Self-organization on mudflats

Eelke Folmer

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Eelke O. Folmer

Introduction

There is something captivating, almost supernatural, about the graceful and synchronized movements displayed by flocks of shorebirds as they fly over intertidal mudflats. Seemingly less dynamic because of its slower pace, but nevertheless just as important, is the development of seagrass beds and the balanced relationships with the physical and biotic environments. The movement patterns of flocks of shorebirds in the sky but also while foraging on mudflats, and the development of the seagrass beds, have in common that their workings are contolled by feedbacks between the elements that constitute the system. That is, through self-organization.

Many systems, in both the natural world and in human society, operate or develop through self-control, i.e. without the involvement of an external regulator. This spontaneous development of a system is denoted self-organization. Globally speaking, it is the process of repeated interactions or feedbacks among elements that make up the system resulting in the spontaneous development of an element-transcending, higher level structure or function, without the intervention of an external regulator. Camazine *et al.* (2001) define self-organization in biological systems as follows: "*a process in which a pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of the system. It is based on local information, without reference to the global pattern*".

Self-organization occurs in a large variety of systems and is a major research topic in amongst others physics, chemistry, economics, psychology, sociology, linguistics, neuroscience and biology[1] (Ball 2004). For example, a major research area in neuroscience is the role of self-organization of the physical base of memory, i.e. encoding of information in the brain through connections between neuronal assemblies (Arbib 2003). A central challenge and research theme in modern sociology and animal behaviour is to link individual decisions to group behaviour and to understand how individual decisions are influenced by the group. Over the last decades research on self-organization in biological systems has rapidly expanded (Solé & Bascompte 2006; Sumpter 2010).

It is important to understand self-organization in systems because it usually is an essential inner process with substantial effects on the macro-dynamics of the system. Particularly, the stability of a system, the occurrence of catastrophes, the presence of alternate states and uncertainty are often related to feedback and propagation mechanisms in the system (Holling 1973; May 1977; Scheffer *et al.* 2001; Haldane & May 2011). This applies especially to complex systems, i.e. sys-

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[1] The interdisciplinary science that seeks to understand how higher level patterns result from the interactions of many elements (i.e. self-organization) is called complexity science.

tems whose elements interact nonlinearly. Due to their nonlinearities, complex systems may spontaneously and rapidly evolve towards unstable critical states, denoted self-organized criticality (SOC) (Bak, Tang, & Wiesenfeld 1988). Sudden, substantial changes in e.g. ecosystems such as large scale fluctuations in populations, pattern formation and extinction cascades[2] are often thought to be related to SOC (Kauffman 1993; Lockwood & Lockwood 1997; Solé *et al.* 1999).

Ecological (and many other natural and social) systems will never be completely self-organized because they will always, though to various extents, depend on one or more external variables (i.e. variables that are exogenous or independent of the system under consideration). Particularly, all the world's ecosystems jointly constitute the biosphere which implies that all ecosystems in some way affect each other and thus depend on each other. Hence, "genuine" external variables do not exist. Nevertheless, the only realistic way to investigate the behaviour of a system is by demarcating it from other systems which can be assumed external to the system under consideration. This requires clear definitions and descriptions of the system's components and of their interactions on time- and spatial scales, as determined by the objectives of the analysis. Particularly, on short-run time scales many variables may be considered to be independent of other variables that in the long run, however, impact on the system.

From a fundamental scientific point of view, as well as for the management of ecosystems, it is important to understand the role of self-organizing processes. Particularly, it is essential to determine the degree to which system-properties are governed by external factors, and the degree to which they are the result of self-organization. Research into the behaviour of a system without considering the inner workings will not lead to adequate models to be used to analyse, predict and manage its development (Lockwood & Lockwood 2008).

Problem statement

There are many unexplored aspects of self-organization in ecology. The present study aims to contribute to the understanding self-organization by considering two different types of systems, some of their feedback mechanisms and their impacts on the higher level structures. The first is the system of foraging shorebirds on mudflats in the Dutch Wadden Sea that behave interdependently in response to other group members. The second is that of seagrasses in the Banc d'Arguin and their reciprocal relationships with the environment, particularly with the sediment characteristics of the soft-bottoms where they grow.

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[2] Secondary extinctions that are triggered by primary extinctions.

A shared aim of the research in the two different systems is methodological, in that statistical models are investigated and applied to determine the strengths of feedback mechanisms. Particularly, in systems of foraging shorebirds, the level of self-organization is the outcome of the opposing forces of conspecific attraction and repulsion due to interference. The adequacy of spatial autoregression to account for, and measure, self-organization in combination with the effects of exogenous environmental factors is evaluated. Based on data collected at the intertidal mudflats of the Banc d'Arguin, the possibilities of using structural equation models are explored to determine the strength of the feedback relationship between seagrass density and sediment grain size. More specifically, in thesis project I have analysed the following topics:

(1) The adequacy of classical resource-based models to predict the distributions of six species of foraging shorebirds, with varying levels of gregariousness, in the Dutch Wadden Sea at landscape level.

(2) The performance of a combination of an interference-based foraging model and a conspecific attraction model to predict the distributions of foraging animals in continuous resource landscapes. This topic is addressed theoretically, by means of simulations and empirically. The model will be applied to explain flocking behaviour of the six different species of foraging shorebirds referred to under (1).

(3) The adequacy of spatial autoregression to measure the impact of self-organization on flocking behaviour. This objective is investigated by means of Monte Carlo simulations.

(4) To gain detailed insight into the behavioural mechanisms of interference. Since self-organization and the distributions of foraging animals in the field are the net outcomes of two opposing forces (spacing out to avoid interference and conspecific attraction to benefit from the presence of conspecifics), understanding of the working of each of the mechanisms separately requires conditions where the opposing mechanism is controlled for. In the present study the focus is on interference competition while controlling conspecific attraction.

(5) To measure the strength of a feedback mechanisms between seagrass density and sediment grain size by means of a non-recursive structural equation model in the Banc d'Arguin, Mauritania.

Below I shall outline the 5 chapters that deal with the above objectives and make up the core of this thesis. Before doing so, I present a synopsis of classical and social foraging theory as well as of collective animal behaviour theory as introduction and framework to the first four objectives. In similar vein, a brief summary of self-organization in seagrass systems is presented as introduction to the fifth objective.

Theories of the spatial distribution of foragers

There are several theories about the spatial distribution of foragers. In this sub-section I will briefly expound why it is imperative to integrate concepts from different theories of animal behaviour for a comprehensive understanding of distributions of foraging shorebirds. The classical Ideal Free Distribution model, based on notions from optimal foraging theory, assumes that animals only suffer from the presence of conspecifics. Social foraging theory, on the other hand is based on the notion that animals may also benefit from each other. In addition, there is the theory of collective animal behavior which is relevant for the explanation of behavior of large numbers of animals. Below, I first describe the conventional optimal foraging theory and the Ideal Free Distribution theory and their limitations. Next I discuss social foraging theory and collective animal behavior theory and the way in which they complement each other.

Opimal Foraging Theory and the Ideal Free Distribution

Optimal foraging theory was developed to understand foraging behaviour and to predict where foragers feed and what they feed on (Emlen 1966; MacArthur & Pianka 1966). It is based on the notion that foragers are economically independent entities that behave to optimize their fitness (Stephens & Krebs 1986). Based on fitness[3] optimization, Fretwell and Lucas (1969) described the equilibrium distribution of individuals across locations which they called the Ideal Free Distribution (IFD). The IFD emerges when all individuals select the most suitable location in terms of the per capita amount of resources (pay-off). Based on density-dependent suitability of the locations and the assumptions that (1) animals have perfect knowledge about the suitability of the locations (i.e. they are "ideal") and (2) are able to freely move between, and enter, habitats at no cost (i.e. they are "free"), the IFD model makes it possible to predict the distribution of animals. The IFD model also predicts that an equilibrium will emerge where no animal can improve its pay-off by unilaterally moving elsewhere. At the equilibrium all animals experience the same pay-off.

Generalized functional response models relate consumption rate to food availability and competitor density. Particularly, consumption rates depend positively on food density and negatively on the level of interference competition that foragers experience from conspecifics[4] (Sutherland 1983). Interference

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[3] Consumption rate is often used as a proxy for fitness.

[4] In this thesis only interference competition will be considered, because competition through depletion plays a minor role for foraging shorebirds on short time scales. Exploitative competition is distinct in that it is an indirect form of competition that operates through depletion of resources.

competition is defined as the reversible negative effect on intake rate through direct effects of the presence of one individual on the other (Goss-Custard 1980). When foragers are ideal and free, and the generalized functional response model is known, it is possible to derive the IFD under interference competition (van der Meer & Ens 1997)[5]. An important limitation of this approach is that only the costs of competition are considered while possible benefits of the presence of conspecifics are ignored[6].

Social foraging theory

Basic in social foraging theory is the notion that a forager's fitness and its behaviour depends on the behaviour of other foragers (Giraldeau & Caraco 2000; Krause & Ruxton 2002). Particularly, a forager may select its foraging location in the vicinity of other foragers to dilute the risk of being depredated (Hamilton 1971; Quinn & Cresswell 2006) or to benefit from the vigilance behaviour exercised by conspecifics (Underwood 1982). Another important reason for foraging animals to locate near other foragers, especially at the search stage, derives from the fact that foraging location decisions require information on the distribution of resources. Social foraging theory acknowledges that the presence of conspecifics may signal food availability (in addition to safety, as mentioned above). This signalling effect is especially relevant for food-searching shorebirds, because intertidal mudflats are large and their benthic prey is buried in the sediment which makes it difficult to obtain information on the distribution of benthic prey by personal sampling. Therefore, the presence and behaviour of other foragers are informative in that they signal the presence of resources (and the absence of danger). Following or joining other foragers may thus be beneficial in that search costs and predation risk are reduced. Particularly, a group of foragers may synchronize their behaviour via behavioural feedbacks to decrease predation costs and to increase foraging opportunities. To sum up, through conspecific interaction, animals can enhance their ability to detect resources and danger in the environment. Particularly, interactions with others allow individuals to evade their own cognitive and perceptive limitations resulting in more accurate and faster decision-making.

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[5] Interference competition can be reduced by spacing out. It should be noted that such cost-reducing behaviour is not included in interference models. Instead, animals are modelled as moving like "aimless billiard balls" (van der Meer & Ens 1997) . These authors noted further that the absence of possible avoidance of interference in interference models is inconsistent from an optimization point of view. It should be pointed out that interference models are also unrealistic in the sense that the size of patches is not explicitly considered and that interactions between animals are simply functions of forager density.

[6] It is interesting to note that Fretwell and Lucas explicitly point out this limitation in their original paper.
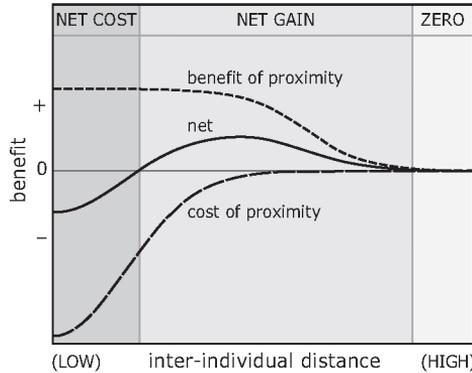
Figure 1.1. Cost and benefit of conspecific proximity as functions of distance between foraging animals. The cost of interference is large on short distances but rapidly decline when inter-individual distances increase. The benefit of sociality is large at short and intermediate distance and levels off to 0 when inter-individual distances increase. The net benefit curve is hump-shaped with the maximum net benefit at intermediate distances.

Locating in the vicinity of conspecifics, however, may lead to increased interference competition. Hence, there is a distance-dependent trade-off between benefits and costs of locating in the vicinity of conspecifics (Figure 1.1). For shorebirds foraging on large open intertidal mudflats the benefits associated with the presence of conspecifics are likely to outweigh the interference costs because food patches tend to be large such that the costs due to interference competition can easily be reduced by spacing out.

Collective animal behaviour
To understand the foraging behaviour of a flock of shorebirds, not only the behaviour of the individuals needs to be understood but also how they act together to form the behaviour of the flock. As pointed out by Gell-Mann (1997) in a different context: *"It is vitally important that we supplement our specialized studies with serious attempts to take a crude look at the whole."*

Models of collective animal behaviour are based on the notion that patterns may arise in large groups of similar individuals through repeated interactions (Sumpter 2010). However, because the flock cannot be described without describing the behaviour of individual foragers, and because the behaviour of individuals must be described with reference to the behaviour of conspecifics, the shaping of flocks is difficult to model[7].

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[7] Collective grouping and movement patterns are not typical for shorebirds but are also observed in insects, fish, mammals and other species of birds.

Understanding the behaviour of large assemblies of individuals has mainly been advanced by mathematical models, individual-based simulations, or a combination of both. Regarding flocking behaviour, simulation is an appealing approach because it proceeds on the basis of simple assumptions about how individuals behave and respond to each other. Computer simulations with multiple agents programmed with simple neighbourhood rules like: "when far away, move towards and when too close, move away" has put forward simple and compelling explanations of seemingly choreographed phenomena (Couzin & Krause 2003; Sumpter 2010). Another advantage of simulation is that it can straightforwardly produce empirically testable hypotheses on patterns of collective behaviour. For these reasons, simulation will be applied below to gain insight into the performance of the food availability-conspecific attraction-interference competition model to predict the emergence of flocks of foraging animals and their spatial distribution.

Self-organization of seagrass systems

Nontrophic interactions that modify abiotic environments and shape communities are common features of ecosystems. In this context ecosystem engineers, i.e. species that fundamentally impact on their abiotic environment[8] (Jones, Lawton, & Shachak 1994; Wright & Jones 2006) play a crucial role. Ecosystem engineers may impact on the development of spatial structure in the environment and affect the availability of resources to other species (Rietkerk *et al.* 2004). However, there may also be reverse effects: the abiotic environment may affect the population dynamics of the engineer (Cuddington, Wilson, & Hastings 2009).

Complexity theory predicts that ecosystems that develop through self-organization may become resilient to change, but may also suddenly shift to alternative states (Levin 1998; Scheffer and Carpenter 2003). It is important to understand the mechanisms of self-organization of ecosystem engineers in relation to exogenous factors because these factors jointly impact on the trajectory and stability of the system. Particularly, the reinforcing feedback between the engineer and its environment may result in the development of a channeled, ordered[9] and resilient ecosystem that in response to changing environmental

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[8] The definition of "ecosystem engineer" is not strict because all species modify their abiotic environment in some way or another on varying temporal and spatial scales.

[9] Kauffman calls self-organizing systems "anti-chaotic" because, despite different initial conditions, the same final state may develop

conditions[10], may be subject to catastrophic shifts (Kauffman 1993; Levin 1998; Scheffer & Carpenter 2003).

Seagrasses growing on intertidal mudflats are ecosystem engineers in that they affect the hydrology and sediment properties. Seagrass may locally promote its own growth in that the canopy reduces mechanical disturbance by reducing water flow velocities. The reduced water flow velocities also reduce erosion and stimulate deposition of fine sediments and associated nutrients. In turn, the accumulated fine sediments influence seagrass growth. Particularly, in silty and anoxic sediments, high concentrations of organic matter also result in the production of hydrogen sulfide that, depending on the concentration, may negatively affect seagrass growth.

Detailed understanding of the feedback mechanism between seagrass density and sediment properties is critical to predict the responses of a seagrass-dominated ecosystem to environmental change. Particularly, it is important to know the strength of the feedback between seagrass growth and the environment in relation to external factors.

Outline of the study

This thesis is made up of two parts. The first deals with self-organization of foraging shorebirds, the second with self-organization in seagrass beds. Below, I first outline the foraging shorebird chapters, next the seagrass chapter.

Part A: Self-organization of foraging shorebirds
This main purpose of this part of the study is to increase understanding of the distribution of foraging shorebirds by addressing research questions 1 - 4. The research questions are addressed conceptually, theoretically, by means of simulation, via observational studies and statistical modeling, and by indoor aviary experiments.

To understand distributions of foraging shorebirds I consider foraging flocks of shorebirds as assemblies of interconnected individuals responding to their exogenous environment and to conspecifics. As noted above, there are positive and negative sides to the presence of conspecifics. The net benefit may be optimized by means of spacing out in such a way that interference is avoided while the benefits of conspecific presence are still gained.

Chapter 2 analyses the distribution of six different species of foraging shorebirds in the Dutch Wadden Sea at landscape level on the basis of a resource

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[10] It should be observed that such a system cannot be too sensitive for else it could not have evolved to its present state in the first place.

based model. The main hypothesis analysed is that resource-based models have better predictive power for interference-sensitive species than for interference-insensitive species because the former are less influenced by conspecific attraction and thus will be more driven by resource availability than the latter. Another hypothesis that will be tested is that species that are interference-insensitive will be more clustered than predicted by the spatial distribution of their food resources because they are more responsive to conspecific attraction such that they follow each other when selecting foraging patches.

Chapter 3 develops a theoretical framework of foraging distributions of gregarious animals in continuous resource landscapes. A classical interference-based foraging model is combined with a conspecific attraction model which is used to simulate distributions of foragers in continuous resource landscapes. In this model the cost of interference and benefits of the presence of conspecifics depend on inter-individual distances. Particularly, it is assumed that interference may be mitigated by maintaining short distances to conspecifics and that the benefits of conspecific presence (causing attraction) operate over larger distances (see Figure 1.1).

Analysis of conspecific attraction has been hampered by the lack of an operational definition and adequate measurement methods. This chapter proposes spatial autoregression to measure self-organization based on the assumption that behavioural feedback amongst shorebirds manifests itself as spatial dependence (i.e. the tendency of foragers to choose locations in the vicinity of other foragers). To account for the fact that animals copy each other's behaviour, the spatial multiplier is proposed to measure the total food effect. Uncertainty in the forager's knowledge about the food distribution and consequently in the spatial distribution of the foragers are included the model. The theoretical model and the adequacy of autoregression are tested by means of numerical simulations.

In Chapter 4 the impact of self-organization in relation to the effects of exogenous factors (i.e. food availability and abiotic habitat characteristics) on the distribution of six species of shorebirds in the Dutch Wadden Sea are considered. The operational definition of conspecific attraction and spatial autoregression introduced in Chapter 3 are applied here. In this chapter the scale of investigation is much smaller and is more behaviourally oriented. The model is estimated on different spatial resolutions to get insight into the modifiable areal unit problem (MAUP), i.e. the problem that regression estimates change by level of aggregation. Lastly, the spatial multiplier is applied to obtain the total food effect.

To evaluate the appropriateness of generalized functional response functions, Chapter 5 investigates the costs and the underlying mechanisms of interference competition by means of experiments with red knots. As noted above, animals

anticipate the presence of conspecifics and may try to avoid physical interactions. In a novel experimental setup with a small moving patch, the behaviour of red knots is analysed to unravel the foundation of interference. Because there may be important differences between individuals of shorebirds, the dominance status is explicitly considered.

Part B: Self-organization in seagrass systems
In Chapter 6 the presence and density of seagrass on the intertidal flats of the Banc d'Arguin and their reciprocal relationships with sediment characteristics is analyzed. The overall objective of the chapter is to contribute to the understanding of the functioning of soft-bottom intertidal seagrass ecosystems. The strength of the feedback mechanisms are estimated by means of a non-recursive structural equation model (SEM).

Chapter 7 synthesizes the findings of the research and discusses possibilities for future research.

2

How well do food distributions predict spatial distributions of shorebirds with different degrees of self-organization?

Eelke O. Folmer, Han Olff and Theunis Piersma

Abstract

Habitat selection models usually assume that the spatial distributions of animals depend positively on the distributions of resources and negatively on interference. However, the presence of conspecifics at a given location also signals safety and the availability of resources. This may induce followers to select contiguous patches and causes animals to cluster. Resource availability, interference and attraction therefore jointly lead to self-organised patterns in foraging animals. We analyse the distribution of foraging shorebirds at landscape level on the basis of a resource-based model to establish, albeit indirectly, the importance of conspecific attraction and interference. At 23 intertidal sites with a mean area of 170 ha spread out over the Dutch Wadden Sea, the spatial distribution of six abundant shorebird species was determined. The location of individuals and groups were mapped using a simple method based on projective geometry, enabling fast mapping of low tide foraging shorebird distributions. We analysed the suitability of these 23 sites in terms of food availability and travel distances to high tide roosts. We introduce an interference sensitivity scale which maps interference as a function of inter-individual distance. We thus obtain interference-insensitive species which are only sensitive to interference at short inter-individual distances (and may thus pack densely) and interference- sensitive species which interfere over greater inter-individual distances (and thus form sparse flocks). We found that interference-insensitive species like red knot (*Calidris canutus*) and dunlins (*Calidris alpina*) are more clustered than predicted by the spatial distribution of their food resources. This suggests that these species follow each other when selecting foraging patches. In contrast, curlew (*Numenius arquata*) and grey plover (*Pluvialis squatarola*), known to be sensitive to interference, form sparse flocks. Hence, resource-based models have better predictive power for interference-sensitive species than for interference-insensitive species. It follows from our analysis that monitoring programmes, habitat selection models and statistical analyses should also consider the mechanisms of self-organization.

Introduction

In the theoretical resource-based literature, animal-habitat relationships are derived from fitness or intake maximization (Fretwell & Lucas 1969; Kacelnik, Krebs & Bernstein 1992). Intake rates are assumed to depend on resource density and interference (Beddington 1975; Ruxton, Gurney & De Roos 1992; Moody & Houston 1995). Under the assumption that animals behave ideally and freely and maximise intake rates, aggregative response functions may be derived (Sutherland 1983; Moody & Houston 1995; Van der Meer & Ens 1997). This approach bases predictions of the spatial distribution of foraging animals on straightforward mechanistic principles.

The empirical resource-based literature takes a phenomenological approach and investigates relationships between habitat characteristics and animal densities statistically (Bryant 1979; Piersma *et al.* 1993; Yates *et al.* 1993; Zwarts, Wanink & Ens 1996; Guisan & Zimmermann 2000; Manly *et al.* 2002; Granadeiro *et al.* 2007). These studies find mixed results and heterogeneous relationships, amongst others because animal densities may depend on habit characteristics in non-linear ways. Specifically, ecological factors may impose upper or lower limits on response variables so that the impacts within and outside the limits substantially differ (Thomson *et al.* 1996; Cade & Noon 2003). Put differently, ecological factors may operate as constraints on, rather than as exact determinants of behaviour. Moreover, multiple limiting factors may interact.

Both the theoretical and the empirical literature are pre-occupied with the negative impacts of co-occurrence of conspecifics while possible benefits are frequently ignored. The presence of many eyes and ears in a group increases the chance that predators (Pulliam 1973; Beauchamp 1998; Krause & Ruxton 2002; Whitfield 2003) or resources (Valone & Templeton 2002; Danchin *et al.* 2004) are detected. Additionally, animals may have developed social behaviour in response to past selection pressures (Byers 1997). Behaviour of individuals thus depends on behaviour of group-members (Sirot 2006). Therefore not only negative aspects of interdependent relationships among individuals must be considered when studying habitat selection but also the positive aspects (Melles *et al.* 2009). It follows that the gregarious nature of animals may be a source of heterogeneity in the relationship between foraging animals and habitat characteristics.

Conspecific attraction is not necessarily beneficial, but may also lead to the selection of suboptimal foraging patches (Giraldeau, Valone & Templeton 2002). Specifically, if predecessors choose suboptimal foraging patches and followers copy their behaviour and select contiguous or nearby patches, a collective mistake results. Hence, conspecific attraction may lead to a mismatch

between the spatial distribution of foraging animals and the spatial distribution of their food. For solitary species the risk of mismatch is smaller because patch selection will be based on expected intake rate only rather than on a combination of expected intake rate and conspecific attraction.

Recently, the concept of self-organisation has been introduced to understand collective animal behaviour of groups without permanent leaders (Camazine *et al.* 2001; Krause & Ruxton 2002; Sumpter 2006). Central to this line of work is the notion that group formation results from repeated interactions among neighbours. These types of models view animals as interacting particles that make movement decisions in response to the locations and movements of their neighbours (Reynolds 1987; Couzin *et al.* 2002). This framework has been useful to understand and predict properties of groups with many individuals, such as insect swarms, fish schools and bird flocks (Sumpter 2006).

Flocks of shorebirds, particularly of dunlin (*Calidris alpina*) and red knot (*Calidris canutus*), may consist of many thousands of individuals displaying synchronized movements in flight, often in response to predation (Piersma *et al.* 1993; Van de Kam *et al.* 2004; Van den Hout, Spaans & Piersma 2008). These flocking patterns are maintained during foraging (Goss-Custard 1970). Despite their ubiquity, flocking patterns tend to be ignored in most studies of low-tide shorebird spatial distributions, as it is generally assumed that animal-habitat relationships only result from individual choices in response to resources and interference (Nehls & Tiedemann 1993; Piersma *et al.* 1993; Van Gils & Piersma 2004; Vahl *et al.* 2005; Van Gils *et al.* 2006; Spruzen, Richardson & Woehler 2008).

We hypothesize that shorebirds choose foraging patches based on exogenous factors (e.g. food availability, danger and travel costs) and, at varying degrees, in response to the presence of conspecifics (Fig. 2.1). Handling time and prey type determine the distance between conspecifics. For instance, oystercatchers (*Haematopus ostralegus*) foraging on bivalves, require long handling times making it possible for competitors to steal prey (kleptoparasitism) (Ens, Esselink & Zwarts 1990; Stillman *et al.* 2002). Hence, oystercatchers are sensitive to interference and therefore maintain relatively large inter-individual distances (Moody *et al.* 1997). In contrast, for species with short handling times (e.g. red knot) the cost of interference is small and animals may easily form dense flocks (Van Gils & Piersma 2004). Hence, they are interference-insensitive, i.e. there is a small impact of interference on spacing behaviour.

The objective of this paper is to test the hypothesis that resource availability and distance to high tide roost are more important determinants of the spatial distributions of interference-sensitive species than of interference-insensitive species. This will be reflected in a larger residual variance of a regression of bird density on these predictors for the latter than for the former. The reason is that
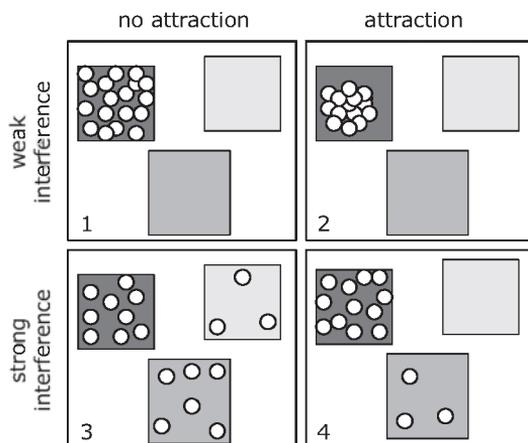
Figure 2.1. Clustering of foraging shorebirds as a function of food availability, attraction and interference. The darker the patch color, the higher the food availability. 1: weak interference and no attraction: clustering at the patch with the highest food density; 2: weak interference and strong attraction: strong clustering at the patch with the highest food density; 3: strong interference and no attraction: weak-to-moderate clustering at the patch with the highest food density and weak clustering at patches with low food densities; 4: strong interference and attraction: moderate clustering at the patch with the the highest food density and weak clustering at the patch with the next highest food density.

in the case of interference-insensitive species systematic predictors (i.e. the joint impact of conspecific attraction and interference-insensitivity) are missing. The hypothesis will be tested, at landscape scale, for six common shorebird species in the Dutch Wadden Sea.

The Wadden Sea is an area *par excellence* to study resource availability–animal density relationships. First, many shorebird species in the Wadden Sea are abundant (Zwarts & Wanink 1993; Van de Kam *et al.* 2004). By focussing on abundant species, the role of accidental relationships (i.e. relationships that may occur by chance) is reduced. Secondly, there is detailed information available on food availability in the Wadden Sea because of an ongoing benthos monitoring programme (Piersma *et al.* 1993, 1995; Van Gils *et al.* 2007; Kraan *et al.* 2009a). Thirdly, there is large variation in food density and in the level of flocking between shorebird species (Goss-Custard 1970). Finally, the Wadden Sea is an open and well-known landscape such that the risk of not identifying possible confounding site characteristics affecting dispersion is small. Moreover, even if they are overlooked, they may not affect the analysis when they are constant between species.

Methodology

The study area

The Dutch Wadden Sea is shallow and contains large soft-sediment flats that emerge twice a day during low tide. The mudflats alternate with permanent channels (Fig. 2.2). The flats are characterized by smooth gradients both in terms of physical properties, such as sediment grain size distributions, and biological properties, such as density of macro-zoobenthic species (Kraan *et al.* 2009a). Due to the semidiurnal tides, the mudflats are accessible to shorebirds approximately twice per day. High tide roosts of non-breeding shorebirds are found on the mainland and on all islands (Koffijberg 2003; Van de Kam *et al.* 2004).

Benthos sampling

As part of a long-term benthic research programme (Piersma *et al.* 1993; Kraan *et al.* 2009a,b), we determined the density of macrozoobenthos in the Dutch Wadden Sea between July and September 2004. Benthos sampling was performed over 250 m grids (Fig. 2.2). The sampling stations were visited by foot during low tide and by boat during high tide (by boat to maximally utilize the number of working hours while in the field).

When sampling by foot, one sample was taken at each station. Each sample consisted of sediment taken down to a depth of 20–25 cm with a core with area of $1/56$ m^2. The top (0–4 cm) layer of the sample was separated from the bottom layer. The top and bottom layers were sieved separately over 1-mm mesh. Since polychaetes are able to move from the bottom to the top part layer, their vertical location in the layer was not recorded. At the same locations, mudsnails (*Hydrobia ulvae*) were also sampled but with a smaller core ($1/267$ m^2) to a depth of 4 cm. Mudsnail samples were sieved over a 0.5 mm mesh. When sampling by boat, at each station two samples were taken, down to a depth of 20–25 cm, each with a core with area of $1/115$ m^2. We took two samples to obtain similar precision of benthos density estimates as in the samples collected by foot. The two samples were sieved jointly. Due to practical limitations, for these samples the top layers were not separated from the bottom layer.

In the field the numbers of adult and juvenile individuals of each macrobenthos species were counted. All molluscs and shore crabs (*Carcinus maenas*) that were retained in the sieve were frozen at –20 °C for later analysis in the laboratory. In the laboratory the lengths of all individual specimens were measured to the nearest 0.1 mm. For bivalves, the flesh was separated from the shell and dried at 55–60 °C. After determination of the dry mass (to the nearest 0.1 mg), the flesh was incinerated at 550 °C for 2 hours. The weights of the ashes were measured to the nearest 0.1 mg. In this way species and length specific values
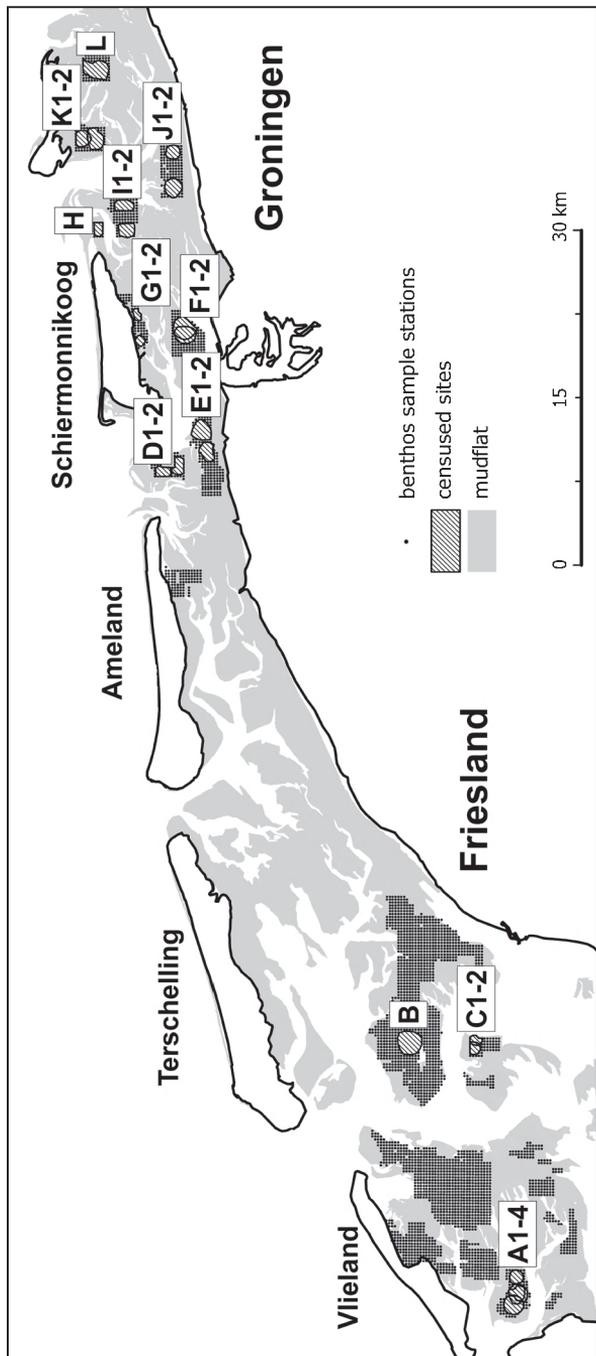
Figure 2.2. Map of the Dutch Wadden Sea. Benthos sampling stations and the sites for which shorebird distributions were mapped are indicated.

for ash-free dry mass (AFDM) were obtained. Further details about prey sampling and analysis can be found in (Piersma *et al.* 1993, 1995, 2003; Kraan *et al.* 2009a).

For the specimens counted in the field and not brought to the lab (polychaetes and isopods), we obtained estimates of energy values from the literature (Appendix S1). Note that the values thus obtained are approximations. This, however, is not a problem in the present analysis, since its objective is to analyse the significance of food as predictor of patch choice and flocking variance rather than precisely estimating and comparing regression coefficients of food variables. Particularly, some inaccuracy in the regression coefficients does not affect the predictive power of the estimated models for the entertained objectives of the paper. Moreover, we also considered higher than conventional (5%) significance levels of the coefficients.

Bird mapping
For the 23 sites that were sampled for benthos, shorebird distributions were mapped (Fig. 2.2). The maps were drawn between three days before and three days after benthos sampling. Several studies (e.g. Piersma *et al.* (1993) and Van Gils *et al.* (2003)), show that depletion and death of benthic species affecting their densities occur over longer time periods than six days.

Benthos sampling and shorebird mapping took place around the centres of the mudflats where submersion times are shortest. This ensures accessibility of the mudflats for most of the time throughout the tide. Observation points were chosen centrally on the mudflats (>1 km away from gullies). Bird distributions were mapped in between two hours before until two hours after low tide. The area of exposed mudflat changes little in this time span so that the spatial distribution of the birds is not affected by tidal movement. Furthermore, disturbance due to the presence of the observer is minimal under these conditions, because the extent of available mudflat is at its largest.

The observer (EOF) arrived at the observation points by foot well before mapping started, so that disturbed birds would have sufficient time to return to the areas through which the observer had arrived. Observations were started in opposite direction from which the observer had arrived. Only Curlew (*Numenius arquata*) seemed disturbed and was never recorded within 200 m from the observer. Positions of individuals and flocks were determined with the aid of GPS, compass and rifle scope with a ranging reticle (mill dots). GPS was used to determine the position of the observer; the compass to determine the observation direction. The rifle scope mounted on the telescope enabled the observer to measure the distance between each individual bird or flock edges and the horizon in terms of mill dots. Based on principles of projective geometry this distance was used to calculate the true distance from the observer (Heinemann

1981). The procedure was regularly calibrated using objects with known locations and true distances. All individual birds and flocks in a 360° circle around the observer were plotted on maps with 100 m grids. Individual birds were plotted as points and flocks as polygons in which the numbers of individuals were registered. In some cases flocks rather than individuals were considered because when the number of birds covering a small area was large it was not feasible to plot all individual positions.

In early morning and late afternoon visibility could be poor due to reflecting light making it impossible to make a full 360° map. In those cases observations in the direction of poor visibility were cancelled. During a single low tide period, depending on the average bird density, either one or two censuses were done on different sites on the same mudflat. A typical census would relate to a circular area with radius between 650 and 800 m. This census area, denoted "site", is the spatial unit of analysis below.

Data preparation

Regarding benthos availability for short-billed birds potentially feeding on small bivalves (i.e. red knot and dunlin), we only considered bivalves in the top-layer (Van Gils *et al.* 2009). Since it was not possible to separate the top and bottom layers for samples collected by boat, we obtained estimates for the top layer benthos in this case by using the proportion of top layer benthos found in samples collected by foot. The proportions of benthos in the top and bottom layers may differ between species, size classes and between the eastern and western Wadden Sea (Van Gils *et al.* 2009). We therefore used species-, size- and location (western (A-C) and eastern (D-L) Wadden Sea (see Fig. 2.2)) specific proportions. For example, if the proportion of top layer ingestible Baltic tellin (*Macoma balthica*, <16 mm) in the samples collected by foot in the eastern Wadden Sea turned out to be 75%, the amount of ingestible top layer Macoma in samples collected by boat in the eastern Wadden Sea was obtained by multiplying the total amount of ingestible *Macoma* by 0.75.

All benthos samples and bird maps were organized in a GIS. Digital point maps of bird distributions were constructed by digitizing the scanned and geo-referenced field maps. Flocks were represented as polygons in which the numbers of birds were registered. The points inside the polygons were distributed evenly (by hand) over the polygon area. Single birds were plotted as individual points.

The points thus obtained were aggregated in 50×50 m grids (i.e. cells) that fully covered the censused sites. The number of birds inside a gridcell was transformed to density and related to its centroid. Only cells with more than 50% of the area inside the site were included in the data set. The resulting lattice formed the basis for calculating occupancy and degree of packing.

For the landscape level analyses, the bird and benthos data sets were aggregated to site level resulting in 23 data points for all species, except red knot where the number of data points is 16. The reason is that the population of red knots in the Wadden Sea is highly variable in August because of turnover of two distinct populations. By the beginning of September members of the *canutus* subspecies have departed while the other subspecies, *islandica*, has arrived (Zwarts, Blomert & Wanink 1992; Piersma *et al.* 1993; Nebel *et al.* 2000; Kraan *et al.* 2009b). For red knot we only considered observations after 1 September.

Bird density was calculated by dividing the total number of individuals by the area of the site corrected for the disturbance effect of the observer. Depending on species-specific sensitivity, we subtracted the area around the observer calculated by $\pi \times r^2$ where r is the distance over which the animals are disturbed. We used the following distances: dunlin and red knot: 150 m, oystercatcher, grey plover (*Pluvialis squatarola*) and bar-tailed godwit (*Limosa lapponica*): 200 m, curlew: 300 m (Spaans, Bruinzeel & Smit 1996). The site level density of each benthos species was calculated by averaging the benthos densities of the sampling stations that were inside the site but outside the disturbed area. A map with locations of high tide roosts was used to calculate the distance between the centroid of each site and the nearest high tide roost (Koffijberg 2003).

Packing of individuals relates to inter-individual distance; it indicates the local density of animals. It was obtained by dividing the density by the proportion of occupied cells (birds ha^{-1}).

Statistical analysis
THE LANDSCAPE-LEVEL MODEL

We investigated the landscape level relationship between the spatial distribution of foraging shorebirds and its predictors with a linear model. The dependent variable is *density* as defined above. To normalize the data, bird densities were log-transformed (Gelman & Hill 2006). We added the value of 1 to avoid taking logarithms of zero.

We used benthos availability and travel distance to high tide roosts as predictors. For each benthos species and sampling station, AFDM values were obtained by summing the AFDMs of the benthos items that were ingestible and accessible (i.e. for red knot and dunlin: only small bivalves from the top layer; for long-billed shorebirds: benthos from both layers). (Appendix S1 gives a synopsis of the literature on the summer diet for the six abundant shorebird species.) Profitability and digestibility may differ widely between prey species, even after adjustment for caloric values (Zwarts & Blomert 1992). Therefore, densities of the prey species were entered as separate variables and not combined to give an overall measure of food availability. To avoid spurious correlations,

we only used the benthos species that were known to be regular prey and reasonably abundant in the Wadden Sea.

Benthos items are assumed to have a positive or zero impact on the dependent variable. Negative impacts are ecologically implausible, because a shorebird may ignore, but will not be deterred, by benthos. As large travel distances from high tide roosts to foraging sites imply extra time and energy costs, they negatively affect density (Dias *et al.* 2006; Van Gils *et al.* 2006; Rogers *et al.* 2006). Therefore we hypothesize a negative impact of this variable. Because there is no *a priori* reason to expect interactions among predictors, and because the number of predictors for some species is large, only linear and additive combinations of the predictors were considered.

For each bird species we applied the following modelling procedure. First, we estimated the initial (full) model based on food availability and distance to high tide roosts. Next, we reduced the initial model applying a stepwise, backward procedure in that predictors with ecologically implausible coefficients were deleted, i.e. a positive coefficient for distance to nearest high tide roost and negative coefficients for benthos items. In the case of several incorrect coefficients, the former was deleted first. Food predictors with negative coefficients were deleted one by one in order of increasing p-values. The model thus obtained is labelled "ecological model". It is plausible on the basis of ecological considerations and permissive in that higher than conventional p-values are accepted.

The ecological model was further reduced on the basis of statistical criteria to find the model with the best predictive power. We therefore selected the final model, from all possible ecological models, on the basis of minimization of the corrected Akaike's information criterion (AICc) (Burnham & Anderson 1998). Data was analyzed with the statistical package R 2.9.0 (R Development Core Team 2009).

Standard deviation of the residuals (σ) and packing
The variance of the residuals of the regression of bird density on food availability and distance to high tide roosts is expected to be higher for gregarious species than for solitary species because of stronger predictive power of benthos for the latter than for the former. This will be reflected by the standard deviation of the residuals (σ). Particularly, for solitary species we expect σ to be smaller than for gregarious species. The relationship between gregariousness and σ was tested by regressing the latter on packing.

Results

Number of birds and density

We counted approximately 26,000 birds at 23 sites on 12 mudflat areas covering a total of 3,943 ha (Fig. 2.2). Dunlin was the most abundant species (12,884 individuals) followed by red knot (5,654 on 16 sites), oystercatcher (5,365), curlew (887), bar-tailed godwit (604) and grey plover (245).

Figure 2.3 presents densities by species and site, showing large variations. The summary in Fig. 2.4A shows that red knot and dunlin had the highest densities, followed by oystercatcher, bar-tailed godwit and curlew, with grey plover having the lowest density. Especially red knot and dunlin showed high variability while the other four species occurred at relatively constant densities between sites (Fig. 2.3). When red knot or dunlins were observed at a particular site, there typically were many of them forming dense flocks. In contrast, grey plover and oystercatcher occurred at all mudflats in relatively constant numbers.

Packing patterns

The packing of individuals varied strongly between species (Fig. 2.4 B). Red knot and dunlin, when encountered, occurred in high local densities. Bar-tailed godwit, grey plover, oystercatcher and curlew showed a much lower degree of packing.

Regression of density on food availability and distance to high tide roosts

Table 2.1 gives the full, ecological and final model estimates including regression coefficients, standard errors as well as several goodness-of-fit measures. The ecological models show that for each bird species there are benthos items with ecologically plausible coefficients. Distance to high tide roost has a correct negative sign for oystercatchers, curlew and grey plovers only.

Compared with the ecological models, the final models generally show a substantial reduction of predictors. For oystercatcher, however, the full and ecological models are the same. Distance to high tide roost has dropped out for every species in the final model. Moreover, we find that for dunlin only *Nereis diversicolor* is a significant predictor; for bar-tailed godwit *Arenicola marina*, *Nephtys hombergii* and *Scoloplos armiger*; for oystercatcher *Nereis diversicolor* and *Cerastoderma edule*; for grey plover *Arenicola marina* and for red knot *Mya arenaria*.

For curlew there are no significant food predictors in the final model. This may be related to the wide variety of prey that curlews select (Appendix S1). Furthermore, individual specialisation on specific prey species probably takes place (Leeman *et al.* 2001; Bolnick *et al.* 2003). Curlews have a preference for large *Carcinus* above other prey species in summer (Goss-Custard, Jones & New-
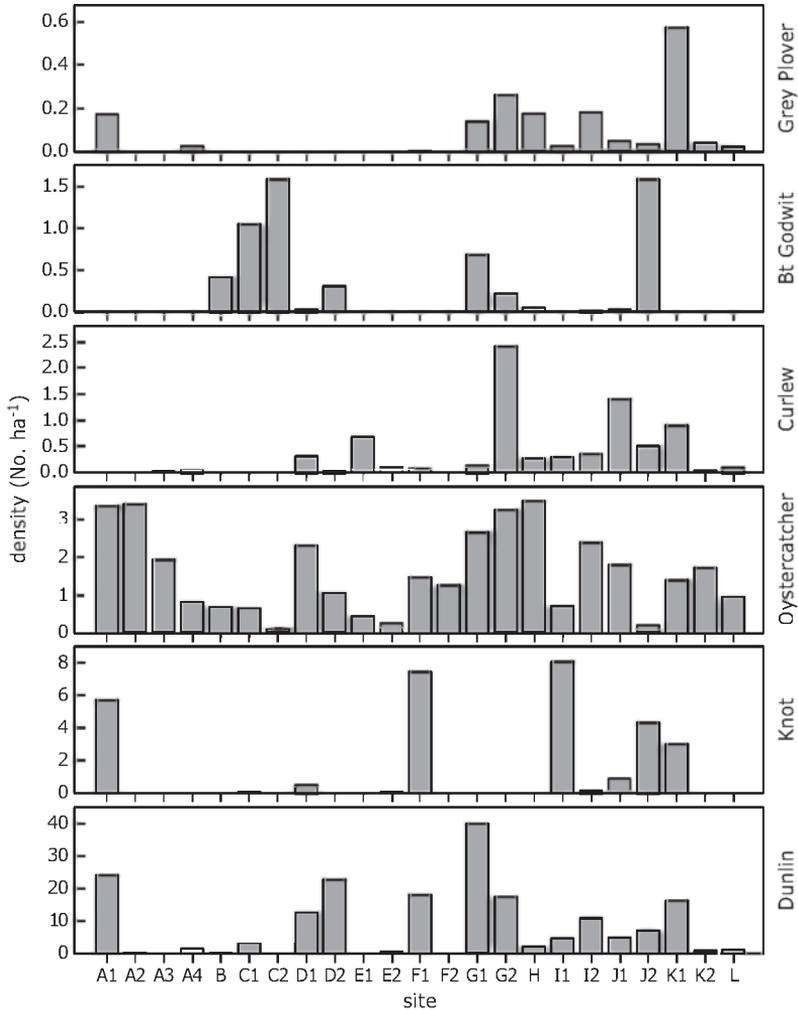
Figure 2.3. Species-specific variation in bird density among sites. Sites ordered from west to east. Each letter corresponds to a unique mudflat. Sites are labelled by a combination of letter and number. Observe the different scales on the y-axis. Panels are ordered from top to bottom in order of increasing variance.

bery 1977; Petersen & Exo 1999; Ens *et al.* 1990). Densities of these large shore crabs were probably not adequately determined by our sampling method. We therefore also tested whether mudflat elevation (obtained from the National Institute for Coastal and Marine Management [RIKZ], The Netherlands, data collected between 1997-2002), silt content (Zwarts, 2004) and distance from
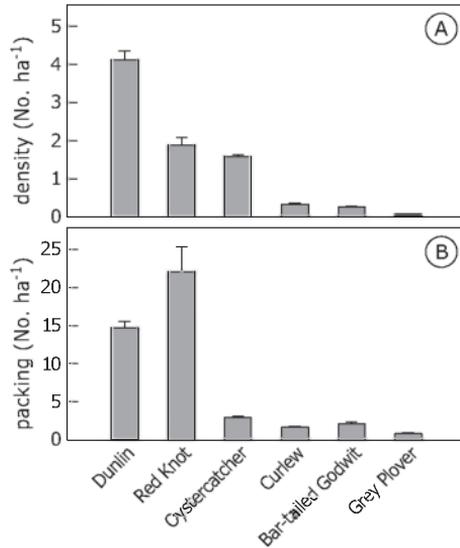
Figure 2.4. (A) Mean density and (B) mean packing of six shorebird species. Length of error bars correspond to standard errors. Packing is calculated by dividing the site density by the proportion of occupied cells. Estimates of packing are based on the sites where more than 5% of the 50×50 m cells were occupied.

high tide roost impacted on curlew density. The final curlew model based on silt content (coefficient = 0.0215, p = 0.003) and mudflat elevation (–0.003, p = 0.052) and distance from high tide roost (coefficient = –0.056, p = 0.112) indicates a preference for muddy and low sites that are near the high tide roosts (R^2 = 0.39 and σ = 0.27). Note that the standard deviation is slightly smaller than for the food model.

As argued above, the missing of systematic predictors is reflected in the R^2s of the final models. The R^2s vary from more than 0.50 for oystercatcher and bar-tailed godwit to less than 0.30 for the gregarious dunlin and red knot. It follows that for gregarious shorebird species important systematic predictors are missing, i.e. the joint impact of conspecific attraction and interference-insensitivity.

Regression of the residual standard deviation (σ) on packing
Figure 2.5 shows that the residual standard deviation (σ) is positively related to packing (slope coefficient 0.032 ± 0.009; F = 14.31; DF = 4; p = 0.019; R^2 = 0.78). As hypothesized, for the solitary species curlew, oystercatcher, bar-tailed godwit and in particular grey plover, we find relatively small σ's but for the gregarious red knot and dunlin large σ's.

Table 2.1. Regression models of shorebird density for six species on landscape scale in the Wadden Sea. The predictors in the full model (white rows) are based on prey species that the various shorebirds have been found to forage on. The ecological model (light grey row) is obtained by ecological model selection: all predictors with implausible signs were deleted in a stepwise, backward selection procedure. The final model is obtained by reducing the ecological model via minimization of AICc. (See text for details on the ecological and statistical model selection procedures.) Standard errors between parentheses below regression coefficients. Significance indicated by asterisks ($p < 0.05$*; $p < 0.01$**; $p < 0.001$***). Abbreviations of the predictors: are: *Arenicola marina*, car: *Carcinus maenas*, cer: *Cerastoderma edule*, cor: *Corophium volutator*, cra: *Crangon crangon*, gam: *Gammarus locusta*, het: *Heteromastis filiformis*, hyd: *Hydrobia ulvae*, lan: *Lanice conchilega*, mac: *Macoma balthica*, mar: *Marenzelleria virides*, mya: *Mya arenaria*, myt: *Mytilus edulis* nep: *Nepthys hombergii*, ner: *Nereis diversicolor*, sco: *Scoloplos armiger*, scr: *Scrobicularia plana*, dhtr: distance to high tide roost (km).

	model	const	dhtr	cer	mac	mya	myt	scr	are	lan	ner	nep	mar	sco	het	cra	cor	car	hyd	R²	σ	AICc	N
dunlin	full	1.21 (1.21)	0.05 (0.22)	-39.58 (34.36)	10.20 (11.49)					0.01 (0.04)	0.02 (0.09)	-1.01 (0.96)	-0.42 (0.69)	0.04 (0.43)	-0.14 (0.61)	0.11 (0.20)	-65.84* (26.68)	2.89** (1.40)	-0.92 (1.04)	0.63	0.96	72.4	23
	ecol	0.22 (0.66)			3.44 (6.68)					0.01 (0.04)	0.07 (0.07)	0.18 (0.70)	0.07 (0.71)	0.16 (0.27)						0.21	1.05	75.7	23
	final	0.68 (0.31)									0.08 (0.04)									0.16	0.95	67.3	23
red knot	full	0.21 (0.92)	0.05 (0.19)	-1.09 (2.23)	0.53 (0.89)	7.73 (5.78)										-0.21 (1.00)		-0.04 (0.98)	-0.57 (1.06)	0.39	0.92	50.6	16
	ecol	0.10 (0.41)			0.39 (0.64)	9.78 (4.80)										0.03 (0.87)		0.31 (0.84)		0.31	0.84	46.7	16
	final	0.39 (0.23)				9.97 (4.29)														0.28	0.76	41.4	16
bar tailed godwit	full	-0.71* (0.24)	0.05 (0.04)		0.07 (0.07)				0.07 (0.04)	-0.01 (0.01)	0.02 (0.02)	0.70 (0.18)		0.12 (0.07)	-0.02 (0.06)			-0.25 (0.17)		0.70	0.22	5.3	23
	ecol	-0.54 (0.22)			0.05 (0.07)				0.05 (0.03)		0.02 (0.02)	0.66 (0.16)		0.08 (0.06)						0.55	0.24	6.3	23
	final	-0.34 (0.15)							0.05 (0.03)			0.54*** (0.14)		0.10 (0.06)						0.50	0.24	5.0	23

|	model	const	dhtr	cer	mac	mya	myt	scr	are	lan	ner	nep	mar	sco	het	cra	cor	car	hyd	R²	σ	AICc	N
oyster-catcher	full	0.49 (0.25)	-0.05 (0.05)	0.01 (0.01)	0.11 (0.08)		0.03 (0.04)	0.10 (0.24)			0.06** (0.02)									0.61	0.32	20.8	23
	ecol	0.49 (0.25)	-0.05 (0.05)	0.01 (0.01)	0.11 (0.08)		0.03 (0.04)	0.10 (0.24)			0.06** (0.02)									0.61	0.32	20.8	23
	final	0.41** (0.11)		0.02 (0.01)							0.06*** (0.01)									0.53	0.31	16.9	23
curlew	full	0.49 (0.34)	-0.04 (0.05)						0.03 (0.04)	-0.01 (0.01)	-0.02 (0.02)					0.00 (0.04)		0.02 (0.19)		0.11	0.35	25.4	23
	ecol	0.13 (0.10)	-0.02 (0.04)						0.02 (0.03)											0.04	0.33	19.3	23
	final	0.23 (0.07)																		0.00	0.32	16.1	23
grey plover	full	0.08 (0.11)	-0.01 (0.02)						0.04 (0.02)	0.00 (0.00)	0.01 (0.01)	0.03 (0.08)		-0.06 (0.03)	-0.03 (0.02)		0.29 (1.25)			0.37	0.11	-27.7	23
	ecol	0.00 (0.07)	-0.01 (0.01)						0.02 (0.02)	0.00 (0.01)	0.00 (0.01)	0.01 (0.07)								0.12	0.11	-28.2	23
	final	0.01 (0.04)							0.02 (0.02)											0.10	0.11	-33.6	23
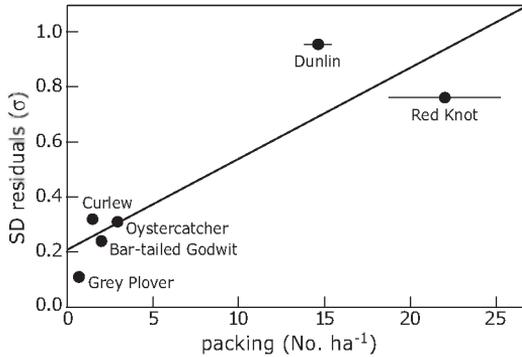
Figure 2.5. Regression of standard deviation of residuals (σ) on packing. σ was obtained from the regression models in Table 2.1. In the regression model shorebird density was ln-transformed so that σ also is on *ln*-scale. Packing is defined as local bird density. The horizontal bars correspond to the standard errors of packing. Regression equation: σ = 0.198 (0.097) + 0.032 (0.009) × *Packing*; p = 0.019; R^2 = 0.78. The numbers between parentheses correspond to standard errors.

Discussion

The main finding of this paper is that the predictive power of a resource based model for the instantaneous spatial distribution of foraging shorebirds deteriorates with the tendency to flock, because the presence of conspecifics may be taken as an indication of the absence of predators or the availability of food (Krause & Ruxton, 2002). Positive feedback in the form of conspecific attraction in combination with insensitivity to interference limits the predictability of the spatial distribution of foraging shorebirds by food availability and distance to high tide roost (Folmer, Olff and Piersma 2010). The mere presence of food availability and absence of conspecific attraction in a bird density model implies a correctly specified model for solitary species, but a misspecified model for gregarious species leading to an increase in residual variance.

We hypothesized handling time to be a decisive factor with respect to the tendency to group or not. The shorter the handling time, the less sensitive a species would be to e.g. kleptoparasitism, and thus the shorter inter-individual distances that need to be maintained and the greater the tendency to flock. Shorebirds such as dunlin and red knot that forage on small prey requiring short handling times do not suffer much from interference of nearby conspecifics allowing them to benefit from nearby conspecifics (Nehls & Tiedemann 1993; Van Gils & Piersma 2004). Such species therefore occupy a relatively small proportion of the suitable habitat which makes it hard to predict their instantaneous distributions. This may also explain why for such species suitable areas

often are not occupied for some time, as observed for red knot by e.g. Piersma *et al.* (1993) and Van Gils & Piersma (2004). Such absences are less common for interference-sensitive species (oystercatchers, grey plovers and curlews) that maintain large minimal distances from conspecifics (Vines 1980; Moody *et al.* 1997). For interference-sensitive species a large proportion of suitable habitat becomes occupied which strengthens the predictive power of a resource based model. For future research, we suggest that attention should also be paid to other factors that may influence inter-individual distances. For example, if small shorebirds were more vulnerable to predation than larger ones, shorebird size would correlate with packing, i.e. small species would flock more densely than large species.

Many studies indicate that complex micro-level relationships may become simple at aggregated levels (Levin 1992). Here we show the opposite: complex patterns at landscape level arise due to small-scale interactions, i.e. flocking behaviour. Hence, the key to prediction and understanding of landscape-level patterns of shorebirds also lies in the elucidation of their social behaviour.

The paper provides some insight into the question whether space or food availability limits population size. It follows from the above that species that are interference-insensitive are merely limited by total food resource stocks, whereas for interference-sensitive species both resource availability and the extent of foraging habitat are important.

Traditionally, miss-matches between the spatial distributions of resources and animals have been explained by perceptual constraints (Abrahams 1986), despotism (Fretwell 1972) and inequality amongst competitors (Parker & Sutherland 1986). The joint impact of conspecific attraction and interference adds an additional explanation: for social species actions based on perceptions (right or wrong) are amplified by the collective behaviour of the members of a group, as suggested by Abrahams (1986).

Adequate management of natural reserves depends on the quality of the information about behaviour and distributions of its animal populations. Monitoring programmes should be designed such that all the behavioural and distributional determinants are addressed. We have shown that, based on the distribution of animals, habitat suitability is more difficult to determine for scarce and gregarious species than for abundant, solitary species. Monitoring programmes should therefore also take into account to the "gregarious nature" of the species. For solitary and abundant species random sampling is adequate. Gregarious species need to be followed over longer periods of time or at larger spatial scales, as shown by Piersma *et al.* (1993) and Colwell *et al.* (2003) who find that the processes driving instantaneous spatial heterogeneity between sites also underlie heterogeneity along the time axis on a day to day basis on mudflats and on roosts.

The finding of this paper that social species tend to occupy a relatively small proportion of the available and suitable habitat contrasts with findings by Piersma et al (1993, 1995) and van Gils et al (2006). They conclude that over a whole season (or even years, Piersma *et al.*, 1993) the cumulative distribution of interference-insensitive shorebird species (red knots), taking the distance to high tide roosts into account, matches relevant food distributions. In these studies the spatial and temporal scales, method of data collection and the statistical models and criteria used differ from the ones employed in the present paper. Comparison of results is hence not straightforward. Further research on the statistical relationships of gregarious species with their exogenous predictors observed over long time periods and large spatial scale is needed to reconcile these findings.

S1 | Synopsis of habitat preferences and benthic prey

Dunlin (*Calidris alpina*)

Dunlins are "generalists" in that they forage on many different species of benthos. Table 1 gives an overview of diet analyses, with a focus on the Dutch Wadden Sea. Nehls and Tiedeman (1993) found for the German Wadden Sea that in late summer and autumn, dunlins tend to select high and sandy mud-flats where both common shrimp (*Crangon crangon*) and shore crab (*Carcinus maenas*) are abundant prey that time of the year (Kuipers & Dapper 1981).

Table S1.1. Summer prey species of dunlin identified in the literature. The numbers in the column "references" denote literature (given in the right hand table) in which the prey under consideration has been found to be part of the diet. If the prey species forms a significant part of the diet, the reference numbers are bold. The column "size class and/or AFDM" gives (1) for bivalve species: the ranges of the lengths that are profitable and ingestible (numbers with-in parentheses refer to references in the right-hand table) (2) for polychaetes and crustacea: the estimated mean length per species or/and approximate energy content (mg AFDM) of an individual as used in our analyses. The given value of approximate energy contents are accompanied with a capital letter corresponding to the source of this information (right hand table). For some species AFDMs could not be identified. In those cases AFDMs of individuals were guessed on the basis of comparison to similarly sized species. If a prey species was found to be reasonably abundant in the Wadden Sea its name is in bold; it is included in the full regression model.

prey	references	size class and/or AFDM (g)
Nereis	**1,2,3, 4,6,7,A**	50 mm (0.086 A)
Nephthys	4	60 mm (0.031 A)
Marenzelleria	**2**	0.005 (guess)
Heteromastus	4, **5**	0.005 (guess)
Lanice	**9,8**	0.07 (guess)
Scoloplos	9	0.01 (guess)
Cerastoderma	**4,7**	<7 mm (guess)
Macoma	3*,4,7	<7 mm (guess)
Crangon	**1,8**	25 mm (0.200 B)
Carcinus	**1,7,8**	0.035**
Corophium	7	6 mm (0.001 A)
Hydrobia	**4**,7	all, num***

	source	sampling location
1	(Nehls & Tiedemann 1993)	Königshafen , GWS
2	(Esselink & van Belkum 1986)	Dollard, DWS
3	Kersten and Piersma in (Smit & Wolff 1980)	Ameland, DWS
4	(Goss-Custard, Jones, & Newbery 1977)	The Wash, UK
5	(Ruiters 1992)	Westerschelde, DD
6	Van de Vlas (1970) in (Leopold *et al.* 2004)	Coast of Gr., DWS
7	(Mouritsen 1994)	Danish WS
8	(Petersen & Exo 1999)	Spiekeroog, GWS
9	(Leopold *et al.* 2004)	Lit. compilation
A	(Zwarts & Wanink 1993)	Coast of Frl. DWS
B	(Kuipers & Dapper 1981)	Dutch WS

num: predictor in number of individuals
guess: educated guess based on similar species
all: all size classes are selected
* Only siphons
** mean of west and east
*** 4 classes [0, 1-10, 11-20, >21] per sample

DD: Dutch Delta   Gr.: Groningen
DWS: Dutch Wadden Sea   Frl.: Friesland
GWS: German Wadden Sea
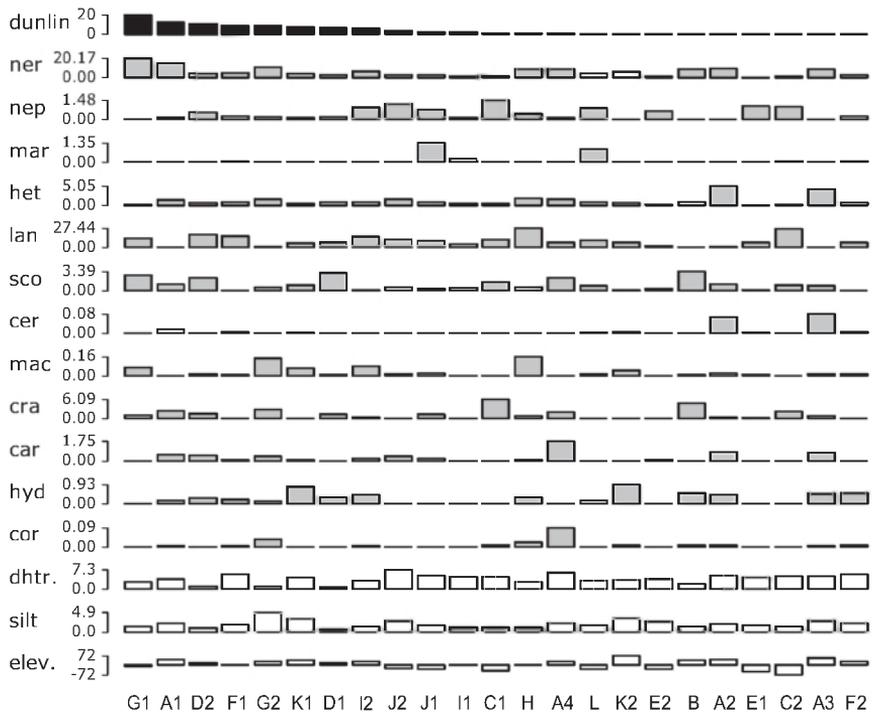
Figure S1.1. Mean density of dunlin (individual ha^{-1}), prey species (g. AFDM m^{-2}) and physical characteristics of all sites. Abbreviations: car: *Carcinus maenas,* cer: *Cerastoderma edule,* cor: *Corophium volutator,* cra: *Crangon crangon,* het: *Heteromastus filiformis,* hyd: *Hydrobia ulvae,* lan: *Lanice conchilega,* mac: *Macoma balthica,* mar: *Marenzelleria viridis,* nep: *Nephthys hombergii,* ner: *Nereis diversicolor,* sco: *Scoloplos armiger,* dhtr.: distance to high tide roost (km), silt: silt content (%), elev.: elevation of mudflat (cm +NAP).

Red Knot (*Calidris canutus*)

Red knot is a specialist tactile feeder mainly probing in the mud for unseen bivalves (Van de Kam *et al.* 2004).

Table S1.2. Prey species of red knot known identified in the literature. The numbers in the column "references" denote the literature (given in the right hand table) in which the prey under consideration has been found to be part of the diet. If the prey species forms a significant part of the diet, the reference numbers are bold. The column "size class and/or AFDM" gives (1) for bivalve species: the ranges of the lengths that are profitable and ingestible (numbers within parentheses refer to references in the right-hand table), and (2) for shore crab and shrimp: approximate energy content of an average individual (mg AFDM) (reference number and estimated mean length in parentheses). The energy contents of the bivalves were determined by incineration. If a prey species was found to be reasonably abundant in the Wadden Sea its name is in bold; it is included in the full regression model.

prey	references	size class and/or AFDM (g)
Macoma	**1,3,4, 5,6**	9 – 16 mm (5,6)
Cerastoderma	1,**3**,5	5 – 12 mm (5)
Mya	5	7 – 17 mm (5)
Scrobicularia	5	7 – 14 mm (5)
Mytilus	3,5	5 – 20 mm (5)
Carcinus	7	0.035*
Crangon	**3**	0.2 (8, based on 25 mm individ.)
Hydrobia	1,**3**,6	all, num**

	source	sampling location
1	(Dekinga & Piersma 1993)	DWS
3	(Piersma *et al.* 1993)	Griend, DWS
4	(Zwarts & Blomert 1992)	
5	(Zwarts, Blomert, & Wanink 1992)	DWS
6	(Goss-Custard *et al.* 1977)	The Wash,UK
7	(Leopold *et al.* 2004)	compilation
8	(Nehls & Tiedemann 1993)	Königshafen , GWS

DWS: Dutch Wadden Sea

Scrobicularia: very few specimens
Mytilus: very few small specimens
all: all size classes are selected
num: predictor in number of individuals
* mean of west and east
**4 classes [0, 1-10, 11-20, >21] per sample
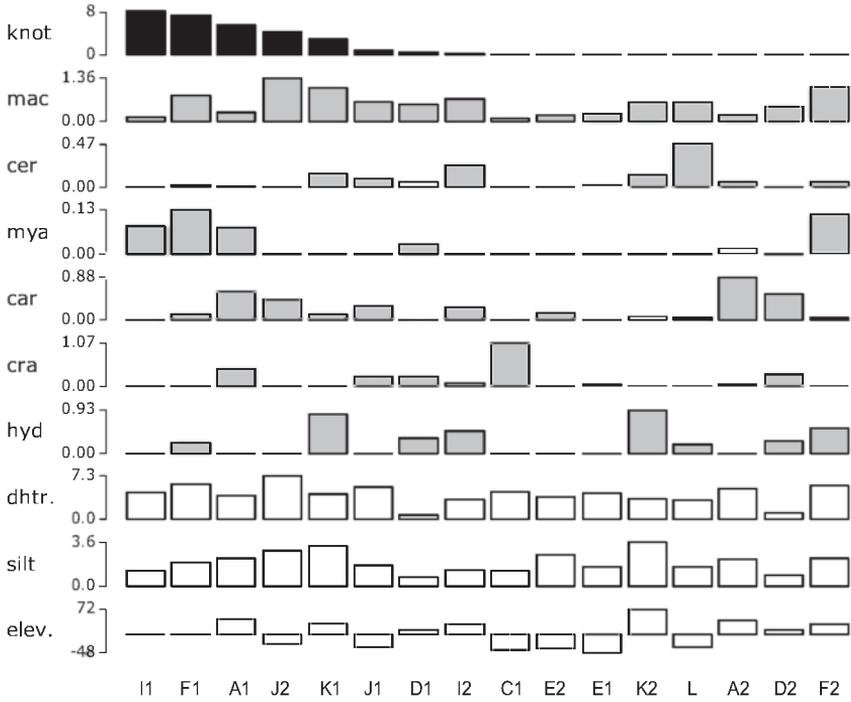
**Figure S1.2.** Mean density of red knot- (individual ha^{-1}), prey species (g. AFDM m^{-2}) and physical characteristics of 16 sites. Abbreviations: car: *Carcinus maenas,* cer: *Cerastoderma edule,* cra: *Crangon crangon,* hyd: *Hydrobia ulvae,* mac: *Macoma balthica,* mya: *Mya arenaria,* dhtr.: distance to high tide roost (km), silt: silt content (%), elev.: elevation of mudflat (cm +NAP).

Bar-tailed Godwit (*Limosa lapponica*)

Bar-tailed godwits mostly forage on worms. Sometimes they also forage on bivalves. They have also been found, for example during high tide, foraging on insect larvae in the nearby inlands (Piersma, Koolhaas, & Dekinga 1993).

Table S1.3. Summer prey of bar-tailed godwit identified in the literature. The numbers in the column "references" denote the literature (given in the right hand table) in which the prey under consideration has been found to be part of the diet. If the prey species forms a significant part of the diet, the reference numbers are bold. The column "size class and AFDM" gives the mean estimated length for each species or/and approximate energy content (mg AFDM) of an individual as used in our analyses. The given value of approximate energy contents are accompanied with a capital letter corresponding to the source of this information (given in the right hand table). For some species AFDMs could not be identified. In those cases AFDMs of individuals were guessed (indicated with "guess") on the basis of comparison to similarly sized species. If a prey species was found to be reasonably abundant in the Wadden Sea its name is in bold; it is included in the full regression model.

prey	refer-ences	size class and/or AFDM (g)		source	sampling location
Nereis	1,2,3	50 mm (0.086 A)	1	Kersten and Piersma (1981) in (Smit & Wolff 1980)	Ameland, DWS
Nephthys	2	60 mm (0.031 A)	2	(Scheiffarth 2001)	Sylt, GWS
Scoloplos	2	0.01 (guess)	3	(Piersma *et al.* 1993)	Paessens, DWS
Arenicola	1,2	0.15 (guess)	A	(Zwarts & Wanink 1993)	
Heteromastus	1	0.005 (guess)			
Lanice	2	0.07 (guess)		DWS: Dutch Wadden Sea	
Macoma	1,2,3	10 – 30 (2)		GWS: German Wadden Sea	
Carcinus	1,2	0.035*			

*mean of west and east
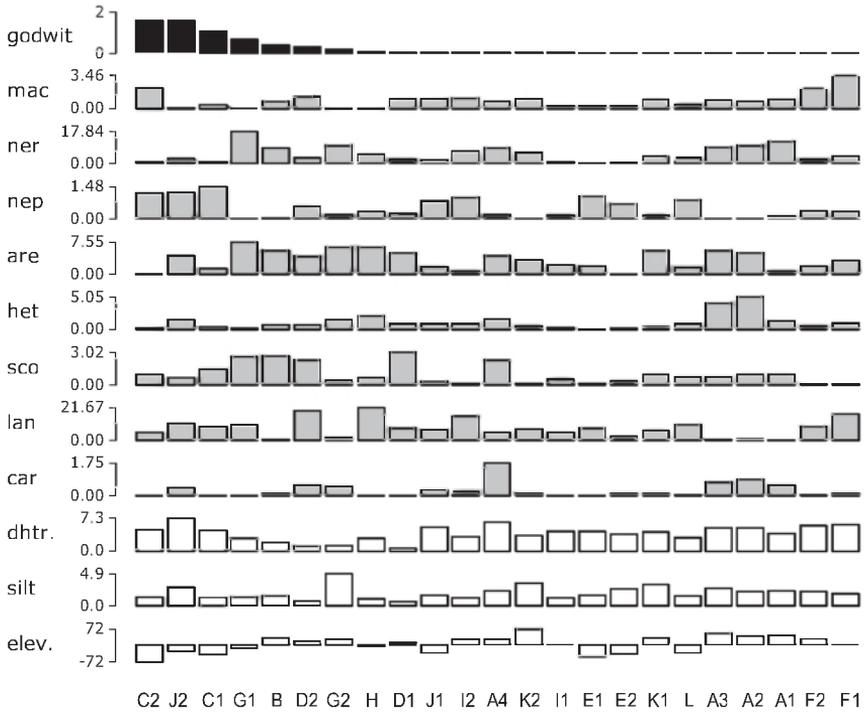
Figure S1.3. Mean density of bar-tailed godwit (individual ha^{-1}), prey species (g. AFDM m^{-2}) and physical variables for 23 sites. Abbreviations: are: *Arenicola marina*; car: *Carcinus maenas*, het: *Heteromastus filiformis*; lan: *Lanice conchilega*; mac: *Macoma balthica*, nep: *Nephthys hombergii*, ner: *Nereis diversicolor*, sco: *Scoloplos armiger*, dhtr.: distance to high tide roost (km), silt: silt content (%), elev.: elevation of mudflat (cm +NAP).

Oystercatcher (*Haematopus ostralegus*)

The oystercatcher is the most studied shorebird species in the Dutch Wadden Sea. Oystercatchers select areas where silt content is less than 5% (Goss-Custard 1996). None of the censused sites contained more than 5% silt on average. Oystercatchers rely on sight when foraging on Nereis diversicolor and probe the sediment when foraging on bivalves (Ens *et al.* 1996).

Table S1.4. Summer prey of oystercatcher identified in the literature. The numbers in the column "references" denote the literature (given in the right hand table) in which the prey under consideration has been found to be part of the diet. If the prey species forms a significant part of the diet, the reference numbers are bold. The column "size class and/or AFDM" gives (1) for bivalve species: the ranges of the lengths that are profitable (numbers within parentheses refer to references in the right-hand table), and (2) for *Nereis*: estimated average length of an individual and between parentheses the energy content of an average individual (mg AFDM) including reference. If a prey species was found to be reasonably abundant in the Wadden Sea its name is in bold; it is included in the full regression model.

prey	refer-ences	size class and/or AFDM (g)
Cerastoderma	**1,2**	>10 mm (1)
Macoma	1,2,3	>10 mm
Mytilus	1,2	>12 (1)
Scrobicularia	1,2	>10 mm (1)
Nereis	**1,2,3**	50 mm (0.086 A)

	source	sampling location
1	(Zwarts *et al.* 1996)	Frisian Coast, DWS
2	(Goss-Custard 1996)	compilation
3	(Ens *et al.* 1996)	Schiermonnikoog, DWS
A	(Zwarts & Wanink 1993)	

DWS: Dutch Wadden Sea
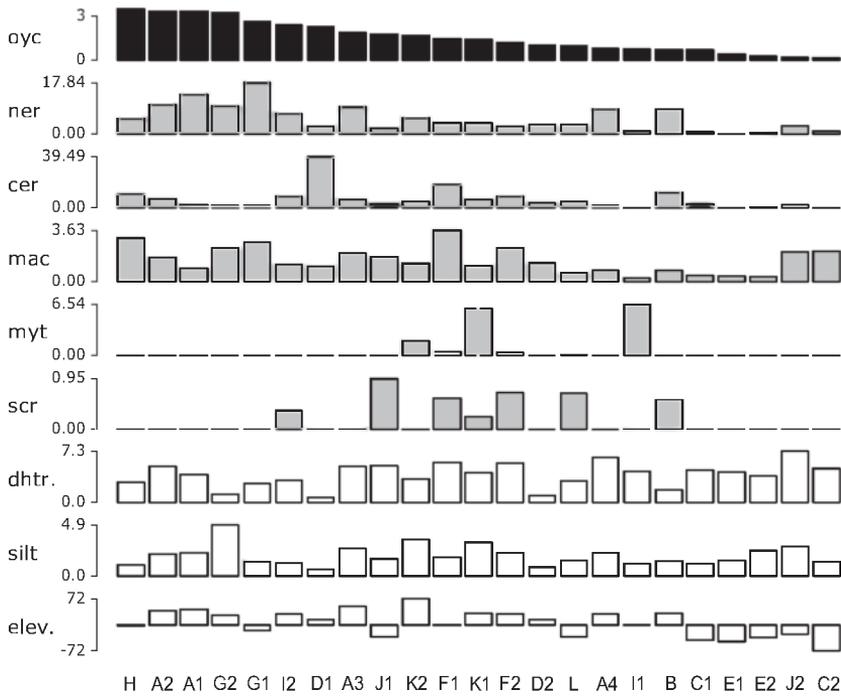
Figure S1.4. Mean density of oystercatcher (individual ha^{-1}), its prey species (g. AFDM m^{-2}) and physical characteristics for 23 sites. Abbreviations: cer: *Cerastoderma edule,* mac: *Macoma balthica,* myt: *Mytilus edulis,* ner: *Nereis diversicolor,* scr: *Scrobicularia plana,* dhtr.: distance to high tide roost (km), silt: silt content (%), elev.: elevation of mudflat (cm +NAP).

Curlew (*Numenius arquata*)

Table S1.5. Summer prey of curlew identified in the literature. The numbers in the column "references" denote the literature (given in the right hand table) in which the prey under consideration has been found to be part of the diet. If the prey species forms a significant part of the diet, the reference numbers are bold. The column "size class and/or AFDM" gives the mean estimated length for each species or/and approximate energy content (mg AFDM) of an individual as used in our analyses. The given value of energy contents are accompanied with a capital letter corresponding to the source of this information (given in the right hand table). For some species AFDMs could not be identified. In those cases AFDMs of individuals were guessed on the basis of comparison to similarly sized species. If a prey species was found to be reasonably abundant in the Wadden Sea its name is in bold; it is included in the full regression model.

prey	references	size class and/or AFDM (g)
Carcinus	**1,2,3,4**	0.035*
Crangon	**2,3**	25 mm (0.200 B)
Arenicola	1,**3**	0.15 (guess)
Cerastoderma	1	small (1,3)
Scrobicularia	1	small (1,3)
Mya	3	small (1,3)
Macoma	1	small (1,3)
Lanice	**1**,2,**4**	0.07 (guess)
Nereis	**1,2,3**	50 mm (0.086 A)

* mean of east and west
Few small mya

	source	sampling location
1	(Goss-Custard *et al.* 1977)	The Wash, UK
2	(Petersen & Exo 1999)	Spiekeroog, GWS
3	(Ens, Esselink, & Zwarts 1990)	Frisian Coast, DWS
4	(Goss-Custard & Jones 1976)	The Wash, UK
A	(Zwarts & Wanink 1993)	Coast of Frl. DWS
B	(Nehls & Tiedemann 1993)	Königshafen , GWS

DWS: Dutch Wadden Sea   Frl.: Friesland
GWS: German Wadden Sea

Notes
Goss-Custard *et al.* found that curlews only select *Carcinus* smaller than 35 mm (carapace width). The largest *Carcinus* in our samples was 20 mm.
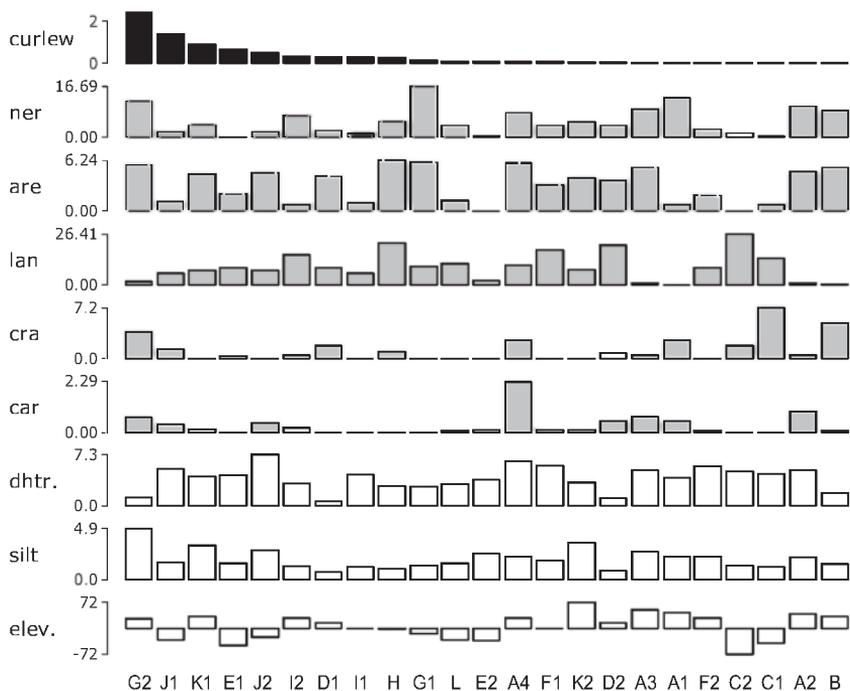
Figure S1.5. Mean density of curlew (individual ha^{-1}), its prey species (g. AFDM m^{-2}) and physical characteristics for 23 sites. Abbreviations: are: *Arenicola marina,* car: *Carcinus maenas,* cra: *Crangon crangon,* lan: *Lanice conchilega,* ner: *Nereis diversicolor,* dhtr.: distance to high tide roost (km), silt: silt content (%), elev.: elevation of mudflat (cm +NAP).

Grey plover (*Pluvialis squatarola*)

Grey plover is a visual hunter; it mainly hunts for large worms on mudflats that contain less than 5% silt. None of the sites that were censused contained more than 5% silt.

Table S1.6. Summer prey species of dunlin identified in the literature. The numbers in the column "references" denote literature (given in the right hand table) in which the prey under consideration has been found to be part of the diet. If the prey species forms a significant part of the diet, the reference numbers are bold. The column "size class and/or AFDM" gives (1) for bivalve species: the ranges of the lengths that are profitable and ingestible (numbers within parentheses refer to references in the right-hand table) (2) for polychaetes and crustacea: the estimated mean length per species or/and approximate energy content (mg AFDM) of an individual as used in our analyses. The given value of approximate energy contents are accompanied with a capital letter corresponding to the source of this information (right hand table). For some species AFDMs could not be identified. In those cases AFDMs of individuals were guessed on the basis of comparison to similarly sized species. If a prey species was found to be reasonably abundant in the Wadden Sea its name is in bold; it is included in the full regression model.

prey	refer-ences	size class and/or AFDM (g)
Nereis	**1,2,3,4**	50 mm (0.086 A)
Scoloplos	**2**	0.01 (guess)
Nephthys		60 mm (0.031 A)
Heteromastus	6	0.005 (guess)
Lanice	**2**	0.07 (guess)
Arenicola	**5**	0.15 (guess)
Macoma	2	small
Cerastoderma	2	small
Carcinus	**2**	0.035*
Corophium	**2,5**	6 mm (0.001 A)

* mean of west and east

	source	sampling location
1	Kersten and Piersma in (Smit & Wolff 1980)	Ameland, DWS
2	(Goss-Custard *et al.* 1977)	The Wash, UK
3	(Esselink & van Belkum 1986)	Dollard, DWS
4	(Ruiters 1992)	Westerschelde, DD
5	(Pienkowski 1983)	Holy Island Sands, Northumberland, UK
6	(Kersten & Piersma)	Ameland, DWS
A	(Zwarts & Wanink 1993)	Coast of Frl. DWS

DWS: Dutch Wadden Sea
DD: Dutch Delta
UK   United Kingdom

Notes

We did not find evidence in the literature that *Nephthys* has been found to be part of the diet of grey plover. We consider it an unlikely a priori hypothesis that grey plover would ignore *Nephthys*; we therefore included it in the full model.
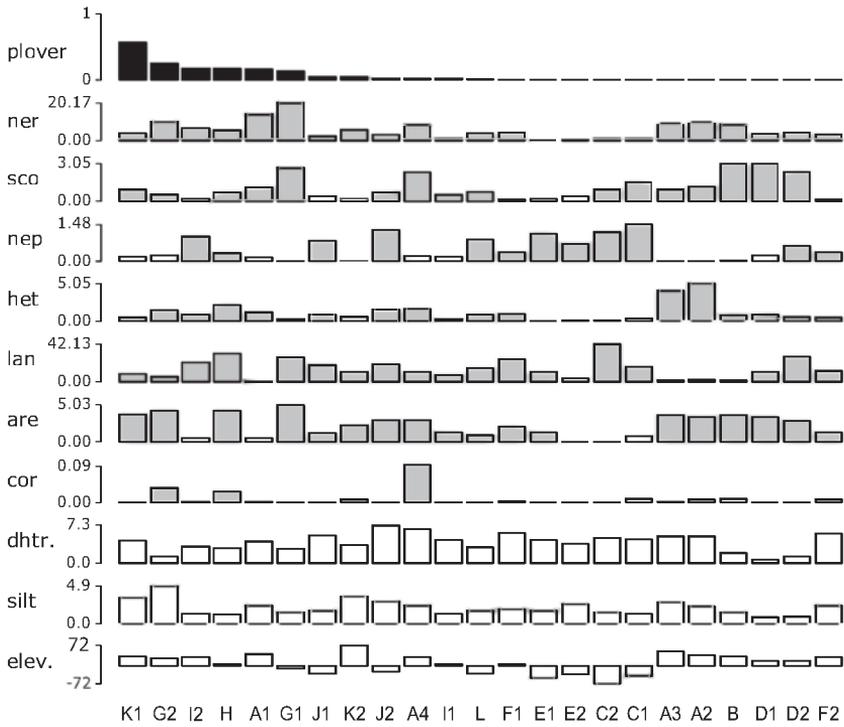
Figure S1.56. Mean density of grey plover (individual ha^{-1}), its prey species (g. AFDM m^{-2}) and physical characteristics for 23 sites. Abbreviations: are: *Arenicola marina,* cor: *Corophium volutator,* het: *Heteromastus filiformis,* lan: *Lanice conchilega,* ner: *Nereis diversicolor,* nep: *Nephthys hombergii,* sco: *Scoloplos armiger,* dhtr.: distance to high tide roost (km), silt: silt content (%), elev.: elevation of mudflat (cm +NAP).

3

The spatial distribution of flocking foragers: Disentangling the effects of food availability, interference and conspecific attraction by means of spatial autoregressive modeling

Eelke O. Folmer, Han Olff and Theunis Piersma

Abstract

Patch choice of foraging animals is typically assumed to depend positively on food availability and negatively on interference while benefits of the co-occurrence of conspecifics tend to be ignored. In this paper we integrate a classical functional response model based on resource availability and interference with a conspecific attraction model and use it to simulate spatial distributions of animals in their continuous resource landscapes. We consider both equilibrium and non-equilibrium distributions. We show that the integrated model produces distributions of foraging animals that closely match the distributions observed in nature. The simulations also show that under information uncertainty the locations of flocks are highly variable when conspecific attraction is strong. We furthermore explain how we can estimate the impacts of conspecific attraction and interference on the distribution of foraging animals by spatial autoregression. On the basis of simulated data we show that the separate impacts of interference and conspecific attraction can be disentangled when prior information on either is available, in addition to information on resource density and predator density, and that the total food effect is given by the spatial multiplier.

Introduction

The understanding of the spatial distribution of foraging animals is one of the most important themes in theoretical and empirical ecological research. The "Ideal Free Distribution" (IFD) model (Fretwell and Lucas 1969) describes the equilibrium distribution of individuals over resource patches based on fitness maximization. When combined with a generalized functional response model that relates food consumption to food availability and competitor density, the IFD model allows prediction of the spatial distribution of foraging animals. The basic theoretical result of this combined model, that we denote the "classical model", is that the degree of aggregation in patchy resource landscapes depends positively on food availability and negatively on interference (Sutherland 1983, Sutherland and Parker 1992, Moody and Houston 1995, van der Meer and Ens 1997).

A shortcoming of the classical approach (besides the unrealistic assumptions that animals are omniscient, have equal competitive abilities, and incur no cost of moving), is that beneficial effects of the presence of conspecifics are ignored (Muller *et al.* 1997). Particularly, the presence of conspecifics dilutes predation risk (Hamilton 1971, Pulliam 1973, Quinn and Cresswell 2006) and it signals the availability of food and safety which reduces search costs, and costs related to exercising vigilance while foraging (Underwood 1982). Hence, the predictive and explanatory power of aggregative response models that do not take into account these self-organizing effects, may be poor for many species (Amano *et al.* 2006, Folmer *et al.* 2010).

The role of signalling has been explored in the animal information literature. It postulates that information about food availability or safety may not be readily obtained by "personal" inspection (Valone and Templeton 2002, Danchin *et al.* 2004, Dall *et al.* 2005). Under such circumstances animals may benefit from cues from conspecifics (Conlisk 1980, Clark and Mangel 1984, Stamps 1988, Valone 1993, Ruxton *et al.* 1995, Valone and Templeton 2002, Danchin *et al.* 2004, Dall *et al.* 2005, King and Cowlishaw 2007). Note that copying behaviour does not necessarily direct animals towards the most rewarding food patch (Beauchamp *et al.* 1997, Sirot 2006, Sumpter and Pratt 2009). Particularly, if predecessors selected a sub-optimal patch, copying may lead to a collective mistake (Beauchamp *et al.* 1997, Giraldeau *et al.* 2002).

In the ecological literature it is widely acknowledged that a better understanding of the impacts of social benefits on foraging (and other types of) behaviour is needed (Fryxell 1991, Fletcher 2006, Nilsson *et al.* 2007, Jeanson and Deneubourg 2007, Campomizzi *et al.* 2008). However, empirical research on the impacts of resource availability, interference and conspecific attraction on the spatial distribution of foraging animals has been hampered by a noticable

lack of a coherent framework to measure conspecific attraction and interference (see also Nathan *et al.* (2008) who argue in a similar vein that lack of a framework hampers the understanding of movement). Here, we present an operational definition based on the notion that conspecific attraction will manifest itself as the tendency of conspecifics to locate in each others' vicinity. (Note the similarity to (2008) who postulate that the structure of a movement path is a reflection of the basic processes that produced it.) This implies that it will show up as positive spatial dependence, i.e. the number of animals at one location is positively correlated with the number of animals at neighbouring locations (controlling for the effects of other location factors). Interference, on the other hand, has a depressing effect on positive spatial dependence, as it induces animals to keep some minimal distance from each other. Hence, both conspecific attraction and interference show up as spatial dependence, but in opposite directions. Interference drives animals away from each other and operates over short distances (Stillman *et al.* 2002, Vahl *et al.* 2005). Particularly, at small spatial scales, the effects of repulsion, due to attempts to reduce costs of interference, will show up as species specific minimal distances between individuals. In contrast, conspecific attraction operates over long distances and makes animals cluster. It follows that at large spatial scales (e.g. whole resource landscapes) the impact of conspecific attraction on spatial dependence will be more pronounced than the interference effect.

Effects of exogenous environmental factors and spatial dependence in the response variable (i.e. spatial autocorrelation) can be estimated by means of spatial autoregressive (SAR) models which combine conventional regression models with a spatial autoregressive structure (Anselin 1988, LeSage and Pace 2009). Thus, estimates of the impacts of interference and conspecific attraction on the one hand, and of exogenous environmental factors on the other, may be obtained by means of estimating a SAR model on the basis of the spatial distributions of animals and food, respectively.

The classical model is based on the assumption of an equilibrium distribution in which no animal has an incentive to find a better foraging site. However, in nature equilibrium distributions hardly, if ever, occur. In a group of foraging animals there are always animals in motion responding to, or anticipating, changing conditions. Particularly, incoming and relocating animals change both conspecific attraction and interference, and hence consumption rates, which may induce on-site individuals to relocate, which induces further relocation, and so on. In this paper we do not only consider the adequacy of measuring conspecific attraction by means of spatial autoregression in equilibrium distributions, but also in non-equilibrium distributions, denoted as "flocks in motion".

The specific objectives of this paper are the following. First, we develop an integrated model based on expected resource availability, interference and

conspecific attraction. Secondly, we simulate spatial distributions on the basis of the integrated model to illustrate how flocking patterns depend on, amongst others, interference and conspecific attraction and show that conspecific attraction decreases the predictability of patch selection. Thirdly, on the basis of simulated data, we analyse the applicability of SAR models to estimate the impact of resource availability, and the joint impact of conspecific attraction and interference, for equilibrium and non-equilibrium distributions. Fourthly, we show that the total (i.e. direct + indirect effects) impact of resource distribution on the spatial distribution of foragers can be estimated by the spatial multiplier. Fifthly, we show how the autoregressive approach can be applied in empirical research. Finally, we discuss some of the simplifying assumptions on which our model is based.

The model

Our integrated classical-conspecific attraction model (integrated model for short) is based on the notion that the selection of a foraging site involves balancing costs and benefits. We assume that if an animal located too close to conspecifics, the costs due to the presence of conspecifics (i.e. interference) would exceed the benefits. The cost of interference and its repulsive effect, however, rapidly level off to zero when inter-individual distance increases (Stillman *et al.* 2002, Seppänen *et al.* 2007). This assumption is based on the notion that interference arises from behavioural interactions (e.g. stealing prey items or fighting) that are only possible amongst nearby animals (Vahl *et al.* 2005). Benefits due to the presence of conspecifics (relating to food availability and safety) decrease at a lower rate with distance than interference costs because individuals can generally observe and benefit from conspecifics that are relatively far away (Fernandez-Juricic *et al.* 2004). Hence, we assume that conspecific attraction operates over larger distances than repulsion. The above assumptions with respect to interference and conspecific attraction are corroborated by the spacing behaviour of e.g. sycamore aphids (*Drepanosiphum platanoides*) (Kennedy and Crawley 1967) and various species of shorebirds (Moody *et al.* 1997, Folmer *et al.* 2010).

Expected consumption rate
We assume that the expected consumption rate at a foraging site (hereafter labeled "cell") is a function of expected resource availability and interference. With respect to expected resource availability, we assume either perfect or imperfect information. Information uncertainty is incorporated by adding stochasticity to Beddington's functional response model (Beddington 1975).

Denoting expectation of a stochastic variable by $'$, the expected consumption rate, C'_i for each cell i is:

$$C'_i = \frac{aR'_i}{1 + ahR'_i + qP_i}$$

where R'_i is the amount of food an animal expects to find in cell i, P_i the number of conspecifics in cell i, q the interference parameter, a the attack rate and h handling time. In the simulations, we model information uncertainty for cell i by drawing from a left-truncated (at 0) normal distribution with mean the true amount of food and standard deviation θ. To simplify the simulations, but without loss of generality, we assume that a and h equal 1.

Conspecific attractiveness and spatial dependence
As noted above, the presence of conspecifics in a cell is taken by searching animals as an indication of food availability or safety. Hence, the presence of conspecifics signals the attractiveness of a location. Conspecific attractiveness of a given cell is a function of the number of its "own" conspecifics, i.e. conspecifics located within the borders of the own cell, and of the number of conspecifics in neighbouring cells. We assume that the conspecific attractiveness of cell i (S_i) increases with the number of conspecifics up to an asymptote as follows:

$$S_i = s \frac{\sum_{j}^{N} W_{ij} P_j}{1 + \sum_{j}^{N} W_{ij} P_j},$$

where N is the total number of cells in the spatial system and W is the spatial weights matrix representing the structure of the spatial system. We assume first-order queen contiguity between cells. That is, $W_{ij} = 1$ if cell i and j have a common border or vertex. Moreover, to allow for conspecific attraction within a cell, we define $W_{ii} = 1$. Finally, $W_{ij} = 0$ elsewhere. W is row-normalized, i.e. each element is divided by the sum of its row elements such that the sum of each row equals 1. By row-normalization, S_i is independent of the number of neighbours of cell i. The term $\sum_{j}^{N} W_{ij} P_j$ indicates that animals are attracted to cell i because of the presence of conspecifics in cell i and in the neighbouring cells. The intensity of conspecific attraction is given by the parameter s.

Note that there are manifold reasons for animals to form groups. Rather than defining a specific attractiveness function, we simply assume that the nearby presence of conspecifics has functional advantages and that the attractiveness of a location relates to the numbers of conspecifics in its near surrounding.

Total attractiveness and leader-follower heterogeneity

Total expected attractiveness of cell i, T_i', is the sum of its expected consumption rate (C_i') and its conspecific attractiveness S_i.

$$T_i' = \frac{aR_i'}{1 + ahR_i' + qP_i} + s \frac{\sum_j^N W_{ij}P_j}{1 + \sum_j^N W_{ij}P_j}$$

In nature, animal populations are heterogeneous with respect to their ability to avoid predation and the knowledge they have of the distribution of resources (Stamps 1988, Krause and Ruxton 2002, van Gils *et al.* 2006). Hence, there is variation in benefits that individuals obtain from locating near conspecifics. This type of heterogeneity is modeled by having a fraction of the population that is insensitive to the "attraction signals" from their conspecifics (i.e. $s = 0$), viz. their choices are based on the expected consumption rate (C_i') only. (In a producer-scrounger model the insensitive type would be considered a producer and the sensitive type an opportunistic scrounger.) Rands and Johnstone (2003) label the insensitive types "leaders", and the sensitive types $(s > 0)$ "followers". We will use this terminology below.

Setup of the simulations

In this section, we first describe how the different resource landscapes in which the foragers select patches, are generated. Next, we present the agent-based patch choice procedure including the properties of the foragers and (re)location rules based on the attractiveness of the cells.

We consider a continuous resource landscape made up of 24 × 24 cells. The amount of food in each cell is generated by drawing a value from the standard normal distribution. Since this may lead to unrealistically large differences in values between adjacent cells, we smooth the landscape by means of a Gaussian 2D convolution filter (Oksanen and Sarjakoski 2005). This smoother preserves the original normal distribution. The level of smoothness is determined by the range of the kernel, r. In the simulations r takes the values 0 (no smoothing), 3 (intermediate) and 5 (strong smoothing). The final resource landscape is obtained by means of inverse standardization, i.e. each smoothed cell value is multiplied by the standard deviation 2 followed by adding the mean 5. Negative values (which because of the selected values of the moments of the distribution will be very rare) will be set at 0.

The numbers of animals that forage in the resource landscape is varied such that the mean densities correspond to 1, 2 and 5 animals per cell. The parameter

s varies between 0 and 1 with steps of 0.1; q varies between 0.1 and 1 with steps of 0.1. With these parameter combinations the resulting distributions range from dense to sparse flocks (Fig. 3.1). The fraction of leaders is 0.1, and, hence, the rest of the population is made up of followers. Of course, when $s = 0$, there are no followers and all individuals find food individually and thus are "leaders".

Individual animals enter the landscape sequentially. Leaders and followers enter in random order. A leader selects a cell on the basis of the highest expected consumption rate C_i'; a follower on the basis of highest expected total attractiveness T_i'. Information uncertainty on the food distribution (θ) for a screening animal is 0 (perfect information) or 2 (incomplete information). (If the animals have perfect information there is no need to locate near conspecifics to reduce search costs. Hence, in the case of perfect information, reduction of costs is related to vigilance and risk dilution only.) We assume no food depletion so that food availability is the same for each individual.

The simulations are agent-based; that is, for each individual we record its position in the landscape and whether it is a leader or follower. Moreover, the expected resource availability of each cell is registered. The number of replications per parameter combination (s, q, r, θ and animal density) is 25. For each replication a new food distribution is generated.

Due to the arrival of new animals, which leads to increased interference and conspecific attraction, the expected and realized total attractiveness for animals already present change. Animals are able to respond to the changing conditions by relocating to other cells. Relocation is simulated as follows. When all the animals have entered the resource landscape, first the leader that is worst off in terms of realized consumption rate (C_i) relocates to a new cell, if it perceives an opportunity for improvement. The new location, $j \neq i$, is chosen on the basis of the highest expected consumption rate (C_j'). Next the follower that is worst off in terms of realized total attractiveness (T_i), that sees opportunity for improvement moves to the cell where expected total attractiveness, T_i', is highest. Note that if relocation does not increase expected consumption rate or total attractiveness, the animals stay in their current cells. The relocation of a leader or a follower is labelled a relocation event. After the first relocation event, the other animals have the opportunity to relocate. The relocation process continues until equilibrium is obtained, i.e. all leaders and followers are in the most attractive cells and have no incentive to move. Individuals remember the resource availability of the visited cells, i.e. R_i is updated after each relocation by removing the stochasticity (associated with imperfect knowledge) of the visited cells. (Obviously, the memory assumption is only relevant for the imperfect information case.) The number of relocation events to obtain equilibrium will be recorded. If no equilibrium is reached within 2000 relocation events, the run is terminated. Note that because of the memory assumption, equilibrium will ultimately emerge.

Evaluation methods

Spatial autoregression

The spatial autoregression (SAR) model combines a conventional regression model with a spatial autoregressive structure. The SAR model estimates the impacts on the number of animals in a cell of the exogenous environmental variables and of the number of animals in neighboring locations weighted by the spatial weights matrix. That is, the SAR model for our integrated model, for cell $i = 1, 2,..., N$, reads:

$$y_i = \beta_0 + \beta_1 x_i + \rho \Sigma_j W_{ij} y_j + \varepsilon_i$$

with $y_i = ln(number\ of\ animals\ +1)$, $x_i = ln(amount\ of\ food\ +1)$, W is defined as above, except that $W_{ii} = 0$ (see below). Row-normalization implies that for cell i, $\sum_j^N W_{ij} \ln(P_j +1)$ is the average (transformed) number of conspecifics in its first order contiguous cells. The regression coefficient β_0 is the intercept, β_1 represents the direct food effect and ρ is the spatial autoregressive coefficient. The number of animals and the amount of food are increased by 1 because of possible zero arguments of the logarithm functions. The spatial autoregressive model will be estimated by means of maximum likelihood (ML). See Anselin (1988) and LeSage and Pace (2009) for details.

In contrast to data generation where $W_{ii} = 1$, $W_{ii} = 0$ in the SAR model. This is because for a single cell there is no spatial dependence by definition (i.e. spatial dependence is between cells only). This does not mean that there could be no conspecific attraction within a given cell. However, to estimate within-cell attraction with a SAR model, spatial disaggregation (splitting up a cell in smaller parts) is required.

Evaluation of the adequacy of the SAR framework for analysis of equilibrium distributions and flocks in motion

We evaluate the adequacy of the SAR framework to estimate the effect of food availability and the joint effect of conspecific attraction and interference for equilibrium distributions and flocks in motion as follows. First, since perfect information always leads to equilibrium, we only consider the case of information uncertainty. Secondly, for a given parameter configuration, we only consider replications for which in one subset of the 25 replications equilibrium distributions were achieved and for the complimentary set flocks in motion. The performance of the SAR framework is evaluated by comparing the differences between the average spatial autoregressive coefficient of equilibrium distributions (ρ_{eq}) and the average spatial autoregressive coefficient for flocks in motion (ρ_{motion}) in the two subsets. Thirdly, the number of relocation events

until equilibrium emerges varies. To get insight into the speed of emergence of an equilibrium (if it emerges) as well as the stability of ρ_{motion} over relocations, we report by classes of relocation events the number of equilibria (u) that have emerged, and the number of flocks in motion (v) as well as the values of ρ_{eq} and ρ_{motion}. The classes are: 1 – 500, 501 – 1000, 1001 – 1500 and 1501 – 2000. We use classes because the number of relocation events for which an equilibrium emerges varies for a given parameter combination. Finally, several parameter configurations will be considered.

Spatial multiplier

Not only do animals in a given cell i attract animals to surrounding cells but also *vice versa*: animals in surrounding cells attract animals to cell i. Specifically, the first individual that settles in the landscape selects a cell i on the basis of its expected consumption rate (direct food effect). Its presence at cell i induces other animals to select cell i or neighbouring cells (first order indirect food effect) which induces other animals to select cell i or neighbouring cells (second order indirect food effect), and so on. Hence, food availablity in cell i does not only impact on the number of animals in cell i, but also in other cells. In other words, food availability in cell i "multiplies" through the spatial system. The average total food effect (direct + all indirect effects) on the number of animals is obtained by multiplying the food regression coefficient β_1 in the SAR model, denoted β_{1SAR}, by the spatial multiplier $1/(1-\rho)$. In other words, the spatial multiplier is the average level by which the direct effect of a factor is multiplied to account for indirect effects in the system to obtain the total effect (LeSage and Pace 2009).

Note that estimating the effect of food availability on the number of foraging animals per cell by ordinary least squares (OLS) (which ignores spatial spillover, i.e. the explanatory variable $\sum_j W_{ij}y_j$ is omitted), is biased because the effect of conspecific attraction is ignored (Beale et al. 2010). Specifically, β_{1OLS}, the regression coefficient of food availability estimated by OLS, is biased, i.e. it over-estimates the direct food effect.

Simulation results

Integrated equilibrium distributions

To get insight into the impacts of various components of the integrated model, especially conspecific attraction and interference, we present various equilibrium distributions in Figure 3.1. This figure shows that for a fixed resource landscape the spatial distribution of omniscient animals ($\theta = 0$) with 10% leaders varies with conspecific attraction and interference. (Observe that conspecific
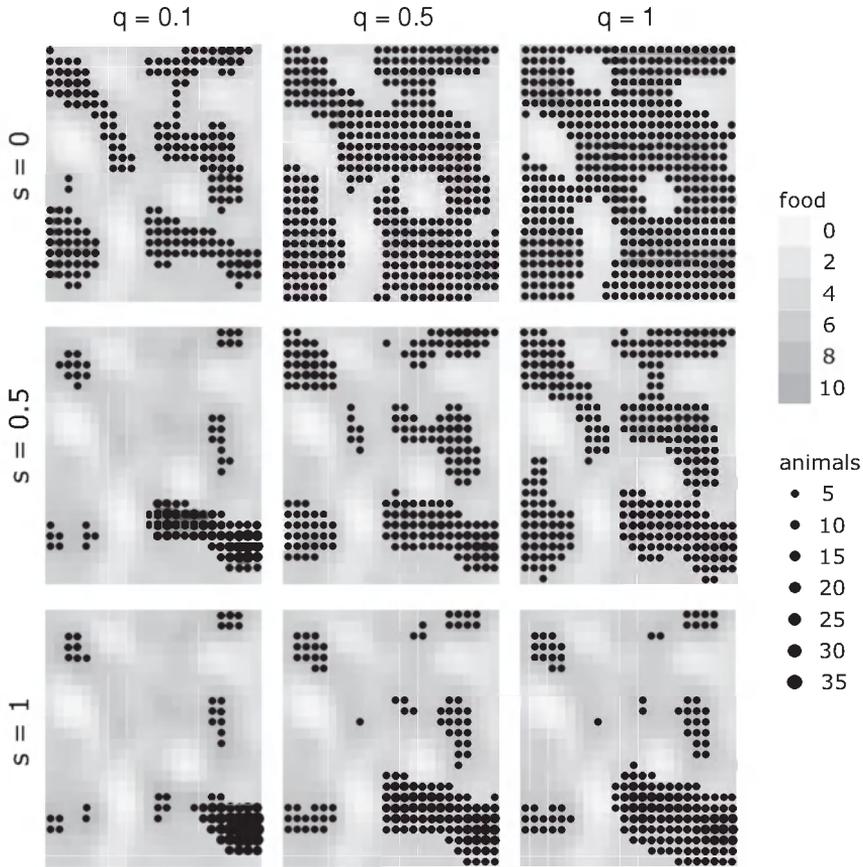
Figure 3.1. Spatial distribution of omniscient animals ($\theta = 0$) in a fixed and smoothed ($r = 5$) 24×24 cells resource landscape with mean animal density equal to 1 individual per cell. Each panel is based on one simulation run for a given combination of s (conspecific attraction parameter) and q (interference parameter). Colour intensity of the landscape represents food density and the size of the dots represent the number of animals.

attractiveness in this case relates to decreased vigilance costs and dilution of predation risk only.) Conspecific attraction results in clustering of animals, whereas interference drives individuals away from each other to cells with lower food availability. Strong interference leads to a spatial distribution of foraging animals that reflects the food distribution more closely. Strong conspecific attraction in combination with weak interference results in dense clusters, whereas strong interference combined with weak conspecific attraction leads to sparsely populated cells and spaced-out distributions.
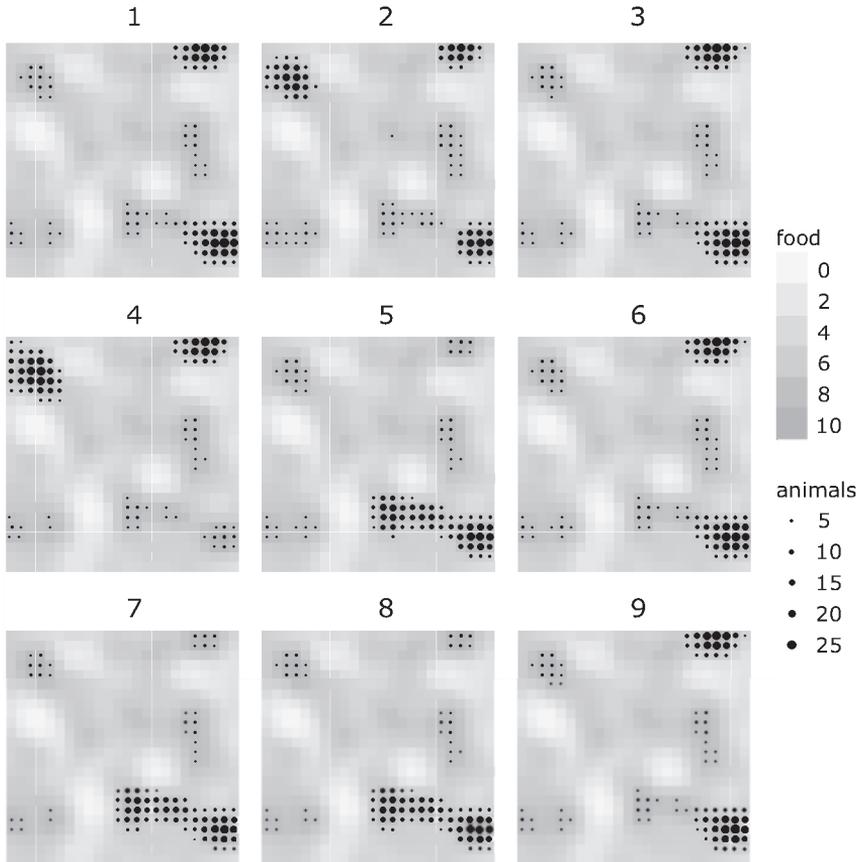
Figure 3.2. Equilibrium distributions of animals that are interference-insensitive ($q = 0.1$), moderately sensitive to conspecific attraction ($s = 0.5$) and with information uncertainty on the food distribution ($\theta = 2$). Each panel shows the outcome of one replication. The 24×24 cells resource landscape is fixed over replications; $r = 5$; animal density = 1 cell^{-1}. See Figure A1 for further details.

Figure 3.2 presents the distributions of 9 independent replications for a fixed resource landscape with animals that are moderately sensitive to conspecific attraction ($s = 0.5$) and interference insensitive ($q = 0.1$). The replications only differ by information uncertainty about the food distribution ($\theta = 2$). The figure shows that the location of the clusters of animals is highly variable and unpredictable under these circumstances. Note that the distributions presented in Fig. 3.2 apply to equilibrium distributions obtained after varying numbers of relocations. When the number of relocations increases, the resulting equilibrium

distributions become more similar to each other because of memory, i.e. individuals remember the resource availability of the visited cells. Note, however, that although they become more similar, they still tend to differ from each other (see Appendix A for further details).

The spatial autoregressive coefficient for equilibrium situations (ρ_{eq}) and flocks in motion (ρ_{motion})

Before going into detail, we make the following observations. First, there are quite a large number of zero counts in the data. This type of data can be analysed by zero-inflated SAR models (Agarwal *et al.* 2002). However, we

Table 3.1. Average ρ_{eq} and ρ_{motion} for animal density 1 and $r = 0$ for selected values of q and s.

relocations		1 – 500		501 – 1000		1001 – 1500		1501 – 2000	
q	s	ρ_{eq}	ρ_{motion}	ρ_{eq}	ρ_{motion}	ρ_{eq}	ρ_{motion}	ρ_{eq}	ρ_{motion}
0.2	0.4		0.86 (0.00) v=20		0.85 (0.00) v=20		0.84 (0.00) v=20	0.82 (0.00) u=5	0.84 (0.00) v=20
	0.6		0.88 (0.00) v=16		0.87 (0.00) v=16	0.86 (0.02) u=3	0.87 (0.00) v=16	0.87 (0.01) u=6	0.87 (0.00) v=16
0.4	0.4		0.86 (0.00) v=18	0.85 (-) u=1	0.85 (0.00) v=18	0.86 (0.01) u=2	0.85 (0.00) v=18	0.84 (0.00) u=4	0.85 (0.00) v=18
	0.6		0.90 (0.01) v=5	0.89 (0.01) u=5	0.89 (0.01) v=5	0.89 (0.00) u=7	0.89 (0.00) v=5	0.89 (0.00) u=8	0.89 (0.01) v=5
0.6	0.0		0.00 (0.01) v=24		0.00 (0.01) v=24		0.01 (0.01) v=24	-0.09 (-) u=1	0.01 (0.01) v=24
	0.2		0.65 (0.01) v=14	0.56 (-) u=1	0.58 (0.01) v=14	0.58 (0.04) u=2	0.54 (0.01) v=14	0.56 (0.01) u=8	0.52 (0.01) v=14
0.8	0.0		-0.01 (0.01) v=14		-0.01 (0.01) v=14	0.00 (0.03) u=4	-0.02 (0.01) v=14	0.00 (0.01) u=7	-0.02 (0.01) v=14
	0.2		0.48 (0.03) v=4	0.45 (0.01) u=5	0.42 (0.03) v=4	0.46 (0.01) u=9	0.42 (0.02) v=4	0.45 (0.02) u=7	0.42 (0.02) v=4
1.0	0.0		-0.02 (0.02) v=8	0.03 (-) u=1	-0.01 (0.01) v=8	0.02 (0.02) u=9	0.02 (0.01) v=8	-0.02 (0.01) u=7	0.01 (0.01) v=8

Notes- u and v: the number of equilibrium distributions and flocks in motion in an interval of relocations, respectively. Standard errors are within parantheses. Averages and standard errors rounded off. (-): no standard error because of one replication only.

found the residuals to approach normality (although they are a bit peaked). Given these characteristics and the purpose of the paper to demonstrate SAR modelling in general, we apply the standard SAR model. However, in empirical applications zero-inflated SAR models may be considered in the case of many zero counts. Secondly, as explained above, comparison of ρ_{eq} and ρ_{motion} is only relevant for the imperfect information case because under perfect information there will always be an equilibrium. Thirdly, consider Table 3.1. To economize on space we do not report results for $s > 0.6$ as they are virtually identical to those for $s = 0.6$. For the same reason we only consider increases of s and q by steps of 0.2, animal density 1 and $r = 0$. The results for other values of these parameters are very similar to the results presented in Table 3.1. A more complete table is presented in Appendix B.

From Table 3.1 the following conclusions emerge: (1) ρ_{eq} and ρ_{motion} hardly differ in most cases. In approximately 85% of the cases the difference is within a two-sided 95 % confidence interval, in approximately 95% of the cases in a two-sided 90% confidence interval; (2) the number of relocations hardly affects the development of the spatial autoregressive coefficients, except in the case of ρ_{motion} for $q > 0.6$. After relatively large changes for less than 1000 relocations, this coefficient stabilizes; and (3) large values of q have a depressing effect on the spatial autoregressive coefficients. This finding follows from the fact that interference induces animals to stay away from each other.

The above implies that the spatial autoregressive coefficient reflects the impacts of conspecific attraction and interference nearly equally well for equilibria and for flocks in motion. This finding is further supported by the stability of the spatial autoregressive coefficient over relocations. Given the above findings there is no need to distinguish between ρ_{eq} and ρ_{motion}. We generically refer to them by ρ. Hence, the analyses below are based on the combined subsets, i.e. the entire set of ρ values.

The spatial autoregressive coefficient as function of the simulation parameters

In this subsection we pay attention to the spatial autocorrelation coefficient as a function of r, animal density and, especially, s and q. As observed in the previous subsection, the results in Table 3.1 hint at a logistic relationship between ρ and its determinants, especially s. Inspired by the results in Fig. 3.1 and Table 3.1, we also included the interaction term $s \times q$ in the model. Therefore, we estimate the following model:

$$\ln(\frac{\rho}{1-\rho}) = \beta_0 + \beta_1 s + \beta_2 q + \beta_3 density + \beta_4 r + \beta_5 sq + \varepsilon$$

with ε the disturbance term and the other variables as defined above.

Separate regressions are performed for perfect and imperfect information. Before going into detail, we observe that in ~2% (1094 out of 49500) of the cases a negative ρ with mean –0.037 was obtained. Because of the *logit* transformation of ρ, these cases were removed from the dataset.

Table 3.2 shows a high overall goodness of fit for each of the two models, as expressed by the R^2. It also shows that the signs of the coefficients of the explanatory variables of the two models are the same and in line with expectations: ρ increases with s and declines with q while animal density has a negative impact, since crowding drives animals to other cells. The coefficient of the interaction term $s \times q$ is positive because s induces animals to locate in each others' vicinity while q restricts the number of animals within cells which leads to large, but sparse flocks. Sparse flocking renders neighbouring cells more similar and thus leads to stronger spatial dependence. An interesting finding is that under imperfect information, the coefficient of s is larger, and the coefficient of q in absolute value is smaller than in the case of perfect information.

From the above it follows that ρ is a function of s, q, r and animal density and varies by information uncertainty. Hence, for given values of q, r and animal density, ρ is a function of s only. Similarly, ρ is a function of q only, if all other variables are known.

An important issue in empirical applications is the sensitivity of the estimates to the scale of observation (Wiens 1989, Levin 1992). As pointed out above, conspecific attraction and interference may occur at various scales. To capture their impacts by means of spatial dependence, the scale at which data on the distribution of animals are available should approximately match the behavioural scales. These scales, however, may not be evident beforehand. We tested how our findings depend on the scale of observation by aggregating adjacent patches and performing the same analysis. The results obtained show that the coefficient of s increases substantially when going from level (1×1) to level

Table 3.2. $\ln(\frac{\rho}{1-\rho})$ as a function of the simulation parameters.

	perfect information	imperfect information
Constant	1.67 (0.02)	1.49 (0.02)
s	2.39 (0.03)	2.53 (0.03)
q	–3.12 (0.03)	–2.40 (0.03)
s × q	2.53 (0.05)	1.74 (0.05)
Animal density	–0.63 (0.00)	–0.56 (0.00)
r	0.29 (0.00)	0.27 (0.00)
R^2	0.86	0.82

Note- predictors: conspecific attraction (*s*), interference (*q*), animal density resource and smoothness (*r*).
Coefficients and standard errors (within parentheses) are rounded off.
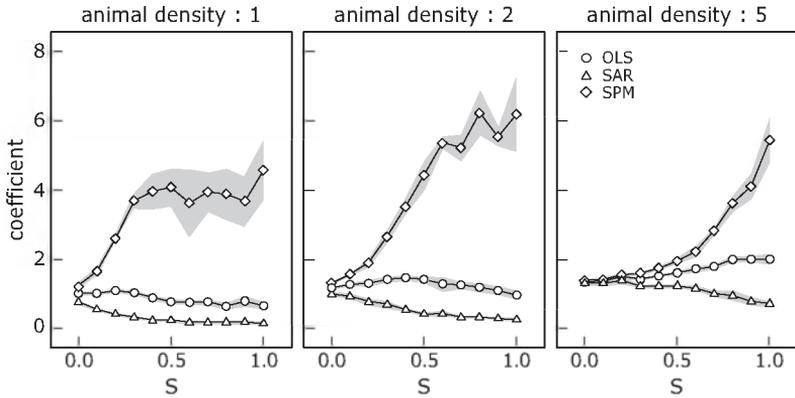
Figure 3.3. Estimated direct and total food effects for an intermediate level of interference ($q = 0.5$), intermediate smoothness ($r = 3$), conspecific attraction (s) as indicated in each panel, animal densities 1, 2, 5 and $\theta = 0$. The 95% confidence intervals are indicated by bands. Confidence intervals for β_{1SAR} and β_{1OLS} are very narrow and therefore do not come through everywhere. OLS = Ordinary Least Squares model; SAR = Spatial Autoregressive model; SPM = Total average food effect based on the SAR regression coefficients and the spatial multiplier. Similar results hold for other values of q and r.

(2×2) while it is constant (perfect information) or decreases slightly (imperfect information) from (2×2) to (4×4). For the coefficient of q there is a monotonic decrease (in absolute value) for both information cases. For animal density and r there are only minor changes, although for the latter there is a change of sign when aggregating (Appendix C).

The decline of the coefficient of q for increasing scale follows from the fact that the impact of interference on the spatial distribution of foragers declines when distance increases, as pointed out in the Introduction. The increase of the coefficient of s follows from the fact that when going from level (1×1) to level (2×2) the similarity, between contiguous regions in terms of foraging animals, increases. However, when going from level (2×2) to (4×4) the similarity decreases. This development of the coefficient of s reflects the tendency for conspecific attraction to level off when distance increases beyond a threshold. The upshot is that the autoregressive model adequately reflects conspecific attraction and interference at various levels of aggregation and makes it possible to gain insight into their separate effects.

The spatial multiplier

In this subsection we address the consequences of ignoring conspecific attraction on the estimator of the food effect. We first compare β_{1SAR} obtained from the SAR model containing both the exogenous variable $x_i = ln(amount\ of\ food$

+1) and the autoregressive term, with β_{1OLS} obtained from the model with x_i only and estimated by ordinary least squares (OLS). Figure 3.3 shows that for s fixed at zero, the OLS and SAR coefficient estimates are equal. However, when s is greater than zero, β_{1OLS} exceeds β_{1SAR} for all animal densities. Hence, ignoring conspecific attraction leads to overestimation of the direct effect of resource availability. Figure 3.3 also shows that β_{1SAR} declines with increasing conspecific attraction for all animal densities which reflects that due to increasing conspecific attraction, the direct impact of food availability decreases.

As observed above, β_{1SAR} only gives the direct impact of food availability, not the total effect, i.e. direct effect plus indirect effects. To obtain the (average) total food effect β_{1SAR} is multiplied by the spatial multiplier. Fig. 3.3 shows that the total effect predicted by the SAR model exceeds the total effect predicted by the OLS model by an order of magnitude. Hence, the interdependent nature of animals reinforces the impact of resource availability on their foraging distribution.

Discussion

Foraging distributions of social animals are complex phenomena. One of the reasons for our poor understanding of the animal-habitat relationships is the unobservable nature of conspecific attraction and interference. In this paper we have shown that they may be measured indirectly by way of their manifestations, i.e. the tendency of conspecifics to locate in each others' vicinity or to stay away from each other, respectively. Conspecific attraction shows up as positive spatial dependence, whereas interference has a depressing effect on it. We have shown that standard statistical methods that ignore spatial dependence (particularly OLS), will give biased estimators and tests of relationships between animals and their resources when they are influenced by conspecific attraction (also see Dormann *et al.* 2007; Beale *et al.* 2010). We have presented the spatial autoregressive model as an adequate alternative that gives unbiased results. Since the estimated spatial autoregressive coefficient is influenced by interference and conspecific attraction as well as animal density, information uncertainty and smoothness of the resource landscape, prior information on these variables is needed to derive estimates of self-organization, i.e. the combined effect of conspecific attraction or interference. In addition, if prior information on conspecific attraction (interference) is also available, the separate effect of interference (attraction) can be obtained. In empirical research, this kind of prior information is sometimes available or can be readily obtained. For example, in shorebird foraging environments information on resource availability and functional responses are available or can be relatively easily collected. For instance, red knots (*Calidris canutus*) are known to be rather interference-insen-

sitive (van Gils and Piersma 2004), and oystercatchers (*Haematopus ostralegus*) interference–sensitive (Vines 1980). Information on the other relevant parameters, i.e. animal density and resource density, can be obtained from spatial population counts and food surveys such as the long run monitoring programs for the Dutch Wadden Sea (van Gils *et al.* 2006; Kraan *et al.* 2009; Folmer *et al.* 2010).

In species distribution datasets there often are many zeros for the dependent variable (Martin *et al.* 2005). This characteristic is often taken as an indicator of the fact that the species under consideration tends to locate in the most suitable habitat which itself is spatially heterogeneously distributed. Here we have proposed a supplementary explanation. Particularly, we have shown that conspecific attraction may lead to large areas with abundant food remaining unoccupied.

We did not investigate the effects of varying attack rates and handling times on the spatial distribution of foragers. However, their effects in our model can be derived from van der Meer and Ens (1997) who show that in Beddington's functional response model (1975) an increasing attack rate will lead to more foragers in rich food patches and that increasing handling times have an opposite effect. An increasing attack rate will have similar effects in our model resulting in smaller but denser flocks. Moreover, the attractiveness of surrounding cells will also increase. Thus, conspecific attraction will further amplify the direct effect of increasing attack rate. Increasing handling time on the other hand will decrease the density of foragers per cell leading to a larger fraction of sparsely populated cells. In this case conspecific attraction will be directed towards a larger number of cells which will lead to spaced-out flocks. This effect is similar to the interference effect.

The simulation results confirm the hypothesis that the impacts of conspecific attraction and interference are virtually the same for equilibrium distributions and flocks in motion, and that their impacts on the distributions of flocks in motion are stable when animals relocate. The explanantion for this finding is that when selecting a foraging patch, an animal is driven by its knowledge of the resource landscape and by the signals from conspecifics. Whether searching is at an early stage or at the final stage is irrelevant in our model; it is always the same mechanisms that drive patch selection. The result implies that analyzing the impacts of interference and conspecific attraction does not require equilibrium distributions. This is an important result for empirical applications because in nature flocks virtually always are in motion.

Another interesting finding is that under information uncertainty, the effect of conspecific attraction on the spatial distribution is larger than under perfect information, in spite of possible higher interference costs. The explanation is that compared to perfect information, the average expected benefit of the presence of conspecifics increases or the expected costs of interference decrease, such that the animals tend to cluster more and spatial dependence increases.

The simulation results imply that if the average consumption rate is not substantially affected by the presence of conspecifics (low interference), populations may benefit from independent individuals (leaders), as long as they select optimal food cells. Resource-rich areas will then be increasingly occupied which decreases the mismatch between the resource and animal distributions. It has been shown that leadership status may be driven by energy stores (Rands *et al.* 2003), body size (Krause *et al.* 1998), age or dominance (Krause and Ruxton 2002), i.e. hungry, large, mature or dominant individuals taking leadership. This implies that heterogeneity amongst interdependent individuals may be beneficial to the population.

The model and simulations presented in this paper focuses on conspecific attraction and interference and abstract from various other factors and processes that also affect the spatial distribution of foragers. For example, we assumed that the proportions of leaders and followers are fixed and that all followers are equally sensitive to conspecific attraction, i.e. all followers having the same s. A more realistic approach would be to have s follow a continuous distribution the shape of which affects the spatial distributions of the foragers. For instance, for the same range, a distribution of s with a fat right tail will result in a more clustered spatial distribution of foragers than when s is drawn from a uniform distribution. It should be noted that drawing s from a continuous distribution rather than from the simple distribution applied above would not basically change the simulation procedure.

In natural populations there are various factors (e.g. energetic state, information, predation risk) that simultaneously affect an animal's level of conspecific attraction which, moreover, may vary for different timescales. The frequency distribution of conspecific attraction of a natural population will, thus, more likely be dynamic rather than fixed. For instance, aggregations of foragers may attract predators which in their turn, *ceteris paribus*, may increase the level of conspecific attraction between the foragers on a short timescale. On longer timescales, increasing age and experience may decrease the level of conspecific attraction. An interesting extension to our model would be to allow for temporal heterogeneity in conspecific attraction of individuals.

Yet another process that may affect foraging distributions (but was ignored here) is resource dynamics. Particularly, spatially heterogeneous depletion and growth of resources is likely to negatively affect the predictability of optimal foraging locations and thus the spatial distribution of foragers and delay or prevent the emergence of equilibria. Our results indicate that in the case of varying resource densities, *ceteris paribus*, the impact of conspecific attraction on the spatial distribution and the importance of leaders will increase. (It should be noted, however, that through time, animals may also learn the spatial distribution of resources which decreases the role of attraction and the importance of

leaders.) However, on short timescales (i.e. the timescales at which flocking takes place) depletion of resources will often be small and the impact on foraging distributions negligible. For instance, in productive intertidal mudflat systems such as the Wadden Sea, where shorebirds forage on benthic prey during low tide, resources are depleted at slow rates. Due to their high reproductive rates, the densities of benthic animals build up fast during spring and summer (Beukema *et al.* 2002, Philippart *et al.* 2010) whereas depletion occurs at a much slower rate during late summer, autumn and winter when shorebird predators are around in greatest numbers (van de Kam *et al.* 2004). For this reason changes in benthos densities have been difficult to detect over time spans shorter than a month (Zwarts *et al.* 1992, Piersma *et al.* 1993, Kraan *et al.* 2009). The resource landscape for foraging shorebirds can, at least in the present case, be considered constant over short timescales. For other systems, resource depletion may be relevant, even in the short run of one visit.

Over longer time spans, however, resource depletion is an important issue. Further development of our understanding of the long run spatial distribution of social foragers in relation to their resources requires integration of social foraging behaviour and resource dynamics. In this context, the role of leadership, learning and interdependency of foragers become important research themes. We expect that the foraging model and the proposed statistical methodology presented in this paper may play a role in this context.

In conclusion, we concur with Lima and Zollner (1996) and Nathan *et al.* (2008) that research on habitat selection at the landscape-scale will benefit from research on animal behaviour on the micro-scale. We also share their conclusion that the main obstacle to the development of population habitat selection models is limited by poor knowledge about the information that animals have about landscape properties. Currently, the theoretical and empirical literature in this area is growing rapidly (van Gils *et al.* 2006, Rogers *et al.* 2006, Wikelski *et al.* 2007). Our study contributes to this literature by showing how conspecific interaction impacts on habitat selection in that it presents an operational definition of the unobservable processes of conspecific attraction and interference and develops a methodology that can disentangle them. It also contributes to research that focuses on the causes and consequences of interdependency among animals in general which is currently an important theme in behavioural research (Couzin *et al.* 2005, Conradt *et al.* 2009, Ramseyer *et al.* 2009, Sumpter 2010).

Appendix A: Development of spatial distributions due to relocations under imperfect information

Figure A1 presents the development of the spatial distributions due to reloca-
tion for equilibrium distributions 3, 4, 5 and 7 in figure 3.2. Observe that for
replications 4 and 7 equilibria are obtained between 1000 and 1500 relocation
which implies that the distributions do not change after 1500. In replications 3
and 6 equilibrium is obtained between 1500 and 2000 relocations.
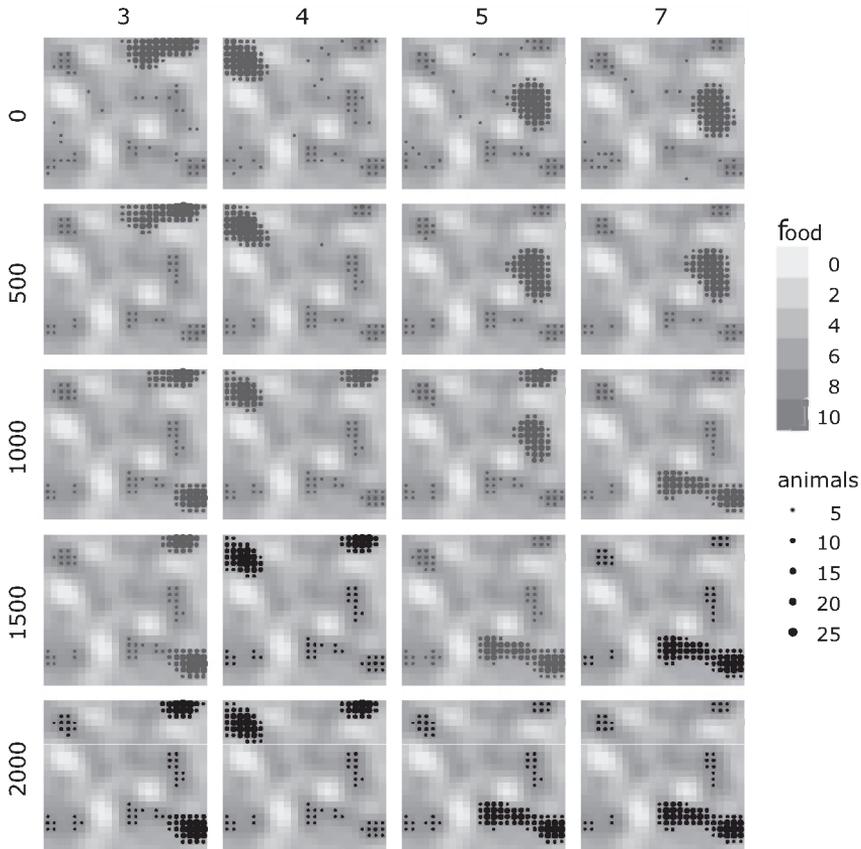
Figure A.1. Development of the spatial distributions 3, 4, 5, 7 presented in Fig 3.2 due to relo-
cations. Animals are interference-insensitive ($q = 0.1$), moderately sensitive to conspecific
attraction ($s = 0.5$) and have imperfect information on the food distribution ($\theta = 2$). Each
column represents the spatial distribution after 0, 500, 1000, 1500 and 2000 relocations. The
24×24 cells resource landscape is fixed for the 4 replications; $r = 5$; animal density = 1 cell^{-1}.
Equilibrium distributions are plotted in black; flocks in motion are grey.

Appendix B: Development of spatial autoregressive coefficients for equilibrium distributions and flocks in motion

This appendix presents a more complete version of Table 3.1 in the main text. Table B1 shows the average spatial autoregressive coefficient for equilibrium distributions (ρ_{eq}) and the average spatial autoregressive coefficient for flocks in motion (ρ_{motion}). A "flock in motion" is a distribution for which no equilibrium was obtained within 2000 relocations. (Due to the memory assumption all distributions will eventually become equilibrium distributions.) Averages are based on the number of replications for which equilibrium and flocks in motion are obtained, respectively. To get insight into the evolution of ρ_{eq} and ρ_{motion} these statistics are reported by classes of relocations: 1 – 500, 501 – 1000, 1001 – 1500 and 1501 – 2000. Classes are used because the number of relocations for which equilibrium emerges varies. Comparison between autoregressive coefficients is not always possible because for some parameter combinations either no equilibrium was reached for any of the 25 replications in which case all distributions are flocks in motion or all 25 replications reached equilibrium.

The basic conclusions that emerge from table S2 is that the spatial autoregressive coefficients are virtually the same for equilibrium distributions and for flocks in motion. Additionally, ρ_{motion} decreases slightly due to relocations. The decrease of ρ_{motion} is strongest after the first relocations.

Table B.1. Average ρ_{eq} and ρ_{motion} for animal density 1 and $r = 0$.

relocations		1 – 500		501 – 1000		1001 – 1500		1501 – 2000	
q	s	ρ_{eq}	ρ_{motion}	ρ_{eq}	ρ_{motion}	ρ_{eq}	ρ_{motion}	ρ_{eq}	ρ_{motion}
0.2	0.0		0.00 (0.01) v=25		-0.01 (0.01) v=25		-0.01 (0.01) v=25		-0.01 (0.01) v=25
	0.2		0.80 (0.00) v=25		0.78 (0.00) v=25		0.77 (0.00) v=25		0.75 (0.00) v=25
	0.4		0.86 (0.00) v=20		0.85 (0.00) v=20		0.84 (0.00) v=20	0.82 (0.00) u=5	0.84 (0.00) v=20
	0.6		0.88 (0.00) v=16		0.87 (0.00) v=16	0.86 (0.02) u=3	0.87 (0.00) v=16	0.87 (0.01) u=6	0.87 (0.00) v=16
	0.8		0.89 (0.00) v=6	0.89 (0.01) u=5	0.89 (0.00) v=6	0.88 (0.01) u=6	0.88 (0.01) v=6	0.88 (0.01) u=8	0.88 (0.01) v=6
	1.0		0.89 (-) v=1	0.89 (0.00) u=8	0.88 (-) v=1	0.89 (0.00) u=11	0.88 (-) v=1	0.89 (0.01) u=5	0.88 (-) v=1

Table B.1. Continued

relocations		1 – 500		501 – 1000		1001 – 1500		1501 – 2000	
q	s	ρeq	ρmotion	ρeq	ρmotion	ρeq	ρmotion	ρeq	ρmotion
0.4	0.0		-0.03 (0.01) v=25		-0.03 (0.01) v=25		-0.03 (0.01) v=25		-0.03 (0.01) v=25
	0.2		0.76 (0.01) v=25		0.71 (0.01) v=25		0.68 (0.01) v=25		0.65 (0.01) v=25
	0.4		0.86 (0.00) v=18	0.85 (-) u=1	0.85 (0.00) v=18	0.86 (0.01) u=2	0.85 (0.00) v=18	0.84 (0.00) u=4	0.85 (0.00) v=18
	0.6		0.90 (0.01) v=5	0.89 (0.01) u=5	0.89 (0.01) v=5	0.89 (0.00) u=7	0.89 (0.00) v=5	0.89 (0.00) u=8	0.89 (0.01) v=5
	0.8	0.90 (0.01) u=2	0.90 (0.01) v=4	0.90 (0.00) u=11	0.90 (0.01) v=4	0.90 (0.00) u=7	0.90 (0.01) v=4	0.89 (-) u=1	0.90 (0.00) v=4
	1.0			0.91 (0.00) u=11		0.91 (0.00) u=9		0.90 (0.00) u=5	
0.6	0.0		0.00 (0.01) v=24		0.00 (0.01) v=24		0.01 (0.01) v=24	-0.09 (-) u=1	0.01 (0.01) v=24
	0.2		0.65 (0.01) v=14	0.56 (-) u=1	0.58 (0.01) v=14	0.58 (0.04) u=2	0.54 (0.01) v=14	0.56 (0.01) u=8	0.52 (0.01) v=14
	0.4	0.85 (0.00) u=2		0.86 (0.00) u=10		0.84 (0.00) u=10		0.84 (0.00) u=3)	
	0.6	0.90 (0.01) u=4		0.90 (0.00) u=17		0.89 (0.01) u=3		0.89 (-) u=1	
	0.8	0.91 (0.00) u=8		0.90 (0.00) u=15		0.90 (0.01) u=2			
	1.0	0.91 (0.00) u=11		0.91 (0.00) u=13		0.91 (-) u=1		0.91 (-) u=1	

Table B.1. Continued

relocations		1 – 500		501 – 1000		1001 – 1500		1501 – 2000	
q	s	Peq	Pmotion	Peq	Pmotion	Peq	Pmotion	Peq	Pmotion
0.8	0.0		-0.01		-0.01	0.00	-0.02	0.00	-0.02
			(0.01)		(0.01)	(0.03)	(0.01)	(0.01)	(0.01)
			v=14		v=14	u=4	v=14	u=7	v=14
	0.2		0.48	0.45	0.42	0.46	0.42	0.45	0.42
			(0.03)	(0.01)	(0.03)	(0.01)	(0.02)	(0.02)	(0.02)
			v=4	u=5	v=4	u=9	v=4	u=7	v=4
	0.4	0.86		0.86		0.84			
		(0.00)		(0.00)		(0.00)			
		u=11		u=11		u=3			
	0.6	0.90		0.89					
		(0.00)		(0.00)					
		u=19		u=6					
	0.8	0.91		0.91					
		(0.00)		(0.00)					
		u=19		u=6					
	1.0	0.92		0.92					
		(0.00)		(0.01)					
		u=21		u=4					
1.0	0.0		-0.02	0.03	-0.01	0.02	0.02	-0.02	0.01
			(0.02)	(-)	(0.01)	(0.02)	(0.01)	(0.01)	(0.01)
			v=8	u=1	v=8	u=9	v=8	u=7	v=8
	0.2	0.42		0.40		0.39		0.37	
		(0.02)		(0.02)		(0.01)		(0.02)	
		u=3		u=8		u=10		u=4	
	0.4	0.85		0.83		0.80			
		(0.00)		(0.01)		(-)			
		u=16		u=8		u=1			
	0.6	0.89		0.89					
		(0.00)		(0.01)					
		u=23		u=2					
	0.8	0.91							
		(0.00)							
		u=25							
	1.0	0.92							
		(0.00)							
		u=25							

Note- u and v: the number of equilibrium distributions and flocks in motion in an interval of relocations, respectively. Standard errors are within parantheses. All figures rounded off. (-): no standard error calculated because of one replication only.

Appendix B: Multi-scale analysis: spatial autoregressive coefficient as a function of the simulation parameters by level of aggregation

In empirical applications it is not always evident what the appropriate observation scale is. We therefore estimated the spatial autoregressive coefficient on data that were aggregated at different levels. Particularly, resource and animal densities were averaged for (2×2) cells and (4×4) cells to render a "new" data set. In the same way as described in the main text, the resulting estimates of ρ were *logit* transformed and regressed against the simulation parameters. Table S3 shows the parameter estimates. To facilitate comparison the estimates on non-aggregated data in Table 3.2 in the main text are also presented (level of aggregation 1×1).

Table C.1. $\ln(\frac{\rho}{1-\rho})$ as a function of the simulation parameters for the original and aggregated data.

Level of aggregation	1 x 1		2 x 2		4 x 4	
	Perfect information	Imperfect information	Perfect information	Imperfect information	Perfect information	Imperfect information
Constant	1.67 (0.02)	1.49 (0.02)	1.38 (0.02)	1.46 (0.03)	0.43 (0.03)	0.61 (0.04)
s	2.39 (0.03)	2.53 (0.03)	3.39 (0.04)	3.42 (0.04)	3.38 (0.05)	3.24 (0.05)
q	-3.12 (0.03)	-2.40 (0.03)	-2.62 (0.04)	-2.22 (0.04)	-2.12 (0.05)	-1.74 (0.06)
s x q	2.53 (0.05)	1.74 (0.05)	2.12 (0.06)	1.85 (0.07)	1.56 (0.08)	1.76 (0.09)
Animal density	-0.63 (0.00)	-0.56 (0.00)	-0.67 (0.00)	-0.57 (0.00)	-0.58 (0.00)	-0.37 (0.00)
r	0.29 (0.00)	0.27 (0.00)	-0.10 (0.00)	-0.20 (0.00)	-0.22 (0.00)	-0.42 (0.00)
R^2	0.86	0.82	0.84	0.77	0.74	0.68

Table C1 shows that the amount of variation in ρ that is explained is high for all the models for both perfect and imperfect information at all levels of aggregation. Furthermore, it shows that the regression coefficients of the variables *s, q, animal density* and the interaction term *s × q* have equal signs for all the levels of aggregation. The effect of *r*, however, is positive for the unaggregated case and turns negative for both the aggregated cases.

4

The relative contributions of resource availability and social aggregation to foraging distributions: A spatial lag modelling approach

Eelke O. Folmer and Theunis Piersma

Abstract

The spatial distribution of foraging animals simultaneously depends on (1) exogenous environmental variables such as resource availability and abiotic habitat characteristics, and (2) the endogenous variable social aggregation made up of the opposing mechanisms of conspecific attraction and conspecific repulsion. In this paper we develop an *exogenous-environment – social aggregation model* and use it to analyse the spatial distribution of six abundant shorebird species in the Dutch Wadden Sea at varying resolutions (150 ×150, 200 × 200 and 250 × 250 m). We estimate the model parameters by spatial autoregression. This approach enables, amongst others, estimation of the direct and indirect effects of an exogenous environmental variable on animal density. The former is given by the regression coefficient and the latter - which is due to the amplification of the direct effect by social aggregation - by the spatial multiplier. At all three levels of resolution and for all species, the explanatory power of social aggregation, measured by Nagelkerke R^2, is larger than the contribution of the exogenous environmental variables food availability, silt content, and elevation of the mudflat together. Social aggregation is stronger for dunlin (*Calidris alpina*), red knot (*Calidris canutus*) and curlew (*Numenius arquata*) than for oystercatcher (*Haematopus ostralegus*), grey plover (*Pluvialis squatarola*) and bar-tailed godwit (*Limosa lapponica*). The total impacts (i.e. direct effect plus indirect impacts) of the exogenous environmental predictors tends to substantially exceed the direct effect.

Introduction

Expected intake rate and predation risk are major determinants of foraging distributions (Brown and Kotler 2004, Stephens *et al.* 2007). Intake rate has been shown to negatively depend on interference behaviour, i.e. interactions such as fighting, stealing prey and monopolization of food patches (Goss-Custard 1980; Sutherland & Koene 1982; Goss-Custard *et al.* 2001; Vahl *et al.* 2005). Interference sensitivity is strongly related to attack distance (Stillman *et al.* 2002), which depends on handling time, which in its turn depends on properties of the predators and their prey (Goss-Custard 1980, Stillman *et al.* 2002, van Gils and Piersma 2004). Animals may reduce the cost of interference by spacing out (Ens *et al.* 1990, Stillman *et al.* 2002, Folmer *et al.* 2011; Chapter 3, Bijleveld *et al.* in press; Chapter 5). The basic result of this literature is that if animals are unconstrained in selecting foraging patches, and merely suffer from the co-occurrence of conspecifics, equilibrium spatial distributions arise such that the marginal pay-off amongst patches is equal (Fretwell & Lucas 1969; Kacelnik, Krebs, & Bernstein 1992; Sutherland 1983).

The conventional patch selection literature ignores that animals may also benefit from the co-occurrence of conspecifics (Underwood 1982; Krause & Ruxton 2002; Nilsson *et al.* 2007; Campomizzi *et al.* 2008). Specifically, the chance of being depredated decreases with group size (Hamilton 1971; Pulliam 1973). Furthermore, the presence of conspecifics provides clues about predation risks (Lima & Dill 1990) and the availability of food (e.g. Camazine *et al.* 2001; Valone and Templeton 2002; Danchin *et al.* 2004; Dall *et al.* 2005; Deygout *et al.* 2010). In addition, for scrounging individuals the nearby presence of foraging conspecifics may provide foraging opportunities in that prey can be obtained by means of stealing (Giraldeau & Caraco 2000; Rutten *et al.* 2010). In a review of the literature, Beauchamp (1998) found that for birds intake rate generally increases with group size. We denote the combination of conspecific attraction and repulsion 'social aggregation' to stress the difference from aggregations resulting from foragers that independently from each other select the same foraging location. The benefits that results from the presence of conspecifics is denoted aggregation economy (Giraldeau and Caraco, 2000).

As mudflats are large and open habitats in which the benthic food stocks are buried in the sediment such that the quality of foraging locations can only be learned by trial and error or by close inspection of the mudflat surface, shorebirds foraging on mudflats are ideal to study the effects of the resource distribution and social aggregation on foraging distributions (Piersma *et al.* 1993, van de Kam *et al.* 2004, van Gils *et al.* 2006). To reduce uncertainty in the search process, shorebirds may benefit from information provided by the presence and behaviour of conspecifics (Clark & Mangel 1984; Valone 2007). The average

costs and benefits of conspecific presence, however, vary from species to species. For example, red knots forage on small buried bivalves which they find by remotely sensing hard objects in soft sediments which they repeatedly probe with their bill (Piersma *et al.* 1998). Once encountered, a prey is retrieved, handled and swallowed intact in seconds (van Gils and Piersma 2004, van de Kam *et al.* 2004). Because prey processing is so short, kleptoparasitism is not possible and therefore red knots are relatively insensitive to interference (Ens, Esselink, and Zwarts 1990). Therefore knots can pack closely at minor costs (van Gils and Piersma 2004). In contrast, grey plovers locate their polychaete prey visually (Kersten & Piersma 1984). For instance, grey plovers can spot worms moving at the surface of the sediment over distances in the order of 10s of meters. However, even when worms are abundant, the fraction that is visually detectable is usually very low (Zwarts and Wanink 1993). Hence, grey plovers are likely to detect the same prey within distances of 10s of meters from each other and thus may incur interference costs. In addition, they may suffer indirectly from each other's presence because of prey depression, i.e. worms decrease their surface movements so as not to be detected by predators (Charnov, Orians, & Hyatt 1976; Goss-Custard 1980; Yates, Stillman, & Goss-Custard 2000). Hence, the presence of conspecifics decreases hunting success over relatively large distances. Thus, for grey plovers interference costs reduce conspecific attraction benefits, and therefore they maintain large inter-individual distances. In a regression for six different species of forager density on food availability and abiotic conditions only, Folmer *et al.* (2010. Chapter 2) found that the residual variance is substantially larger for red knot than for grey plover. This result is in line with the hypothesis that the former are driven by conspecific attraction and food availability, and the latter mainly by food availability.

Although conceptually, its impact on foraging behavior is fairly straightforward, the precise way in which social aggregation should be included in a regression specification is complex. Hence, research on the impacts of resource availability and social aggregation on the spatial distribution of foraging animals has been hampered by the lack of a methodology that allows estimation of their separate effects (Beauchamp 1998; Sumpter 2010).

In a previous paper (Folmer *et al.* 2011), we showed that social aggregation manifests itself as spatial interdependence between neighbouring foraging areas, i.e. an observation (the number of foraging animals) associated with one location depends on the observations (the numbers of foraging animals) at other locations. Furthermore, we suggested to estimate and to test the *exogenous-environment - social aggregation model* by spatial autoregression (SAR). By means of Monte Carlo simulations we showed that SAR performs well on gridded data. The imposition of a grid of some resolution may, however, lead to the modifiable areal unit problem (MAUP). That is, the chosen grid imposes an

arbitrary measurement system on the spatial process of foraging site selection. As shown by others (e.g. Openshaw 1984; Fotheringham & Wong 1991; Holt *et al.* 1996; Jelinski & Wu 1996; Heywood, Cornelius, & Carver 1998; Fortin & Dale 2005, Schneider 2009), MAUP can affect parameter estimates in regression analysis. We demonstrated, however, that multi-scale analysis (Wiens 1989) can be applied to obtain robust estimates of the relationship between predictors and response variables. Finally we showed that spatial dependence in the response variable implies that the direct impact of an exogenous environmental predictor like food availability is amplified by the interdependent behaviour of the foraging animals. We demonstrated that SAR allows estimation of the direct effect and the total effect (direct plus all indirect effects), the latter by means of the spatial multiplier.

The purpose of the present paper is to estimate the impacts of exogenous predictors and social aggregation on foraging distributions of six abundant shorebird species in the Dutch Wadden Sea at three spatial resolutions using the SAR methodology previously presented by Folmer *et al.* (2011).

Study area and data collection

The Dutch Wadden Sea
The Dutch Wadden Sea is shallow and contains large soft-sediment flats that emerge approximately twice a day during low tide during which they are accessible to shorebirds. Intertidal flats alternate with permanent channels. The flats are characterized by smooth gradients both in terms of abiotic features, such as sediment grain size (Zwarts *et al.* 2004), and biological properties, such as density of macrozoobenthos (Kraan *et al.* 2009). The six most abundant wader species are dunlin, red knot, oystercatcher, curlew, grey plover and bar-tailed godwit. The analysis focuses on these species because they are found in sufficiently large numbers for adequate statistical analyses and because there is large variation in flocking patterns between these species.

Data collection and preparation
As part of a long-term benthic research programme (Piersma *et al.* 1993; Kraan, van der Meer, *et al.* 2009), the density of macrozoobenthos was determined in the eastern and western Dutch Wadden Sea in July and September 2004. Benthos sampling was performed over 250 m grids in confined areas at 23 mudflats (sites). For each bird species at each sample station, we determined which prey items were available (not buried too deeply) and ingestible (smaller than maximum length and larger than minimum length) (Zwarts & Wanink 1993). For bivalves we determined the energetic value by measuring the ash free dry mass

(AFDM) in the laboratory (for details see Piersma, de Goeij, *et al.* 1993, Piersma *et al.* 1995, Kraan, van Gils *et al.* 2009). For the specimens that were counted in the field and not brought to the lab (polychaetes and isopods) we obtained estimates of their energetic value from the literature (see Folmer *et al.* 2010 for details).

Maps of the foraging shorebird on the 23 sites were taken from Folmer *et al.* (2010) and combined with maps of the distributions of species-specific harvestable benthos. The locations of individual birds and flocks could be determined with a precision of approximately 50 m while the benthos data were sampled on a 250 × 250 m grid. Finer resolutions than the 250 × 250 m grid of benthos biomass densities were obtained by thin plate spline interpolation (TPS). The interpolation was obtained by minimization of the residual sum of squares between the data and the predicted surface, constrained by a roughness penalty (Green & Silverman 1993; Wood 2006). The smoothing parameter is automatically chosen by generalized cross validation (GCV). Thin plate spline interpolation is simple, requires no knowledge of spatial model parameters and is suitable for positively skewed data.

For red knots a subset of the 23 sites were included in the analysis. The reason is that the population of red knots in the Wadden Sea is highly variable in August because of turnover of two distinct populations. By the beginning of September members of the *canutus* subspecies have departed while the other subspecies, *islandica*, has arrived (Zwarts, Blomert & Wanink 1992; Piersma *et al.* 1993b). For red knot we only considered the 16 sites observed after 1 September.

Individual birds were aggregated in grids that fully covered the censused sites (Figure 4.1). The numbers of birds inside the cells were transformed to densities (No × ha^{-1}). The density of a species in each cell was related to the exogenous environmental variables, i.e. density of prey (AFDM × m^2), mudflat elevation (m +NAP , the standard Dutch elevation reference) and silt content (% weight) of the sediment (obtained from Zwarts *et al.* 2004), and to the endogenous variable social aggregation (i.e. the density of birds in neighbouring cells). With respect to the density of prey, we included all relevant benthic species identified as food in the literature that were reasonably abundant (see supplementary material in Folmer *et al.* 2010 for further information about the benthic species included). Some cells were partially outside the censused site boundaries. They were included in the data set, if at least 50% of the area was inside the site.

To account for the disturbance caused by the presence of the observer, cells located near the observation point were removed from the datasets. Depending on species specific sensitivity to observer disturbance, we removed the cells whose centroids were within the following distances from the observer: dunlin
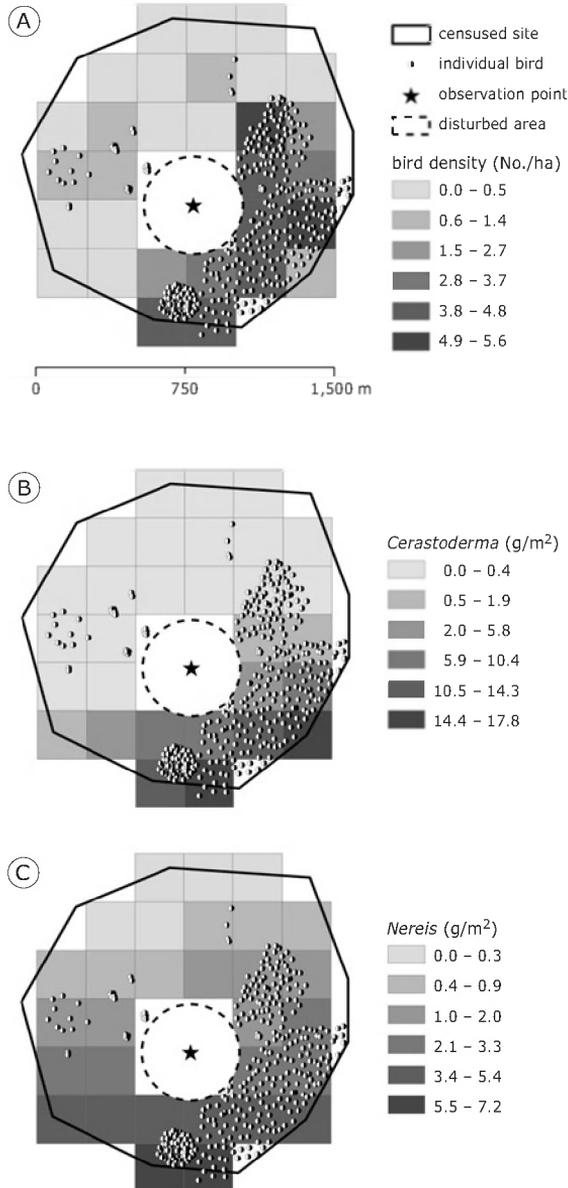
Figure 4.1. An example of a site with the locations of individual oystercatchers and food resources; resolution: 250 × 250 m. The dots denote individual birds (all three panels). Panel A: Mean bird density (No × ha^{-1}); Panel B: Cockle (*Cerastoderma edule*) biomass (ash free dry mass) (g × m^{-2}); Panel C: Biomass (AFDM) of the polychaete *Nereis diversicolor* (g × m^{-2}). The "hole" in the middle is the disturbed area around the observer. Cells with centroid within the disturbed area are removed from the dataset. For further details see Methods.

and red knot: 150 m, oystercatcher, grey plover and bar-tailed godwit: 200 m, curlew: 300 m (Spaans, Bruinzeel, & Smit 1996). The resulting lattices contained all relevant information for statistical analysis, i.e. bird and prey densities, the abiotic habitat characteristics and the geographical coordinates of each cell.

Each site was divided into cells of 250 × 250 m, 200 × 200 m and 150 × 150 m, respectively. The data sets consisted of the aggregate of the cells over the sites. The total number of observations (which varies by cell size) for each species is given in Table 4.1. To check the robustness of the results, we estimated models for the 250 × 250 m, 200 × 200 m, and 150 × 150 m resolutions.

Statistical analysis

The spatial lag model

We estimated the *exogenous-environment – social aggregation model* by means of the spatial lag model which is made up of two systematic components, i.e. the spatial autoregressive component representing social aggregation and the set of exogenous variables representing the exogenous environment. The spatial lag model (Anselin 1988, Haining 2003, LeSage and Pace 2009) (in matrix notation) reads:

$$y = \rho Wy + X\beta + \varepsilon$$

where y is an $n \times 1$ vector of observations on the dependent variable (in the present case bird density), X is an $n \times k$ data matrix of explanatory variables with associated coefficient vector β, ε is an $n \times 1$ vector of error terms which follows a normal distribution, i.e. $\varepsilon \sim N(0, \sigma^2 1_n)$. W is the $n \times n$ spatial weights matrix and ρ the spatial autoregression coefficient or spatial lag parameter. The spatial weights matrix W represents spatial dependence (or connectivity) among the observations. Various types of W matrices may be employed (see Fortin and Dale 2005). We defined cells as spatially dependent, if the distance between their centroids was less than or equal to 750 m. The limit of 750 m is based on the assumption that it is roughly the maximum distance over which the benefits of conspecific attraction extend. Spatial dependence was measured by inverse distance. That is, $W_{ij} = 1/d_{ij}$ if the distance between the centroids of cell i and j <750 m and $W_{ij} = 0$ elsewhere. Moreover, a cell is considered non-dependent with itself, i.e. $W_{ii} = 0$. W was row-normalized, i.e. each element was divided by the sum of its row elements so that the sum of each row equals 1. Left-multiplication of the vector y by the row-normalized matrix W (W_y) gives for each cell the mean y in its spatially dependent regions. The parameter

ρ reflects spatial dependence in the sample. That is, it measures the average impact of spatially dependent cells on observations in the vector y caused by social aggregation.

In SAR, the regression coefficient of an exogenous environmental variable does not represent the total change in y in response to a unit change in that variable, as in a standard linear model, because the indirect impacts due to autocorrelation are not taken into account. That is, an exogenous variable in a given cell attracts birds which in their turn attract other birds to the own and neighbouring cells (first order indirect effect) which in their turn attract birds to the own and neighbouring cells (second order indirect effect) and so on (see LeSage and Pace 2009 for details). To obtain the total effect the indirect effects also need to be taken into account (Folmer et al. 2011). The total effect (direct + all indirect effects) of a given exogenous variable on animal density can be obtained by multiplying its SAR coefficient by the spatial multiplier $1/(1-\rho)$. Estimates and standard deviations of the total effects were obtained by means of MCMC simulation (for details see LeSage and Pace 2009 and the documentation of the spdep package in R (Bivand et al. 2008a)).

Model specification

The dependent variable is the density of birds (No $\times$ ha^{-1}) in each cell of the lattice. To reduce skewness the response variable was ln-transformed before estimation (Gelman & Hill 2006). The argument of the ln-function was increased by half the smallest non-zero value observed to avoid arguments equal to 0.

Regarding the explanatory variables, we started the analysis with a model that included the autoregressive component, all relevant benthos species that were reasonably abundant, and the abiotic variables silt content and elevation of the mudflat (see Folmer et al. 2010). The skewness of the distributions of the food-variables and the non-linear relationships between forager density and food density (van der Meer and Ens 1997) were handled by ln-transformation of the food variables. Again, to avoid zero arguments, every argument was increased by half of the smallest non-zero value observed. The abiotic predictors were not transformed.

We estimated by means of spatial autoregression (SAR) all models ranging from the full model with all relevant exogenous predictors and the autoregressive term included to a social aggregation model with intercept and autoregressive term only. Models with negative coefficients of prey variables were considered implausible. Since we did not have a priori expectations about the signs of silt content and elevation for neither bird species, negative and positive coefficients were considered ecologically plausible.

To assess the relative importance of plausible exogenous environmental predictors and social aggregation, we compared the full model and the model with social aggregation only (i.e. the benchmark) by means of the Nagelkerke R^2 (Nagelkerke 1991):

$$R^2 = \frac{1 - \left[\dfrac{L(M_{intercept})}{L(M_{SAR})}\right]^{2/n}}{1 - \left\{L(M_{intercept})\right\}^{2/n}}$$

where n is the number of observations, $L(M_{intercept})$ and $L(M_{SAR})$ are the log-likelihood values of models with intercept only and the two types of SAR models (type 1: intercept + spatial autoregressive component only, and type 2: intercept + spatial autoregressive component + exogenous variables), respectively. Improvement in terms of variance explained between both types of models was given by the difference between both R^2s. We also estimated the AICs of a model without and with the spatial autoregressive component. The best three models based on the AIC value and exogenous environmental variables with ecologically plausible signs are presented in Table 4.1.

We used the R environment version 2.13.1 (R Development Core Team 2009) for the statistical analyses including geographical interpolation. Specifically, the procedure of interpolation and geographical overlaying was automated by applying functions from the packages *fields* (Furrer, Nychka, & Sain 2009), *maptools* (Lewin-Koh *et al.* 2008), *sp* (Pebesma & Bivand 2005; Bivand, Pebesma, & Gómez-Rubio 2008b) and *spatstat* (Baddeley & Turner 2005). We used the package *spdep* (Bivand *et al.* 2008a) to estimate the spatial lag model by means of maximum likelihood and to calculate the total effects of the exogenous predictors including the associated dispersion measures (standard deviations).

Results

Before turning to the estimations, we observe that because of conspecific attraction, large parts of the mudflats tend to be unoccupied in a cross-section (Folmer et al, 2010). To reduce the resulting skewness the dependent variable was log-transformed. The frequency distributions of the log transformed response variables (ln (No $\times$ ha^{-1} + c) (where c is half the smallest non-zero value) thus contained a peak at the left end. The frequency distributions of the residuals after SAR estimation, however, turned out to be close to normal (though a bit peaked, Figure 4.3), which means that the maximum likelihood estimator is consistent and asymptotically normal.
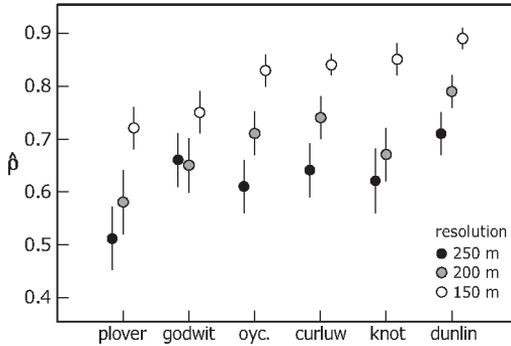
Figure 4.2. Spatial dependence ($\hat{\rho}$) by resolution and shorebird species in the Dutch Wadden Sea.

The following patterns emerge from Table 4.1. First, there is evidence of MAUP, since the estimated coefficients for both social aggregation and the exogenous environmental variables vary by resolution. However, the following robust patterns emerge. First, for all species for all resolutions the estimated autoregression coefficients ($\hat{\rho}$) are significant at 5% level. This result is supported by the substantial differences in AICs between the models with and without the SAR component. Furthermore, $\hat{\rho}$ increases with resolution which is due to the increase in similar adjacent cells.

Secondly, as argued above, $\hat{\rho}$ is the net outcome of the two opposing mechanisms conspecific attraction and repulsion. This implies that drawing conclusions about each mechanism separately requires external information (Folmer *et al.*, 2011). For the six species under consideration this kind of information exists. Particularly, bar-tailed godwit, grey plover, oystercatcher and curlew are known to be interference-sensitive and red knot and dunlin insensitive. Hence, we expect smaller $\hat{\rho}$'s for the former four species than for the latter, especially at smaller scales. The results in Table 4.1 are in line with this expectation (see also Figure 4.2).

Thirdly, the exogenous predictors follow a similar pattern as social aggregation in that the best, second best and third best models vary by resolution. However, for a given species the same environmental variables frequently show up as relevant predictors at various resolutions. In addition, for a given species for a given resolution, the best, second best and third best model tend to differ only slightly in terms of AIC and Nagelkerke R^2. Possible explanations for this are the low predictive power of the exogenous variables and high multicollinearity between them. This is supported by the small differences in AIC between the best and successive models (ΔAIC), suggesting that the best models are only marginally better than the second and third best models. Given these findings,
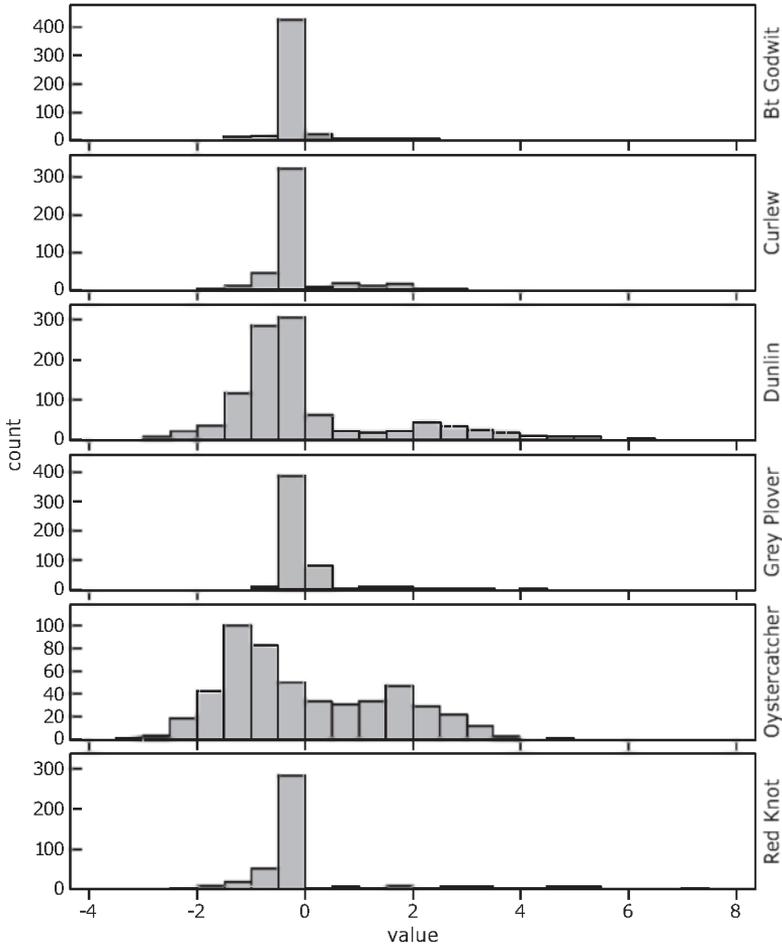
Figure 4.3. Histograms of residuals of the best SAR models by species at 250 × 250 m scale.

we accept all the food items and abiotic habitat characteristics that have been identified by the best three models as relevant predictors.

Table 4.1 shows that for dunlin the prey species *Nereis diversicolor, Heteromastus filiformis* and *Carcinus maenas* are the main exogenous predictors, for red knot *Carcinus maenas, Mya arenaria, Macoma balthia* and silt content , for oystercatcher *Cerastoderma edule, Macoma balthia, Nereis diversicolor* and silt content, and for bar-tailed godwit *Nereis diversicolor, Lanice conchilega, Arenicola marina, Heteromastis filiformis* and elevation. *Lanice conchilega*, is the most important food predictor for curlew. Furthermore, curlews are relatively more

abundant on relatively low and silty mudflats. Finally, *Nephtys hombergii* and *Lanice conchilega* and *Nereis diversicolor* are the most important prey variables for grey plover. In addition, this species shows a preference for mudflats with relatively high silt content.

The most striking result in Table 4.1 is that social aggregation outweighs the exogenous predictors in terms of explanatory power. Comparison of the Nagelkerke R^2s of the models with intercepts and autoregressive component only versus the models with intercepts, autoregressive component and exogenous predictors shows that for the latter this statistic is only slightly higher than the former for all species at all levels of resolution.

The regression coefficients of the exogenous environmental predictors represent their direct effects only. The full impact of an exogenous predictor is given by its total impact (also presented in Table 4.1). To obtain the total effects, the coefficients of the exogenous predictors were multiplied by the spatial multiplier. The main finding is that the total effect outweighs the direct effect (represented by the regression coefficient), a result that holds for all species at all resolutions. Obviously, the larger the coefficient of an exogenous predictor and the larger the degree of social aggregation, the larger the total impact is. For instance, for dunlins the spatial autocorrelations are highest at resolution 150 × 150 m. Hence, the difference between the regression coefficients of the exogenous predictors (direct impacts) and the corresponding total impacts are largest for this resolution.

Discussion

Although its relevance has been widely acknowledged in the behavioural and theoretical literature, the empirical analysis of foraging patch selection in the case of social aggregation has been hampered by the methodological problems to directly measure it. However, ignoring social aggregation as an explanatory variable in empirical analysis of foraging behaviour is likely to lead to misleading results. Particularly, in regression analysis the estimators of the regression coefficients of the variables included in the model and their variances are biased, if social aggregation is omitted as an explanatory variable (Legendre 1993; Lichstein *et al.* 2002; Keitt *et al.* 2002; Beale *et al.* 2010). In this paper we have operationalised social aggregation as spatial dependence and applied spatial autoregression to estimate the full *exogenous environment – social aggregation model* to overcome the problem of bias due to omitted variables.

The results presented above substantiate the importance of social aggregation. Indeed, more than that, we have found that for all the species at all three levels of resolution social aggregation outweighs the exogenous predictors in

terms of explanatory power. These results substantiate the notion that the group represents a central component of the environment for different species of foraging shorebirds. However, the small differences in explanatory power between the models with constant and autoregressive component on the one hand and the full models with constant, autoregressive component and exogenous predictors on the other, do not imply that the exogenous predictors played a negligible role in foraging location choice. On the contrary, food availability, elevation or silt content may have played a decisive role in the choice of the foraging sites at the initial site selection stage. For instance, expected prey availability may have led to the collective selection of a location by a flock or may have influenced location choices by leading animals whose choices were copied by followers.

When animals respond to both the presence of conspecifics and environmental cues, the interpretation of the regression coefficients becomes more complicated due to the need to take the indirect effects generated by social aggregation into account. That is, food availability initially attracts animals (direct effect) that attract conspecifics and so on (indirect effects). The total effect consists of the sum of the direct and indirect effects. We did not only estimate the direct effects, but, by means of the spatial multiplier, also total effects of exogenous predictors and found that the total effects tend to substantially exceed the direct effects. Note that typically only direct effects are considered in habitat selection models (Campomizzi *et al.* 2008).

The coefficients of social aggregation and of the exogenous variables change in opposite directions by resolution. Particularly, whereas the relative contributions of social aggregation increase with resolution, the contributions of the exogenous variables decrease, and vice versa. This suggests that there may be some scale-dependent replacement between social aggregation and the exogenous predictors. Indeed, for models made up of the same exogenous environmental predictors, the total impacts were more constant than the regression coefficients for the three resolutions.

The findings in this paper are in line with field studies in that the level of spatial dependence was highest for dunlins and red knots, followed by curlews, oystercatchers, bar-tailed godwits and grey plovers. These results are supported by other field observations of spatial distributions of these species (Goss-Custard 1970; Piersma 1985).

We have found that the amount of variance explained by environmental predictors is low. This is not due to the fact that all sampled mudflats are similar in resource availability. Previous studies (Kraan, van der Meer, *et al.* 2009; Kraan, van Gils, *et al.* 2009; Kraan *et al.* 2010) have shown that there is substantial variation in food availability across sites. Hence, the small impacts of food availability found here cannot be ascribed to the fact that food is abundant and more

or less uniformly distributed so that location selection is irrelevant. An additional conclusion is that the tendency of shorebirds to aggregate leads to suitable habitat remaining unoccupied. It follows that when animals tend to aggregate , stochasticity in site choice plays a larger role than when all shorebirds would independently select a foraging patch.

Acknowledgements

Table 4.1. (Next pages) Effects of exogenous variables and social aggregation ($\hat{\rho}$) on the density of six shorebird species in the Wadden Sea on resolutions 250 × 250 m, 200 × 200 m and 150 × 150 m.

Bench: benchmark model, i.e. intercept and autoregressive term only (see Methods). The ecologically plausible models are ordered on the basis of Akaike's information criterion (AIC). Model 1,2,3: model with lowest, next lowest and third lowest AIC, respectively. S: Number of sites; N: number of cells; elev: elevation; silt: silt content (%); Are: *Arenicola marina*; Car: *Carcinus maenas*; Cer: *Cerastoderma edule*; Cra: *Crangon crangon*; Het: *Heteromastis filiformis*; Lan: *Lanice conchilega*; Mac: *Macoma balthica*; Mya: *Mya Arenaria*; Nep: *Nephtys hombergii*; Ner: *Nereis diversicolor*; ρ: spatial autoregression coefficient (social aggregation); the number between parentheses: the standard error; Significance: *: $P < 0.1$; **: $P < 0.05$; ***: $P < 0.01$; ****: $P < 0.001$; Wald p: Wald statistic p-value; AIC.sar: Akaike's information criterion for the model including the spatial autoregressive term; ΔAIC: difference in AIC.sar with respect to the best model; AIC.lm: AIC for the model without spatial autoregressive term; R^2: Nagelkerke R^2; TI: the total impact of the exogenous predictor obtained by the spatial multiplier ($\frac{\beta}{1-\rho}$); estimate and standard error of the total impact is obtained by means of MCMC simulation (see Methods).

Table 4.1A. Dunlin

S = 23	Model	Const	Ner	Het	Car	ρ	Wald.p	AIC.sar	ΔAIC	AIC.lm	R^2	Model nr
	bench	-46.22 (9.87)				0.72 (0.04)	<0.001	2036.3		2188.1	0.25	1
	1 TI	-52.91 (10.75)	6.25 (3.46) 22.00 (10.88)			0.71 (0.04)	<0.001	2035.0		2179.4	0.26	2
250 N = 530	2 TI	-40.43 (15.33)	6.01 (3.46) 19.93 (12.41)		2.15 (1.96) 7.53 (6.82)	0.71 (0.04)	<0.001	2035.8	0.8	2177.2	0.26	3
	3 TI	-43.60 (10.10)		4.89 (3.88) 14.05 (5.79)		0.71 (0.04)	<0.001	2036.8	1.8	2183.3	0.25	5
	bench	-28.69 (6.54)				0.80 (0.03)	<0.001	3039.9		3305.2	0.27	1
	1 TI	-33.22 (7.19)	4.09 (2.44) 19.85 (10.93)			0.79 (0.03)	<0.001	3039.1		3293.1	0.27	2
200 N = 851	2 TI	-23.56 (9.90)	4.08 (2.43) 18.90 (10.33)		1.61 (1.19) 7.88 (5.87)	0.79 (0.03)	<0.001	3039.2	0.1	3286.6	0.27	3
	3 TI	-18.98 (9.47)			1.62 (1.20) 7.64 (6.05)	0.79 (0.03)	<0.001	3040.1	1.0	3298.5	0.27	4
	bench	-12.03 (3.62)				0.89 (0.02)	<0.001	5034.8		5621.7	0.32	1
	1 TI	-7.12 (5.58)	1.86 (1.13) 17.36 (9.57)		0.98 (0.68) 9.37 (7.18)	0.89 (0.02)	<0.001	5033.8		5597.5	0.32	2
150 N = 1552	2 TI	-13.48 (3.76)	1.88 (1.13) 17.27 (10.32)			0.89 (0.02)	<0.001	5033.9	0.1	5605.5	0.32	3
	3 TI	-5.57 (5.49)			1.00 (0.68) 9.25 (5.83)	0.89 (0.02)	<0.001	5034.5	0.6	5613.3	0.32	4

Table 4.1B. Red Knot

S = 16 Model	Const	Silt	Mac	Car	Mya	ρ	Wald.p	AIC.sar	ΔAIC	AIC.lm	R^2	Model nr
bench	-78.67 (14.53)					0.63 (0.06)	<0.001	1348.1		1412.5	0.15	1
1 TI	-65.71 (17.16)				1.91 (1.40) 5.03 (3.40)	0.62 (0.06)	<0.001	1348.3		1408.3	0.15	14
250 N = 408 / 2 TI	-74.91 (15.34)			2.77 (2.18) 7.68 (5.77)		0.62 (0.06)	<0.001	1348.6	0.3	1405.4	0.15	21
3 TI	-95.92 (21.59)	9.52 (6.95) 26.15 (17.17)		3.62 (2.24) 9.42 (6.00)		0.60 (0.07)	<0.001	1348.7	0.4	1399.0	0.16	24
bench	-58.26 (10.53)					0.68 (0.05)	<0.001	1980.0		2064.2	0.12	1
1 TI	-49.82 (12.19)				1.21 (0.90) 3.47 (2.60)	0.67 (0.05)	<0.001	1980.2		2059	0.13	14
200 N = 652 / 2 TI	-55.84 (11.07)			1.97 (1.50) 6.35 (4.45)		0.66 (0.06)	<0.001	1980.4	0.2	2054.4	0.13	17
3 TI	-70.20 (15.21)	6.54 (4.82) 20.39 (14.81)		2.63 (1.56) 7.46 (4.80)		0.65 (0.06)	<0.001	1980.5	0.3	2047.4	0.13	19
bench	-19.60 (4.40)					0.85 (0.03)	<0.001	3155.3		3407.0	0.19	1
1	-17.72 (4.55)		1.33 (0.90) 9.42 (6.84)			0.85 (0.03)	<0.001	3155.1		3402.6	0.19	6
150 N = 1203 / 2 TI	-14.10 (5.86)				0.68 (0.50) 4.65 (3.38)	0.85 (0.03)	<0.001	3155.4	0.3	3395.1	0.19	10
3 TI	-13.49 (5.84)		1.13 (0.92) 7.24 (6.38)		0.56 (0.51) 3.56 (3.54)	0.85 (0.03)	<0.001	3155.9	0.5	3393.7	0.19	18

Table 4.1C. Oystercatcher

S = 23	Model	Const	Silt	Mac	Car	Ner	ρ	Wald.p	AIC.sar	ΔAIC	AIC.lm	R^2	Model nr
	bench	-36.77 (8.57)					0.66 (0.05)	<0.001	1894.0		1998.9	0.19	1
	1 TI	-43.18 (8.98)			4.14 (2.76) 11.18 (6.98)	3.51(2.30) 8.78 (5.94)	0.61 (0.05)	<0.001	1889.5		1970.7	0.20	41
250 N = 509	2 TI	-40.46 (9.02)		6.38 (4.40) 17.11 (10.24)		4.27 (2.13) 10.35 (5.34)	0.61 (0.05)	<0.001	1889.6	0.1	1969.5	0.20	44
	3 TI	-41.92 (8.91)				5.14 (2.04) 13.96 (5.65)	0.62 (0.05)	<0.001	1889.7	0.2	1974.5	0.20	46
	bench	-23.97 (5.95)***					0.74 (0.04)	<0.001	2886.7		3069.8	0.20	1
	1 TI	-24.60 (6.08)			2.85 (1.56) 9.36 (5.51)		0.71 (0.04)	<0.001	2881.8		3036.7	0.21	24
200 N = 821	2 TI	-27.45 (6.52)		4.98 (3.00) 17.10 (10.49)		3.42 (2.07) 11.08 (7.41)	0.70 (0.04)	<0.001	2882.4	0.6	3028.4	0.21	32
	3 TI	-25.52 (6.02)		4.90 (3.07) 16.29 (11.12)	3.66 (1.48) 13.26 (5.33)		0.72 (0.04)	<0.001	2882.5	0.7	3044.6	0.21	33
	bench	-10.27 (3.35)					0.85 (0.02)	<0.001	4708.8		5121.3	0.24	1
	1 TI	-10.38 (3.36)			2.38 (0.82) 14.43 (5.10)		0.83 (0.03)	<0.001	4702.1		5075.9	0.25	21
150 N = 1500	2 TI	-9.88 (3.40)		2.09 (1.65) 12.32 (10.24)	2.08 (0.85) 12.37 (5.01)		0.83 (0.03)	<0.001	4702.5	0.4	5062.3	0.25	28
	3 TI	-13.49 (7.48)	1.51 (3.24) 7.81 (18.71)		2.33 (0.82) 14.59 (5.63)		0.83 (0.03)	<0.001	4703.9	1.8	5076.6	0.25	34

ESTIMATIONS OF FOOD EFFECTS AND SOCIAL AGGREGATION

Table 4.1D. Bar-tailed Godwit

S = 23	Model	Const	Elev	Ner	Are	Lan	Het	ρ	Wald.p	AIC.sar	ΔAIC	AIC.lm	R^2	Model nr
250 N = 509	bench	-76.79 (11.70)						0.67 (0.05)	<0.001	1056.0		1190.9	0.24	1
	1 TI	-78.59 (11.94)	-10.36 (7.06) -30.27 (23.02)					0.66 (0.05)	<0.01	1055.9		1179.3	0.24	20
	2 TI	-79.36 (11.96)				1.27 (0.88) 3.65 (2.66)		0.66 (0.05)	<0.001	1056.0	0.1	1181.4	0.24	22
	3 TI	-81.10 (12.22)	-15.50 (7.93) -43.54 (22.35)	1.32 (0.98) 3.43 (2.63)				0.65 (0.05)	0.003	1056.1	0.2	1169.9	0.24	26
200 N = 821	bench	-64.69 (9.39)						0.67 (0.05)	<0.001	1225.1		1377.2	0.17	1
	1 TI	-68.93 (9.79)	-12.51 (4.84) -33.98 (14.47)	1.64 (0.80) 4.23 (2.37)				0.65 (0.05)	<0.001	1221.8		1355.1	0.18	2
	2 TI	-70.52 (9.93)	-13.32 (4.89) -36.52 (12.51)	1.48 (0.82) 4.06 (2.39)	1.06 (0.96) 3.06 (2.91)			0.64 (0.05)	<0.001	1222.6	0.8	1349.6	0.18	4
	3 TI	-68.16 (9.81)	-12.74 (4.85) -36.88 (12.98)	1.33 (0.90) 3.93 (2.53)			0.68 (0.94) 1.89 (2.77)	0.65 (0.05)	<0.001	1223.3	1.5	1356.4	0.18	7
150 N = 1500	bench	-32.77 (4.99)						0.77 (0.03)	<0.001	1716.1		2028.1	0.19	1
	1 TI	-34.66 (5.21)	-5.86 (2.94) -24.06 (12.85)	0.56 (0.35) 2.17 (1.47)				0.75 (0.04)	<0.001	1715.6		1989.8	0.19	9
	2 TI	-33.43 (5.07)	-3.57 (2.60) -14.60 (11.16)					0.76 (0.04)	<0.001	1716.2	0.6	2010.2	0.19	21
	3 TI	-33.21 (5.12)	-4.36 (2.75) -17.81 (12.95)				0.41 (0.48) 1.71 (2.09)	0.76 (0.04)	<0.001	1717.4	1.8	2007.8	0.19	56

Table 4.1E. Curlew

S = 23	Model	Const	Elev	Silt	Len	ρ	Wald.p	AIC.sar	ΔAIC	AIC.lm	R^2	Model nr
250 N = 460	bench	-70.30 (10.84)				0.67 (0.05)	<0.001	1132.8		1250.3	0.23	1
	1 TI	-73.67 (11.28)	-20.03 (9.32) / -56.96 (27.59)			0.64 (0.05)	<0.001	1130.3		1228.2	0.24	4
	2 TI	-80.23 (14.77)	-23.53 (10.60) / -67.56 (29.20)	3.22 (4.74) / 9.62 (12.91)		0.64 (0.05)	<0.001	1131.8	1.5	1228.3	0.24	17
	3 TI	-74.03 (11.33)	-18.71 (10.33) / -49.80 (29.10)		0.26 (0.80) / 8.36 (2.31)	0.64 (0.05)	<0.001	1132.2	1.9	1226.7	0.24	20
200 N = 747	bench	-41.85 (6.66)				0.76 (0.04)	<0.001	1613.7		1840.8	0.26	1
	1 TI	-44.16 (6.96)	-13.93 (6.16) / -51.42 (26.29)			0.74 (0.04)	<0.001	1610.6		1803.7	0.27	3
	2 TI	-44.51 (7.00)	-12.44 (6.80) / 48.89 (26.72)	1.22 (3.19) / 3.09 (12.75)	0.34 (0.52) / 1.21 (2.23)	0.73 (0.04)	<0.001	1612.3	1.7	1799.3	0.27	13
	3 TI	-46.58 (9.30)	-15.18 (6.93) / -53.58 (24.41)			0.74 (0.04)	<0.001	1612.5	1.9	1804.8	0.27	17
150 N = 1357	bench	-19.28 (3.34)				0.85 (0.02)	<0.001	2330.7		2744.3	0.26	1
	1 TI	-19.79 (3.45)	-5.61 (3.68) / -33.34 (20.75)			0.84 (0.02)	<0.001	2330.4		2700.4	0.27	15
	2 TI	-19.61 (3.41)		1.18 (1.88) / 7.43 (12.33)	0.35 (0.34) / 2.28 (2.25)	0.84 (0.02)	<0.001	2331.6	1.2	2717.7	0.26	25
	3 TI	-22.15 (5.10)	-6.79 (4.13) / -40.71 (28.06)			0.84 (0.03)	<0.001	2332.0	1.6	2699.4	0.27	41

Table 4.1E: Grey Plover

S = 23	Model	Const	Silt	Nep	Lan	Ner	ρ	Wald.p	AIC.sar	ΔAIC	AIC.lm	R²	Model nr
	bench	-105.7 (14.91)					0.56 (0.06)	<0.001	837.28		893.08	0.11	1
	1 TI	-126.25 (17.61)	6.55* (3.01) 12.82 (6.36)	2.64* (1.03) 5.45 (1.99)		2.56* (1.29) 5.47 (2.77)	0.51 (0.06)	<0.01	832.24		874.95	0.13	2
250 N = 509	2 TI	-129.28 (17.82)	7.02 (3.03) 13.96 (6.02)	2.26 (1.07) 4.53 (2.27)	0.67 (0.50) 1.48 (1.01)	2.75 (1.30) 6.02 (2.66)	0.50 (0.07)	<0.01	832.47		873.55	0.13	3
	3 TI	-121.68 (17.27)	7.19 (3.01) 15.68 (7.04)	2.03 (0.99) 4.42 (2.30)			0.53 (0.06)	<0.01	834.13		882.53	0.12	9
	bench	-76.01 (10.63)					0.62 (0.05)	<0.001	1090.3		1172.5	0.10	1
	1 TI	-90.49 (12.44)	4.76 (2.01) 11.85 (4.68)	1.75 (0.65) 4.12 (1.62)		1.58 (0.87) 3.65 (2.35)	0.58 (0.06)	<0.001	1084.5		1149.4	0.11	2
200 N = 821	2 TI	-87.38 (12.19)	5.14 (2.00) 12.50 (4.92)	1.43 (0.62) 3.63 (1.56)	0.27 (0.38) 0.65 (0.87)		0.59 (0.05)	<0.001	1085.7		1157.4	0.11	3
	3 TI	-91.91 (12.56)	4.96 (2.03) 11.79 (5.06)	1.66 (0.66) 4.03 (1.64)		1.66 (0.88) 3.95 (2.01)	0.57 (0.06)	<0.01	1086.0		1148.9	0.11	4
	bench	-38.99 (5.71)					0.73 (0.04)	<0.001	1208.0		1378.7	0.11	1
	1 TI	-44.10 (6.54)	2.29 (1.14) 8.44 (3.83)	0.64 (0.39) 2.50 (1.35)			0.72 (0.04)	<0.001	1207.1		1362	0.11	2
150 N = 1500	2 TI	-45.09 (6.64)	1.96 (1.06) 6.81 (4.14)		0.35 (0.21) 1.27 (0.72)		0.71 (0.04)	<0.001	1207.1		1359.6	0.11	3
	3 TI	-45.14 (6.62)	2.50 (1.15) 8.49 (3.75)	0.51 (0.40) 1.69 (1.42)	0.27 (0.22) 1.04 (0.82)		0.71 (0.04)	<0.001	1207.5		1359.9	0.11	4

5

Experimental evidence for cryptic interference among socially foraging shorebirds

Allert Imre Bijleveld, Eelke Olov Folmer and Theunis Piersma

Abstract

Foraging rate and the distribution of foragers depend on prey distribution in conjunction with inter-individual interactions. Generalized functional response models predict intake rates and spatial distributions of foragers on the basis of resource distribution and interference competition. The adequacy of these models depends on how well they capture the foragers' essential behavior. In this paper we report on the results of a foraging experiment designed to examine the mechanisms of interference competition using red knots *Calidris canutus* that feed on buried bivalves. Red knots are rarely observed to interfere in the field, but this does not imply absence of interference. Our experimental setup minimized resource depletion which allowed us to quantify interference competition as the decline in intake rate as a function of group size, with prey density and social status as additional treatments. We found that intake rate and searching efficiency decreased with group size and that dominant birds had higher intake rates than subordinates. Additionally, time spent searching for prey increased with group size. The decrease in intake rate was not due to conventional interference mechanisms (such as kleptoparasitism and time spent interacting with conspecifics), but to "cryptic interference", i.e. avoidance of physical encounters with conspecifics. To accurately predict intake rates and foraging distributions, theory and models need to account for the possibility that animals anticipate and try to avoid, at costs, physical encounters with conspecifics (i.e. conflicts that would make conventional interference behavior visible).

Introduction

Intake rate and the distribution of foraging animals depend on the distribution of resources and the presence of conspecifics (Krebs, 1972). The latter can be both beneficial and detrimental (Stephens *et al.*, 2007; Danchin *et al.*, 2008; Sumpter, 2010; Folmer *et al.*, 2011). Conspecific presence can be beneficial because it provides information on food availability (Krause and Ruxton, 2002; Valone, 2007; Danchin *et al.*, 2008; Bijleveld *et al.*, 2010) and predation risk (Lima and Dill, 1990; Krause and Ruxton, 2002). In addition, it dilutes the risk of being depredated (Hamilton, 1971; Lima and Dill, 1990; Quinn and Cresswell, 2006). The presence of conspecifics may also lead to interference competition with negative effects on intake rate (Goss-Custard, 1980; Sutherland, 1983; Tregenza, 1995; Johnson *et al.*, 2006; Klaassen *et al.*, 2006).

If animals behaved ideally and freely (Fretwell and Lucas, 1970), intake rates and foraging distributions could be predicted using generalized functional response models (van der Meer and Ens, 1997; Smallegange and van der Meer, 2009). Such models combine prey density and parameters that capture the negative effect of nearby conspecifics to predict intake rates, which in turn may be used to predict spatial foraging distributions (Beddington, 1975; Sutherland, 1983; Ruxton *et al.*, 1992; Bautista *et al.*, 1995; Holmgren, 1995; Tregenza, 1995; Johnson *et al.*, 2006; van Gils *et al.*, 2006).

There exist two classes of generalized functional response models to describe and predict intake rates in standing stock situations: phenomenological and mechanistic models (van der Meer and Ens, 1997). Both have been used to describe and predict intake rates for various species (Bautista *et al.*, 1995; Smallegange and van der Meer, 2009; van der Meer and Smallegange, 2009; Gyimesi *et al.*, 2010) including shorebirds (Piersma *et al.*, 1995; Stillman *et al.*, 1997; Goss-Custard *et al.*, 2006; van Gils *et al.*, 2006; Rutten *et al.*, 2010a).

Phenomenological generalized functional response models are based on statistical relationships between intake rate and competitor density and summarize interference into one parameter (Hassell and Varley, 1969; Sutherland and Koene, 1982). Mechanistic generalized functional response models are derived from basic behavioral processes which are modeled as transitions between mutually exclusive behavioral states (e.g. searching, handling, fighting). Transition rates are assumed to be constant functions of competitor density. However, these models do not take into account that animals may anticipate events and adjust behavior accordingly. Hence, they assume that animals act as "aimless billiard balls" (van der Meer and Ens, 1997). Mechanistic models are considered superior to phenomenological models because they are more generic than case-specific phenomenological models (Stillman *et al.*, 1997; van der Meer and Ens, 1997; Smallegange and van der Meer, 2009). Whether a mechanistic general-

ized functional response model adequately predicts intake rate and the spatial distribution depends on how well it captures the foragers' essential behavior. Particularly, small differences in the relationship between intake rate and group size (i.e. interference) can have a large influence on the predicted foraging distributions (van der Meer and Ens, 1997). Interference has become a central topic in behavioral ecology, but the current understanding of the behavioral mechanisms of interference competition is still incomplete (van der Meer and Ens, 1997; Vahl *et al.*, 2005b). The mechanisms of interference competition are generally assumed to be kleptoparasitism and time lost in aggressive interactions (Tregenza, 1995; Stillman *et al.*, 1997; Smallegange and van der Meer, 2009).

In the field, the various mechanisms of interference competition are not necessarily observed, because animals may space out to avoid or mitigate interference costs while maintaining the benefits of conspecific presence (Vahl *et al.*, 2007; Folmer *et al.*, 2010; Gyimesi *et al.*, 2010). That is, foragers will trade-off the benefits and costs of social foraging which will lead to "spaced-out gregariousness" (Kennedy and Crawley, 1967). The degree of spacing between social foragers will depend on the net benefits of the presence of conspecifics (Folmer *et al.*, 2011). In the field only the net effect of conspecific attraction and interference on the spatial distribution of foraging animals can be observed (Folmer *et al.*, 2010), and the relative strengths of each of the separate mechanisms can only be assessed indirectly (Folmer *et al.*, 2011). Therefore, detailed information on the mechanisms of interference competition cannot be obtained from field observations (Vahl *et al.*, 2007; Gyimesi *et al.*, 2010; Rutten *et al.*, 2010a). To gain insight into the various mechanisms of interference, experiments are needed.

The objective of this study is to obtain insight into the mechanisms of interference for a gregarious forager to underpin and improve upon generalized functional response models. We used red knots *Calidris canutus*, a species that does not show typical interference behavior in the field (van Gils and Piersma, 2004). We studied foraging behavior at different competitor densities while ensuring minimal prey depletion to avoid confounding of resource competition and interference competition (Vahl *et al.*, 2005b; Smallegange *et al.*, 2006). Because prey density and social status also influence interference competition, these factors are incorporated as treatments.

Methods

birds

Red knots are medium-sized shorebirds that outside the breeding season usually feed on mollusks (Zwarts and Blomert, 1992; Piersma *et al.*, 1993; Piersma   *et*

al., 1998; van Gils *et al.*, 2003a). Their short prey handling times and the fact that prey items are swallowed in their entirety (Piersma *et al.*, 1995) reduce opportunities for kleptoparasitic acts (Ens *et al.*, 1990; van Gils and Piersma, 2004).

The experimental animals, 23 knots of the *islandica* subspecies (Piersma, 2007), were captured with mistnets on 7 and 8 February 2005 in the western Dutch Wadden Sea (53°15'N, 5°15'E). The birds were housed in two indoor aviaries at the Royal Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands. Each aviary, 4.5 m × 1.5 m surface × 2.5 m height, contained a fresh water tray. To keep the aviary floors and the feet of the birds clean, salt water was constantly flowing over the floors. The light was kept at a constant light regime (12:12 h L:D) and temperatures were kept constant at 12°C. To avoid different dominance hierarchies to develop in the two aviaries, every day membership to aviary groups were assigned randomly. A metal identification ring was fitted to the right tibia together with plastic color rings on each tarsus for individual recognition. After the experiment, in June 2005, the birds were returned to the field. The experiment complied with Dutch law regarding animal experiments under permits issued by the DEC-KNAW.

The staple food and experimental prey items were blue mussels *Mytilus edulis*, a mollusk that commonly occurs in the diet of free-living knots (Zwarts and Blomert, 1992; Dekinga and Piersma, 1993). Every other week fresh mussels were collected from the basalt groins at Den Helder (52°57'N, 4°43'E). After collection, bundles of mussels were disentangled and sorted based on length. Mussels smaller than 20 mm were used as staple food and mussels between 8 and 12 mm were used as experimental prey items.

Experimental setup

Inspired by Smallegange, van der Meer & Kurvers (2006), we kept prey density relatively constant by minimizing prey depletion as follows. In the experimental arena (7 m by 7 m) an elevated lane (6.5 m long, 0.7 m wide and 0.3 m deep) was filled with sand in which the prey items were buried at approximately 3 cm depth (Fig. 5.1). The water in the arena was kept at such a level that only the lane was above water and accessible for the birds. The lane was covered with a polyester sheet which contained a square hole of 0.7 m × 0.7 m in which the knots were able to forage; this hole is the food patch. During a trial the sheet was rolled onto a beam that was driven by an electrical motor so that it smoothly slid across the lane from one end to the other at an average speed of 1 cm s^{-1} which mimics the receding water line in the field. As the food patch moved across the lane, new prey became available and the area that had been foraged upon disappeared underneath the sheet.
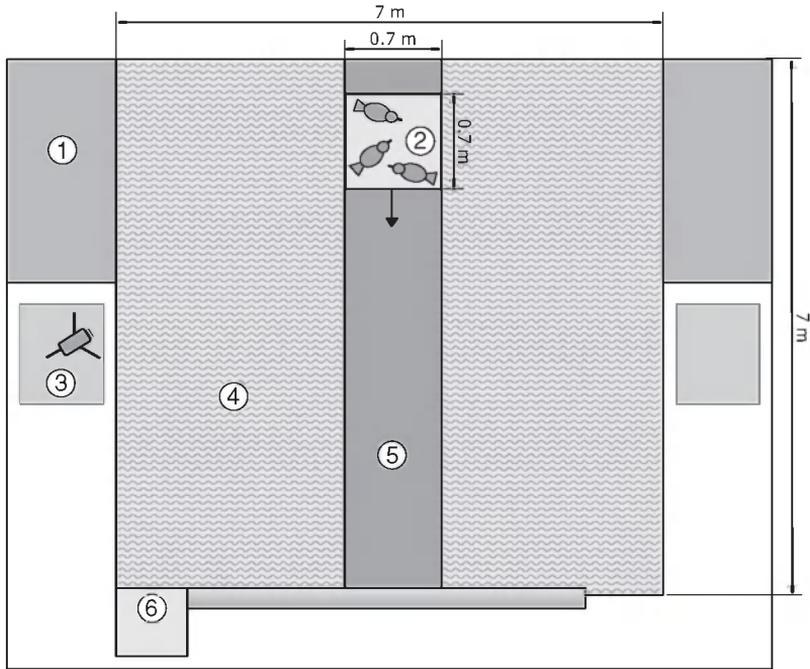
Figure 5.1. The experimental shorebird facility: 1) aviary, 2) food patch, 3) observation hide, 4) water, 5) covered lane and 6) electrical engine with beam to roll the sheet on. 2, 4 and 5 make up the experimental "arena".

Social status

Prior to the interference trials, we obtained the social status of each experimental animal as follows. We covered the lane with a large quantity of mussels over which the patch moved. After 14 h of fasting, all 23 knots were released in the arena to forage. The number of aggressive interactions between foraging individuals, i.e. threatening, charging (moving towards conspecifics) and receding, was recorded, as were the winners and losers of each interaction. Individuals that retreated were taken as losers. The trial ended when the sheet reached the end of the lane; when one individual had taken control of the patch; or when one individual interacted extremely aggressive towards other birds. The red knot that dominated the group was isolated from the rest and the above procedure was repeated with the reduced group. We repeated the procedure until a group of individuals remained that rarely interacted. The whole procedure was repeated five times per day for four consecutive days.

In a group of 23 birds there are $(23 \times 22) / 2 = 253$ combinations of paired individuals between whom interactions can take place. The 20 repetitions gave

a total of 771 interactions between 207 pairs. On the basis of the interactions we calculated a dominance coefficient for each individual as follows. We assumed transitivity, that is, we assumed that if bird A is dominant over B and B is dominant over C, then A is dominant over C, i.e. a linear dominance hierarchy. We estimated dominance coefficients by means of logistic regression, where X_{ij} , which is the number of victories of bird i over j, is binomially distributed with parameters p_{ij} , the probability of bird i winning the pair-wise confrontation, and N_{ij} the total number of disputes between bird i and j. A dominance coefficient d is estimated for each individual and the expected logit p_{ij} equals the difference Δd between the pair's dominance coefficients. In practice it means that the rows of the design matrix are formed by all pair wise combinations of individual birds with the value 1 for the reference bird in the pair, -1 for the partner, and 0 elsewhere (van der Meer, 1992; Tufto *et al.*, 1998). Hence, the estimated dominance coefficients represent the social statuses of the birds and allow estimating the probability of winning a pair-wise confrontation as $e^{\Delta d} / (1 + e^{\Delta d})$.

On the basis of their social status, individuals were divided into three groups (Fig. 5.2): nine subordinates, five intermediates (focal bird group) and nine dominants. The average dominance coefficient per group was: subordinates -1.2 (SE 0.2, N = 13), focal birds –0.3 (SE 0.07, N = 5) and dominant individuals 0.8 (SE 0.2, N = 13) (Fig. 5.2).

Interference experiment

From May till June 2005 the foraging behavior of the focal birds was studied under various combinations of bird- and prey densities, and in relative subordinate or dominant social positions. The level of interference competition was set by group size which ranged from two to eight including the focal bird of which there was one per trial. Because we used a fixed patch size (0.5 m^2), competitor density is linearly related to group size.

Two levels of prey density were used: low and high (20 and 30 mussels m^{-2}, respectively). These densities are in line with the densities encountered in the field (Dekker and Beukema, 2007) and are sufficiently low to prevent digestive constraints (van Gils *et al.*, 2005), as indicated by the fact that all birds kept foraging until the end of the trials. The prey items were buried into the lane at predetermined positions with 1 cm^2 accuracy, which allowed retrieving remaining prey items after each trial. To avoid that birds learned the spatial distribution of prey items, we randomly selected one of the two available configurations of burial positions for each trial.

Social status treatment consisted of composing the group around the focal bird at a trial with birds randomly chosen from either the pool of subordinates or dominants. Accordingly, the same focal bird was either the most dominant or
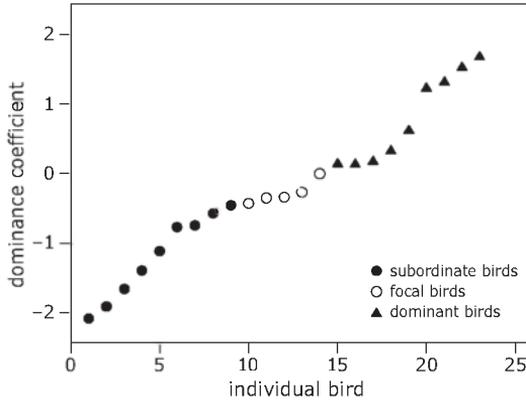
Figure 5.2. Social status of experimental birds ranked by dominance coefficients. The five intermediate birds were selected as focal birds.

the most subordinate member of the group. Observe that social status may be influenced by group size. However, it turned out that a subordinate bird rarely attacked a dominant bird and that subordinates suffered more from the presence of dominants than the other way around. We thus conclude that the hierarchy was reflected in the experiments with smaller groups.

The different combinations of treatments consisted of manipulating group size (7 levels, varying from 2–8), prey density (2 levels) and social status (2 levels) resulting in 28 trials per focal bird and 140 trials in total. We ran between 2 and 10 trials per day. We maintained a random order in which the trials were carried out over the 29 days of experimentation.

The knots were fasted for 12 h during the night before each experimental day, and at least 60 min before each trial (i.e. larger than the time needed to digest the consumed prey, van Gils *et al.*, 2005). The trial lengths were short enough to ensure that all birds were highly motivated to forage during the trials. Thirty minutes before the trial the birds were released into one of the two randomly chosen aviaries adjacent to the "arena" (Fig. 5.1) to accommodate. Hereafter, a sliding door between the aviary and the arena was opened so that the birds could enter the arena. The trial started 30 s after the first bird entered the patch. At that moment the electric engine was started to move the food patch. The trial ended when the patch had moved halfway the length of the lane. For efficiency reasons, the lane was split into two sections of equal length and each section was used for one trial. At the end of a trial, the arena, but not the adjacent aviary, was darkened to make the birds fly to the lightened aviary. The polyester sheet was then moved one patch-length so that unexploited mudflat was available for the next trial with new birds. The second trial of a session

lasted for the remainder of the lane. The average duration of a trial was 241 s (SD = 12.8). As the beam with the sheet thickened when winding up, the average speed of the moving patch was slightly larger in the second trial which explains the variance in trial duration. This effect is negligible because the standard deviation is less than 13 seconds on a mean of 241 s and we randomly assigned trials to one of the two lane sections. After a session of two trials the remaining prey were dug out and counted per trial to get an estimate of prey depletion. New prey items for the following session were then buried according to the method described above.

All trials were recorded on video by an observer who was positioned in a hide near the patch (Fig. 5.1). The videotapes were analyzed using The Observer 5.0 Event recorder (Noldus Information Technology, Wageningen, The Netherlands). The Observer software allowed measurements of time budgets with an accuracy of 0.04 s per behavioral bout.

Following Vahl *et al.* (2005b), we measured the time spent by the focal birds in a trial on the following, mutually exclusive, behaviors: *searching* (probing the sediment in search of prey, either while moving or standing still), *watching* (watching the surroundings while standing still with the bill at an upward angle of at least 45 degrees with the sediment; note that this may include watching conspecifics), *moving* (taking steps with the bill at an upwards angle of at least 45 degrees with the sediment), *interacting* (both attacking (i.e. moving towards conspecifics aggressively) and evading (i.e. moving away from attacking conspecifics), *handling* (touching prey with bill until swallowed, lost or dropped), and being *off-patch* (not on the food patch). In addition, we scored the number of prey intakes and vigilance acts (head up while tilting the head sideways at least 45 degrees; note that in the wild vigilance behavior is used to detect approaching raptors (Cresswell, 1994)). On average, a focal bird showed approximately one vigilance act per trial. Because of the absence of predators the birds may have experienced the experimental area as a safe environment (van den Hout *et al.*, 2010). Vigilance was not included as a fraction in the time budget, because a vigilance act takes less than a second and constitutes a marginal part of the total time budget (Piersma *et al.*, 1995). Instead, we used vigilance rates calculated as the number of vigilance acts divided by trial duration (*vigilance*, # min^{-1}). Handling times are also very short. They were averaged per trial (*handling*, s).

Statistical analyses

One focal bird rarely foraged during trials. Its average intake rate was close to zero, whereas the other four individuals had substantially higher intake rates. The hypothesis of equal average intake rates for the five focal birds was rejected (ANOVA, $F_{4,135} = 3.1$, $P = 0.02$), while it was not rejected for the four focal

birds without the outlier (ANOVA, $F_{3,108} = 0.5$, $P = 0.69$). Therefore the outlier was omitted from further analyses which gave an adjusted sample size of 112.

The average experienced prey density per trial (D m^{-2}) was calculated by averaging the initial and final prey density. To normalize the distribution of model residuals we ln-transformed average experienced resource density. Average intake rate (*IR*, # s^{-1}) per trial was obtained by dividing the number of prey intakes by the duration of the trial. Average searching efficiency (cm^2 s^{-1}) per trial was calculated by $1 / (T_s \times D)$ (i.e. instantaneous rates of discovery, Holling, 1959), where T_s is the average searching time per prey item, and D the average experienced resource density.

The following behaviors of the focal bird were analyzed: (1) the time spent off-patch relative to the trial duration. The proportion of time spent off-patch was analyzed using a generalized linear mixed model with binomial errors and focal bird as random intercept. The following on-patch behaviors were analyzed as proportions of time spent on-patch: (2) searching, (3) watching, (4) moving, (5) interacting. The proportions 2 – 5 are "sum constrained", i.e. they sum up to one. The sum constraint was accounted for by *ln*-ratio-transformation (Aitchinson, 1986; Kucera and Malmgren, 1998). That is, the dependent variables 2 – 5 are

$$y_i' = \ln \left(\frac{y_i}{(\prod_{i=2}^{n=5} y_i)^{\frac{1}{4}}} \right),$$

where y_i is the fraction of time spent on behavior i. Zeroes were replaced by $\delta = 100\% \times 0.5 \times 0.04 / $ average trial time, which gives half the smallest percentage unit that behavior was recorded in (Aitchinson, 1986). Note that 0.04 s is the duration of one video frame.

Additionally, (6) handling and (7) vigilance were determined as explained above. Both were *ln*-transformed to normalize the data. To avoid possible zeroes in the *ln*-transformations of vigilance, we increased the argument by one.

The impacts of experimental treatments on intake rate, searching efficiency, time budget, handling time and vigilance rate were analyzed in R v2.11.1 (R Development Core Team, 2011) using general linear mixed models with focal bird as random intercept. Because experienced prey density, *IR*, and searching efficiency were negatively and non-linearly related to group size, the latter was *ln*-transformed.

We started the statistical analyses with models including all experimental treatments and their interactions as explanatory variables. The models were simplified by removing non-significant terms ($P > 0.05$) from the initial model applying a step-wise backward procedure: (i.e. terms were removed one by one

in order of decreasing p-values, Quinn and Keough, 2005). However, regardless of statistical significance, the main effects of experimental treatments were retained in the final model. Normality of residuals was judged by visual inspection of QQ-plots (Miller, 1986).

Results

Experienced resource density

Experienced prey densities slightly declined with ln(group size). The average experienced prey density declined by -0.17 (SE 0.02, $F_{1,108} = 70.3, P < 0.01$) with ln(group size) and at approximately equal rates for both prey densities ($F_{1,108} = 2.6, P = 0.11$) and social status treatments ($F_{1,108} = 0.4, P = 0.53$).

Interference

During the 112 trials we observed only 4 events in which prey items were stolen from conspecifics (i.e. kleptoparasitism). Table 5.1A and Figure 5.3A show that *IR* was significantly lower in the low prey density treatment than in the high density treatment (-0.008 s^{-1} SE 0.002). In addition, *IR* declined linear-

Table 5.1. Intake rate (# s^{-1}) and searching efficiency (cm^2 s^{-1}) models. The treatments are: prey density (high and low), social status of focal birds (subordinate and dominant), and *ln*-transformed group size (number of individuals, including focal). The reference case (intercept at group size = 0) is the high prey density treatment for focal birds in subordinate positions.

	Response variables	Predictors	Coefficient	SE	P
A) Fixed effects	Intake rate (# s^{-1})	Intercept**	0.066	0.005	<0.01
		Group size**	-0.028	0.003	<0.01
		Prey density (low)**	-0.008	0.002	<0.01
		Social status (dominant)*	0.005	0.002	0.04
Random effects		Focal bird	SD = 0.000		
		Residual	SD = 0.013		
B) Fixed effects	Searching efficiency	Intercept**	54.32	4.12	<0.01
	(cm^2 s^{-1})	Group size**	-22.47	2.36	<0.01
		Prey density (low)	0.43	2.15	0.84
		Social status (dominant)	1.23	2.15	0.57
Random effects		Focal bird	SD = 1.79		
		Residual	SD = 11.37		

* treatment significant at the .05 level
** treatment significant at the .01 level
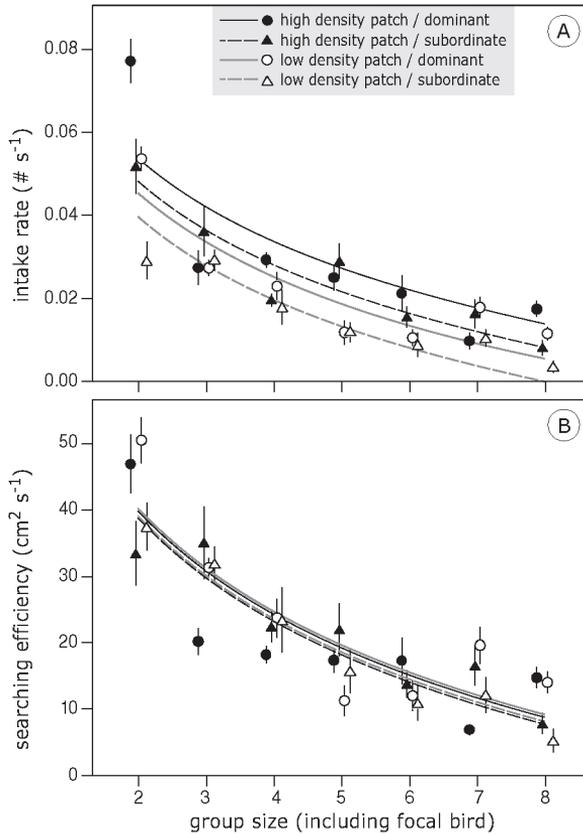
Figure 5.3. Intake rate (# s^{-1}) (panel A) and searching efficiency (cm^2 s^{-1}) (panel B) as functions of group size. The plotted lines are based on the final regression models (Table 5.2). Vertical bars denote standard errors of the means. The values on the x-axis are adjusted for graphical representation.

ly with ln(group size). The decline was approximately equal for both prey densities (–0.028 SE 0.003; Fig. 5.3A and Table 5.1A). The *IR* of a focal bird in a dominant position was on average 0.005 s^{-1} (SE 0.002) higher than when it was in a subordinate position. The interactions between ln(group size) and social status, and ln(group size) and prey density were non-significant indicating that the negative impact of ln(group size) on *IR* did not vary by these treatments. Searching efficiency declined linearly with ln(group size) (–22.47 SE 2.36, Table 5.1B, Fig. 5.3B), but was not affected by either prey density or social status.

Time budgets

Focal birds spent tended to spend less time off-patch when they were in domi-
nant positions than when they were in subordinate positions (Table 5.2A).
However, the fraction of time spent off-patch did not differ by prey density or
by group size.

From Table 5.2B and Figure 5.4A it follows that the fraction of time spent
searching for prey was larger on the low prey density patch than on the high
prey density patch. Moreover, it varied by social status: focal birds in dominant

Table 5.2. Time budget models. The different behaviors are time spent off the food patch
(off-patch), searching for prey (searching), watching with head up (watching), moving
(moving), interacting with conspecifics, i.e. attacking or retreating (interacting), handling
prey (handling), and vigilance. Treatments and reference case as in Table 5.1. Model esti-
mates refer to transformed data (see methods).

		Behaviors	Predictors	Coefficient	SE	*P*
A)	Fixed effects	Off-patch	Intercept	-1.53	0.80	0.05
			Prey density (low)	-0.08	0.53	0.88
			Social status (dominant)	-1.11	0.57	0.05
			Group size	0.07	0.13	0.60
	Random effects		Focal Bird	SD = 0.00		
			Residual	SD = 0.16		
B)	Fixed effects	Searching	Intercept**	1.54	0.21	< 0.01
			Prey density (low)*	0.29	0.14	0.04
			Social status (dominant)**	0.83	0.14	< 0.01
			Group size*	0.07	0.04	0.04
	Random effects		Focal Bird	SD = 0.00		
			Residual	SD = 0.74		
C)	Fixed effects	Watching	Intercept*	-0.74	0.29	0.01
			Prey density (low)*	0.30	0.14	0.03
			Social status (dominant)**	1.35	0.37	< 0.01
			Group size**	0.18	0.05	< 0.01
			Social status (dominant) x Group size*	-0.16	0.07	0.02
	Random effects		Focal Bird	SD = 0.21		
			Residual	SD = 0.72		
D)	Fixed effects	Moving	Intercept**	-2.42	0.33	< 0.01
			Prey density (low)**	1.21	0.38	< 0.01
			Social status (dominant)**	0.51	0.14	< 0.01
			Group size**	0.32	0.05	< 0.01
			Prey density (low) x Group size*	-0.17	0.07	0.02
	Random effects		Focal Bird	SD = 0.35		
			Residual	SD = 0.75		

positions spent more time searching than when they were in subordinate positions. An interesting finding is that the proportion of time spent searching for prey increased with group size.

The fraction of time spent watching increased with group size. It was also larger on the low prey density patch than on the high prey density patch (Table 5.2C, Fig. 5.4B). For subordinates the fraction of time spent watching was smaller than for dominants, but the significant interaction between social status and group size suggests that this difference was mitigated by group size.

Table 5.2. Continued

	Behaviors	Predictors	Coefficient	SE	P
E) Fixed effects	Interacting	Intercept	0.79	0.56	0.16
		Prey density (low)*	-0.93	0.36	0.01
		Social status (dominant)**	-1.90	0.36	< 0.01
		Group size**	-0.41	0.09	< 0.01
Random effects		Focal Bird	SD = 0.30		
		Residual	SD = 1.88		
F) Fixed effects	Handling	Intercept**	-0.64	0.10	< 0.01
	time (s)	Prey density (low)	-0.11	0.06	0.09
		Social status (dominant)*	0.13	0.06	0.04
		Group size	-0.02	0.02	0.11
Random effects		Focal Bird	SD = 0.06		
		Residual	SD = 0.31		
G) Fixed effects	Vigilance	Intercept	0.05	0.09	0.62
	(# min^{-1})	Prey density (low)	0.00	0.04	0.94
		Social status (dominant)**	0.47	0.11	< 0.01
		Group size	0.01	0.01	0.73
		Social status (dominant) x Group size**	-0.07	0.02	< 0.01
Random effects		Focal Bird	SD = 0.09		
		Residual	SD = 0.22		

* treatment significant at the .05 level
** treatment significant at the .01 level
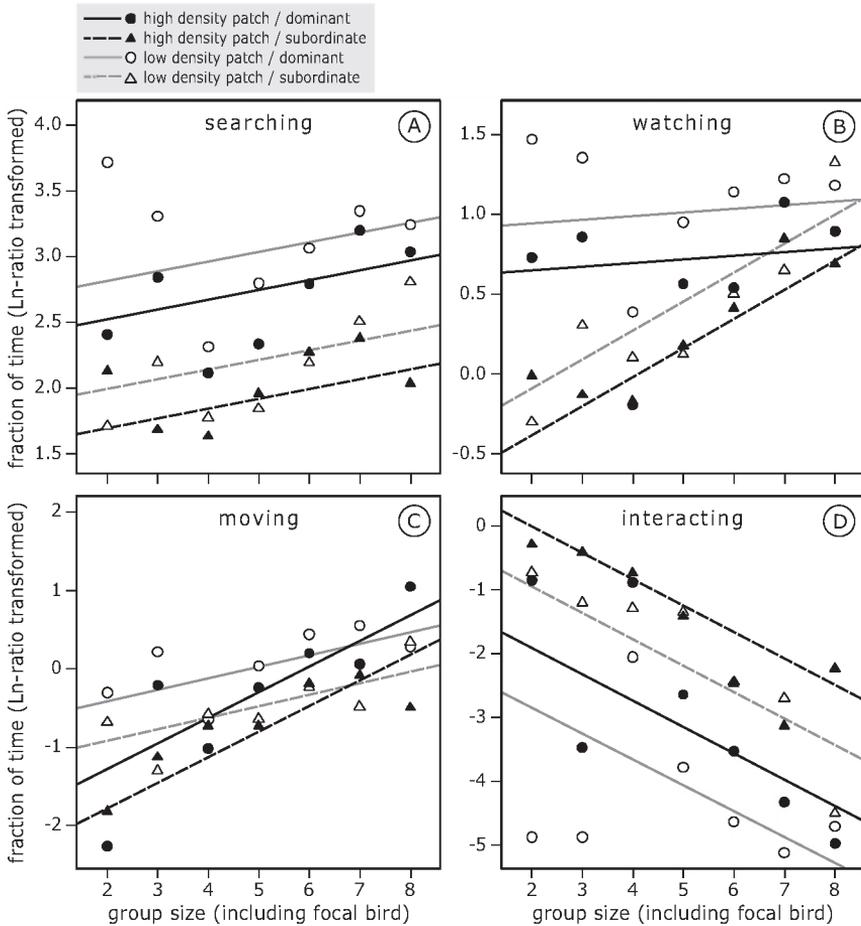
Figure 5.4. Mean transformed fractions of time spent on searching for prey (A), watching (B), moving on the food patch (C) and on interacting with conspecifics (D). The plotted lines are model estimates for prey densities and social status (Table 5.2). Note the differences in range on the vertical axes between panels. Each point in the graph represents the mean value.

The fraction of time spent moving increased with group size (Table 5.2D, Fig. 5.4C). For small group sizes the fraction of time spent moving was higher on the low prey density patch than on the high prey density patch. However, this difference decreased with group size. Additionally, birds in dominant positions spent more time moving than when the birds were in subordinate positions.

The proportion of time spent interacting decreased with group size and was lower on the low prey density patch than on the high prey density patch (Table

5.2E, Fig. 5.4D). In addition, birds in dominant positions spent less time on interactions than in subordinate positions.

Table 5.2F shows that prey density nor group size had significant effects on handling times. Birds in a dominant position, however, had larger handling times than when they were in a subordinate position.

Birds in dominant positions tended to be more vigilant than in subordinate positions. However, this effect was mitigated by group size as indicated by the significant negative interaction between group size and social status.

Discussion

One main finding of this study is that increasing group size had a negative effect on intake rate. It declined by 93% on the low prey density patch and 78% on the high density patch when group size increased from two to eight. Another important result is that the decline was not due to conventional mechanisms of interference competition. We observed only four cases of kleptoparasitism during the 112 trials and time spent interacting with conspecifics decreased with group size. The reduction in intake rate coincided with a decline in searching efficiency. Furthermore, the time budget models showed that with an increase in group size the time spent searching, watching and moving increased.

To avoid that decreased intake rate due to resource depletion is incorrectly attributed to interference competition as group sizes increase, resource depletion needs to be controlled for (Vahl *et al.*, 2005b; Smallegange *et al.*, 2006). Previous experiments accounted for prey depletion by using unnaturally high prey densities or by using very short trial durations (Vahl *et al.*, 2005b; Gyimesi *et al.*, 2010; van Dijk *et al.*, 2012). In experiments with shore crabs *Carcinus maenas* Smallegange *et al.* (2006), kept prey densities constant by replenishing consumed prey. In our experiment prey density declined 21% when group size increased from 2 to 8 birds. This effect was much smaller than the negative impact of group size on intake rate even though the effects of group size on the other behaviors were smaller than that on intake rate. The methods used here lead to substantially reduced depletion effects compared to comparable interference experiments (Vahl *et al.*, 2005b). Moreover, in our experimental setup we were able to study interference mechanisms in trials of approximately 4 minutes at naturally occurring prey densities (Vahl *et al.*, 2005b; Gyimesi *et al.*, 2010; Rutten *et al.*, 2010a; van Dijk *et al.*, 2012).

As noted in the Introduction, mechanistic functional response models generally assume that the main mechanisms of interference competition are kleptoparasitism and time lost in agonistic interactions. In oystercatchers *Haematopus ostralegus*, for instance, it has indeed been found that kleptoparasitism and time

spent interacting with conspecifics increased with forager density while intake rate declined (Sutherland and Koene, 1982; Ens and Goss-Custard, 1984). For shore crabs *Carcinus maenas* Smallegange *et al.* (2006) observed that aggressive interactions increased with group size, but that kleptoparasitism rarely occurred. Our results are consistent with the negative effect of group size on intake rate, but the common mechanisms of interference competition were virtually absent or operated in the opposite direction. Kleptoparasitism rarely occurred while time spent interacting declined. However, we found that time spent searching increased with group size, which was also observed in an interference experiment with mallards *Anas platyrhynchos* (van Dijk *et al.*, 2012). Absence of kleptoparasitism was probably due to short handling times (similar results were obtained by van Gils *et al.*, 2003b; van Gils and Piersma, 2004; Vahl *et al.*, 2005b). The decrease in time spent interacting, and the increase in time devoted to searching with increasing group size, could be the result of scrambling for prey (Clark and Mangel, 1986; Grant, 1993; Dubois and Giraldeau, 2005). Additionally, a reduction in vigilance with group size could allow more time to be spent searching for prey (Pulliam, 1973; Beauchamp, 2003, 2009). In our study, the already low vigilance rates (overall one act every 2.4 minutes) indeed decreased with increasing group sizes. However, the amount of time gained from a reduction in vigilance was very small.

Larger group sizes led to more time spent on watching and moving as well as to a decrease in searching efficiency. We hypothesize that these behaviors resulted from birds shunning aggressive interactions. Time spent watching increased with group size, because our knots had to increasingly divert their attention between searching for prey and avoiding interactions with conspecifics which in turn reduced searching efficiency (Goss-Custard, 1976; Dukas and Kamel, 2001). Time spent moving increased with group size, because our knots increasingly had to avoid collisions with conspecifics. Because this may disturb preferred search paths (e.g. to avoid revisiting the same, depleted locations) it reduced searching efficiency (Cresswell, 1997). We follow Gyimesi *et al.* (2010), in suggesting to label the decline in intake rate due to covert avoidance behavior and associated reduced searching efficiency "cryptic interference": these mechanisms are not the typical overt interference mechanisms.

Dominant birds are less susceptible to interference competition (Ens and Goss-Custard, 1984; Stillman *et al.*, 1996), because they may displace subordinates and monopolize food patches (Vahl *et al.*, 2005a; Rutten *et al.*, 2010b). Consequently, subordinates spend time avoiding dominants at the cost of foraging time (Stillman *et al.*, 1997; Smallegange and van der Meer, 2009) or at the cost of selecting less preferred foraging locations (Dolman, 1995; Rutten *et al.*, 2010b). In line with these results, we found that intake rates were higher when focal birds were dominant than when they were subordinate. Searching efficien-

cies, however, did not differ between dominance treatments. Dominant birds had higher intake rates because they spent more time on the food patch searching for prey. Subordinate birds on the other hand more often avoided encounters with conspecifics, and were more often excluded from the food patch as indicated by the fact that they spent more time off-patch.

Our experiments have shown that red knots incur decreased intake rates from avoiding encounters with conspecifics. In the field this is rarely observed because mechanisms are cryptic (Gyimesi *et al.*, 2010) and because suitable foraging areas are often large enough (van Gils *et al.*, 2006; Kraan *et al.*, 2009a; Kraan *et al.*, 2009b), such that encounters and physical hindering are minimal while maintaining the benefits of group foraging (Goss-Custard, 1976).

Interference models have been used to predict spatial distributions of different species of shorebirds at various spatial scales (e.g., Stillman and Goss-Custard, 2010; Quaintenne *et al.*, 2011). For instance, Quaintenne *et al.* (2011) explain the distribution of red knots between wintering areas in NW Europe, including sites in The Netherlands, UK and France, by means of an interference model. Their model is parameterized on the basis of small scale experiments, but applied to explain and predict distributions of red knots over large spatial and temporal scales. The explanation of Quaintenne *et al.* (2011) is therefore (implicitly) based on the notion that interference may operate over large spatial and temporal scales. Our results do not support this hypothesis, since they indicate that knots attempt to avoid direct encounters with conspecifics. Furthermore, in intertidal areas, knots have sufficient opportunities to "space out gregariously" because foraging areas are extensive (Kraan *et al.*, 2009a; Kraan *et al.*, 2009b). Indeed, in the field aggressive interactions and kleptoparasitism between knots are rarely observed.

As explained in the Introduction, a prerequisite for mechanistic generalized functional response models to adequately predict intake rate and spatial distributions is that it adequately captures the foragers' essential behavior. Uncertainty about the mechanisms of interference hampers the validity and generality of predictions from such models. The mechanisms of interference competition that we observed challenge the assumed mechanisms in the existing functional response models (that we know of). For instance, Smallegange and van der Meer (2009), considering a state of conspecifics avoidance, suggest that their model, and in principle any mechanistic model, may be extended to various situations by expanding the set of behavioral states. However, this requires unambiguous definitions, non-overlapping states and unambiguous observations of behavioral states. In our experiment such unambiguous assignments were perhaps not possible despite detailed behavioral observations. For instance, part of the behavior that we scored as 'searching' could have been a combination of avoiding conspecifics whilst probing. Moreover, since it already is difficult to

disentangle behavioral states in an experiment, in the field this will be nearly impossible (Gyimesi *et al.*, 2010).

The phenomenological 'Hassell and Varley model' allows for a decline of searching efficiency with group size (Hassell and Varley, 1969), but all behavioral mechanisms are aggregated into one interference parameter. Hence, this model is unable to fully capture the interference mechanisms and lose their generality (van der Meer and Ens, 1997; Smallegange and van der Meer, 2009).

Our results showed that current generalized functional response models do not adequately capture the interference mechanisms that we have observed. Therefore, the aggregative response functions (i.e. the predicted distributions of foragers across food patches) are imprecise. Perhaps better predictions and understanding of interference may be obtained when current models are elaborated to take into account the fact that animals behave in ways such that agonistic interactions are anticipated and covertly avoided (i.e. cryptic interference).

6

Seagrass - sediment feedback: an exploration using a non-recursive structural equation model

Eelke O. Folmer, Matthijs van der Geest, Erik Jansen,
Jan A. van Gils, T. Michael Anderson, Theunis Piersma, Han Olff

Abstract

The reciprocal effects between sediment texture and seagrass density may play an important role in the dynamics and stability of intertidal coastal ecosystems. However, this feedback relationship has been difficult to study empirically on ecosystem scale, so that knowledge is mainly based on theoretical models and small scale (experimental) studies. In this paper we apply a non-recursive structural equation model (SEM) to empirically investigate on large spatial scale the mutual dependence between seagrass (*Zostera noltii*) density and sediment texture on the pristine seagrass-dominated intertidal mudflats of the Banc d'Arguin, Mauritania. The non-recursive SEM allows consistent estimation and testing of the presence of a feedback loop between sediment and seagrass while statistically controlling for the effects of nutrients and abiotic stress. The estimation results support the hypothesized negative feedback: grain size decreases with seagrass density, while fine grain size has a negative impact on seagrass density. Another finding is that seagrass density increases with sediment organic material content, however, up to a threshold level beyond which it levels off. In combination with decreasing grain size due to capture and stabilization of sediment by seagrass, accumulation of organic matter creates hypoxic sediment conditions leading to the production of toxic hydrogen sulfide which slows down seagrass growth. The (statistically significant) negative feedback loop implies that intertidalseagrass modifies its own environment, thus controlling growing conditions. To the best of our knowledge, this study is one of the first to demonstrate a negative feedback relationship in ecosystems by means of a non-recursive SEM.

Introduction

Ecosystem engineers are species that modulate habitats, thus changing their own and/or other species' environment (Hastings and others 2007; Wright and Jones 2006; Jones and others 1994). Based on this definition, seagrass is an ecosystem engineer that impacts on soft-bottom intertidal ecosystems (Bouma and others 2009; Olff and others 2009; van de Koppel and others 2005). Seagrasses affect local hydrodynamics, geomorphology and sediment properties in intertidal ecosystems and may thus influence their own growing conditions (Koch 2001; de Boer 2007). Particularly, seagrass meadows may locally capture and stabilize sediments and thus influence the turbidity of the water column. To get insight into the impact of seagrass on the turbidity state of the ecosystem, it is important to understand the reciprocal relationships between sediment properties and seagrass density.

Because of methodological problems and data limitations (see section Discussion for details), empirical analyses of feedback relationships in ecosystems, which are drivers of alternative stable states (Levin 1998; Gunderson and Holling, 2001), are difficult to perform (Scheffer and Carpenter 2003). Knowledge of feedback relationships between seagrass density and sediment texture is mainly based on small-scale field measurements, and localized experiments (de Boer 2007). In this paper, we empirically investigate across an extensive spatial scale the mutual dependence between the density of the seagrass species *Zostera noltii* Hornem. and sediment texture on the pristine, seagrass-dominated intertidal mudflats of the Banc d'Arguin, Mauritania (Wolff and Smit 1990; Honkoop and others 2008). As a general introduction to the research topic and as background information to the model estimated below, we present a brief review of the empirical literature. The review relates to various species of seagrass, and not to *Z. noltii* solely.

In a review of experimental and observational field studies on various species of seagrass, de Boer (2007) suggests a positive feedback loop between seagrass and sediment via reduction of the turbidity of the water column. Due to resistance of the seagrass meadows, water flow velocity is attenuated which reduces erosion and stimulates deposition of sediment and associated nutrients (Gacia and others 1999, Koch 2001; Bos and others 2007, Widdows and others 2008, van Katwijk and others 2010). In addition, reduced flow velocity and depositions of fine sediments and nutrients may facilitate the development of biofilms by benthic microalgae (diatoms) and cyanobacteria (Paterson and Black 1999; Herman and others 2001; Widdows and others 2008). These organisms excrete exopolymeric substances (EPS) which form connective filaments between particles. The filaments build up erosion-resistant biofilms which stabilize the sediment (Grant and others 1986; Miller and others 1996;

Paterson and Black 1999; Herman and others 2001, Van de Koppel and others 2001). For instance, Widdows and others (2008) found that in the German Wadden Sea the seagrass species *Z. noltii* stabilizes sediments via increased microphytobenthos abundance. These effects may independently or concomitantly lead to net positive sedimentation that may decrease the turbidity of the water column which increases irradiance and thus the rate of photosynthesis when seagrass is inundated during high tide.

In addition to the positive feedback loop that operates via reduction of turbidity of the water column, seagrasses may locally promote their own growth in the following ways. First, by decreasing water currents and waves, seagrass meadows reduce the constant movement of sediment and hydrodynamic drag which negatively affect shoots (Fonseca and Bell 1998; Koch 2001; Madsen and others 2001). Second, seagrasses may reduce negative effects of desiccation (Boese and others 2005) by exposure to air by retaining receding water (Powell and Schaffner 1991) which benefits photosynthesis and growth. Third, accumulation of fine sediments, due to reduced water movement, decreases the permeability of the sediment (Koch 1999) which promotes water accumulation at the surface of the mudflat at low tide which further reduces desiccation. Finally, growth may also be promoted by increased trapping of organic material as a source of nutrients. However, higher concentrations of organic matter lead to increased microbial decomposition to the point at which anaerobic conditions and H2S production may begin to negatively affect seagrass density (Goodman and others 1995; Terrados and others 1999; Koch 2001).

Theoretical and empirical investigations suggest that positive feedback interactions may drive ecosystems into alternative stable states or regimes (Scheffer and others 2001). Consequently, ecosystems may show qualitative shifts in system dynamics under changing environmental conditions (Levin 1998; Scheffer and Carpenter 2003). Specifically, when unfavorably disturbed, an ecosystem with extensive seagrass meadows may change from a vegetated to a bare state from which recovery may be difficult, even when the original conditions are restored (Suding and others 2004; van der Heide and others 2007). Hence, insight into potential feedbacks between seagrass density and environmental factors, such as sediment texture, are critical to understanding the responses of seagrass-dominated ecosystems to environmental change.

In this paper, we analyze the interactions between the seagrass *Z. noltii* and its self-engineered environment by deploying a structural equation model (SEM) based on spatial cross-sectional data. SEM, as a multiple equation model, allows explicit modeling of the non-recursive feedback relationship between seagrass density and grain size, thus controlling for inconsistency and simultaneity bias (Bollen and Long 1993). We estimate the seagrass density – sediment SEM by maximum likelihood (ML) under the assumption of normally distributed

variables (which is the standard estimation procedure of a SEM). If the likelihood function is correctly specified, the ML estimator is consistent, asymptotically efficient and asymptotically normally distributed under weak regularity conditions (Bollen and Long 1993; Kline 2010). However, even in the case of deviation from normality, it is still consistent, though the standard errors should be interpreted carefully (Bollen and Long 1993). (Observe that estimators which do not take the interdependency between dependent and explanatory variables into account like OLS, are inconsistent and subject to simultaneity bias.)

Sediment-seagrass interactions are best studied over large spatial (or temporal) scales that exhibit large variations in seagrass density and sediment characteristics. The near pristine intertidal flats of the Banc d'Arguin, Mauritania, covering a surface of about 500 km2 meet this requirement, which makes them an ideal study system.

We analyzed the reciprocal relationship between *Z. noltii* seagrass density and median grain size while controlling for the effects of organic matter content of the sediment and abiotic stress. We collected data by field sampling and remote sensing. The latter is an efficient and accurate method for studying seagrass meadows on intertidal mudflats (Ferguson and Korfmacher 1997)
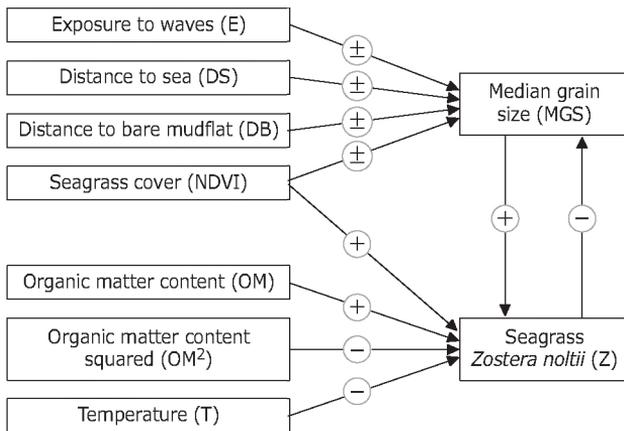

Figure 6.1. The conceptual Seagrass density (Z) – Median grain size (MGS) model. MGS decreases with Z and Z increases with MGS rendering a negative feedback loop. Z is furthermore determined by the exogenous variables organic matter content (OM_c), organic matter content squared (OM_c^2), average of the normalized difference vegetation index of the area surrounding the observed location (NDVI) as proxy for hydrodynamic stress and desiccation proxied by at satellite temperature (T). In addition to local Z, MGS furthermore depends on hydrodynamic stress and erodibility measured by wave exposure (E), distance to sea (DS), distance to bare patches (DB) and NDVI. +: positive effect; -: negative effect; ±: ambiguous effect. See text for further details.

because of the strong contrast between vegetated and non-vegetated areas at low tide (Altenburg and others 1982; Mumby and others 1997).

Before discussing data collection, SEM and empirical results in detail, we first present the theoretical underpinnings of the seagrass-sedimentation model, i.e. the rationale of the explanatory variables included in the model.

Conceptual model: determinants of seagrass density and sediment grain size

At the heart of the model is the reciprocal relationship between local above-ground seagrass (*Zostera noltii*) density (Z) and the local median grain size (MGS) of the sediment (Figure 6.1) (e.g. Madsen and others 2001; de Boer 2007, Widdows and others 2008), where "local" indicates that we are interested in the interaction between seagrass and sediment in each other's immediate vicinity (i.e. the same plot). Particularly, Z depends on the properties of the sediment and MGS is affected by the capacity of seagrass to capture and stabilize sediment. Z further depends on the availability of nutrients (Koch 2001) and abiotic stress levels. MGS depends on wave exposure and factors that attenuate hydrodynamic stress (Paterson and Black 1999).

Reciprocal sediment-seagrass interaction
The model shown in Figure 6.1 has two endogenous variables: local Zostera density (Z) (measured as ash-free dry mass (AFDM) of leaves in g m^{-2}) and median grain size (MGS) which is a measure of coarseness of the sediment. Z and MGS are mutually dependent, i.e. Z impacts on MGS and vice versa. Z is hypothesized to have a negative impact on MGS because of attenuation of flow velocities which stimulates deposition of fine material from the water column to the sediment surface (Amos and others 2004; Widdows and others 2008; van Katwijk and others 2010).

In turn, in already fine sediments, an increase in MGS is expected to have a positive effect on Z because the coarser the sediment, the better the pore water exchange with the water column which reduces the anoxic condition of the sediment. Particularly, sulfate reduction by bacteria leading to increased sulfide concentrations declines and oxidation of sulfide increases in coarse sediments through increased oxygen transport in to the sediment (Koch 2001).

Organic matter
Z is also influenced by the concentration of organic matter (OM) in the sediment which is the major source of organic nitrogen and phosphorous. Hence, OM is expected to promote seagrass density, though up to a threshold. On the

basis of a review of several studies, Koch (2001) concludes that the growth of seagrass is constrained in sediments with mass concentrations of organic matter that are higher than 5%. Hence, the effect of OM initially is positive, levels off, reaches a peak and finally decreases. So, we expect Z to be a unimodal function of OM which is accounted for by including both OM and OM^2 in the model. The hypothesized unimodal relationship implies that OM has a positive and OM^2 a negative sign.

Note that in the long run there also may exist a feedback of Z on OM in that leaves, roots and rhizomes ultimately decompose to organic matter (Mateo and others 2006). It may, however, take years for leaves, roots and rhizomes to subside (in the case of leaves) to a depth where it can degrade such that the nutrients become available to seagrass roots (Mateo and others 1997). We therefore did not model a direct impact of Z on OM or nutrients due to this discrepancy in time scales between processes. Furthermore, Hemminga and Nieuwenhuize (1991) found that on the Banc d'Arguin a large part of the particulate carbon present in the surface sediment originates from above-ground biomass. It follows that in this model (which only considers current states of and interactions between the variables) OM and OM^2 are exogenous in that they are not influenced by Z.

Hydrodynamic stress and desiccation of seagrass

Hydrodynamic stress, caused by currents and waves, negatively impacts on seagrass density because it inflicts direct damage to the plants or causes uprooting due to erosion of sediment (Fonseca and Bell 1998; Koch, 2001). Since we had no information on currents and wave exposure, we used seagrass cover surrounding a particular observation point (irrespective of the density at the sample point) as a proxy. The use of this proxy is based on the assumption that seagrass at a given sample location is sheltered by seagrass in its vicinity. That is, we assume hydrodynamic stress to be low at locations that are surrounded by areas that are densely covered with seagrass (Fonseca and others 1982; Ward and others 1984; Madsen and others 2001; Widdows and others 2008).

On the basis of a Landsat 7 satellite image recorded on 22nd January 2003 (resolution 25 m), we obtained seagrass cover surrounding the sample plot. We calculated the proxy for a given station as the average of the normalized difference vegetation index (NDVI) across the surrounding pixels. The surrounding area was defined as an annulus with the sampling station as centroid. The radius of the inner circle was 25 m and the radius of the outer circle 75 m. (All pixels of which the centers fell within the annulus were included in the calculation of the average). Note that the radius of 25 m of the inner circle and the distance of 50 m between the inner and outer circle of the annulus around the sample stations implies a substantial buffer to the sampling stations, so that the

risk of compounding Z and NDVI is moderate to small (correlation coefficient = 0.54). At the same time, the distance to the sampling station is not too large to miss the dampening effects of currents and waves within the annulus. Hence, NDVI can be considered an adequate indicator of shear stress. On the basis of the above considerations we hypothesize a positive impact of NDVI on Z at the sampling stations.

We did not collect information on desiccation damage, plant water potential or photo-oxidative stress (due to long exposure to strong light). Therefore, we proxied these variables by temperature of the mudflat. Specifically, desiccation is affected by several temperature-related factors including the duration of the exposure of the mudflat to sunlight at low tide, moist retention capacity of the sediment, the color (albedo) of the mudflat, and the amount of seagrass in the near-surroundings. Relatively low temperatures prevail at mudflats that fall dry for only short periods during the tidal cycle , or with water tables close to the soil surface (both due to low elevation) and for mudflats with high moist retention capacity. Since higher temperatures correspond to longer desiccation, and longer exposure to strong light, we hypothesize a negative impact of T on Z.

Powell and Schaffner (1991) show that seagrass meadows prevent desiccation by moist retention which is a function of NDVI. Hence, in addition to T which is a proxy with a negative impact on Z, NDVI is a proxy with a positive impact via mitigating desiccation.

Hydrodynamic stress and MGS

In addition to local (micro-level) seagrass density (Z), MGS may be influenced by hydrodynamic conditions at macro- (exposure to waves from the open sea) and meso-levels (on the mudflat), and by erodibility of the sediment. Hydrodynamic conditions at macro-level are included in the MGS equation by means of a dummy variable that distinguishes between sampling stations on mudflats that are directly exposed to waves from the open sea and sampling stations at sheltered locations within the bay behind other mudflats (see Figure 6.2 and Figure A2 in the supplementary appendix A for an overview of the geography of the Banc d'Arguin). The level of exposure (E) takes the value 0 for inner sampling stations and 1 for outer stations. (This classification is in line with local observations by the authors of wave intensity from observation towers at the different mudflats during various expeditions in different months over various years). Everything else equal, we expect a positive sign for E because the deposition rate of fine grains will be lower under high wave intensity conditions than under low wave intensity conditions.

The hydrodynamic conditions at meso-level are a function of distance to sea (DS) and NDVI. The longer the distance waves travel over the shallow mudflats (DS), the more energy they dissipate (Le Hir and others 2000). In addition, the

higher NDVI, the more waves are damped (Koch and others 2006). Hence, everything else equal, DS and NDVI are expected to have negative signs because small sediment particles are only deposited under calm hydrodynamic conditions, i.e.at large DS and high NDVI.

A final indicator of hydrodynamic conditions affecting MGS is distance to bare patches (DB). Particularly, sampling stations in the vicinity of bare patches (which contain coarse sediment) may receive relatively coarse sediment that is locally translocated. Hence, *ceteris paribus*, DB is expected to have a negative impact on MGS.

The above effects of E, DS and NDVI may be mitigated by erodibility of the sediment and possibly even change their expected signs. Sand may erode more easily than clay and silt because (1) it has a rougher surface than clay and thus is more easily moved by flowing water, and (2) small particles are more cohesive and hence more resistant to flowing water (Black and others 2002; van Rijn 2007). However, in mixtures of course and fine sediment, clay and silt particles may be washed out together with sand particles. Erodibility thus depends on the texture of the sediment. Another determinant of erodibility is the presence of biotic films of extracellular polymeric substances, formed by microphytobenthos. Biotic films increase the smoothness of the surface which in its turn increases hydrodynamic stress thresholds and thus have a stabilizing effect, i.e. a negative impact on erodibility (Black and others 2002; Peterson and Black 1999; Widdows and others 2000; Widdows and others 2008).

The positive sign of E is likely to be mitigated and could even turn negative when only sediment made up of fine particles can sustain the hydrodynamic stress and a larger fraction of the coarse particles is deposited at the inner flats. The signs of DS, and NDVI are also subject to opposing forces. On the one hand, we expect negative signs for DS and NDVI since both represent reduced hydrodynamic stress. However, erodibility of the sediment may weaken their negative signs. For DB we expect a positive effect because of more hydrodynamic stress in the vicinity of bare patches and the nearby presence of coarse sediment. Again, erodibility may mitigate this effect.

The variables E, DB, DS and NDVI strongly overlap in that they are all proxies for hydrodynamic stress, which may lead to multicollinearity. In this case, one or more of the proxies are estimated highly inaccurately and may turn out to be insignificant. We handled this problem by means of stepwise, backward selection.

Study area

The study area is the Iwik region (Figure 6.2) which is an accessible part of the intertidal area of the Banc d'Arguin (19°60' - 19°33'N, 16°33' - 16°35'W) off the
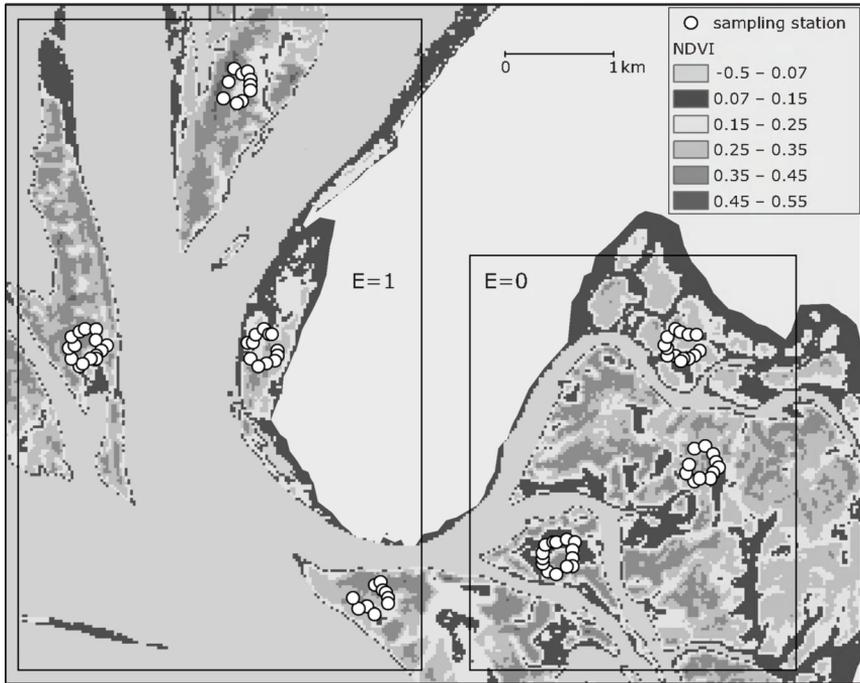
Figure 6.2. The mudflats of the study area and sampling stations. The colors of the mudflats and sea represent NDVI, as calculated from a LANDSAT 7 ETM+ scene recorded on 22nd January 2003. The rectangles represent subareas that differ in hydrodynamic stress due to the level of wave exposure (E). Waves in the outer subarea (E = 1) are larger than in the more sheltered area (E = 0).

coast of Mauretania. The study area can roughly be divided into land, sea, sebkha and mudflats (Altenburg and others 1982, Wolff and Smit 1990). Sebkhas are sandy, saline flats situated above the mean spring high-tide level and are free of vegetation and infauna. The extremely muddy intertidal mud-flats (in our samples: min MGS = 33.6 μm, max = 219.3 μm; mean MGS = 103.7 μm; sd = 56.7 μm, Table B1 in supplementary appendix B) are dominated by *Z. noltii* (Wolff and Smit 1990; van Lent and others 1991; Honkoop and others 2008), a common seagrass species of intertidal zones in Europe and North-West Africa (Hemminga and Duarte 2000). Four of the intertidal mud-flats on which data was collected were substantially more exposed to waves than the remaining three, more sheltered mudflats (Figure 6.2; See Figure A2 in supplementary appendix A for an overview of the whole intertidal area of the Banc d'Arguin).

Data collection

NDVI and Temperature

NDVI and at satellite temperature were obtained from a single scene from the Landsat 7 Enhanced Thematic Mapper plus (ETM+) instrument that covered the whole area of interest (Path 206 and row 046). The image was recorded on the 22 January 2003 at 11:20 AM GMT and resampled to a spatial resolution of 25×25 m. (It is the latest suitable Landsat7 image recorded at low tide before the SLC device of the satellite failed.) Low tide in Dakar on this date was at 5:37 AM GMT. Low tide in the Iwik region follows on average circa 4h 50m after Dakar (Altenburg and others 1982; Wolff and Smit 1990). The image was therefore recorded circa 53 minutes after the lowest tide ensuring that the mudflats were not inundated during recording of the image. Cloud cover was 0.09%. A false color image is presented in the online appendix.

NDVI was calculated from the Landsat image as NDVI = (NIR – RED)/(NIR + RED) where RED and NIR are the digital numbers (DN) corresponding to the spectral values in the red and near-infrared regions, respectively. As mentioned above, we estimated seagrass density in the vicinity of a sampling station by the average of the NDVI within an annulus with the sampling station as centroid, radius of the inner circle 25 m and radius of the outer circle 75 m.

Temperature of the mudflat (T) was estimated by band 6-2 (high gain) of the ETM+ instrument which measures the emitted radiation in the thermal IR region of the electromagnetic spectrum. Band 6-2 measures spectral radiance at 60 m resolution. To reduce noise and to obtain physically based values of temperature, the DN of band 6-2 was converted to an at satellite reflectance value. To obtain at satellite temperatures (in Kelvin) from these measures we applied NASA's (2009) transformation:

$$T_K = \frac{K2}{1\mathrm{n}(\frac{K1}{L_\lambda}+1)}$$

where T_K is temperature in Kelvin, K1 = 666.09 and K2 = 1282.71 are constants and L_λ is the determined spectral radiation.

To determine the minimum distance between a sampling point and the sea (DS), the study area was classified into sea, land, sebkha, bare and seagrass covered mudflats by supervised classification (Supplementary material A). DS was determined by calculating the shortest path from a sampling station to the class "sea" (as determined by the habitat classification procedure in supplementary appendix A).

Seagrass and sediment sampling procedures

The survey area was divided into seven sub-regions (Figure 6.2) which in their turn were subdivided in annuli with an outer radius of 200 m and an inner radius of 100 m. Each annulus was split into 16 equally-sized and equally-shaped parts. In each part, a sampling station was randomly selected. The sampling procedure thus yielded $7 \times 16 = 112$ observations. The field work was carried out in March-April 2007.

At each station, a seagrass sample was taken with a circular core with a surface area of 0.0038 m^2 and 10 cm depth into the sediment. The content was sieved over a 500-μm mesh. The material retained on the sieve was stored in a plastic bag, frozen at −18°C and transported to The Netherlands, where each sample (without detritus) was sorted into either leaves or below-surface components (roots and rhizomes). The ash-free dry masses (AFDM) of the seagrass leaves and below-surface components were determined via the loss-on-ignition method. That is, samples were dried at 60°C for a minimum of 72 hours, weighed and then incinerated at 550°C for 4 hours after which the remaining ashes were weighed again. The difference between the first and the second measurements gives the AFDM of the leaves in the sample (Z, in g m^{-2}).

At each station a separate sediment sample was taken to a depth of 10 cm by pressing a PVC tube in to the sediment. The sediment sample was also stored in a plastic bag, frozen at −18°C and transported to The Netherlands where grain-size distribution of each sample was determined using a particle size analyzer (Beckman Coulter Model LS 230). From the grain size distribution the median (MGS) was calculated. Total organic matter content (OM$_c$) of the sediment was determined by loss-on-ignition of a approximately 0.5 g sub-samples as described above. (For details on particle size and organic content measurement see Honkoop and others (2008)). The percentage mass of organic matter in our samples with seagrass ranged from 0.74% to 11.43% (mean = 4.28 and sd = 3.13). The findings in the review by Koch (2001) imply that the concentrations in many of our samples are in the detrimental range due to H$_2$S production.

Of the 112 seagrass samples, 12 were lost during processing. Moreover, 8 sediment samples were lost during freeze-drying. After matching the seagrass dataset with the sediment dataset, data from 98 sampling stations were available for the SEM analysis.

Statistical analysis

As a first step, we checked the data for possible non-linearities by means of pairwise scatter plots of the dependent variables and their explanatory variables (Supplementary material B Figure B1). Except for the relationship

between Z and OM, the relationships turned out to be highly linear. Single equation regression of Z on its exogenous variables showed that OM has a positive sign and OM^2 has a negative sign (Supplementary material B). Both coefficients are statistically significant ($p < 0.05$). Hence, the Z - OM relationship is curvilinear, as hypothesized above. The collinearity between OM and OM^2 was reduced by mean centering (Kline 2010), i.e. the mean value of OM was subtracted from the OM values to obtain OM_c. OM_c was squared to obtain OM_c^2. The correlation between OM_c and OM_c^2 is 0.67.

Next, we estimated the system of equations model outlined above on the basis of the covariance matrix of the observed variables by means of the Maximum Likelihood (ML) procedure in the software package Lisrel 8.80 (Student Edition) (Jöreskog and Sörbom 1996). The regression coefficients were standardized (a standardized coefficient represents the standard deviation change in the dependent variable resulting from a standard deviation increase of a predictor variable) so that their magnitudes are independent of the measurement scales. Hence the explanatory variables can be directly compared and the most important ones can be directly identified by inspection of their coefficients.

As a first step, we estimated the full model (Figure 6.1). This and subsequent models were evaluated on the basis of overall goodness of fit statistics and signs and significance of the estimated regression coefficients. Particularly, we considered models with χ^2 with $P > 0.05$, and regression coefficients with P-value $<$ 0.05 acceptable. The full model was trimmed in a backward elimination fashion while considering overall goodness of fit. That is, variables with regression coefficients with P- values >0.05 were eliminated in order of increasing significance (decreasing P-values). We selected the best fitting model based on minimization of Bayesian Information Criterion (BIC).

Note that the models estimated below are identified because they meet the necessary and sufficient condition for identification in a simultaneous two-equations model that each equation contains at least one exogenous variable with a nonzero coefficient that is excluded from the other equation (Bollen and Long, 1993).

Estimation results

The $\chi^2 = 10.23$, df $= 5$, $P = 0.07$ (Table 6.1 and Figure 6.3), indicate a relatively poor fit. All signs of the coefficients of the determinants of Z (i.e. MGS, OM_c, OM_c^2, T, and NDVI) were as expected and significant, except T which was positive (standardized coefficient $= 0.01$; $P = 0.98$). Particularly, the impact of MGS on Z was positive and significant (standardized coefficient $= 4.99$; $P < 0.05$). The impact of Z on MGS was negative and significant (standardized

Table 6.1. Structural equation models for seagrass density (Z) and sediment coarseness (MGS). The initial model was trimmed by means of stepwise elimination of insignificant predictors. See main text for statistical analysis. Standard errors in parentheses below (standardized) structural coefficients. 1: initial model; 2 – 4: intermediate models; 5: final model.

		Z	MGS	OMc	OMc²	T	NDVI	E	DS	DB	χ^2	df	P	RMSEA[1]	BIC[2]	AIC	NFI[3]
1	Z		4.99 (2.01)	5.32 (1.94)	-2.47 (0.90)	0.01 (0.29)	1.37 (0.52)				10.23	5	0.07	0.10	-12.70	107.96	0.98
	MGS	-1.47 (0.46)					0.12 (0.32)	-0.31 (0.15)	0.08 (0.14)	0.04 (0.27)							
2	Z		4.98 (1.90)	5.31 (1.90)	-2.46 (0.87)		1.37 (0.51)				5.85	4	0.21	0.07	-12.49	85.71	0.99
	MGS	-1.47 (0.45)					0.11 (0.32)	-0.31 (0.15)	0.08 (0.14)	0.04 (0.27)							
3	Z		4.94 (1.86)	5.27 (1.85)	-2.44 (0.84)		1.36 (0.50)				2.92	3	0.40	<0.00	-10.83	66.89	0.99
	MGS	-1.45 (0.43)					0.14 (0.26)	-0.31 (0.15)	0.08 (0.14)								
4	Z		4.56 (1.46)	4.89 (1.46)	-2.28 (0.68)		1.28 (0.42)				3.32	4	0.51	<0.00	-15.02	65.27	1.00
	MGS	-1.28 (0.21)						-0.29 (0.13)	0.07 (0.13)								
5	Z		4.32 (1.24)	4.66 (1.26)	-2.18 (0.59)		1.23 (0.38)				1.59	3	0.66	<0.00	-12.17	49.59	1.00
	MGS	-1.23 (0.19)							-0.32 (0.12)								

1. Root Mean Square Error of Approximation
2. Bayesian Information Criterion
3. Bentler-Bonnett NFI

ESTIMATION OF A SEAGRASS-SEDIMENT FEEDBACK BY MEANS OF SEM
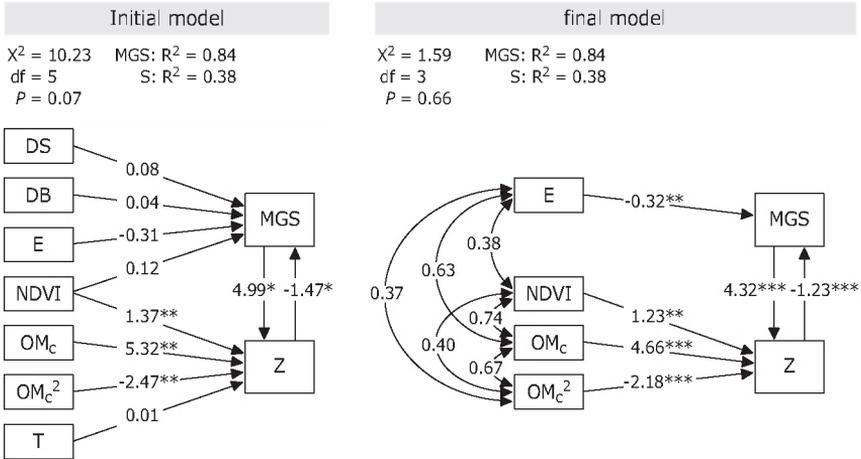
Figure 6.3. Graphical representations of the initial and final MGS-Z SEM. Arrows represent hypothesized causal influence of one variable on another. Dark arrows indicate a significant positive relationship. Structural coefficients are standardized. Significance levels are denoted by means of asterisks: $* = P < 0.05$, $** = P < 0.01$, $*** = P < 0.001$. Intermediate models are presented in Table 6.1. Curved arrows represent significant correlations between the exogenous variables.

coefficient $= -1.47$; $P < 0.01$).. Of the exogenous predictors of MGS (E, DB, DS) only E was significant and negative (-0.31, $P < 0.05$).

The model was trimmed by first deleting T as a predictor for Z and next DB, NDVI and DS as predictors for MGS (Table 6.1). The final model (5 in Table 6.1) had substantially better fit ($\chi^2 = 1.59$, df $= 3$, $P = 0.66$) than the initial model (Figure 6.3). Even though the fit of the intermediate models as measured by NFI were satisfactory, model 5 was selected as the final model on the basis of a superior fit according to BIC, χ^2 and significance of coefficients.

Discussion

The final (accepted) model strongly supports the hypothesized relationships. Particularly, all coefficients have the expected signs and are significant at 5% levels or less. Consistent with the hypothesized negative feed back, the accepted structural model shows a reciprocal relationship in which the impact of MGS on Z is positive and the reverse effect of Z on MGS is negative. Z increases with MGS, indicating that on the extremely silty mudflats of the Banc d'Arguin, seagrass thrives in relatively coarse sediment. The negative impact of Z on MGS implies that the median grain size of the sediment decreases with higher sea-

grass density, which has a negative impact on Z. The model furthermore confirms that NDVI in the immediate vicinity of a sample location is an indicator of reduced shear stress and desiccation which positively impacts on seagrass density. The final model also supports the curvilinear relationship between OM_c and Z. OM_c has a positive coefficient and OM_c^2 a negative coefficient which implies that seagrass density increases with organic material content up to a point beyond which the density levels off. The model furthermore shows that the level of exposure to waves (E) has a significant, negative impact on MGS, probably because only the fine particles are cohesive enough to resist being washed away such that in the outer sampling stations small particles dominate. DB, DS, NDVI as proxies of hydrodynamic stress were not retained in the final model. As a last point, temperature (T) turned out to be a poor proxy for abiotic stress. This could be due to small variations or because it is an ambiguous measure for desiccation and photo-oxidative stress. Particularly, temperature may increase with the albedo of the mudflat which depends on seagrass cover (seagrass is darker than sand).

From the above it follows that seagrasses control their own habitat by engineering activities, in particular, they stabilize the abiotic environment while slowing their own growth (Bagdassarian and others 2007). We have thus revealed and quantified a locally operating micro-scale process (i.e. the negative feedback loop) with substantial consequences for the macro-scale properties of the ecosystem. First, the negative feedback regulates seagrass density and sediment dynamics which reduces water turbidity, which is a basic growth requirement for seagrass in the ecosystem. Second, the local impacts of hydrodynamic stress on seagrass are reduced by surrounding seagrass meadows. Third, seagrass reduces its own growth by capturing fine sediment. These three processes imply that self-organization of seagrass in the Banc d'Arguin is important for the abiotic and biotic state and development of the ecosystem. Particularly, within the current boundary conditions, the biotic components of the ecosystem and the geomorphology are self-controlled via feedback interactions. These findings reveal the driver that keeps the ecosystem in its stable (seagrass) state which is important from a fundamental ecological point of view as well as from a conservation perspective (Levin 2005).

The analysis has also revealed the ambiguity of the interaction between biotic components of the ecosystem and geomorphology. We have argued on the basis of the literature review that erosion and sedimentation are influenced by the density of seagrasses and hydrodynamic factors like waves and currents, whose effects are influenced by the distance over which they travel over the shallow intertidal mudflats (Widdows et al 2008). In addition, the literature review revealed that the impact of hydrodynamic stress on grain size also depends on the erodibility of the sediment (Black and others 2002; van Rijn

2007). We found that grain size was smaller at the borders of the mudflats near the sea and at the outer flats where wave action is stronger than at the inner flats. This contradicts findings in other intertidal areas where the opposite is usually found. However, as pointed out above, other variables, like erodibility, may have impacted on the sign of the effect of E. Further research, including hydrodynamical modeling, is needed to disentangle the opposing effects of shear stress and erodibility on these seagrass dominated mudflats.

Recently, it has been discovered that as a consequence of changing land use, the influx of relatively coarse dust from the Sahara (which is coarser than river sediment) to the Atlantic coastal area has increased, relative to the influx of river sediment (Mulitza and others 2010). Our model predicts that the resulting increase in sediment coarseness will lead to an increase in seagrass density. Satellite images recorded since 1973 provide provisional evidence for this (Olff unpublished data). It remains to be analyzed to what extent this is due to increased grain size.

The feedback loop and processes of self organization considered here were studied under the assumption of a stable state. However, the stable state conditions may be subject to gradual development and and exogenous perturbations which may change the behavior of the system. However, the gradual development and perturbations show up on longer time scales than the ones implicitly considered in this paper. For instance, seagrass brings dead organic matter to the sediment (by capturing OM from the watercolumn and by own root production) which may affect seagrass density in the long term. Various studies including Smith and others (1984) and Koch (2001) show that too high densities of organic matter may be detrimental to seagrass survival and growth because of the production of toxic hydrogen sulfide by anaerobic sulfate reduction. However, oxygen released from roots during the day oxidizes sulfide and reduces its concentration and thus its toxic impact (Smith and others 1984, Koch 2001, Clavier and others 2011). Hence, also in the long run seagrasses control the quality of their habitats (import of organic matter) while they alleviate the negative impact on the short term (by oxygen import). Specifically, over time, when the seagrass - OM ratio decreases, the density of seagrass starts to level off or to decline , which reduces oxygen transport to the sediment, which further reduces seagrass density, and so on. Under such conditions, seagrass may disappear abrubtly. However, van der Heide and others (submited manuscript) have recently shown experimentally that the infaunal, lucinid bivalve *Loripes lacteus* which contains endosymbiontic sulfur-oxidizing bacteria, reduces the sulfide concentration in the sediment and thus enhances the growth of *Zostera noltii*. Whether self-induced collapses could occur due to the above-mentioned processes depends on the rates of organic matter accumulation, decomposition, oxygen transport and sulfide consumption.

In addition to the factors which continuously influence the ecosystem, seagrass density is subject to erratic shocks. For example, storms may cause erosion which (temporarily) reduces seagrass density and may even lead to its local disappearance (Larkum and West 1990, Piersma unpubl. observations). Analyses of the effects of erratic events, such as storms, require different modeling approaches than the one applied here that operate continuously. However, insight into the regularly operating mechanisms is a prerequisite for understanding seagrass ecosystems responses to erratic shocks.

Conclusions and Future Directions

The SEM approach presented in this paper analyzes feedback mechanisms in ecological systems on the basis of cross-sectional data to get insight into system dynamics. As such, it forms a complementary or alternative method to the commonly used time series approach (Scheffer and Carpenter 2003). Since cross-sectional data (capitalizing on spatial heterogeneity) can usually be more readily obtained than time series data, particularly for slowly changing variables, we expect the SEM approach to be valuable in empirical applications. The results obtained here lend support to further applications of SEM to ecosystem cross-sectional spatial data analysis, particularly with respect to feedback mechanisms

Whereas SEM, including non-recursive models, is common in other disciplines, such as psychometrics, sociology and economics (Owens 1994; Jedidi and others 1997; Burns and Spangler 2000), its use has been limited in ecosystem sciences, although it was introduced in this field in 1991 already by Johnson and others (1991). Its limited application is surprising as many ecological systems include feedbacks. Several studies that have attempted to estimate non-recursive SEMs up until now have been unsuccessful (e.g. Veen and others 2010; Laughlin and others 2010; Anderson and others 2010), and to the best of our knowledge ours presents the first successful estimation of a reciprocal feedback SEM in ecosystem sciences. Why previous attempts have failed is unknown. It could be because of peculiarities of the ecosystems studied or because of the data. This question deserves further investigation because this approach has the potential to contribute to filling the gap between theory and empirics (Grace and others 2010).

The results presented in this paper add to our understanding of the natural functioning of a pristine intertidal seagrass ecosystem. This understanding is important because seagrass ecosystems, which provide several essential marine services, are worldwide at a decline. Because of increasing human pressure on coastal ecosystems, climate change and sea level rise preservation of remaining systems, and development of restoration programs are urgently needed.

Seagrass ecosystem services range from providing habitat for foraging shorebirds to spawning grounds for fish and shrimp. Furthermore, they are a direct food source for grazing animals such as turtles, gastropods and isopods (Hemminga and Duarte 2000). This applies especially to a pristine seagrass-dominated mudflat ecosystems like the Banc d'Arguin. Its main seagrass species *Z. noltii* occurs in very high densities which has led to high densities of macro-zoobenthos (Dittmann 2002; Cardoso and others 2004;Honkoop and others 2008). Since macro-zoobenthos is key food for shorebirds (e.g. Piersma and others 1993; van Gils and others 2012) and different species of fish (Jager 1993), these predators are ultimately dependent on the ecosystem engineering properties of the seagrasses.

Supplementary material A: Habitat Classification

The main mudflat area of the Banc d'Arguin was classified into sea, land, sebkha, bare and seagrass covered mudflats by applying the "Maximum Likelihood supervised classification" function in the Spatial Analyst toolset within ArGis^{TM} (ESRI ArcMap 9.2 1999 – 2006) on the remotely sensed Landsat7 image (bands 1–8) which includes various color bands, two temperature bands and a 15 m resolution panchromatic band. The classification function is a multispectral image interpretation algorithm in which the classification process is supervised by the user by defining classes of training samples in the study area to which the images are compared by the algorithm (Girard 2003). Training points were obtained from a false color image on which land, water and sebkha, bare patches and seagrass meadows were clearly distinguishable (Figure A1). To minimize ambiguity, training samples were chosen some distance away from the (often diffuse) boundaries between habitat types. Isolated pixels were removed with a majority filter with 8 neighbors.

Reliability of the above habitat classification (Figure A2) was evaluated in three ways. First, we compared the outcome to ground-truth control field observations that were obtained at several stations within the main mudflat area (presented in Figure A2), (Observe that these are different from the sampling stations in the Iwik region (the study area).) Secondly, we compared the produced habitat map with the false-color image (Figure A1) on which the different types of habitat are clearly distinguished. Thirdly, we obtained the confidence of the habitat assignment as the probability of correct classification (Figure A3). Particularly, the Maximum Likelihood classifier assigns to each cell the probability that it was correctly classified. It produces 14 confidence levels (1 = highest, 14 = lowest).

Land and water could most reliably be distinguished from each other and from the other categories. As expected, differentiation between sebkha, bare- and seagrass covered mudflats was less accurate. Misclassifications occurred near gullies and near the borders between habitats. For example, one sample point in a seagrass habitat located near a gully was misclassified as bare mudflat. This was probably due to a thin layer of water covering the sample location; the reflectance of a water covered seagrass habitat is very similar to that of bare habitat. Three other sample points that in reality were located on bare mudflats were classified as seagrass habitats. These misclassifications were probably due to the presence of seagrass in the vicinity of each of these three points affecting the mean reflectance of the 25 × 25 m pixels containing the stations.

At the time of image recording, some parts of the mudflats were inundated due to the incoming tide from the west. (The image was recorded 40 minutes
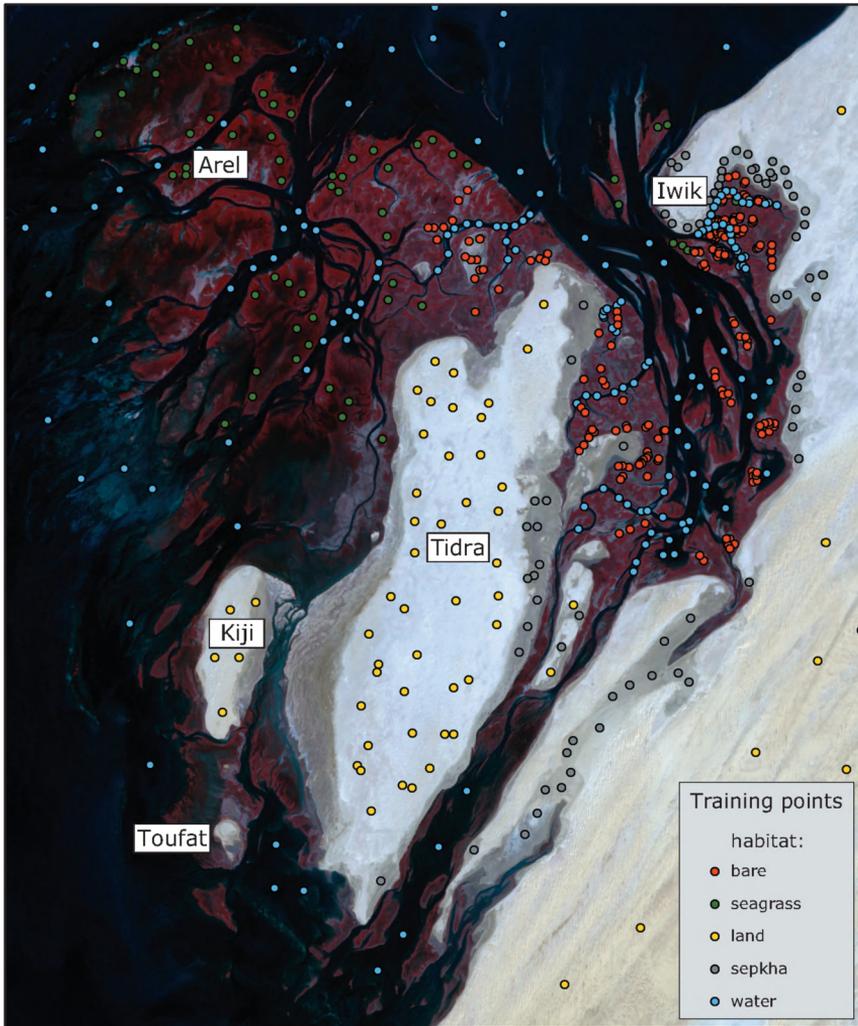
Figure A.1. False-color composite Landsat image of the Banc d'Arguin recorded on 22nd January 2003. In the false-color composite, the color red corresponds to near infra-red (band4); green to red (band 3) and blue to green (band 2). Cloud cover during image recording was 0.09%. The training points used for the supervised classification (result shown in Figure A2) are shown with dots. Five types of habitat are distinguished: Bare intertidal mudflat, Seagrass covered mudflat, Land (desert), Sebkha (irregularly flooded floodplain) and Water.

after low tide at Iwik. The tidal cycle in the west precedes the one in the east.) Therefore, the likelihood of misclassification is largest north-west of Arel and north of Kiji. This suspicion is confirmed by the low confidence levels of the classification procedure in these areas (Figure A3).
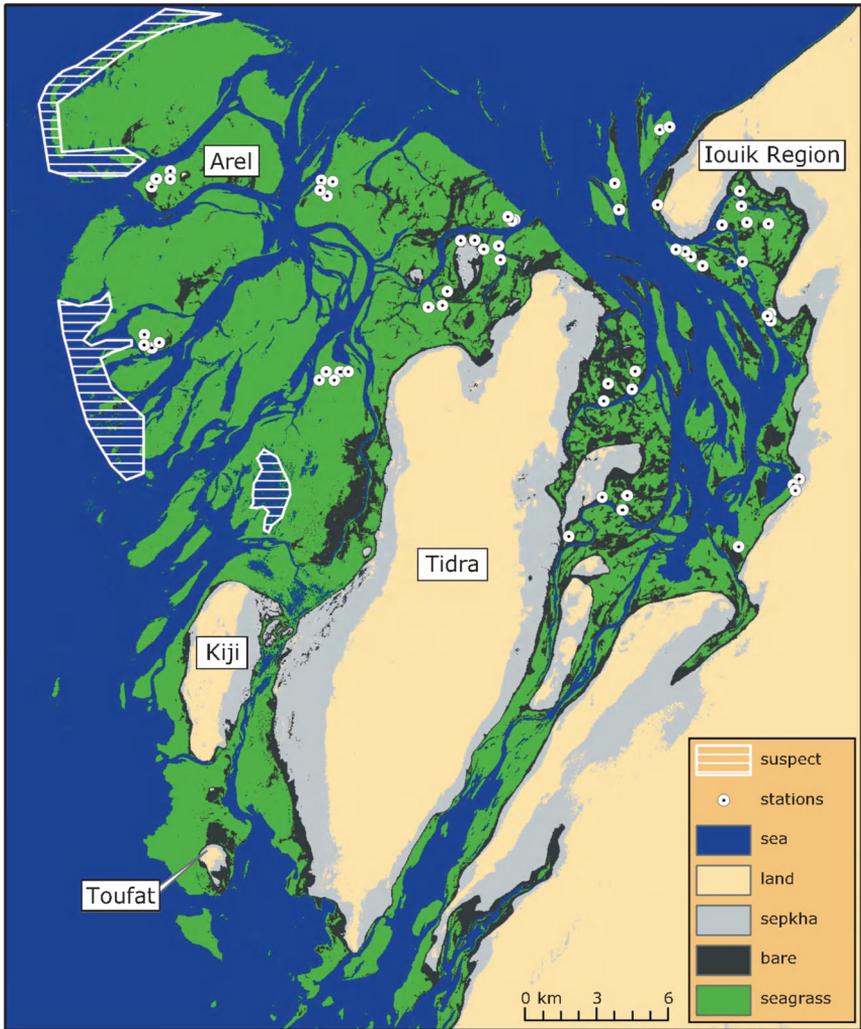
Figure A.2. Banc d'Arguin area classified into five habitats. The map is based on a supervised classification of Landsat TM image recorded on 22nd January 2003. Isolated pixels were removed with a majority filter with 8 neighbors. On the intertidal flats bare and seagrass habitats are distinguished. The hatched areas (north of Kiji and northwest of Arel) were probably falsely classified as sea due to the incoming tide. The stations represent sampling locations which should not be confused with the training points that were used for the classification.
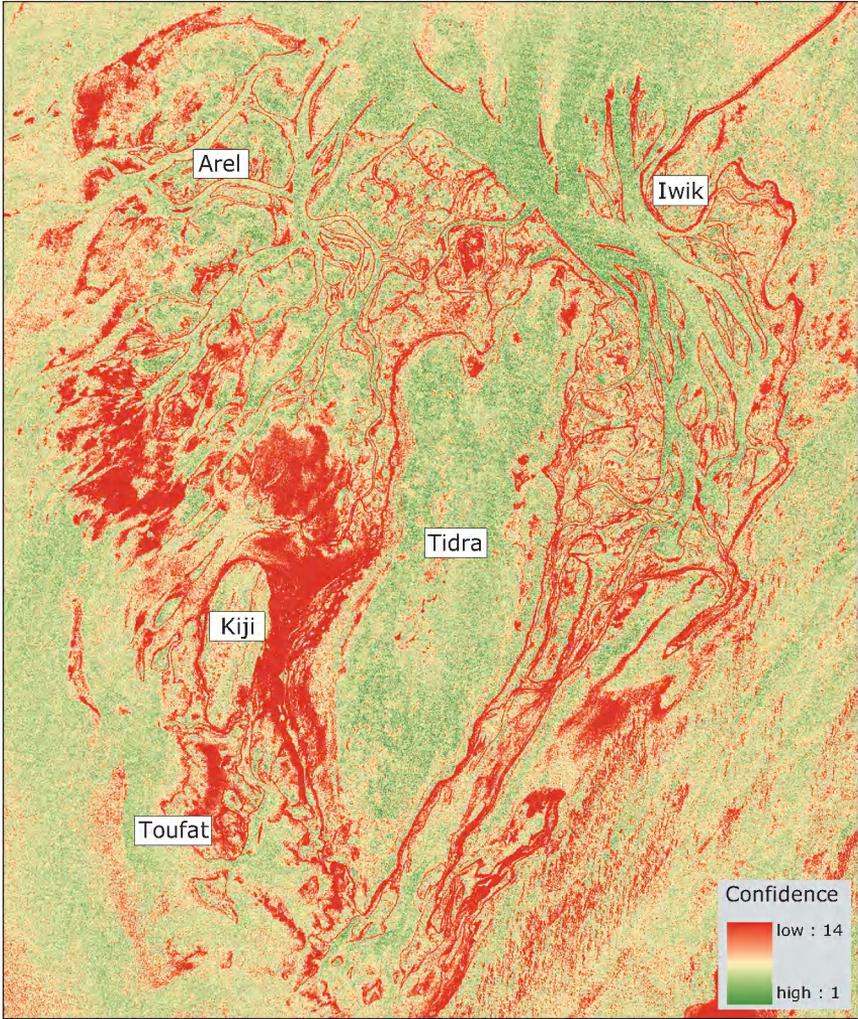
Figure A.3. Confidence of the classification of the Banc d'Arguin area. The confidence of classification in Error! Reference source not found. is represented by the color.

Supplementary material B: Relationships between dependent variables and predictors and summary statistics
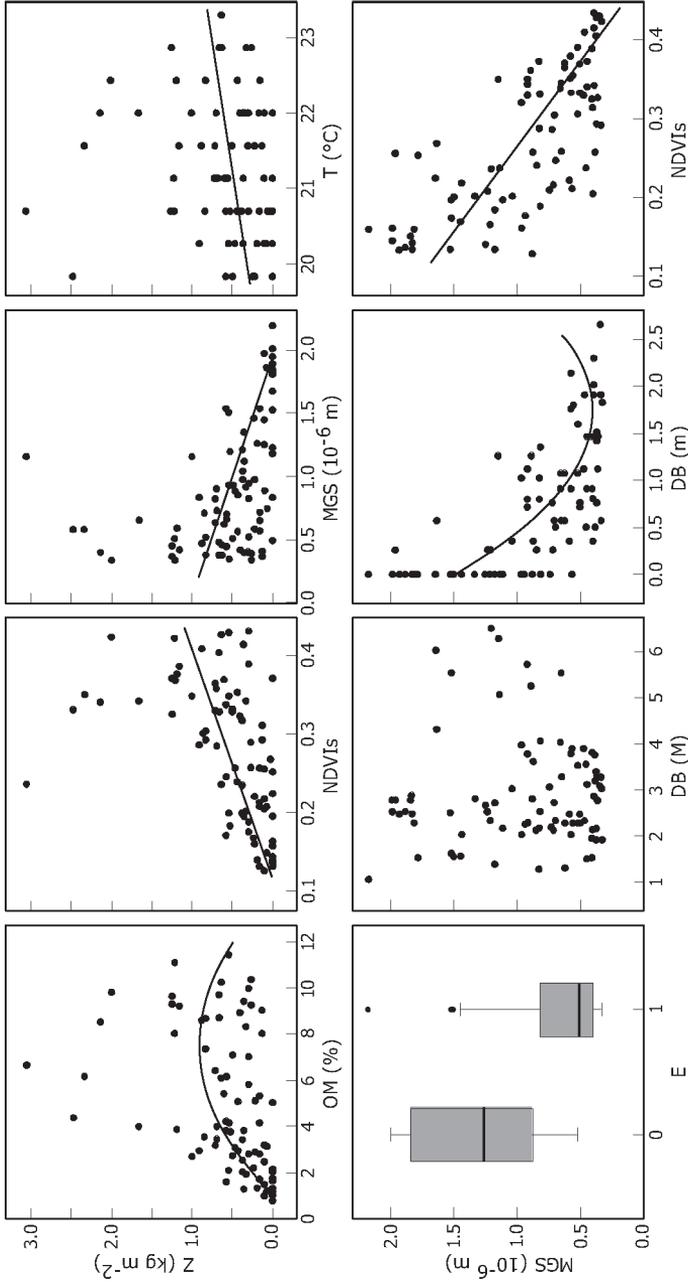

Figure B.1. Scatter plots showing the univariate relationships between the dependent variables (S and MGS) and the predictors that enter the structural equation model. The plots include curves that indicate statistically significant relationships ($P < 0.05$). The initial models included a linear and a quadratic term. If a model contained an insignificant coefficient it was removed from the model by first deleting the squared term. If next the linear predictor was insignificant no curve was drawn in the scatter plot.

Table B.1. Summary statistics: mean and standard deviation (sd).

	S (kg x m^{-2})	MGS (µm)	OM (%)	OM^2	T (°C)	NDVIs	E	DS (km)	DB (km)
mean	4.77 x 10-2	103.7	4.28	27.98	21.1	0.259	0.48	0.292	0.060
sd	5.84 x 10-2	56.7	3.13	34.64	0.8	0.092	0.50	0.120	0.068

Table B.2. Input Covariance matrix to the SEM. The variables in this matrix have been rescaled such that one unit of S corresponds with 100 g x m^{-2}; MGS in 10^{-4} m. OM in %; T in °C; NDVI is dimensionless; E an indicator variable 0 or 1; DS and DB in 100 m. (In the covariance matrix we use the unconventional unit of 10^{-4} m instead of 10^{-6} m (μm) so that the variable is better scaled with the other variables. To obtain a scale in line with the scales of the other variables OM is measured in 10 g.

	S	MGS	OM	OM^2	T	NDVIs	E	DS	DB
S	0.34								
MGS	-0.17	0.32							
OM	0.88	-1.49	9.78						
OM^2	8.25	-14.54	105.56	1199.84					
T	0.10	-0.28	1.61	16.54	0.71				
NDVIs	0.03	-0.04	0.21	2.20	0.04	0.01			
E	0.06	-0.16	0.99	10.38	0.22	0.02	0.25		
DS	0.09	-0.00	-0.28	-3.47	0.05	0.01	-0.19	1.44	
DB	0.20	-0.27	1.53	16.43	0.25	0.06	0.13	0.04	0.46

Table B.3. Correlation matrix of the variables included in the SEM. OM$_c$ and OM$_c^2$ are mean centered; see main text for details.

	S	MGS	OM$_c$	OM$_c^2$	T	NDVIs	E	DS	DB
S	1								
MGS	-0.51	1							
OM	0.48	-0.84	1						
OM^2	0.11	-0.31	0.67						
T	0.21	-0.59	0.61	0.31	1				
NDVIs	0.54	-0.75	0.74	0.40	0.49	1			
E	0.21	-0.58	0.63	0.37	0.51	0.38	1		
DB	0.50	-0.71	0.72	0.47	0.43	0.88	0.37	1	
DS	0.13	0.00	-0.08	-0.08	0.05	0.09	-0.31	0.05	1

ESTIMATION OF A SEAGRASS-SEDIMENT FEEDBACK BY MEANS OF SEM

7

General dicussion

Eelke O. Folmer

The research problem

Intertidal mudflats are important habitat for various kinds of wildlife of which migratory birds are the most conspicuous (van de Kam *et al.* 2004). Theory and empirical models describing the ecological processes that govern intertidal mudflats and the populations of species that depend on them are required to understand and predict the responses of the system to a changing environment. The main objective of this thesis is to contribute to the understanding of the role of self-organization at mudflats, with self-organization defined as the process of repeated interactions or feedbacks among elements that make up the system resulting in the spontaneous development of an element-transcending, higher level structure or function (Chapter 1).

Discovery of causation in ecological systems requires models describing how current states and process have evolved from past states and processes (Cressie & Wikle 2011). Typical for ecological systems in general, but especially for ecological systems in which self-organization plays an important role, is that they are difficult to study. The main reason is that required information may be hard to obtain from field observations or from experiments (Hilborn & Mangel 1997). In addition, patterns of interest may have developed over long periods of time and may vary by spatial and/or temporal scales (Holling 1973; Levin 1992). Further complexity arises from the fact that ecological systems usually develop under self-organization, i.e. that patterns emerge from past states, which feedback on current behaviour and future developments of the system (Kauffman 1993; Gunderson & Holling 2001; Levin 2005). Therefore, to discover causation in complex ecological systems, it is important to have methodologies that enable estimation and testing of hypotheses about presumed feedback processes. The challenge taken up in this thesis is to get insight into some aspects of self-organization on intertidal mudflats by means of statistical modeling of observed manifestations in a cross sectional setting and in an experiment.

Self-organization and its impacts on higher level structures are considered in this thesis in two types of ecological systems. The first is the system of foraging shorebirds on mudflats in the Dutch Wadden Sea, particularly their behaviour in relation to conspecifics and the resulting spatial distributions. For that purpose we developed a model that integrates different strands of literature, and a methodology for empirical analysis of field observations. In addition, we conducted an experiment with red knots to gain insight into possible hidden (cryptic) interference competition which might affect their spatial distribution, but is difficult to observe in the field because knots tend to space out. The second system is that of seagrass meadows in the Banc d'Arguin that maintain a reciprocal relationship with the abiotic environment. Also for this system the emphasis is

on the development of a methodology to empirically analyse the reciprocal relationships.

In the remainder of this chapter, I will summarize and integrate the main results of the various chapters and present some suggestions for future research. I will first discuss the system of foraging shorebirds, next the seagrass–sediment system.

Foraging shorebirds

The research questions
On the rhythm of the tides, shorebirds recurrently select foraging locations in vast intertidal resource landscapes like the Wadden Sea. A system of mudflats needs to satisfy various conditions to carry large populations of shorebirds. One basic requirement is high productivity. The productivity in terms of macrozoobenthos of the Wadden Sea is generally high which allows large numbers of foraging shorebirds to satisfy their energetic demands (Beukema 1979; Beukema, Cadee, & Dekker 2002; van de Kam *et al.* 2004). Zwarts and Wanink (1993), however, have shown that the mere presence of prey is not sufficient; prey items also need to be within reach (not buried too deeply) and profitable (i.e. be of correct size: large enough so that they contain sufficient meat to outweigh the cost of handling and small enough to be handled and swallowed). Furthermore, the duration of exposure of the mudflats during low tide has to be sufficiently long so that shorebirds have enough time to satisfy their energetic demands (Zwarts *et al.* 1996; Goss-Custard *et al.* 2001). (Note that foraging time can be prolonged by moving between mudflats in the same direction as, and ahead of, the tidal wave (Van Gils *et al.*, (2006)). Finally, daily energetic demands can only be met when local benthos densities are sufficiently high so that birds need not spend too much time searching. This implies that birds must find resource rich foraging areas quickly.

The vastness of the landscape and the absence of landmarks to navigate by, make it difficult for shorebirds to find and remember suitable foraging locations. In addition, the possible presence of predators requires perpetual vigilance. To increase foraging success and to elude the risk of predation, shorebirds can make use of the information that is (inadvertently) signalled by the presence and behaviour of other foragers. It is therefore advantageous for shorebirds to form groups to benefit from each other's presence. Foraging in a group, however, may also entail costs in the form of interference competition (Goss-Custard 1980; Sutherland & Koene 1982; Sutherland 1983; Goss-Custard *et al.* 2001).

The scientific literature on spatial distributions of foraging populations has mainly been in the tradition of the Ideal Free Distribution (IFD) assumptions

and generalized functional response (GFR) models. This literature has developed largely independently from the literature on behavioural processes underlying group formation based on interdependent decision making. The former strand explains spatial distribution of foraging animals in terms of fitness (or intake rate) optimization, i.e. it assumes that animals maximize their pay-off by selecting optimal foraging locations. The latter, behavioural approach, models movement and alignment of individuals in response to conspecifics (e.g. Sumpter 2010 for an overview).

Chapter 1 ("*Introduction*") describes the basic notions of three (complementary) types of animal distribution models, i.e. the IFD model, the generalized functional response model and social grouping models that form the conceptual framework for the subsequent chapters. In the chapter I specify the objectives and research questions of the foraging shorebirds part of the thesis[1], viz. whether generalized functional response models adequately describe spatial distributions of foraging shorebirds, and, if not, how they should be substituted for or supplemented with behavioural models which explicitly take into account the fact that animals aggregate in response to each other.

The main findings

Chapter 2 ("*How well do food distributions predict spatial distributions of shorebirds with different degrees of self-organization?*") tests models that only contain exogenous environmental variables (resources and distance to high tide roost) as predictors of the spatial distributions of shorebirds at landscape level. It analyses the relationship by regressing the density of six species of foraging shorebirds in the Dutch Wadden Sea with varying levels of gregariousness on resource density and distance to high tide roost. The main finding of the chapter is that the predictive power of a model based on environmental variables only, as measured by the residual variance, deteriorates with the tendency to flock. For instance, interference-insensitive species like red knot (*Calidris canutus*) and dunlins (*Calidris alpina*) were found to cluster more densely than predicted by the spatial distribution of their food resources. In contrast, for curlew (*Numenius arquata*) and grey plover (*Pluvialis squatarola*), which are known to be sensitive to interference and to form sparse flocks, the residual variance was substantially smaller and the predictive power substantially larger. We arrived at the conclusion that positive feedback in the form of conspecific attraction in combination with (in)sensitivity to interference, limits the predictability of the instantaneous spatial distribution of foraging shorebirds on the basis of models with exogenous predictors only.

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[1] Chapter 1 is the general Introduction and also contains the problem statement and research questions relating to the seagrass-sediment chapter. This part of chapter 1 will be discussed in the summary of chapter 6

The mere presence of food availability and absence of conspecific attraction in an animal density model implies a correctly specified model for solitary species, but a misspecified model for gregarious species which leads to an increase in residual variance. Hence, in general, to adequately predict the behaviour and the spatial distribution of foragers both the exogenous environmental predictors (i.e. the availability of food and distance to high tide roosts) and the presence of conspecifics (endogenous) need to be taken into account.

The spatial distribution of animals in relation to conspecifics, particularly their inter-individual distances, may be used as an indication of the net outcome of attraction and repulsion. In a homogeneous resource environment it would be straightforward to discern whether animals are attracted to or repulsed by each other because clustering would be the outcome of inter-individual interaction solely. In an environment with heterogeneously distributed resources it is more difficult to discern interaction effects because the social forces operate concurrently with attraction due to the presence of resources.

Van der Meer and Ens (1997) show that under IFD assumptions, similar functional response functions may lead to very dissimilar aggregative response models. This implies that some model from this set of aggregative response models (in which conspecific attraction is not included) might fit some consumer- resource data set - which is the outcome of both exogenous and endogenous factors - well. In practice this leads to searching for a model from the set to fit the data at hand (e.g. Quaintenne *et al*. 2011). Since the set contains many models, this search is usually successful. The basic flaw of this approach is that while these aggregative response models may describe distributions of social foragers well, they do not provide an explanation. Because of the expected benefits to group foraging and the relatively vast areas of suitable foraging habitat, I have argued in the Introduction that it is implausible to *a priori* discard conspecific attraction as a predictor of the distribution of foragers in general and of shorebirds in the Wadden Sea in particular. The findings in Chapter 2 support this argument. In the subsequent chapters 3 and 4 this issue is further analysed.

In chapter 3 (*"The spatial distribution of flocking foragers: Disentangling the effects of food availability, interference and conspecific attraction by means of spatial autoregressive modeling"*) we have taken up the challenge to develop and test a methodology to separate resource effects from conspecific attraction and interference competition effects. Based on notions from the literatures on GFR models, social foraging and collective animal behaviour, we constructed a simple model combining an interference-based functional response model with a model accounting for the benefits of conspecific presence to predict the distributions of foraging animals in continuous resource landscapes. The model is based on the notion that selection of a foraging site involves balancing costs and bene-

fits related to the presence of conspecifics, given environmental conditions like food availability. It assumes that when an animal locates close to conspecifics, interference costs exceed the benefits. The cost of interference (which leads to repulsion), however, rapidly levels off when inter-individual distance increases. Benefits due to the presence of conspecifics decrease at a lower rate with distance than interference costs.

Another important issue considered in this chapter is the system of spatial measurement unit, i.e. the grid system. In van der Meer and Ens' (1997) interference-based foraging models, "patches" are assumed to be homogeneous spatial entities with constant food and predator densities. Empirical testing of foraging models, however, requires operationalization of the abstract constructs "patches" as well as measurement procedures (Bivand, Pebesma, & Gómez-Rubio 2008). Because benthos densities are spatially autocorrelated (i.e. the density at one patch is related to the densities at surrounding patches) (Kraan *et al.* 2009), it is difficult, if not impossible, to unambiguously delimit "patches" from the perspective of foraging shorebirds. We therefore modelled the food resources in the landscape as being spatially autocorrelated, continuously and smoothly distributed over spatial units (grid cells) rather than as spatially discontinuously distributed with large jumps between patches.

As is well-known, the imposition of a grid of some resolution may lead to the modifiable areal unit problem (MAUP), i.e. the chosen grid imposes an arbitrary measurement system on the spatial system of food and bird density which can affect parameter estimates in regression analysis. By means of multi-scale analysis, however, it is possible to compare estimates on various resolutions and thus get a sense of their robustness.

By means of simulations we showed that the integrated model produced distributions of foraging shorebirds that are close to those observed in nature. The simulations furthermore showed that under information uncertainty and when conspecific attraction is strong, the locations of flocks are highly variable. This prediction of the model is in line with the findings of Chapter 2, namely that the predictive power of a model based on environmental variables (resources and distance to high tide roost) only, as measured by the residual variance, deteriorates with the tendency to flock.

As mentioned above, one specific objective of this thesis was to develop a methodology to measure the mechanisms underlying self-organization. For conspecific attraction and interference competition we proposed to measure them by means of their spatial manifestations. This approach is based on the fact that these mechanisms show up as the tendency of conspecifics to locate in each other's vicinity or to stay away from each other, respectively. That is, *ceteris paribus*, conspecific attraction shows up as positive spatial dependence, whereas interference has a depressing effect on it.

Since interference and attraction show up as spatial dependence, we proposed to estimate their impacts on the foraging distribution by means of a spatial autoregressive model, i.e. the spatial lag model. We showed that the spatial lag model gives adequate estimates of the impacts of resource availability and of the combined effect of conspecific attraction and interference for equilibrium and non-equilibrium distributions. Furthermore, the chapter shows under which conditions the separate impacts of conspecific attraction and interference can be disentangled.

As mentioned above, it may *a priori* not be known at what scales self-organization operates. Therefore, the applied methodology needs to be robust and give consistent estimates at various resolutions. We therefore investigated the correspondence between the simulation parameters (particularly interference and conspecific attraction parameters) and their estimates across spatial scales (obtained by aggregating adjacent grid cells). The results showed that, at least in the case of one exogenous (food) predictor, the estimators of the coefficients of self-organization and food are robust over a wide range of spatial scales.

The regression coefficients of the exogenous variables in a spatial lag model represent their direct effects on the dependent variable. However, feedback between foragers in the context of self-organization implies that the total effect of an exogenous variable is different from the direct effect. Particularly, food availability induces foragers to locate in a given cell (direct effect) which, due to conspecific attraction, induces other animals to locate in the same cell or in neighbouring cells (first-order indirect effect) which induces other foragers to locate in their vicinity (second-order indirect effect) and so on. Hence, feedbacks among the foragers resulting in clustering amplifies the direct effect of the exogenous variable. The chapter introduced the spatial multiplier to account for the indirect effects caused by positive feedbacks among the foragers to obtain the total impacts of the exogenous predictors.

In chapter 4 ("*Estimating the relative contributions of resource availability and self-organization to explain foraging distributions: A spatial lag modelling approach*") we developed an *exogenous-environmental – self-organization model* and used it to re-analyse the spatial distribution of the six abundant shorebirds species in the Dutch Wadden Sea (considered in Chapter 2) at three resolutions. We estimated the model by means of spatial autoregression (developed and tested in Chapter 3). The main finding was that for all species, at all three levels of resolution, the explanatory power of self-organization - as measured by the Nagelkerke R^2 - is substantially larger than that of the exogenous environmental variables food availability, silt content and elevation of the mudflat together. We also found that for dunlin (*Calidris alpina*) and red knot (*Calidris canutus*) the impact of self-organization is stronger than for curlew (*Numenius arquata*), oystercatcher (*Haematopus ostralegus*), grey plover (*Pluvialis squatarola*) and

bar-tailed godwit (*Limosa lapponica*). Another important finding was that the total effect of the exogenous environmental predictors substantially exceeds the direct effect.

The high levels of spatial autocorrelation and relatively low predictive power of the exogenous predictors imply that conspecific attraction is an important factor to predict instantaneous shorebird distributions. It does, however, not imply that exogenous predictors are unimportant for foraging location choice. Particularly, the exogenous predictors may have led to the collective selection of a location by a flock, or may have influenced the choice of a location by leading animals whose choices were copied by followers.

In a study of the distribution of red knots around the small island of Griend in the Dutch Wadden Sea, Piersma *et al.* (1993, 1995) found that the spatial distribution of foraging red knot summed over multiple tidal cycles were in line with the spatial distribution of food availability. Indeed, summing or averaging observations over time could increase the correlation between animal density and food availability because the likelihood of rich foraging areas remaining unvisited decreases with time or foraging bouts (i.e. number of foraging cycles in response to the tide). However, this result is not at odds with the above findings. In fact, the micro-level behaviour of social attraction is instrumental in improving the correspondence between foraging distribution and food distribution (van Gils 2004). Positive feedback in micro-level behavioural processes may result in non-linear correlations between exogenous variables and the response variable at macro-levels (i.e. thresholds) (Sumpter 2010). To investigate the role of social attraction on 'summed' foraging distributions of shorebirds in large and complex intertidal landscapes, further research of macro-level patterns in realistic settings, based on behavioural assumptions, will be required. More importantly, while summed or averaged animal densities may provide insight into the importance of different areas and their food sources, they are basically uninformative of the micro-level behavioural processes of patch choice.

In the field, non-breeding red knots *Calidris canutus* while feeding on buried bivalves on intertidal mudflats, are rarely observed to interfere. This, however, need not imply the absence of any form of interference[2] because the spatial distribution of foragers is the net result of animals attempting to avoid interference competition while retaining the benefits related to the presence of conspecifics. To assess possible interference behaviour, optimal conditions for its occurrence including high competitor density and absence of confounding factors such as

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[2] Note the similarity to the explanation of Lima and Dill (1990) who state that the fact that few killed animals does not imply that the effect of predation is negligible on the population of prey.

food depletion, should prevail. We created such conditions in an experiment the results of which are presented in Chapter 5 (*"Experimental evidence for cryptic interference among socially foraging shorebirds"*).

In the indoor experiment we set up foraging patches of constant size with constant prey density, but varied the numbers of conspecific competitors on the patch. In this setup there was minimal resource depletion so that interference competition could be distinguished from competition arising from depletion. The setup allowed quantification of the intake rate as a function of flock size, prey density and social status. We studied the behaviour of red knots by means of time-budget analysis to identify the source of possible interference competition. We found that intake rate and searching efficiency decreased with flock size and that dominant birds had higher intake rates than subordinates. Particularly, the proportion of time spent searching for prey, moving and watching to avoid physical encounters with conspecifics, increased with group size. The decrease in intake rate was not due to kleptoparasitism or more time spent on aggressive interactions, i.e. conventional interference mechanisms, but rather to what we defined "cryptic interference", i.e. avoidance of physical encounters with conspecifics.

The results are consistent with the fact that red knots space out in a gregarious fashion while foraging in the wild. An important implication of our results is that (generalized) functional models need to take into account the possibility that animals may anticipate physical encounters and will attempt to avoid them (see the next section for further details).

Some theoretical implications

In this subsection I present some theoretical implications of the findings summarized above.

Emotions and behavioural states in complex (social) environments

Based on the findings of this thesis I have argued that the ideal free distribution approach in combination with fitness functions does not provide satisfactory models of shorebird foraging distributions. One reason for this is that this approach assumes that animals can flexibly adopt to various circumstances and develop optimal behaviour (to maximize fitness); even if the situation and problems at hand are difficult or costly to solve (Tinbergen 1981). The inadequacy is particularly true for gregarious animals for which fitness also depends on the actions of the group (of which the individuals are members). McNamara and Houston (2009) suggest that progress in this area can be made by further integration of ethology and ecology, particularly by incorporating into the latter
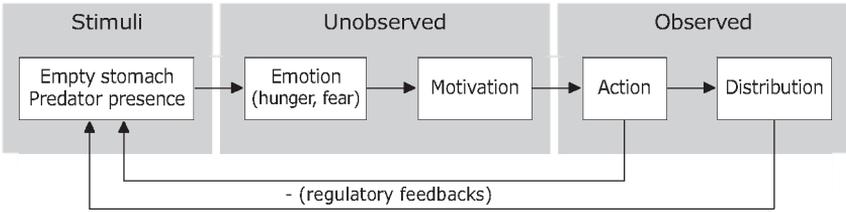
Figure 7.1. The relationships between stimuli, emotions, motivation, action and spatial distribution of foragers.

the evolution of behavioural mechanisms. In this regard they emphasize the role of emotions which play a pivotal role in the evolution of optimal behaviour. Emotion is roughly defined as an animal's psychosomatic state (i.e. "feelings") resulting from integration of external (presence of food, mates, predators) and internal stimuli (e.g. hunger, memory). For example, beneficial conditions are (or evolve to become) associated with pleasure and contentment while detrimental circumstances are associated with anxiety, distress and uneasiness (Dawkins 1990). Emotions thus aid animals to perform mental accounting of potential benefits and detriments which enable them to develop and follow simple rules. Because emotion integrates internal and external stimuli, it acts as a simple and robust driver of motivation which in its turn directs and energizes behaviour. Rules that map stimuli, to emotions, emotions to motivation and motivation to behaviour may evolve such that in most situations, including new and unexpected situations, rational and optimal behaviour emerges.

As depicted in Figure 7.1, an animal's acts (i.e. the change of the behavioural state) will feed back onto stimuli such that the displayed behaviour will tend to normalize an animal's emotional state (i.e. it is a regulatory feedback). For example, if an animal feels frightened, it will act (e.g. move away from the danger) such that its feeling of fear decreases. Similarly, if a forager finds itself located too far away from its group members (stimulus) it will feel uneasy (emotion) and move towards the group (act) which reduces its fear.

Mechanistic behavioural models as depicted in Figure 7.1 are difficult to operationalize because motives are difficult, if not impossible, to observe, especially in the field. In this thesis I have argued that in the case of self-organisation and its underlying mechanisms of conspecific attraction and repulsion, motivation is reflected by its manifestations, i.e. spatial dependence which allows operationalisation and measurement of motivation. One basic result of this thesis therefore is the operationalisation and measurement of motivation by means of its manifestations.

Memory versus information from conspecifics

The world of animals is complex in that they continuously need to adequately respond to new, unexpected and possibly ambiguous inputs and signals in various kinds of (changing) environments. The world of socially foraging animals is especially complex because, in addition to the complexity of the exogenous environment, they need to 'understand' each other (i.e. they need to be empathic, that is, to be able to read the intentions of conspecifics and to develop a response to their behaviour). Natural environments of animals in general and of social animals in particular, are too complex for the development of rules that make an animal behave optimally in every possible situation (Mangel & Clark 1986; McNamara & Houston 2009). Instead, animals are likely to develop rules that perform well in most situations (McNamara & Houston 2009). An example is Hirvonen *et al.*'s (1999) memory model in which individuals adjust the rate of devaluation of their memory on the basis of previous foraging success. In stable environments animals show low memory devaluation rates; in unstable environments high rates. The reason is that the likelihood of a repetition of a situation in the former case is higher than in the latter. Hence, the value of information is higher in the former case. Application of this simple rule results on average in adequate and appropriate foraging behaviour in different kinds of environments.

From this thesis it follows that information transferred by the presence of foraging conspecifics may supplement an animal's memory (e.g. Danchin *et al.* 2004, Dall *et al.* 2005). Instead of storing information on foraging locations in its memory, the searching animal may exploit information signalled by the presence of foraging conspecifics to choose a foraging location. However, the spatio-temporal structure of prey distribution will influence the role of information transfer between foragers searching for prey. For instance, when resources are uniformly distributed, the presence of foragers does not contain information value. However, when resources are heterogeneously distributed, and "patches[3]" are large enough so that they cannot be monopolized, competition for food or space will not be strong. In such cases it will be beneficial to locate in the vicinity of other foragers.

One corollary is that when the resource landscape changes, the significance of the information in the form of the presence of foragers will change too. For instance, in the Wadden Sea, in late summer, when macrozoobenthos densities are high, there are peaks in the resource landscapes. During that season the amount of information signalled by the presence of shorebirds is high. However, the need for food (and thus for information) is relatively low during late sum-

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[3] The enclosed surface (polygon) in which resource density is high enough to meet the energetic demands.

mer compared to winter periods. If the peaks are depleted first, there will be homogenization of the resource landscape resulting in a decrease in the amount of information conveyed by the presence of foragers. However, in fall and winter energy demand increases due to decreasing temperatures (Wiersma & Piersma 1994) which increases the value of information for foraging shorebirds. Thus, while requirements for information are highest during winter, the amount of information conveyed is lowest.

Suggestions for future research

From the above it follows that evolutionary consistent models of foraging behaviour and distributions for interdependent animals are to be based on emotions and motives. In this thesis I have focussed on the links between motivation, action and the distribution of foragers and the feedback of the latter to motivation, in line with McNamara and Houston (2009) who point out that it is important to integrate evolutionary ethology with ecology. Particularly, understanding of foraging behaviour requires that it is studied within the context of the ecological system, since this is the setting in which an animal's behaviour has evolved.

To better understand the full system of stimuli, emotion, motivation, action and distribution of collective foragers in the wild, it is important to consider interdependent behavioural states and dynamics (i.e. the switching between behavioural states) in the context of the spatial distribution of resources. This requires a combination of field observation, mathematical modelling and experiments[4]. Field observations of behaviour and of spatial distributions of social foragers will provide insight into how spatial distributions arise from social interactions and interactions with prey. The use of geo-locators fixed on animals, particularly geo-locators that are able to register the presence and behaviour of nearby geo-locators, is particularly relevant in this context. Experiments with multiple foragers will be useful to assess relationships between emotion (i.e. the integration of internal and external stimuli), motivation and interdependent (movement) behaviour. The information thus obtained can be applied to gain insight into the conditions, including the social forces, which drive behaviour in the field.

When there is positive feedback between individual foragers, the behaviour of the group is not trivially "scaled up" to the group, because the system may become self-organized (Parrish & Edelstein-Keshet 1999) such that it behaves as a unit. To investigate how self-organisation arises from individual behaviour

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[4] In this context it is righteous to quote Begon, Harper and Townsend (1996) who state that *"Ecology is a meeting ground of the naturalist, the experimentalist, the field biologist and the mathematical modeller"*.

(including movement behaviour in response to conspecifics), spatial simulation models with parameters obtained from field observations and experiments will be useful to investigate whether micro-scale behaviour may lead to matching macro-patterns. Agent- and state-based models naturally lend themselves to include decision rules describing switches between behavioural states of individuals in a heterogeneous group of interdependent foragers. If the behavioural states that an individual (or agent) can exhibit, and if the rates at which they make transitions between these states can be determined, a model of foraging (and possibly other kinds of) behaviour including movement can be constructed. The behaviour of foragers may thus be modelled in a relatively straightforward manner.

An interesting specific research topic within the above framework is to gain a more detailed insight into the relationship between memory and information received or conveyed by conspecifics. Particularly, does the substitution between memory and information conveyed by conspecifics vary by individual characteristics, such as age or experience? Conversely, does the value of information conveyed by conspecifics vary by individual characteristics, such as age, size or sex? This kind of questions could be at first instance addressed in indoor experiments where foraging behaviour is observed under different types of populations composition, e.g. with and without leaders, different age cohorts, etc.

A disadvantage of agent-based models is that they easily become complex so that under different parameter settings similar macro-patterns may arise. The fact that the model generates patterns that match reality is no guarantee that the living system follows the same rules as the simulation model. By considering the whole living system, from micro-level to macro level the risk of choosing "wrong" parameters may be reduced.

The seagrass – sediment system

A species is considered to be ecosystem engineer when it has substantial impacts on the functioning and stability of ecosystems by affecting the abiotic environment which in its turn impacts on other biota and the own species (Jones *et al.* 1994, Wright and Jones 2006, Hastings *et al.* 2007). There has been substantial interest in ecosystem engineers, amongst others because of the role they may play in the development and resilience of ecosystems (Holling 1973; Gunderson & Holling 2001; de Boer 2007; Bouma *et al.* 2009).

The impacts of ecosystem engineers can last longer than the lifetime of an organism. In addition, ecosystem engineers may be important factors in the stability of systems in that they may drive the state of the system towards a stable "basin of attraction". The loss of an ecosystem engineer therefore could cause a

system to move away from a stable state and lead to a decrease in resilience (Holling 1973; Gunderson & Holling 2001). Because of their potential to radically change ecosystems and their impacts on stability, ecosystem engineers have also received considerable attention from management as instruments to restore ecosystems to desired states (Byers *et al.* 2006).

All organisms in an ecosystem affect each other in some way or another and their interactions vary in time and space. In the Introduction I argued that the only realistic way to study the development of systems is by demarcating them from external factors that can be considered constant for the purpose of the study. In practice this means that presumed unimportant interactions are considered constant. This, however, is a challenging task in the case of ecosystem engineers because their (initial) biotic impacts or interactions may be small on small spatial or temporal scales while their substantial abiotic effects may show up on larger scales (Hastings *et al.* 2007). Furthermore, the biotic interactions may depend on the abiotic conditions. It is therefore important to consider the spatio-temporal hierarchy of biotic and abiotic interactions and the history of systems when investigating the effects of engineers. Ecological data, however, are generally too poor to assess the spatio-temporal hierarchy of biotic and abiotic interactions.

Non-trophic interactions between ecosystem engineers and abiotic environments are common features of intertidal ecosystems (Bouma *et al.* 2009). Because the effects of ecosystem engineers may only show up over long spells of time, their long-term impacts on the system are difficult to investigate within short time frames. Hence, there is need for methodologies that enable estimation of interaction effects between engineers and their environments based on data collected over short periods of time. The objective of the final chapter was to estimate the feedback effects between the ecosystem engineer seagrass and sediment by means of a non-recursive structural equation model (SEM) on spatial cross-sectional data (Chapter1).

The effect of seagrass on sediment is relatively robust and predictable (compared to e.g. predator prey relationships) which makes the process relatively insensitive to extrinsic factors. This implies that the interaction between sediment and seagrass is a predictable driver of the system. Particularly, it provides stability and generates a constant environment for other biota. Furthermore, by means of its engineering activities seagrass may ameliorate abiotic stress which makes it possible that it occupies otherwise intolerable areas (Bertness & Leonard 1997). The fact that engineers may ameliorate abiotic stress raises the question of what limits its occurrence and its engineering activities.

Detailed understanding of the feedback between seagrass density and sediment properties is critical for the prediction of the responses of a seagrass-dominated ecosystem to environmental change. Particularly, it is important to know

the strength of the feedback between seagrass density and the environment in relation to external factors.

In Chapter 6 ("*Self-inhibition of seagrass beds through sediment modification revealed with a non-recursive structural equation model*") we took up the challenge to estimate the negative feedback relationships between an engineer and its abiotic environment in relation to exogenous factors on the basis of cross-sectional data. Particularly, we used a non-recursive structural equation model (SEM) to estimate the reciprocal strengths of the relationships between seagrass density and sediment grain size in the pristine, seagrass-dominated intertidal mudflats of the Banc d'Arguin. We identified a statistically significant negative feedback loop which implies that intertidal seagrasses change their environment to ultimately limit their own growing condition.

Suggestions for future research
Cross-sectional data could be used to assess the dynamics of the system because in different locations of the study area the system is in different stages of development. In other words, the dynamics showed up in spatial patterns which form the basis for inference of temporal dynamics. An important topic for future research would be to collect time series data for the different locations and to compare the estimates of the feedback relationship between seagrass and sediment based on this kind of data with the non-recursive SEM estimates based on cross-sectional data.

To obtain insight into the robustness of the approach, it would also be useful to investigate the SEM approach by means of simulation. Particularly, a spatio-temporal model of seagrass and sediment interaction (which of course could include other relevant variables such as hydrodynamics and bathymetry) could be tested by estimation of impacts on the basis of simulated data in different stages of development.

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ENGLISH SUMMARY
Self-organization on mudflats

The main objective of this thesis is to contribute to the understanding of the role of self-organization on mudflats, with self-organization defined as the process of repeated interactions or feedbacks among elements that make up the system, resulting in the development of an element-transcending, higher level structure or function. The main part of this thesis is about the behaviour, site choice and spatial distribution of foraging shorebirds in relation to abiotic factors, food resources and conspecifics. The research is theoretical, empirical and statistical. The empircal work was conducted in the Dutch Wadden Sea and in the experimental shorebird facilities at the Netherlands Institute for Sea Research (NIOZ). A smaller part of the thesis is about the feedback between sediment and seagrass which determines the density and distribution of seagrass, at the mudflats of the Banc d' Arguin, Mauretania.

There are two connecting elements between the two seemingly different topics. Firstly, seagrass has substantial impacts on the presence and density of food resources for shorebirds. A second connecting element is the conceptual and methodological similarity as a consequence of the fact that in both ecosystems endogeneity and self-organization play a crucial role. Specifically, the behaviour of shorebirds, such as the selection of foraging location, depends on the behaviour of conspecifics while the growth and density of seagrass is affected by its own density via modification of sedimentation and erosion.

In this summary I will first describe the chapters about the spatial distributions of foraging animals. Next, I will summarize the chapter about the seagrass-sediment feedbacks.

Spatial distributions of socially foraging shorebirds

Ecology is the science that deals with explaining and predicting numbers and spatial distributions of organisms in ecosystems . Behavioural ecology is the branch of ecology dealing with animal behaviour in an ecological and evolutionary context. To analyse patterns of (socially) foraging shorebirds I have chosen a behavioural approach. The chapters about the spatial distribution of shorebirds are based on the following motivations and considerations.

While in intertidal ecosystems there are generally a limited number of foraging locations that are very rich in resources, it is not efficient to forage simultaneously with many conspecifics at such locations. The reason is that the lack of space would cause foragers to interfere with each other leading to lower intake rates than could be achieved at locations less resource-rich but with fewer competitors. The phenomenon that intake rate decreases due to the presence of conspecifics, but not due to depletion of resources, is called interference competition. If shorebirds had perfect knowledge of the spatial distribution of

resources (i.e. they knew how much food is available at all locations), of the spatial distribution of competitors and if the costs of movement were negligable, then the foraging individuals would distribute themselves such that all would obtain the highest possible intake rate. This distribution is called the Ideal Free Distibution(IFD). The basic theory was introduced by Fretwell and Lucas (1969) and has since then been further developed and applied to explain and predict distributions of foraging animals including shorebirds. A basic assumption of the IFD theory is that the quality of a location decreases with the number of individuals that uses that location (i.e. it assumes negative density dependence).

Although the IFD theory is central to behavioural ecology, it neglegts the fact that there are important advantages to the presence of conspecifics. A theory that incorporates both advantages and disadvantages of the presence of conspecifics is the social foraging theory (Giraldeau & Caraco 2000 and Krause & Ruxton 2002). A basic notion in social foraging theory is that animals may benefit from the presence of conspecifics because it reduces the risk to become prey. Another central notion of this theory is that the presence of foraging conspecifics provides information about the presence of food and the absence of predators.

Signalling of information is especially relevant for food-searching shorebirds because they recurrently (every low tide period) have to find foraging locations on the large intertidal mudflats in which their benthic prey is buried in the sediment. This makes it difficult and time consuming to obtain information on the distribution of benthic prey by individual sampling. Therefore, they take the presence and behaviour of other foragers as signals of the presence of resources (and the absence of danger). Following or joining foraging conspecific may thus be beneficial in that search costs and predation risk are reduced.

The advantanges and disadvantages of the presence of conspecifics depend on the distance between the individuals. On short distances the costs due to interference competition outweigh the benefits due to reduction of search costs and predation risk. At larger distances the benefits are greater than the costs because interference competition rapidly declines with inter-individual distance . This implies that there is a distance dependent trade-off between benefits and costs of locating in the vicinity of conspecifics. The distance dependent trade-off between on the one hand interference competition and on the other reduction of search costs and of risk is an optimization problem that determines location choice in the vicinity of conspecifics. For shorebirds foraging on large open intertidal mudflats, the benefits associated with the presence of conspecifics are likely to outweigh the interference costs because food patches tend to be large such that the costs due to interference competition can easily be reduced by spacing out. Hence, most shorebird species live in groups which vary by local density (or packing).

I have argued that the spatial distribution of foraging shorebirds depends on the density of resources, habitat characteristics and on self-organization. The goal of this part of the thesis is to obtain further insight into the relevance of self-organization for foraging shorebirds by analyzing their foraging distribution patterns.

In **chapter 2** we analysed on landscape scale the foraging densities of six common shorebird species that vary in their level of packing. At 23 intertidal mudflats spread out over the Dutch Wadden Sea, the spatial distribution of the six species was determined. The locations of individuals and groups were mapped using a simple method based on projective geometry. We developed a measure for the level of packing and analysed the suitability of the 23 sites in terms of food availability and travel distances to high tide roosts. We found that interference-insensitive species like red knot and dunlins are more closely packed than interference sensitive species like curlew, oystercatcher and grey plover, which are known to be sensitive to interference. In addition we regressed foraging density against the availability of resources and distance to high tide roosts. The regression analysis showed that food and habitat provide better explanations for foraging densities of solitary than for gregarious species. It follows from our analysis that monitoring programmes, habitat selection models and statistical analyses of foraging behaviour should also consider the mechanisms of self-organization.

In **chapter 3** we integrated a classical functional response model based on resource availability and interference competition with a conspecific attraction model. By means of simulations we investigated the spatial distributions of foragers in their resource landscapes which varied by spatial dependence. We found that the integrated model produces distributions of foragers that match distributions of foraging shorebirds observed in the Wadden Sea. The simulations also showed that when foragers have uncertain information about the distribution of resources, the locations of flocks are highly variable when conspecific attraction is strong.

The attraction among individuals causes endogeneity in the system in that individuals at one location is influenced by the presence of conspecifics at other locations and vice versa. This implies that in a regression model of the number of foraging individuals containing self-organization as an explanatory variable is subject to simultaneity which would render the usual OLS estimator biased and inconsistent. We solved this problem by applying maximum likelihood spatial autoregression. We showed that the spatial autoregressive coefficient in the spatial lag model reflects the level of self-organization. On the basis of simulated data we furthermore showed under which conditions the separate impacts of interference and conspecific attraction can be disentangled. Lastly we showed that with the spatial multiplier, a function of the spatial autoregressive coeffi-

cient, the total effect of exogenous predictors (like food availability) on the spatial distribution of foraging animals may be estimated.

In **chapter 4** we reanalysed the data from chapter 2 by means of the spatial lag model which we introduced and tested in chapter 3. In stead of aggregating the data to landscape level (as in chapter 2) we made use of grids of cells of different sizes (150×150, 200×200 and 250×250 m). Within each gridcell we determined the bird and prey density. In the regression analysis we explicitly accounted for self-organization, measured as spatial dependence between cells. As shown in chapter 3, this methodology enables estimation of the direct and indirect effect of resource availability on the density of foragers. An important result was that at all three levels of resolution and for all species, the explanatory power of self-organization (measured by Nagelkerke R^2) is larger than the contribution of the exogenous environmental variables food availability, silt content, and elevation of the mudflat together. Averaged over all cell-sizes, self-organization is stronger for dunlin, red knot and curlew than for oystercatcher, grey plover and bar-tailed godwit. However, the effect of self-organization was dependent on the scale at which it was measured. The total impacts (i.e. direct effect plus indirect impacts) of the exogenous environmental predictors tends to substantially exceed the direct effect.

In **chapter 5** we present the results of an experiment with red knots designed to examine the behavioural mechanisms of interference competition in detail. To avoid confusing intake rate decline due to resource depletion and intake rate decline due to interference competition, we set up the experiment such that resource depletion was minimal. The set up thus allowed us to quantify interference competition as the decline in intake rate as a function of group size, with prey density and social status as additional treatments. The most important finding was that intake rate and searching efficiency decrease with group size and that dominant knots have higher intake rates than subordinates. Additionally, time spent searching for prey increased with group size.

The decrease in intake rate was not due to conventional interference mechanisms (such as kleptoparasitism and fighting), but to the fact that knots lost time avoiding physical encounters with conspecifics (which we denote "cryptic interference"). An important implication of our results is that the mechanistic functional response models (mathematical descriptions of the relationships between intake rate on the one hand and resource and competitor density on the other) are incomplete because they do not take into account the fact that animals may anticipate physical encounters with conspecifics and try to avoid them, though at a costs. To accurately predict intake rates and foraging distributions, theory and models need to account for cryptic interference.

Seagrass-sediment interactions

Typical for ecological systems in general, but especially for ecological systems in which self-organization plays an important role, is that they are difficult to study. The main reason is that information may be hard to obtain from field observations, and that patterns of interest may have developed over long, unobserved, periods of time and may vary by spatial and/or temporal scales. Our understanding of these types of systems often comes from conceptual models, mathematical models based on simplifying assumptions and from small scale experiments. Therefore, to identify and analyse causation in these types of complex ecological systems, it is important to have methodologies that enable estimation and testing of hypotheses about presumed feedback processes on the basis of cross section data obtained from field observations.

In **chapter 6** we present the results of our research on the reciprocal interaction between seagrass and sediment at the intertidal mudflats of the Banc d'Arguin, Mauretania. The reason that we investigated the interactions between these elements is that they may play an important role in the dynamics and stability of intertidal ecosystems. We used a non-recursive structural equations model (SEM) to analyse the interdependencies between seagrass and sediment. This type of SEM makes it possible to estimate feedbacks controlling for the effects of nutrients, and abiotic stress due to waves and currents. We found that grain size decreased with seagrass density, and that fine grain size had a negative impact on seagrass density. Another finding was that seagrass density increased with sediment organic material content, however, up to a threshold beyond which it leveled off. In combination with decreasing grain size, accumulation of organic matter created hypoxic sediment conditions leading to the production of toxic hydrogen sulfide which slows down seagrass growth. The negative feedback loop implies that intertidal seagrass modifies its own environment, thus controlling its own growing conditions.

Synthesis

Chapter 7 ends the thesis with a synthesis of the previous chapters and suggestions for further research. It first discusses the usefulness of spatial autoregressive models and SEM for modeling ecological systems in which endogenous processes are important. Usually, to gain insight into the development of ecological systems, use is made of concepts and models which depict the way in which the current state and behaviour of the system follow from previous states and developments. Empirical testing of these types of models is usually based on timeseries. However, in self –organizing ecological systems this type of analysis

is often difficult to perform because processes evolve slowly and historical developments areoften unknown. In the previous chapters we have shown that cross section data analysed with spatial autoregressive models and non-recursive structural models provide an alternative to obtain insight in the often invisible and slowly evolving ecological processes. In this context I have also suggested to combine a SEM with latent variables (made up of a structural model in terms of the latent variables and a measurement model for the latent variables) and a spatial autoregressive model to improve the analyses in chapter 4, amongst others to solve the problem of multicolinearity between exogenous predictors.

The thesis has identified some limitations of current distribution models of socially foraging animals. One is the incomplete modelling of possible complex interactions between individuals. Inspired by ideas of amongst others McNamara and Houston (2009) and Sumpter (2010) who plead for stronger integration ofindividual behaviour, evolution and ecology, I have described some elements that could lead to more realistic and accurate distribution models. They are based on the notion that individual behaviour results from emotions or the psychosomatic state of the individual. Emotions develop under the influence of external (presence of food, mates and predators) and internal (e.g. hunger) stimuli, experience and memory. Emotions are thus the product of external and internal factors and can act as robust drivers of motivation and behaviour. Rules or 'internal algorithms' that map stimuli to emotions, emotions to motivation and motivation to behaviour may evolve such that in most situations, including new and unexpected ones, rational and optimal behaviour emerges. Since foraging behaviour of social individuals depends on the behaviour of other individuals, agent-based models in which individuals have memory and can anticipate the behaviour of conspecifics (for example move away from conspecifics) are potentially useful. Even though agent-based models easily may become complex, they have several advantages. Particularly, model parameters may be estimated by means of experiments and physiological measurements. These models can be further tested via field observations and used to analyse spatial distributions. The most important reason to use these types of models is the possibility to realistically scale up from individual behaviour to the behaviour of groups.

Zelf-organisatie op wadplaten

Dit proefschrift gaat over zelf-organisatie in intergetijde ecosystemen. Onder zelf-organisatie wordt in dit verband verstaan de herhaalde interacties en terugkoppelingen tussen elementen van het ecosysteem, waardoor zich spontaan structuren of functies ontwikkelen, die de elementen overstijgen. Het grootste deel van dit proefschrift betreft gedrag, locatiekeuze en verspreiding van voedselzoekende steltlopers in relatie tot abiotische factoren, voedsel en soortgenoten. Dit onderzoek is theoretisch, empirisch en statistisch van aard. Het empirische onderzoek heeft plaatsgevonden in het Nederlandse deel van de Waddenzee en in de experimentele voorziening (wadunit) van het Nederlands Instituut voor Zeeonderzoek (NIOZ). Een kleiner deel is gewijd aan de mechanismen die ten grondslag liggen aan de verspreiding en dichtheid van zeegras op wadplaten in de Banc d'Arguin, Mauretanië.

Er zijn twee verbindende elementen tussen de twee ogenschijnlijk verschillende thema's. Ten eerste, zeegras heeft belangrijke effecten op de aanwezigheid en de dichtheid van voedsel voor steltlopers. Ten tweede zijn er conceptuele en methodologische overeenkomsten bij de bestudering van beide ecosystemen die voortvloeien uit het feit dat bij beide systemen endogeniteit en zelforganisatie een belangrijke rol spelen. Meer in het bijzonder, het gedrag van steltlopers, zoals de keuze van foerageer locaties, hangt mede af van het gedrag van soortgenoten, terwijl de groei en dichtheid van zeegras op een bepaalde locatie medebepaald worden door de eigen dichtheid via de effecten op sedimentatie en erosie.

In deze samenvatting behandel ik eerst de hoofdstukken over de ruimtelijke verspreidingen van foeragerende steltlopers en vervolgens het hoofdstuk over zeegras – sediment interactie.

Ruimtelijke verspreidingen van sociaal foeragerende steltlopers

Ecologie is de wetenschap die zich bezig houdt met de verklaring en voorspelling van aantallen en verspreiding van organismen in ecosystemen. Gedragsecologie is de tak van de ecologie die zich richt op het gedrag van dieren waarbij de ecologische en evolutionaire context centraal staat. Om patronen in de verspreiding van (sociaal) foeragerende steltlopers te analyseren heb ik in dit proefschrift voor een gedrags-ecologische benadering gekozen. De hoofdstukken over de ruimtelijke verspreiding van steltlopers zijn gebaseerd op de volgende uitgangspunten en overwegingen.

Hoewel er in intergetijde ecosystemen doorgaans sprake is van een beperkt aantal zeer rijke voedselrijke locaties, is het niet efficiënt om met veel soortgenoten tegelijkertijd op deze locaties te foerageren. De reden is dat het gebrek aan ruimte interferentie tussen fouragerende soortgenoten teweeg brengt

waardoor de foerageersnelheid lager komt te liggen dan op minder voedselrijke rijke plekken met een kleiner aantal concurrerende soortgenoten. Het fenomeen dat foerageersnelheid afneemt ten gevolge van de aanwezigheid van en competitie met soortgenoten, onafhankelijk van voedsel depletie, wordt interferentie competitie genoemd. Indien steltlopers perfecte kennis zouden hebben van de ruimtelijke verdeling van voedsel (d.w.z. zouden weten hoeveel voedsel er op de verschillende locaties aanwezig is), van de ruimtelijke verdeling van hun foeragerende soortgenoten en de kosten van verplaatsing verwaarloosbaar zouden zijn, dan zouden de foeragerende individuen zich zodanig verdelen dat allen de hoogst mogelijke voedselopname zouden hebben. De verdeling die zo ontstaat, wordt de Ideaal Vrije Verdeling genoemd (Ideal Free Distribution (IFD) in het Engels). Dit eenvoudige concept is eind jaren 60 bedacht en gespecificeerd door Fretwell en Lucas (1969) en is sindsdien theoretisch nader uitgewerkt en met wisselend succes toegepast op allerlei locatiekeuze- en verspreidingsvraagstukken. Een belangrijke aanname in het IFD concept is dat de geschiktheid van een locatie afneemt met het aantal individuen dat gebruik maakt van die locatie.

Hoewel het IFD concept een belangrijke plaats inneemt in de gedragsecologie, schiet het ernstig tekort doordat het voorbij gaat aan het feit dat er ook belangrijke voordelen verbonden kunnen zijn aan de aanwezigheid van soortgenoten. Een theorie die met zowel de voor- als nadelen van de aanwezigheid van soortgenoten rekening houdt is de sociale foerageertheorie (Giraldeau & Caraco 2000; Krause & Ruxton 2002). Deze theorie gaat er van uit dat foerageren in de nabijheid van soortgenoten het risico verlaagt om zelf ten prooi te vallen. Een ander uitgangspunt van deze theorie is dat de aanwezigheid van foeragerende soortgenoten informatie verschaft over de aanwezigheid van voedsel en afwezigheid van predatoren.

De informatie functie is van groot belang voor steltlopers omdat zij op het ritme van het getij gedurende elke laagwater periode opnieuw geschikte foerageerlocaties moeten vinden. Aangezien de benthische prooien van steltlopers in het sediment ingegraven zijn, is het moeilijk om informatie over de verspreiding ervan te verkrijgen. In een dergelijke situatie verschaft de aanwezigheid van foeragerende soortgenoten belangrijke informatie over de aanwezigheid van prooien. Kortom, interacties met soortgenoten maakt het mogelijk voor individuele steltlopers om hun cognitieve en perceptuele beperkingen te compenseren waardoor sneller en/of meer accurate beslissingen genomen kunnen worden.

De voor- en nadelen van de aanwezigheid van soortgenoten hangen af van de afstand tussen de individuen. Op korte afstanden overheersen de kosten ten gevolge van interferentie, terwijl op grotere afstand de voordelen overheersen vanwege reductie van de zoekkosten naar voedsel en van predatie gevaar. Dit betekent dat er sprake is van een optimalisatievraagstuk in de vorm van een uitruil tussen de kosten en baten van foerageren in de nabijheid van soortgenoten.

De uitruil van afstandsafhankelijke kosten en baten resulteert in aantrekking en afstoting tussen soortgenoten. Omdat steltlopers forageren op weidse open wadplaten kunnen zij de nadelen van concurrentie reduceren door afstand tot elkaar te houden. Tegelijkertijd kunnen zij de voordelen van sociaal forageren behouden door bij elkaar in de buurt te blijven. De meeste soorten wadvogels leven dan ook in groepen die per soort variëren in dichtheid (mate van clustering).

Hierboven heb ik gesteld dat de ruimtelijke verspreiding van foragerende steltlopers afhangt van voedsel dichtheid en habitat karakteristieken en van de mate van zelf-organisatie (het netto effect van de uitruil van kosten en baten). Het doel van het eerste deel van het proefschrift is om inzicht te verkrijgen in het belang van zelf-organisatie voor foragerende steltlopers door hun verspreidingspatronen te analyseren.

In **hoofdstuk 2** hebben we op landschaps niveau (23 wadplaten in de Nederlandse Waddenzee) de forageerdichtheid onderzocht van zes algemeen voorkomende soorten steltlopers, die variëren qua clustering. We registreerden op gedetailleerde kaarten voor ieder van de zes soorten de forageer verspreidingen. Tevens werd de beschikbaarheid van voedsel en de afstand van iedere forageerlocatie tot de dichtstbijzijnde hoogwater vluchtplaats bepaald. Verder hebben we een maat voor clustering ontwikkeld, die afhangt van interferentie gevoeligheid en aantrekking tussen individuen (sociale attractie). We hebben gevonden dat soorten die ongevoelig zijn voor interferentie ('sociale' soorten), zoals de kanoet en bonte strandloper, meer geclusterd forageren dan interferentie gevoelige soorten ('solitaire' soorten), zoals de wulp, scholekster en zilverplevier. Tevens hebben we forageerdichtheid geregresseerd op de beschikbaarheid van voedsel en afstand tot de dichtstbijzijnde hoogwatervluchtplaats. De uitkomst van deze regressieanalyse was dat voedsel en/of habitat betere verklaringen en voorspellingen van forageerdichtheid geven voor solitaire soorten dan voor sociale soorten. Dit hoofdstuk onderstreept het belang van modellen en monitoringsprogrammas waarin zelf-organisatie expliciet wordt meegenomen.

In **hoofdstuk 3** hebben we een klassiek interferentie-forageer model geïntegreerd met een sociaal attractie model. Met behulp van simulaties hebben we de kenmerken van forageerlocaties en –forageerdichtheden onderzocht en een ruimtelijk autoregressief model getest om sociale attractie en interferentie te schatten. Daartoe hebben we voedsel landschappen met variërende ruimtelijke afhankelijkheid gesimuleerd. Met behulp van het geïntegreerde forageer model hebben we verspreidingen van foragerende individuen in de voedsel landschappen gegenereerd. De verspreidingen varieerden van volledig voedsel gedreven tot verspreidingen waarin sociale attractie domineerde. De typen verspreidingen correspondeerden goed met patronen van foragerende steltlopers

die in de Waddenzee zijn geobserveerd. De simulaties lieten zien dat wanneer individuen geen perfecte informatie hebben over de verspreiding van het voedsel en wanneer sociale attractie sterk is, de plaatskeuze van groepen individuen sterk kan variëren.

Wanneer de aanwezigheid van individuen op een bepaalde locatie het aantal individuen op andere locaties beïnvloedt en omgekeerd, ontstaat endogeniteit. Dit heeft gevolgen voor een regressiemodel dat het aantal individuen op een bepaalde locatie (mede) verklaart uit het aantal individuen op andere locaties. In dit geval geldt dat de gebruikelijke OLS schatter van de regressiecoëfficiënten vertekend en inconsistent is. Om dit probleem op te lossen hebben we gebruik gemaakt van ruimtelijke maximum likelihood autoregressieve modellen. We hebben aangetoond dat de ruimtelijke autoregressie coëfficiënt (dat wil zeggen, de coëfficiënt van de ruimtelijk vertraagde afhankelijke variabele) in dergelijke modellen het effect van zelf-organisatie weergeeft. Op basis van de gesimuleerde data hebben we verder onderzocht hoe en onder welke condities de afzonderlijke effecten van interferentie en inter-individuele aantrekking geschat kunnen worden. Tot slot hebben we aangetoond dat met de ruimtelijke multiplier, die een functie is van de autoregressie coëfficiënt, het totale effect van een exogene variabele, zoals de beschikbaarheid van voedsel, op de verspreiding van foeragerende individuen geschat kan worden.

In **hoofdstuk 4** hebben we de data uit hoofdstuk 2 geanalyseerd met behulp van ruimtelijke autoregressieve modellen, zoals we die in hoofdstuk 3 ontwikkeld en getest hebben. Echter in plaats van de data te aggregeren op landschapsniveau (zoals in hoofdstuk 2) hebben we in dit hoofdstuk gebruik gemaakt van rasters van cellen van verschillende grootte (150 × 150, 200 × 200 and 250 × 250 m). Binnen iedere gridcel hebben we vogel- en voedseldichtheden bepaald. Naast voedsel en habitat variabelen hebben we in de regressieanalyse expliciet rekening gehouden met zelf-organisatie, gemeten als ruimtelijke afhankelijkheid tussen de cellen. Zoals in hoofdstuk 3 aangetoond, maakt deze methode het mogelijk om zowel de directe als de indirecte effecten van de beschikbaarheid van voedsel en milieu factoren op de dichtheid van steltlopers te schatten. Een belangrijke uitkomst van de analyse was dat op alle schaalniveaus en voor alle soorten zelforganisatie belangrijker is dan de exogene factoren (in termen van verklaarde variantie, bepaald aan de hand van de Nagelkerke R^2). Gemiddeld over de verschillende resoluties bleek zelf-organisatie als verklarende variabele belangrijker te zijn voor de bonte strandloper, kanoet en wulp dan voor de scholekster, zilver plevier en rosse grutto. Echter, het effect van zelf-organisatie bleek afhankelijk te zijn van het schaalniveau waarop deze geschat wordt. Verder hebben we gevonden dat de totale effecten (directe plus indirecte effecten) van de exogene factoren substantieel groter zijn dan de directe effecten.

In **hoofdstuk 5** hebben we de uitkomsten gepresenteerd van een experiment met kanoetstrandlopers dat als doel had inzicht te verschaffen in de mechanismen die ten grondslag liggen aan interferentie competitie. In de opzet van het experiment was sprake van minimale voedsel depletie om te voorkomen dat een afname in opname snelheid ten gevolge van lagere voedseldichtheid ten onrechte geïnterpreteerd zou worden als het gevolg van interferentie competitie. De belangrijkste uitkomst was dat de opname snelheid en zoek-efficiëntie afnemen met groepsgrootte en dat dominante individuen een hogere opnamesnelheid hebben dan ondergeschikte. Tevens hebben we gevonden dat de tijd besteed aan het zoeken naar voedsel toeneemt met groepsgrootte.

De afname in opnamesnelheid werd niet veroorzaakt door conventioneel interferentie gedrag (zoals het stelen van voedsel en interacties als vechten) maar vooral door het feit dat kanoeten tijd kwijt zijn aan het vermijden van fysieke interacties met soortgenoten (cryptische interferentie). Op grond hiervan hebben we geconcludeerd dat theorie en modellen rekening dienen te houden met de mogelijkheid dat dieren anticiperen op de aanwezigheid en het gedrag van soortgenoten, veelal door ze te ontwijken om fysieke interacties tevoorkomen. Een belangrijke implicatie van onze resultaten is dat de mechanistische functionele response modellen (mathematische beschrijvingen van de relaties tussen de snelheid van voedsel opname enerzijds en voedseldichtheid en aantal soortgenoten anderzijds) onvolledig zijn omdat zij geen rekening houden met anticipatie en cryptische interferentie.

Zeegras-sediment interacties

Interacties tussen twee of meer elkaar beïnvloedende ecosysteem elementen zijn doorgaans moeilijk te bestuderen omdat de gevolgen van de interacties zich vaak zeer langzaam ontwikkelen. Kennis over dit soort systemen komt daarom vooral van conceptuele en op vereenvoudigende veronderstellingen berustende wiskundige modellen en van experimenten op kleine schaal waarin een deel van de processen constant zijn of gecontroleerd worden. In **hoofdstuk 6** hebben we de resultaten weergegeven van ons onderzoek naar de wederzijdse beïnvloeding van zeegras en sediment in het intergetijde systeem van de Banc d'Arguin, Mauretanië. De reden dat we de interactie tussen deze systeem elementen onderzocht hebben, is dat algemeen wordt aangenomen dat zij een belangrijke rol spelen in de dynamiek en stabiliteit van intergetijde ecosystemen. We hebben een niet-recursief structurele vergelijkingen model (non-recursive structural equations model (SEM)) gebruikt om de wederzijdse afhankelijkheid tussen zeegras en sediment te analyseren. Dit type SEM maakt het mogelijk om terugkoppelingen (feedbacks) te schatten, waarbij gecontro-

leerd wordt voor de effecten van nutriënten en van abiotische stress ten gevolge van golven en stroming. We hebben een negatieve terugkoppeling gevonden tussen zeegras dichtheid en korrelgrootte van het sediment. We vonden ook dat de dichtheid van zeegras toeneemt met de concentratie aan organisch materiaal in het sediment, echter tot een drempelwaarde waarna de dichtheid afneemt. Zeegras vangt fijn sediment in wat een negatief effect heeft op zeegras doordat er anoxische omstandigheden ontstaan wat de concentratie van het giftige sulfide verhoogt. De resultaten impliceren dat zeegras de eigen omgeving controleert en daarmee de eigen groei reguleert.

Synthese

Hoofdstuk 7 sluit het proefschrift af met een synthese van de voorgaande hoofdstukken en suggesties voor verder onderzoek. Het beschouwt eerst de bruikbaarheid van ruimtelijk autoregressieve modellen en SEM voor het modelleren van ecologische systemen waarin endogene processen een rol spelen. Om de ontwikkeling van ecologische systemen te modelleren wordt veelal gebruik gemaakt van modellen die weergeven hoe de staat en het gedrag van het systeem op een bepaald tijdstip volgen uit voorgaande toestanden en uit ontwikkelingsprocessen. Empirisch vertaalt zich dit meestal in de analyse van tijdreeksen. Echter, in zelf-organiserende ecologische systemen wordt dit type analyse bemoeilijkt doordat processen langzaam verlopen en historische ontwikkelingen vaak niet bekend zijn. In de voorgaande hoofdstukken hebben we aangetoond dat analyse van cross sectie data met ruimtelijke autoregressieve modellen en niet-recursieve structurele modellen een alternatief bieden om inzicht te krijgen in de (vaak onzichtbare) ecologische processen. In dit verband heb ik tevens gesuggereerd om een koppeling te maken tussen enerzijds SEM met latente variabelen (bestaande uit een structureel model in termen van latente variabelen en een meetmodel voor latente variabelen) en anderzijds ruimtelijke autoregressieve modellen teneinde de analyses in hoofdstuk 4 te verfijnen, vooral om het multicollineariteit probleem te ondervangen.

Het proefschrift heeft duidelijk gemaakt wat de beperkingen zijn van de huidige verspreidingsmodellen voor sociaal foeragerende dieren. Zo is een belangrijke beperking de onvolledige modellering van de (complexe) interacties tussen individuen. In **hoofdstuk 7** beschrijf ik de uitgangspunten van een model waarmee mogelijkerwijs realistischer en meer accurate verspreidingsmodellen te ontwikkelen zijn. Ik sluit me hierbij aan bij de ideeën van McNamara en Houston (2009) en Sumpter (2010) die pleiten voor een sterkere integratie van gedrag, evolutie en ecologie. Het vertrekpunt is dat individueel gedrag voortkomt uit de emoties of de psychosomatische staat van een individu. Emo-

ties ontwikkelen zich onder invloed van verschillende externe prikkels (zoals de aanwezigheid van voedsel, soortgenoten, predatoren), interne stimuli (zoals honger) en ervaring en geheugen. Emotie is daarom de resultante van de integratie van interne en externe factoren en is daarmee een robuuste catalysator van motivatie en gedrag. De interne 'algoritmen' of gedragsregels die de vertaling van stimuli tot emoties, emoties tot motivatie en motivatie tot gedrag bepalen, kunnen zodanig evolueren dat op termijn in veel situaties rationeel en optimaal gedrag ontstaat. Aangezien het forageer gedrag van sociale soorten afhangt van het gedrag van andere individuen, ligt het voor de hand om gebruik te maken van zogenaamde agent-based modellen waarin individuen een "staat van honger" en geheugen hebben en anticiperen op het gedrag van soortgenoten (bijvoorbeeld soortgenoten uit de weg gaan). Hoewel dit type van modellen snel complex kan worden zijn er niettemin belangrijke voordelen aan verbonden. Zo kunnen model parameters bepaald worden met behulp van experimenten in combinatie met fysiologische metingen. De modellen kunnen vervolgens in experimenten nader getoetst worden en vervolgens gebruikt worden om ruimtelijke verspreidingen te analyseren. Het belangrijkste argument om dit type modellen te ontwikkelen is de mogelijkheid om op realistische wijze op te kunnen schalen van het gedrag van individuen naar het gedrag van groepen.

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