Untying the knot

Mechanistically understanding the interactions between social foragers and their prey

Allert I. Bijleveld

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Mechanistically understanding the interactions between social foragers and their prey

Royal Netherlands Institute for Sea Research

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Promotor
Prof. dr. T. Piersma

Copromotor
Dr. J.A. van Gils

Beoordelingscommissie
Prof. dr. F.J. Weissing
Prof. dr. A.M. de Roos
Prof. dr. J.M. Fryxell

to R

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The Blind Men and the Elephant: A Hindoo Fable

John Godfrey Saxe (1872)

It was six men of Indostan
To learning much inclined,
Who went to see the Elephant
(Though all of them were blind),
That each by observation
Might satisfy his mind

The *First* approached the Elephant,
And happening to fall
Against his broad and sturdy side,
At once began to bawl:
“God bless me! but the Elephant
Is very like a wall!”

The *Second*, feeling of the tusk,
Cried, “Ho! what have we here
So very round and smooth and sharp?
To me ’tis mighty clear
This wonder of an Elephant
Is very like a spear!”

The *Third* approached the animal,
And happening to take
The squirming trunk within his hands,
Thus boldly up and spake:
“I see,” quoth he, “the Elephant
Is very like a snake!”

The *Fourth* reached out an eager hand,
And felt about the knee.
“What most this wondrous beast is like
Is mighty plain,” quoth he:
” ‘Tis clear enough the Elephant
Is very like a tree!”

The *Fifth*, who chanced to touch the ear,
Said: “E’en the blindest man
Can tell what this resembles most;
Deny the fact who can
This marvel of an Elephant
Is very like a fan!”

The *Sixth* no sooner had begun
About the beast to grope,
Than, seizing on the swinging tail
That fell within his scope,
“I see,” quoth he, “the Elephant
Is very like a rope!”

And so these men of Indostan
Disputed loud and long,
Each in his own opinion
Exceeding stiff and strong,
Though each was partly in the right,
And all were in the wrong!

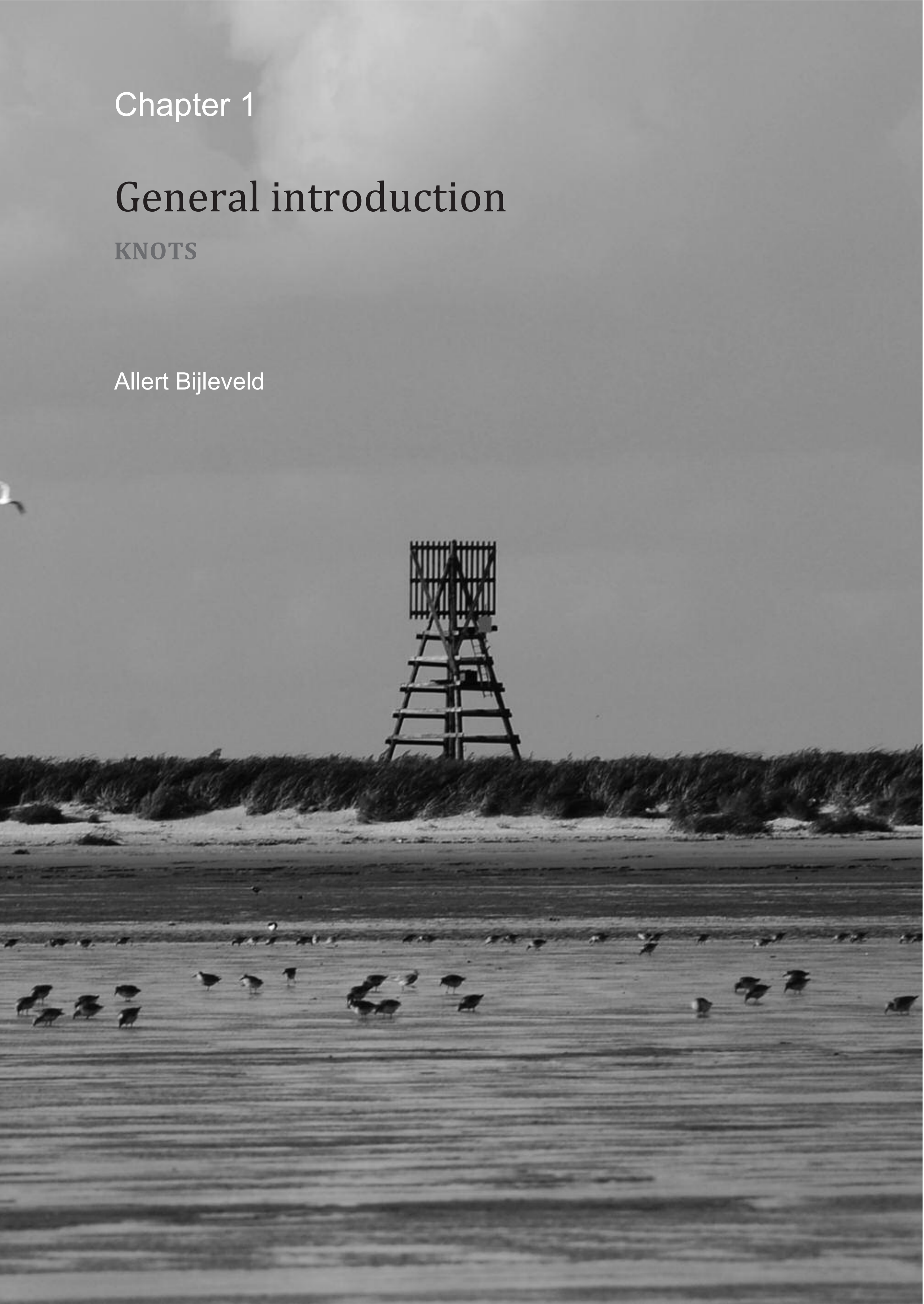
So oft in theologic wars,
The disputants, I ween,
Rail on in utter ignorance
Of what each other mean,
And prate about an Elephant
Not one of them has seen!

Chapter 1

General introduction

KNOTS

Allert Bijleveld



KNOTS – PART I

Walking the mudflats of the Dutch Wadden Sea fuels one's fascination for nature. Twice a day, vast areas of mudflat are exposed for a few hours. In this short time-window, many thousands of birds need to find food to survive. Most birds feed on small worms and shellfish that live buried in mudflats that, at first glance, appear to show little variation. Only when one digs in the mud, one realises that some parts of the mudflats contain much more food than others. Likewise, on some mudflats birds clump together in flocks of several thousand individuals, while on others a handful of birds are widely spread out. This makes one wonder how the birds find their scattered and concealed food on mudflats that look so uniform. Do they use each other to find food? Are some individuals more successful in finding their prey than others? Why did they choose to forage there, and not elsewhere?

Questions like these highlight the focus of my thesis and are fundamental to ecologists, scientists that study the interactions between organisms and their environment. I will stand on the shoulders of giants (Table 1.1) and continue three decades of research on red knots *Calidris canutus islandica* (Fig. 1.1, hereafter called knots) in an effort to identify and untie the mechanisms that drive their foraging decisions and spatial distributions in the field. Even though this research mainly concerns knots, the mechanistic understanding that we pursue is certainly not limited to this single species. In fact, knots serve as a model

Table 1.1 The shoulders of giants that I stand on. This Table shows the different PhD students and theses on knots and their prey, which have been defended at the University of Groningen.

Year	Auteur	Title
1994	Theunis Piersma	Close to the edge: energetic bottlenecks and the evolution of migratory pathways in knots
1997	Leo Zwarts	Waders and their estuarine food supplies
2004	Jan A. van Gils	Foraging decisions in a digestively constrained long-distance migrant, the red knot (*Calidris canutus*)
2006	Wouter K. Vahl	Interference competition among foraging waders
2007	Jeroen Reneerkens	Functional aspects of seasonal variation in preen wax composition of sandpipers (Scolopacidae)
2008	Deborah M. Buehler	Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants
2010	Casper Kraan	Spatial ecology of intertidal macrobenthic fauna in a changing Wadden Sea
2010	Piet J. van den Hout	Struggle for safety: adaptive responses of wintering waders to their avian predators
2011	Jutta Leyrer	Being at the right place at the right time: interpreting the annual life cycle of Afro-Siberian red knots
2012	Eelke O. Folmer	Self-organization on mudflats
2013	Matthijs van der Geest	Multi-trophic interactions within the seagrass beds of Banc d'Arguin, Mauritania: a chemosynthesis-based intertidal ecosystem

Figure 1.1 Group of foraging knots (*Calidris canutus islandica*) on intertidal mudflats in the Dutch Wadden Sea. Note that some birds have found a cockle (*Cerastoderma edule*) that they are about to swallow whole. Photo courtesy by Jan van de Kam.

allowing us to understand principles that are commonly found in nature, including human nature. Such an understanding is of general interest from a basic scientific perspective (the intrinsic value of understanding the world around us), as well as from an applied science or conservation perspective. Especially in light of a rapidly changing world (e.g., due to climate change, land reclamations, natural resource extraction, etc.), the need for nature conservation managers to predict animal spatial distributions is growing, which requires an understanding of species distributions.

FORAGING THEORY

Foraging theory is central to ecology and has been studied and refined over many decades (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Charnov 1976, Pyke et al. 1977, Clark and Mangel 1984, Lima 1985, Mangel and Clark 1986, Stephens and Krebs 1986, Krebs 2001, Stephens et al. 2007). A forager's survival and reproductive success (fitness) will depend on how well they can acquire food (energy and nutrients). Food intake rate is, therefore, often assumed to be correlated with fitness (Kacelnik et al. 1992). Foraging theory has provided a deep understanding of how forager's decide what to eat, where to eat it, and when to look somewhere else to feed. At the base of foraging theory is the functional response that describes a forager's intake rate as a function of prey density

(Holling 1959). The exact shape of the functional response depends on how searching and handling time limit intake rate. The most widespread is the 'type II' functional response (Fig. 1.2) that shows a decelerating increase in intake rate to a plateau that is set by handling time, i.e. at high prey densities foragers almost immediately find their prey and are continuously handling them.

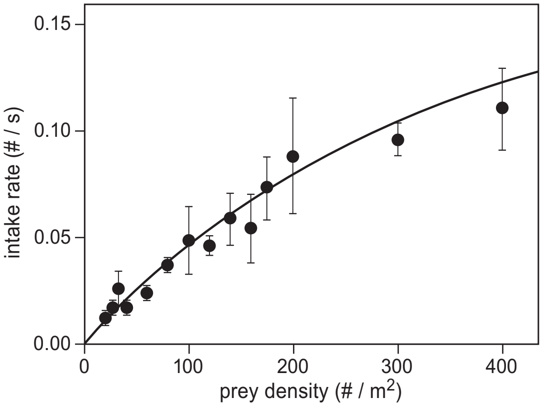


Figure 1.2 The functional response of knots feeding on Balthic tellins (*Macoma balthica*) and edible cockles (*Cerastoderma edule*). These data were gathered from captive knots in controlled experiments (Piersma et al. 1995), and pooled for both prey species as the functional response parameters were indistinguishable. The dots represent means and bars represent standard errors. The solid line represents Holling's disc equation: $IR = a \times N / (1 + a \times N \times T_h)$, where a forager's predicted numerical intake rate is given by IR (n s^{-1}), searching efficiency or area of discovery by a (5.7 cm^2 s^{-1}), prey density by N (n m^{-2}), and prey handling time by T_h (3.8 s). We reproduced this graph from van Gils (2004, Box II).

PREDICTING SPATIAL FORAGING DISTRIBUTIONS

Prey are often distributed in patches where prey density is higher than the surrounding area (Kraan et al. 2009a). Assuming that animals aim to maximize intake rate (fitness), one would expect foragers to aggregate in those patches with the highest prey densities (Sutherland 1983, Tregenza 1995). Clearly, predators are found much more spread out, and the question is why not all foragers are found in the patch with the highest prey density? As predators aggregate they increasingly interfere with each other, which decreases their intake rate (Goss-Custard 1980, Johnson et al. 2004, Vahl et al. 2005b, Smallegange et al. 2006). When predators aggregate even more, their intake rate drops below the intake rate that they could acquire on a different patch with lower food density but also with less competition (Fig. 1.3). Ultimately, foragers will distribute themselves in such a way that they all experience a similar intake rate, i.e. they obey what is known as the 'ideal free distribution' (Fretwell and Lucas 1970). Ideal-free distributions are null-models that are built on simplifying (and hence usually unrealistic) assumptions. For

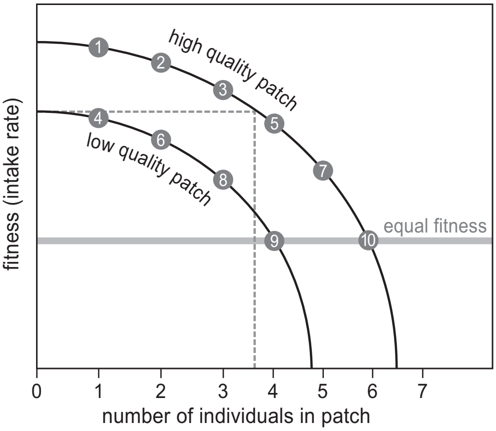


Figure 1.3 The 'ideal free distribution'. The two solid curves represent two food patches, one of low and one of high quality in terms of intake rates. The numbers in grey circles indicate the order in which 10 foragers will choose between patches. Foragers are expected to go to the patch that maximises their intake rate (fitness). They will, therefore, first go to the high quality patch. As the group size of foragers increases, their intake rate will decrease. At a group size of between 3 and 4 foragers, the intake rate in the high quality patch drops below that of the low quality patch (without foragers). The fourth forager will therefore go to the low quality patch where its interference-free intake rate will be highest at that time, and so forth. Finally, six foragers will gather on the high quality patch and four on the low quality patch; all of them with the same intake rate (as indicated by the horizontal grey bar).

instance, foragers are assumed to have perfect knowledge about the possible intake rates across all patches that are available to them, and to incur no costs for moving between patches. Nevertheless, such null-hypotheses help us understand spatial distributions (Sutherland 1983, Parker and Sutherland 1986, Bautista et al. 1995, Sutherland 1996, van der Meer and Ens 1997, van Gils et al. 2006b).

BENEFITS OF SOCIALITY

As discussed above, a main cost of foraging in groups is competition for resources. Group foraging (social foraging) is beneficial as well and animals are often attracted to each other (Folmer et al. 2012). The benefits of group foraging include increased safety in numbers (Pulliam 1973), increased time that could be spent foraging rather than on anti-predation vigilance (Lima 1995), and the accessibility of foraging information (Clark and Mangel 1984, Valone 1989, Danchin et al. 2004, Dall et al. 2005, Valone 2007, Giraldeau and Dubois 2008). Animals face tremendous uncertainty in nature. Information gained from others can help individuals make more accurate and faster estimates of patch resource density (Clark and Mangel 1984, 1986, Valone 1989), which allows foragers to maximise their intake rate by wasting less time in unprofitable patches (Charnov 1976, Templeton and Giraldeau 1996, Smith et al. 1999, van Gils et al. 2003b). Information from others can also indicate the location of food (local enhancement, Thorpe 1956, Pöysä 1992). Many different species use local enhancement to select where to eat (Galef and Giraldeau 2001), which is especially beneficial when food is clumped and patches are large enough not to be monopolized (Beauchamp 1998); if patches are small, dominant foragers can exploit food discoveries of subordinates (Vahl and Kingma 2007).

INDIVIDUAL VARIATION

Within species and populations, individuals differ in their behaviour, which can affect foraging decisions that drive spatial distributions (Parker and Sutherland 1986). Based on foraging theory there should, however, be one optimal foraging decision that maximises intake rate and thus fitness (Stephens and Krebs 1986). The observed between-individual variation in foraging behaviour was often seen as noise around an animal's calculated optimal behaviour, i.e. 'the raw material on which natural selection acts, rather than as the end product of natural selection' (Wilson 1998). However, individuals of many species have been shown to vary consistently in their behaviour across contexts, yielding the notion of 'animal personalities' (Koolhaas et al. 1999, Gosling 2001, Dall et al. 2004, Sih et al. 2004a, Sih et al. 2004b, Réale et al. 2007, Carere and Maestripieri 2013). An animal's personality is commonly quantified on the basis of standardized measurements of aggressiveness, boldness, exploration, sociability and activity (Réale et al. 2007). These personality traits have been shown to relate to ecologically relevant traits such as social dominance (Armitage and Van Vuren 2003, Dingemanse and de Goede 2004), risk-taking (Bell 2005, Bell and Sih 2007), social information use (Kurvers et al. 2010b), habitat use (Boon et al. 2008, Minderman et al. 2010, van Overveld and Matthysen 2010), and foraging behaviour (Wilson and McLaughlin 2007). Only recently, animal personality research has become firmly grounded in evolutionary ecology and life-history theory (Réale et al. 2007, Stamps 2007, Wolf et al. 2007, Biro and Stamps 2008, Careau et al. 2008, Réale et al. 2010a, Réale et al. 2010b, Wolf and Weissing 2010, Dall et al. 2012, Wolf and McNamara 2012). Nonetheless, the evolutionary origin and maintenance of phenotypic variation in animal personality is still intensely debated (Dingemanse and Réale 2005, Dingemanse and Wolf 2010, Dall et al. 2012, Wolf and McNamara 2012).

KNOTS – PART II

Knots are migratory shorebirds (Fig. 1.4) that breed on large territories in High-Arctic tundras between June and July (Davidson and Wilson 1992, Piersma 2007). During the non-breeding season they live in tidal areas of Western Europe (Piersma 2007, Quaintenne et al. 2010, Piersma 2012). Around high tide, they aggregate (roost) on exposed areas in large and dense flocks (Piersma et al. 1993a). Around low tide, they search for food in large groups of up to several thousand individuals (Piersma et al. 1993a). Over short time-scales (weeks) their foraging locations tend to be unpredictable,

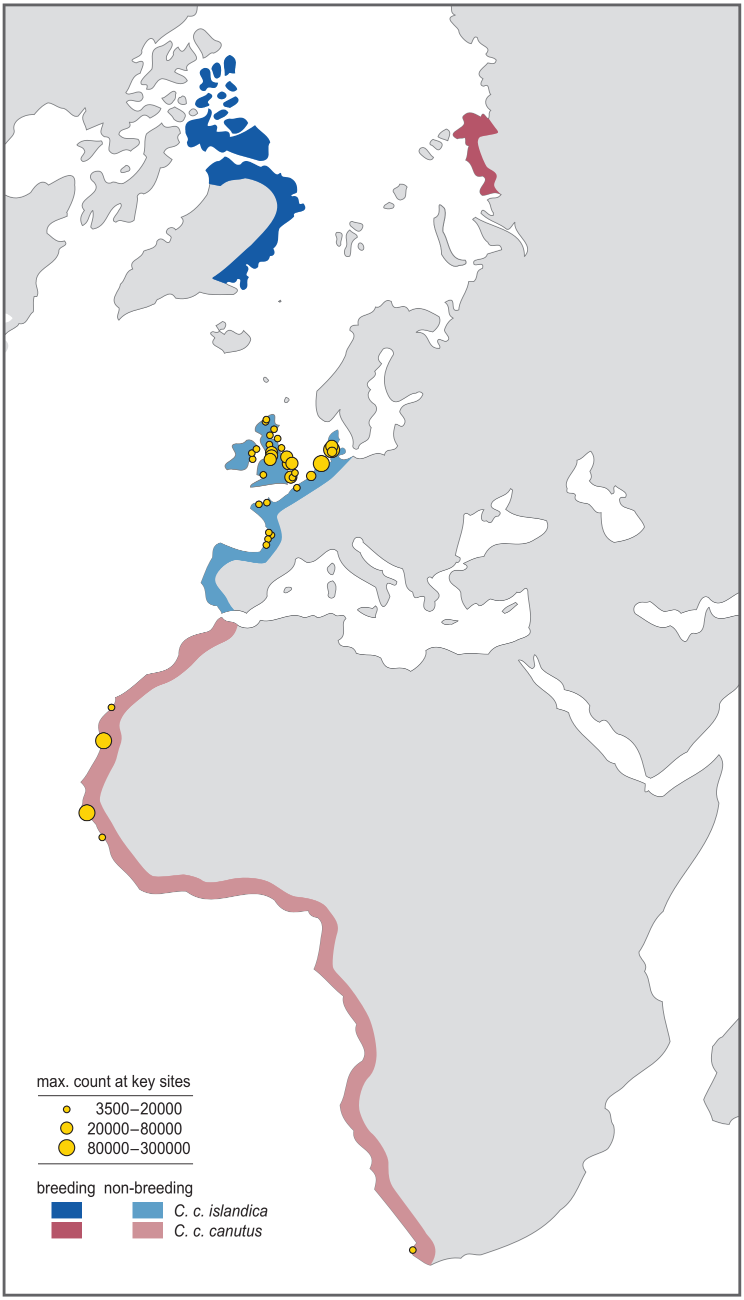


Figure 1.4 Spatial distribution of two subspecies of knots: *Calidris canutus canutus* and *islandica*. The *canutus* subspecies can be found in the Dutch Wadden Sea during periods of migration between their breeding sites in Siberia and their overwintering sites in Africa. The *islandica* subspecies breeds in Greenland and Canada and overwinters in mudflats across Western Europe, including the Dutch Wadden Sea. The work that we present in my thesis focusses on the *islandica* subspecies. This figure was reproduced from Davidson and Piersma (2009).

which is attributed to their strong social attraction (Folmer et al. 2010), mobility (van Gils et al. 2005b), and the large spatial extent of foraging opportunities (Kraan et al. 2009a). Within each low-tide period, knots fly tens of kilometres across exposed mudflats in search of buried hard-shelled molluscs, such as Baltic tellins *Macoma balthica* and edible cockles *Cerastoderma edule* (Zwarts and Blomert 1992, Piersma et al. 1993a, van Gils et al. 2005b). Knots have pressure sensitive organs in the tip of their bill, which enable them, by repeatedly inserting their bill in soft wet sediments, to remotely touch-sense hard-shelled prey over a distance of several cm (Piersma et al. 1998). When found, knots swallow their prey whole and are, therefore, limited to ingesting prey smaller than 16-18 mm (Zwarts and Blomert 1992, Piersma et al. 1993a). To crush the shells, they require a strong muscular stomach that is known as a gizzard (van Gils et al. 2003a, Battley and Piersma 2005). With an ultrasound scanner, gizzard mass can be measured in living birds (Dietz et al. 1999, Dekinga et al. 2001). Under controlled experimental conditions, gizzard mass was found to be flexible within individuals and changes in response to the ratio of flesh to shell mass of their prey (prey quality). The size of the gizzard sets an upper limit to the amount of shell mass that can be processed and thus limits daily intake rates (van Gils et al. 2003a). The lower the prey quality, the larger the gizzard must be to process the ballast shell material necessary to uphold their required energy intake rates.

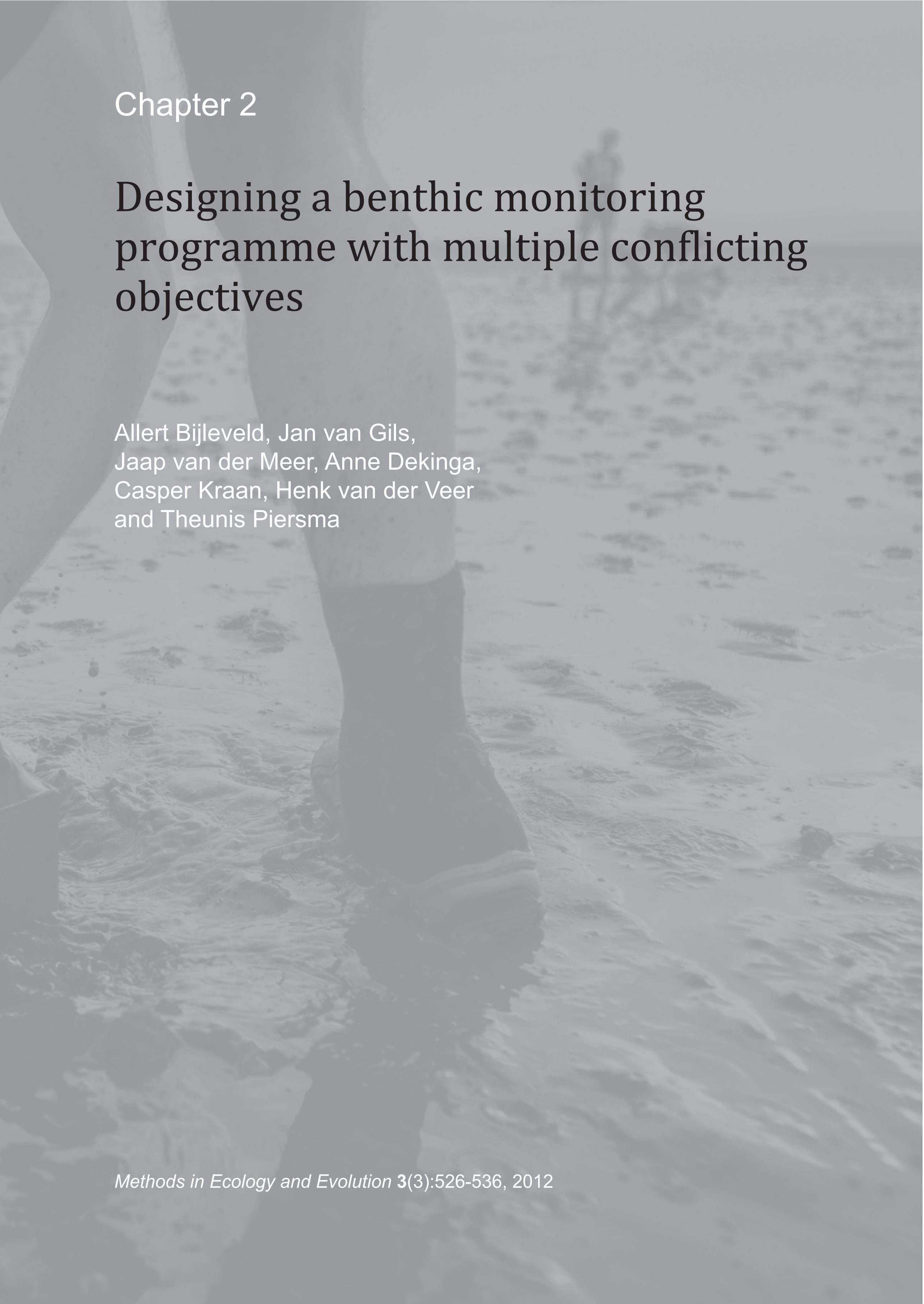
THESIS OUTLINE

My thesis is divided into four sections. In the first section we develop methodology that we build on subsequently. Monitoring programmes can have multiple objectives with conflicting demands on the optimal sampling design. In **Chapter 2**, we develop a novel sampling method that allows for estimating temporal and spatial changes, as well as accurately mapping macrobenthic prey densities on intertidal mudflats. In order to track the small-bodied knots at fine spatial and temporal scales across nonbreeding habitats, in **Chapter 3** we report on the development of a novel light-weight tracking method. In the second section we untie the effects of sociality on the foraging behaviour of knots. In **Chapter 4**, we first show the costs of social foraging, which differ between dominant and subordinate knots. Then we investigate the information benefits of social foraging. In **Chapter 5**, we dust-off the controversial information-centre hypothesis from the 1970s and show how knots could use high-tide roosts to gain inadvertent information on where, on what and with whom to forage. In **Chapter 6**, we show that knots indeed use the foraging success of their flock mates to decide where to forage and that social foraging increases their foraging efficiency proportional to flock size. We also show that knots consistently differ in the effort they put into searching for food patches and that some individuals readily and consistently exploit the searching effort of their flock mates.

This leads up to the third section of my thesis in which we show how individual variation in both predators and prey is crucial for understanding foraging decisions and distributions. In **Chapter 7**, we experimentally establish that knots have personalities. They consistently differ in their exploratory behaviour; some readily explore a novel environment while others are more sedentary. We also show how variation in exploratory behaviour drives variation in gizzard mass and explained their spatial distribution in the wild. Then, in **Chapter 8**, we switch from the predator's perspective to that of the prey and show the effect that predation by knots has on the density, length, and body composition of cockles and discuss their potential for adaptive anti-predation responses. In **Chapter 9**, we illustrate that due to negative density-dependence among cockles, knots are faced with a trade-off between prey quantity and quality. Opposing the common notion that predators achieve the highest intake rate at the highest prey densities, we predicted that knots would achieve the largest intake rates at intermediate prey densities. By sampling prey quantity and quality and tracking the spatial distributions of knots in the wild, we indeed show that knots selected locations with intermediate prey densities. I conclude my thesis with the fourth section that contains **Chapter 10**. Here, I highlight some of our findings that I discuss in a broader context and suggest avenues for future research.

Section I

Methodology



Chapter 2

Designing a benthic monitoring programme with multiple conflicting objectives

Allert Bijleveld, Jan van Gils,
Jaap van der Meer, Anne Dekinga,
Casper Kraan, Henk van der Veer
and Theunis Piersma

Methods in Ecology and Evolution **3**(3):526-536, 2012

SUMMARY Sound conservation and management advice usually requires spatial data on animal and plant abundances. The expense of programmes to determine species distributions and estimates of population sizes often limits sample size. To maximize effectiveness at minimal costs, optimizations of such monitoring efforts are critical. A monitoring programme can have multiple objectives with demands on the optimal sampling design that are often in conflict. Here we develop an optimal sampling design for monitoring programmes with conflicting objectives, building on an existing intertidal benthic monitoring programme in the Dutch Wadden Sea and simulation models bounded in their parameter spaces by these data. We distinguish three possible objectives: (1) estimation of temporal changes and spatial differences in abundance, and (2) mapping, i.e. prediction of abundances at unsampled locations. Mapping abundances requires model-based analyses using autocorrelation models. Such analyses are as good as the model fits the data; therefore, the final objective was (3) accurately estimating model autocorrelation parameters. To compare sampling designs, we used the following criteria: (1) minimum detectable difference in mean between two time periods or two areas, (2) mean prediction error, and (3) estimation bias of autocorrelation parameters. Using Monte Carlo simulations we compared five sampling designs with respect to these criteria (i.e. simple random, grid, two types of transects, and grid with random replacements) at four levels of naturally occurring spatial autocorrelation. The ideal sampling design for objectives (1) and (2) was grid sampling and for objective (3) random sampling. The sampling design that catered best for all three objectives combined was grid sampling with a number of random samples placed on gridlines. Grid sampling with a number of random samples is considered an accurate and powerful tool with the highest effectiveness. This sampling design is widely applicable and allows for accurate estimates of population sizes, monitoring of population trends, comparisons of populations/trends between years or areas, modelling autocorrelation, mapping species distributions, and a mechanistic understanding of species distribution processes.

INTRODUCTION

Spatially explicit data on animal abundances comprise key data for ecologists and are essential for a sound underpinning of conservation and management plans (Underwood 1997, Krebs 2001). Collecting such data is expensive and labour intensive, and therefore monitoring programmes are practically constrained by the number of sampling units (Andrew and Mapstone 1987, Field et al. 2005). Smaller sample sizes reduce the accuracy of the estimates (e.g. total abundances), or the power to detect significant impacts (Quinn and Keough 2002). Hence, it pays selecting a sampling design that minimises the number of sampling units and maximises the accuracy of the estimates (Thompson 1992). Monitoring programmes can have multiple objectives such as describing spatial patterns and temporal trends in species abundance, or impact assessments and each objective, can have a different optimal sampling design. Optimising sampling designs between monitoring objectives that explicitly consider spatial autocorrelation has received little attention so far and is the objective of this paper.

Hitherto the ecological literature has paid much attention to designing sampling programmes aiming at detecting the impact of a specific treatment in an area (Green 1979, Underwood 1991, Stewart-Oaten et al. 1992, Underwood 1997, Stewart-Oaten and Bence 2001). So called 'beyond BACI designs' (Before-After Control-Impact) are now regarded as the most appropriate for spatial sampling for impact assessments (Underwood 1991, 1994, Schmitt and Osenberg 1996). Usually, multiple sites are sampled within an area, several locations per site, and several sampling units per location. The results are analyzed by nested ANOVA where the overall variance is allocated to different variance components according to the spatial scale of sampling. Such models are powerful for impact assessment, but they ignore spatial autocorrelation which can provide additional biological information (Sokal and Oden 1978b, Kraan et al. 2009a, Kraan et al. 2009b). As such, the monitoring of spatial autocorrelation warrants to become a monitoring objective itself.

In contrast to the nested ANOVA approach, the geostatistical literature (Diggle and Ribeiro 2007) and some of the ecological literature (Sokal and Oden 1978a, b, Legendre 1993, Keitt et al. 2002, Fortin and Dale 2005, Dormann et al. 2007), have emphasized explicitly modelling spatial autocorrelation. Usually spatial autocorrelation is modelled as a declining function of Euclidean distance between sampling units (Cliff and Ord 1981, Upton and Fingleton 1985). Hence, geostatistical approaches advocate model-based inference by estimating an underlying spatial autocorrelation model allowing for predictions at unsampled locations (i.e. mapping, Ripley 1981, Cressie 1993). Another advantage of explicitly modelling spatial autocorrelation is that this provides an understanding of the mechanisms (e.g. competition, landscape structure) underlying the observed spatial distributions (Bergström et al. 2002, Klaassen et al. 2006c, de Frutos et al. 2007, Lagos et al. 2007, Kraan et al. 2009b, van Gils 2010).

The NIOZ Royal Netherlands Institute for Sea Research maintains long-term benthic monitoring programmes for detecting temporal and spatial changes in abundance from either natural or anthropogenic causes (Piersma et al. 2001, Beukema and Dekker 2006, van Gils et al. 2006a, Dekker and Beukema 2007, Kraan et al. 2007, van Gils et al. 2009). Additionally, mapping macrobenthic invertebrates enables predictions on the spatial distribution of their predators, such as birds and fish (van Gils et al. 2005b, van Gils et al. 2006b). Currently, the NIOZ monitoring programme is limited to the western Dutch Wadden Sea, but is to be extended to cover the entire Dutch Wadden Sea for monitoring effects of gas extraction. The aim of this study is twofold. First, building on the existing benthic monitoring efforts at NIOZ, we aim to determine an optimal sampling design for monitoring programmes that have multiple conflicting objectives. Second, we apply this sampling design to the Dutch Wadden Sea. We focus on the following objectives: (1) estimation of temporal change and spatial differences in abundance between two years or two areas. Because comparisons between years or areas depend on similar analytical principles, they can be combined into one objective. (2) Predicting species abundances at unsampled locations, i.e. mapping. Such predictions, using model-based inference, are only as good as the match between the estimated model parameters and the data, and therefore an additional objective was (3) accurately estimating autocorrelation model parameters. Comparisons between sampling designs were based on: (1) the minimum detectable difference between means of two time periods or areas, (2) the mean prediction error, and (3) the estimation bias, i.e. the number of times the autocorrelation parameters were inestimable and the difference in simulated and estimated autocorrelation parameters . With respect to these criteria, we compared one novel with four regularly applied sampling designs.

METHODS

General approach

Using field data, the most parsimonious autocorrelation structure was fitted, model parameters estimated and four extreme, but realistic levels of autocorrelation selected. These autocorrelation models were then used to simulate spatially autocorrelated data with a normal distribution and according to different sampling designs compared regarding the previously mentioned criteria.

Field data

From 1996, building on a tradition of station-intensive and transect-based monitoring (Beukema 1976, Beukema and Dekker 2006, Dekker and Beukema 2007), the NIOZ has monitored population densities of macrobenthic invertebrates across 225 km^2 of intertidal mudflats in the western Dutch Wadden Sea (van der Meer 1997, Piersma et al. 2001). Between July and September each year, between 1,807 and 2,762 stations were sampled. Sample stations were arranged according to a grid sampling design with 0.25 km inter-sample distance. Sampling stations were located by handheld Global Positioning System (GPS, Garmin 60, Olathe, Kansas, U.S.A.). At each station one core (1/56 m^2) to a depth of 20-25 cm was collected, washed over a 1-mm mesh sieve and numbers of each species were counted. To allow comparisons between groups (objectives 1 and 2), the analyses were based on the difference in densities between two successive years (2005 and 2006) and restricted to the five most abundant bivalve (*Cerastoderma edule*, *Macoma balthica*, *Mya arenaria*, *Abra tenuis* and *Ensis americanus*) and polychaete species (*Scoloplos armiger*, *Heteromastus filiformis*, *Nereis diversicolor*, *Nephtys hombergii* and *Lanice conchilega*).

Statistic framework

Generalised Least Squares (GLS) methods are model-based analyses for spatially autocorrelated data, as well as for spatial predictions necessary for the three objectives. GLS are widely used in spatial statistics (Cressie 1993) and spatial ecology (Dormann et al. 2007). Spatial GLS assumes that autocorrelation (i.e. covariance) is a function of (Euclidean) distance between sampling units (Cliff and Ord 1981, Upton and Fingleton 1985), and fits a spatial autocorrelation function (SAF) to field data in order to estimate covariance between sampling units.

Autocorrelation, expressed as the commonly used Moran's I, was calculated for discrete distance classes into a correlogram (Sokal and Oden 1978a, Cliff and Ord 1981, Legendre and Fortin 1989). Several SAFs were fitted to the correlogram. The most parsimonious fit was provided by the exponential SAF (van der Meer and Leopold 1995):

$$AC(h) = \begin{cases} b_0 e^{b_1 h} & \text{if } h > 0 \\ 1 & \text{if } h = 0 \end{cases}$$

Using nonlinear least-squares, autocorrelation AC was fitted as a continuous function of distance h with b_0 being the autocorrelation for distances close to zero (local autocorrelation) and b_1 denoting the decline in autocorrelation with distance. Autocorrelation at distance zero is 1 by definition and therefore omitted for estimation of b_0 and b_1. The autocorrelation model was fitted to the distance matrix, which gives pair wise distances between sampling units, and multiplied by the variance of the response variable σ^2 to obtain an estimate of the variance-covariance matrix Σ (van der Meer and Leopold 1995).

Sampling designs

Five designs were compared: (1) simple random sampling, (2) grid sampling, (3, 4) transect sampling (with one or with five sampling units per station respectively) and (5) grid sampling with random replacements. (1) Simple random sampling is the most common sampling method in ecology (Fig. 2.1A) and often combined with stratified sampling (Armonies and Reise 2003). (2) For grid sampling, sampling stations are usually spaced in a lattice (Herman et al. 2001) and, in this study, located in the centre of a grid cell (Fig. 2.1B). (3) Transect sampling (Fig. 2.1C) consisted of transects with random starting locations and a random heading in which 9 additional stations were equally spaced (Beukema 1976, Yates et al. 1993). (4) Transect sampling with multiple sampling units is similar to transect sampling, but at each of 10 transect sampling stations an additional four sampling units were taken within 400 m2 (Beukema 1974). (5) Grid sampling with random replacements is based on the "lattice-plus-closed-pair-design" by Diggle & Lophaven (2006).

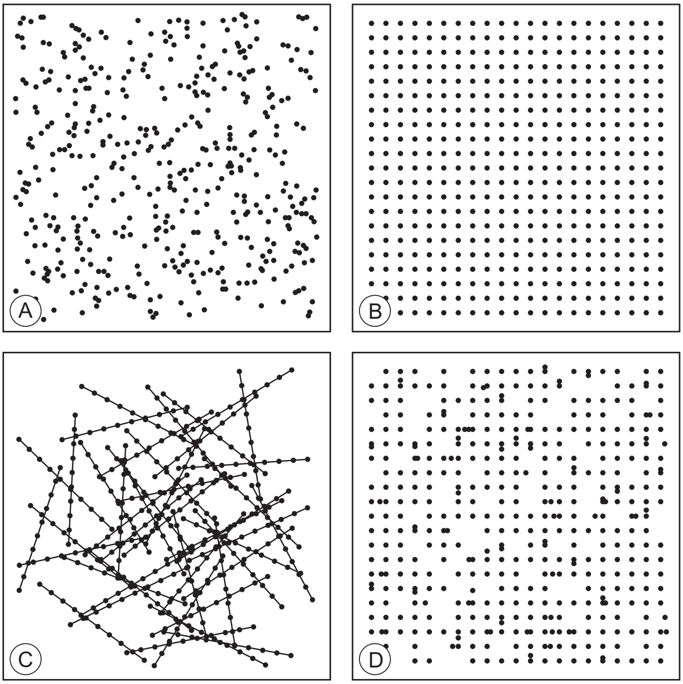


Figure 2.1 The different sampling designs compared in this study. (A) Simple random sampling, (B) grid sampling, (C) transect sampling with either one or five sampling units per station and (D) grid sampling with random replacements.

Similar to grid sampling, sampling units are equally spaced on a grid, but 10% of these stations were replaced to a random position on both a vertical and horizontal gridline (Fig. 2.1D). *Replaced* instead of added to maintain equal sample sizes for between sampling design comparison, and replaced *onto gridlines*, because sampling stations are hereby more easily located in the field than is the case for completely random locations. This reduces sampling costs while maintaining most statistical advantages of random sampling (Diggle and Lophaven 2006).

Data simulation

On a 10 x 10 km surface area, sampling stations were selected according to the different sampling designs. The distance between sampling stations was 0.25, 0.5, 0.75 and 1 km (i.e. sample sizes of 1681, 441, 196 and 121 respectively). This coincided with an expected distance between sampling units of 0.12, 0.24, 0.36 and 0.45 km for simple random sampling (Clarke and Evans 1954). At a given inter-sample distance, designs have different sample sizes. To compare power of sampling designs for each inter-sample distance, sampling designs were restrained to the sample size of grid sampling. For example, at an inter-sample distance of 1 km the sample size of grid sampling consisted of $11 \cdot 11 = 121$ sampling units. The sample size of transect sampling is a multiple of the length of one transect (i.e. 9 inter-sample distances). To maintain equal sample sizes we truncated the last transect so the total sample size equalled that of grid sampling. Sample stations were simulated on 100 km^2 plus a margin of 0.5 times the inter-sample distance. Sample stations were restricted to this area and starting locations of transects were reassigned if any sample station would reach beyond this area. Consequently, diagonal transects are more likely to occur than transects parallel to the gridlines (Fig. 2.1C). This sampling bias will be large if the area is small relative to the inter-sample distance (Thompson 1992). With an inter-sample distance of 1 km, for instance, the length of transects would measure the entire 10 km width or length of the area. This bias also occurs in the field, and as we were interested in field implications of different sampling designs, it was accepted as realistic.

The variance-covariance matrix Σ was calculated using four extreme, but naturally occurring, levels of autocorrelation. Based on field data estimates of autocorrelation parameters, we modelled either weak or strong local autocorrelation (b_0), with a shallow or steep decline in autocorrelation with distance (b_1). Spatially autocorrelated response variables were simulated for each sampling design and inter-sample distance, using Cholesky decomposition (i.e. given a symmetric positive definite matrix, the Cholesky decomposition is an upper triangular matrix with strictly positive diagonal entries such that $A = U^T U$) (Ripley 1981, Cressie 1993, Dormann et al. 2007). A weight matrix W was derived from the variance-covariance matrix $\Sigma = W^T W$, and normally distributed, spatially autocorrelated response variables were calculated by $\varepsilon = W^T \xi$ with ξ drawn from the standard normal distribution ($\mu = 0$ and $\sigma^2 = 1$).

Comparison criteria

The minimum detectable difference (MDD) between two populations (objective 1) was calculated with the standard error of the mean (se): $MDD = se \cdot (t_{\alpha,n-1} + t_{\gamma,n-1})$ and $\alpha = 0.05$ and $\gamma = 0.20$, i.e. the minimum detectable difference 80% of the time at a significance level of 0.05 (Quinn and Keough 2002). The mean and se were calculated with GLS following Cliff & Ord (1981). We calculated the variance of the mean using ordinary least squares (OLS, corresponding to GLS analyses with $b_0 = 0$ and $b_1 = 0$). With OLS variance, the fraction of independent data points in the autocorrelated sample (i.e. effective sample size n*, Griffith 2005) could be estimated by dividing OLS-variance through GLS-variance.

A common method for spatial predictions at unsampled locations is kriging (see Ripley 1981, Upton and Fingleton 1985, Cressie 1993, Haining 2003). For objective (2) we calculated the mean prediction error using ordinary kriging for which the calculations are available elsewhere (Ripley 1981, Cressie 1993, Fortin and Dale 2005, Furrer et al. 2013). To estimate the mean prediction error we randomly selected 100 locations on the 100 km^2 simulated area. For each location we calculated the prediction error and the resulting 100 prediction errors were averaged.

For objective (3) we fitted a SAF to simulated autocorrelated data at four levels of autocorrelation. We recorded how often autocorrelation parameters were inestimable and calculated the difference between simulated and estimated autocorrelation parameters, i.e. estimation bias. The SAF was fitted over 2/3 of the maximum distance between pairs of sample units and the width of distance classes was 1/3 of the inter-sample distance, hereby, the sample size per distance class was at least 10. Autocorrelation parameters were not estimable when the SAF could not be fitted or estimates of $b_0 > 2$, $b_1 > 0$ and $b_1 < -10$.

All analyses followed Monte Carlo simulations in which the above criteria were averaged over 1,000 runs. The estimation of the mean prediction error was calculated based on 200 rather than 1,000 runs, because of time consuming calculations and small Monte Carlo variance in the mean prediction error.

All calculations and simulations were performed with R v2.6 (R Development Core Team 2008) using the following packages: *PBSmapping* (Schnute et al. 2008), *ncf* (Bjornstad 2006), *spatstat* (Baddeley and Turner 2005) and *fields* (Furrer et al. 2013).

RESULTS

Field data

On the basis of 2,695 sampling stations covered both in 2005 and 2006, density differences between years could be calculated. These data, used to estimate a species correlogram, consisted of many zeros and were therefore not normally distributed. There are no transformation routines that could adequately normalize the data, but sample sizes were large enough for the effect of non-normality to be small. Moreover, many zero counts do not change the pattern of the correlogram (Bergström et al. 2002). For each species, σ^2 was estimated and b_0 and b_1 were estimated from a correlogram (Fig. 2.2A). The parameter estimates for b_0 ranged from 0.03 to 0.66 and for b_1 from –3.12 to –0.34 (Table 2.1). Depending on the level of autocorrelation, the effective sample size (percentage of independent data points, n*) ranged from 3% to 28% (Table 2.1).

Simulated data

Based on field estimates (Table 2.1), we used $b_0 = 0.1$ or $b_0 = 0.5$ and $b_1 = -0.5$ or $b_1 = -3$ (Fig. 2.2B) to simulate different levels of spatially autocorrelated normally distributed data. The combinations of autocorrelation parameters approximated *C. edule* ($b_0 = 0.32$, $b_1 = -0.76$; strong local autocorrelation, long range of autocorrelation), *A. tenuis* ($b_0 = 0.66$, $b_1 = -3.12$; strong local autocorrelation, short range), *H. filiformis* ($b_0 = 0.13$, $b_1 = -0.58$; weak local autocorrelation, long range). None of the selected species showed the combination of weak local autocorrelation and a short range.

MDD - Objective (1)

The level of autocorrelation decreased with increased inter-sample distance, because sampling units were increasingly outside each other's range of influence. Nonetheless, the decrease in MDD (i.e. increased power) with longer inter-sample distance was outweighed by the stronger increase in MDD caused by reduced sample sizes. Therefore, MDD increased for all sampling designs as inter-sample distance increased (Fig. 2.3). Grid sampling allowed for the smallest MDD for most inter-sample distances. Simple random

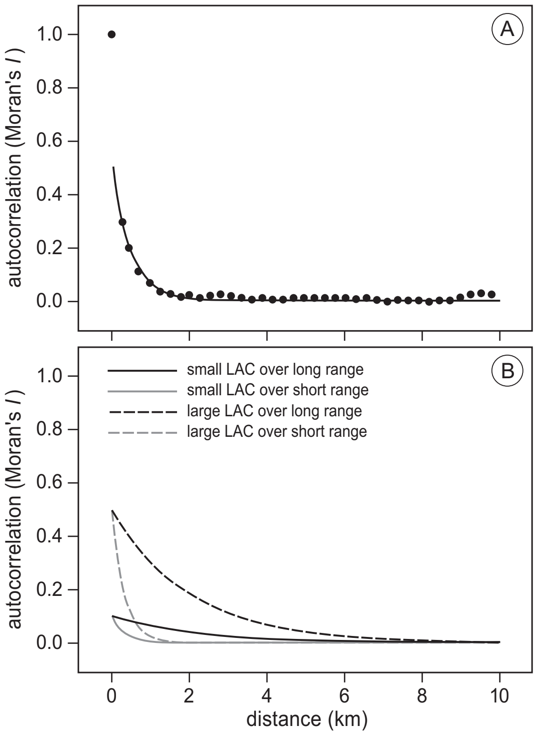


Figure 2.2 Autocorrelation as function of distance for (A) field and (B) simulated data. (A) An example for fitting autocorrelation (*AC*) as function of distance (*h*) from field data for *Nereis diversicolor*, where $AC(h) = 0.50\ e^{-2.11h}$. Note that distance class zero is not included in the fit (see Methods). (B) Autocorrelation functions of four simulated levels of autocorrelation with weak or strong local autocorrelation (LAC) combined with a shallow or steep decline in autocorrelation with distance.

Table 2.1 Estimates of spatial autocorrelation function parameters based on field data. For each species are given: local autocorrelation b_0, steepness of decline in autocorrelation with distance b_1, and percentage effective sample size n* (see methods).

Species	b_0	b_1	**n* (%)**
Cerastoderma edule	0.32	-0.76	5
Macoma balthica	0.05	-0.50	13
Mya arenaria	0.05	-0.34	8
Abra tenuis	0.66	-3.12	19
Ensis americanus	0.03	-0.42	18
Scoloplos armiger	0.21	-0.40	3
Heteromastus filiformis	0.13	-0.58	7
Nereis diversicolor	0.50	-2.11	14
Nephtys hombergii	0.38	-3.02	28
Lanice conchilega	0.23	-1.29	13

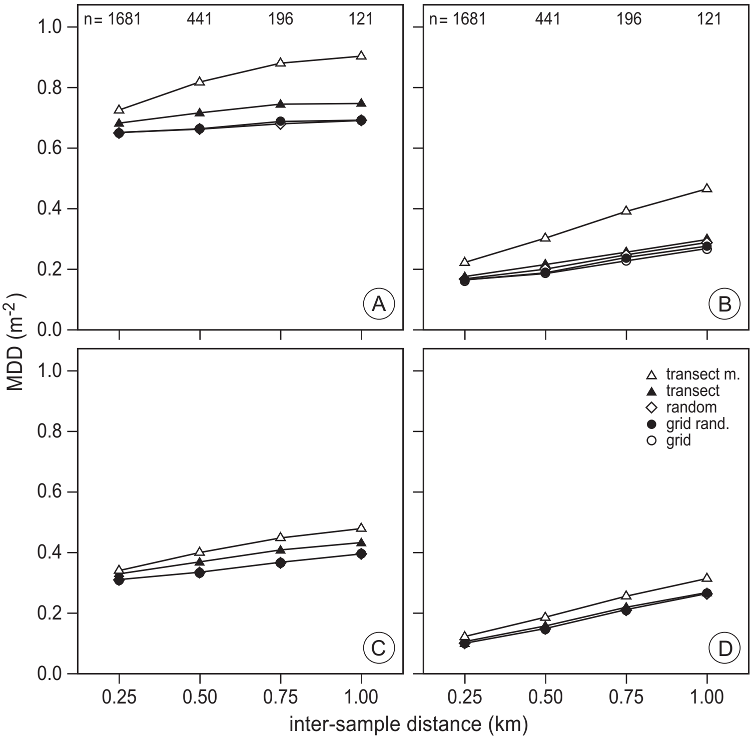


Figure 2.3 Minimum detectable difference (MDD) at different levels of autocorrelation for: transect sampling with either multiple (transect m.) or a single sample per station (transect), simple random sampling (random), grid sampling with random replacements (grid rand.) and grid sampling (grid). The x-axis gives distance between sampling stations which is inversely related to sample size. Each panel represents different simulated levels of autocorrelation: (A) strong local autocorrelation and a long range of autocorrelation, (B) strong local autocorrelation and a short range, (C) weak local autocorrelation and a long range and (D) weak local autocorrelation and a short range.

and grid sampling with random replacements also provided small MDD. Both transect sampling designs consistently showed a larger MDD than the other sampling designs. Between autocorrelation levels, strong local autocorrelation (Fig. 2.3A-B) resulted in a larger MDD than weak local autocorrelation (Fig. 2.3C-D). Additionally, a long range of autocorrelation (Fig. 2.3A and 2.3C) resulted in a larger MDD than a short range (Fig. 2.3B and 2.3D). The differences in MDD between sampling designs were more pronounced for strong local autocorrelation over a short range (Fig. 2.3B).

Prediction error - Objective (2)

Sample size and the level of autocorrelation were reduced with an increase in inter-sample distance, and therefore, the prediction error increased with inter-sample distance (Fig. 2.4). With decreased autocorrelation, kriging interpolations became less accurate and the prediction error more or less approached the simulated variance of 1 (Fig. 2.4C-D).

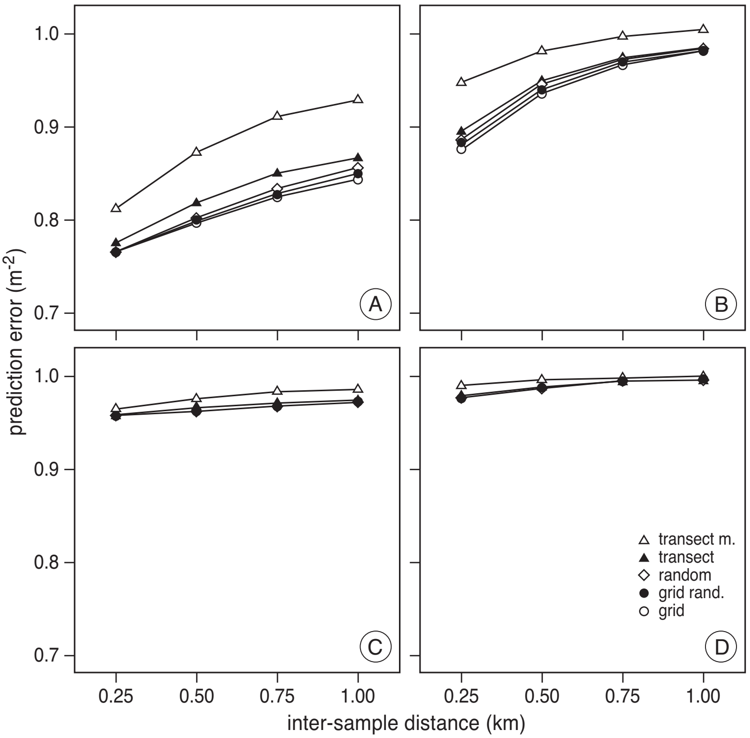


Figure 2.4 Mean prediction error of kriging given for sampling designs at different levels of autocorrelation. For an explanation on the x-axis, legend and panels A-D, see caption of Fig. 2.3.

Grid sampling allowed for smallest prediction errors for all inter-sample distances (Fig. 2.4A-D), followed by grid sampling with random replacements, simple random sampling, transect sampling and transect sampling with multiple sampling units. Between autocorrelation levels, strong local autocorrelation (Fig. 2.4A-B) resulted in smaller prediction errors than weak local autocorrelation (Fig. 2.4C-D). Additionally, a long range of autocorrelation (Fig. 2.4A and 2.4C) resulted in smaller prediction errors than a short range of autocorrelation (Fig. 2.4B and 2.4D).

Estimation bias of autocorrelation parameters - Objective (3)

The smaller the level of autocorrelation, the less often the autocorrelation parameters were estimable (Fig. 2.5). An increase in inter-sample distance, therefore, reduced the number of times the autocorrelation parameters were estimable (Fig. 2.5). Overall, random sampling allowed for estimating the SAF most often.

The smaller the sampling distance, the more accurate the estimate of local autocorrelation (b_0) (Fig. 2.6). As inter-sample distance increased b_0 was overestimated using most sampling designs. Because multiple sampling units were taken within a small range, transect sampling with multiple sampling units was most accurate for estimating b_0 (Fig. 2.6),

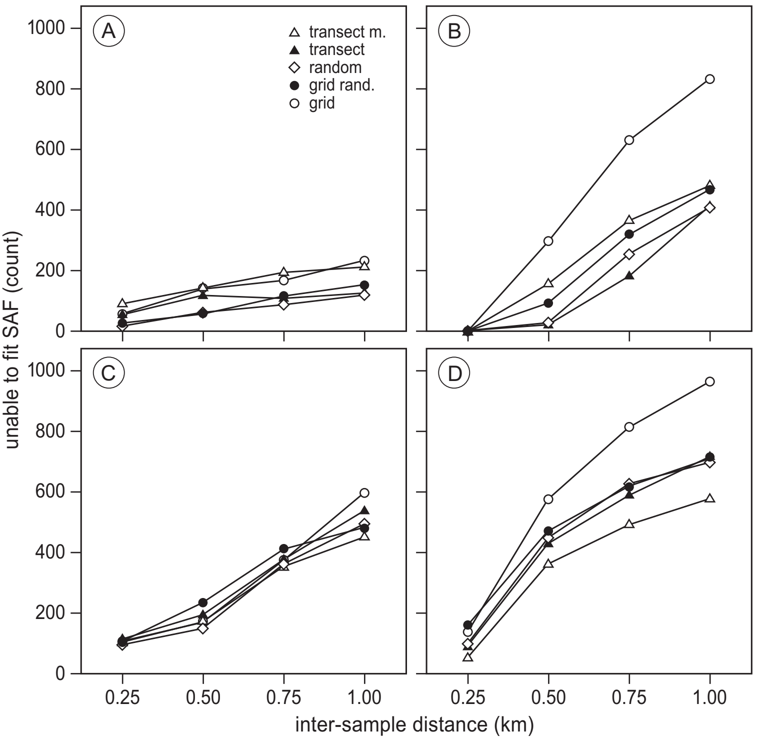


Figure 2.5 Count of inestimable spatial autocorrelation function (SAF) from 1000 simulation runs for different sampling designs at different levels of autocorrelated data. For an explanation on the x-axis, legend and panels A-D, see caption of Fig. 2.3.

especially at low levels of autocorrelation (Fig. 2.6D). Grid sampling showed the largest estimation bias (Fig. 2.6).

The decline in autocorrelation with distance (b_1) was often underestimated (Fig. 2.7). The estimation bias of b_1 was larger with low levels of autocorrelation (Fig. 2.7D) than with high levels of autocorrelation (Fig. 2.7A) and increased with inter-sample distance (Fig. 2.7). Grid sampling with random replacements was the most accurate in estimating b_1 followed by random sampling (Fig. 2.7). Both transect sampling designs showed the largest estimation bias.

Combining the three sub-criteria for estimating autocorrelation structure, the best performing sampling design was dependent on the level of autocorrelation. For low levels of autocorrelation, random sampling performed best, but for intermediate and high levels of autocorrelation, grid sampling with random replacements performed best. At our average overall level of autocorrelation random sampling performed best closely followed by grid sampling with random replacements.

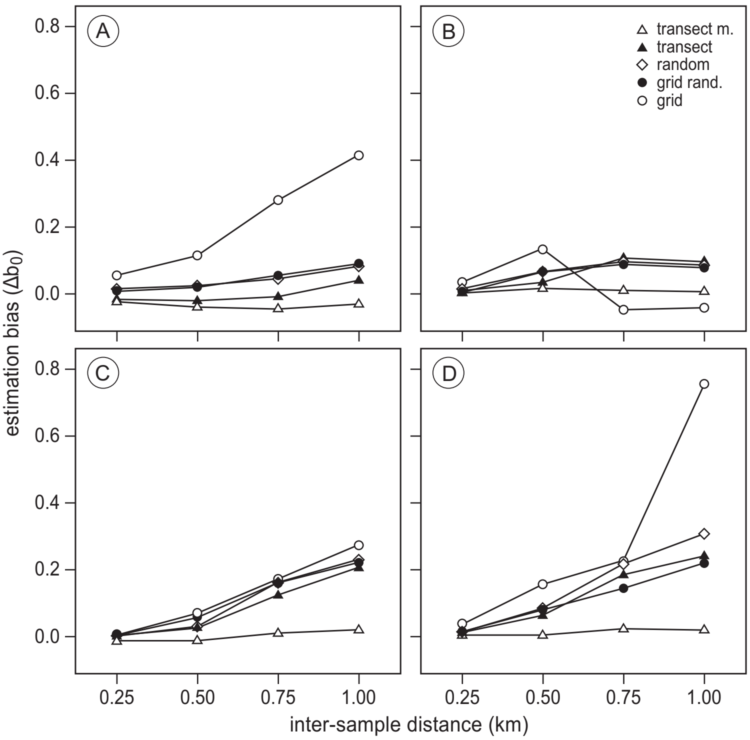


Figure 2.6 Estimation bias of local autocorrelation for different sampling designs at different levels of autocorrelated data. The difference is given between the simulated and estimated local autocorrelation (Δb_0). For an explanation on the x-axis, legend and panels A-D, see caption of Fig. 2.3.

DISCUSSION

The ideal sampling design per objective

COMPARISON BETWEEN YEARS OR AREAS

In ecology one often observes positive spatial autocorrelations (Legendre and Fortin 1989). Statistical power for comparisons between, for instance, the mean abundances of an organism in two areas, is thus reduced. This can be illustrated by the 'effective sample size' (Table 2.1), i.e. the proportion of sampling units that consists of non-autocorrelated independent data points (Griffith 2005). The higher the level of autocorrelation, the smaller the effective sample size and the smaller the power of model-based inference. Indeed, our results show that low levels of autocorrelation resulted in large power (i.e. small MDD) to detect changes between years or areas (objective 1). Between all levels of autocorrelation grid sampling revealed the largest power.

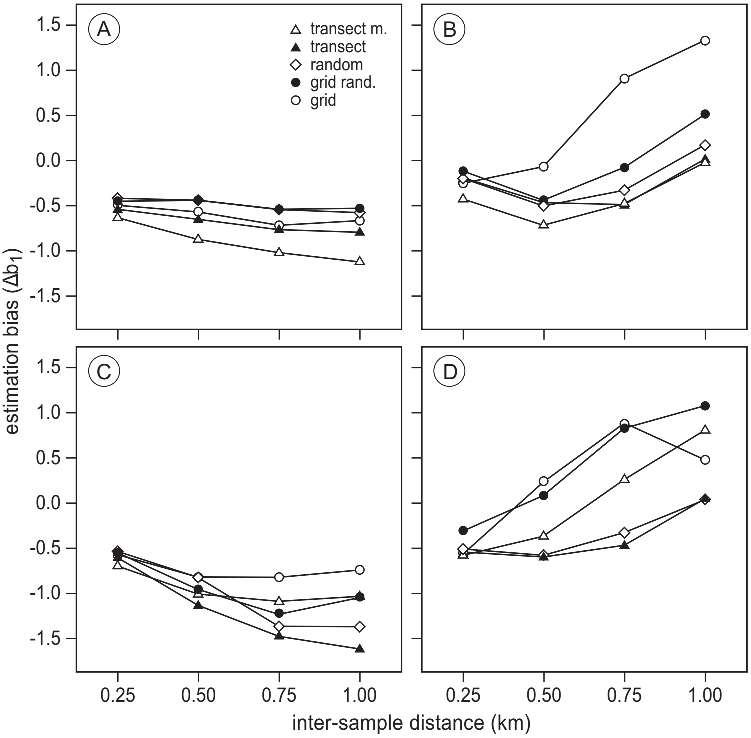


Figure 2.7 Estimation bias of decline in autocorrelation for different sampling designs at different levels of autocorrelated data. The difference is given between the simulated and estimated decline of autocorrelation with distance (Δb_1). For an explanation on the x-axis, legend and panels A-D, see caption of Fig. 2.3.

MAPPING SPECIES ABUNDANCES

The stronger the spatial autocorrelation, the more accurate interpolations of abundances at unsampled locations as the interpolated values are weighed more strongly and by more surrounding sampling units (Cressie 1993, Diggle and Ribeiro 2007). Also, designs that satisfy the uniformity condition (e.g., surface-covering sampling designs) allow for more accurate kriging predictions (Pooler and Smith 2005, Marchant and Lark 2007). Our results are consistent with this understanding. The prediction error was smallest with the highest levels of autocorrelation and with grid sampling which covers the entire surface and conforms to the uniformity condition.

ESTIMATION OF AUTOCORRELATION PARAMETERS

Grid sampling was the best sampling design for objectives (1) and (2). However, note that in our study we simulated autocorrelated data with known autocorrelation parameters. In the analysis of field data autocorrelation parameters need to be estimated from the data itself. For estimating autocorrelation parameters (objective 3), grid sampling performed worst, although the fit of these parameters to the data determine the validity of model-based inference (Gregoire 1998, Haining 2003, Little 2004). For accurate parameter estimations, spatial sampling designs should include small distances between sampling units (Diggle and Lophaven 2006). Our results showed that those designs that included small inter-sample distances allowed for the most times the SAF could be fitted and the most accurate estimates of autocorrelation parameters. Overall, random sampling performed best in estimating autocorrelation structure closely followed by grid sampling with random replacements.

The ideal sampling design between objectives

For this study we were interested in a sampling design that allowed for the best results between three monitoring objectives: estimation of temporal changes and spatial differences in abundance, prediction of abundances at unsampled locations and accurately estimating autocorrelation model parameters. None of the sampling designs suited all objectives. Therefore, the objectives need to be compromised to find the best overall sampling design. A procedure ideally suited for finding a compromise between sampling designs is Pareto-optimization (Steuer 1986). Using Pareto-optimization we can identify superior sampling designs using the following criterion: no other sampling design produces improved results concerning a particular objective without at the same time producing worse results for another. A further selection from those sampling designs that fit the above criterion requires arbitrary weighing of sampling objectives. We ranked all sampling designs according to the different monitoring objectives (Table 2.2). For objective (3) we averaged the rankings for sub-objectives to obtain an overall ranking. For objectives (1) and (2), grid sampling was the best sampling design, closely followed by grid sampling with random replacements. For objective (3) random sampling performed best, closely followed by grid sampling with random replacements. The worst sampling

Table 2.2 Ranking of sampling designs according to different monitoring objectives, i.e. minimum detectable difference (MDD), mean prediction error, the accuracy in fitting the spatial autocorrelation function (SAF). The different sampling designs are transect sampling with multiple (Transect M) or a single sample per station (Transect), simple random sampling (Random), grid sampling with random replacements (Grid Rand.) and grid sampling (Grid). Three Pareto-optimal solutions exist (indicated by *): Random, Grid Rand. and Grid. Weighing all monitoring objectives equally, grid sampling with random replacements (indicated in bold) is the ideal compromise between objectives.

	MDD	prediction error	SAF
Transect M.	5	5	4
Transect	4	4	3
Random*	3	3	1
Grid Rand.*	**2**	**2**	**2**
Grid*	1	1	5

design for objective (1) and (2) was transect sampling with multiple sampling units and for objective (3) it was grid sampling. Following Pareto-optimization we identified three optimal solutions: grid sampling, random sampling and grid sampling with random replacements. For all objectives, grid sampling with random replacements was a close runner up and showed substantially improved performance compared to grid sampling on objective (3). Weighing all three monitoring objectives equally, grid sampling with random replacements is the best compromise between objectives.

In this study, we *moved* 10% of grid sample stations to randomly selected sample positions on gridlines to maintain equal sample sizes for correct comparisons between sampling designs. Therefore, we lost homogenous surface coverage which increased the prediction error. The constraint of equal sample size does not apply in the field and, therefore, the ideal sampling design for similar objectives would be surface-covering grid sampling with a percentage of sampling stations randomly placed on gridlines *additional* to the grid design (see Online Supporting Information for R-code to create such a sampling design). The main effect of *adding* random samples instead of *replacing* is that the homogenous surface coverage is preserved which decreases the prediction error. Grid sampling allows for large statistical power in comparisons between years or areas as well as small prediction errors at unsampled locations and the *additional* random sampling allows for accurate estimates of autocorrelation parameters. The lower the level of autocorrelation, the higher the percentage of additional random sampling units needs to be for accurately estimating the autocorrelation function. The level of autocorrelation depends on the scale of the sampling effort, i.e. the ratio of inter-sampling distance to autocorrelation range. The higher the ratio, the lower the level of autocorrelation. Increasing the percentage of random sampling units will increase levels of autocorrelation and allow for more accurate estimates of autocorrelation parameters. On the other hand, the higher the level of autocorrelation in the data, the larger the MDD.

In practice sampling programmes are more complicated than we have simulated here. For instance, in order to increase power and reduce prediction error, one might want to use environmental variables as covariates or apply environmental stratification, where autocorrelation varies among strata. Optimising sampling designs in such cases will be slightly more difficult, but can be achieved along similar principles as we have opted here.

Issues of non-normality

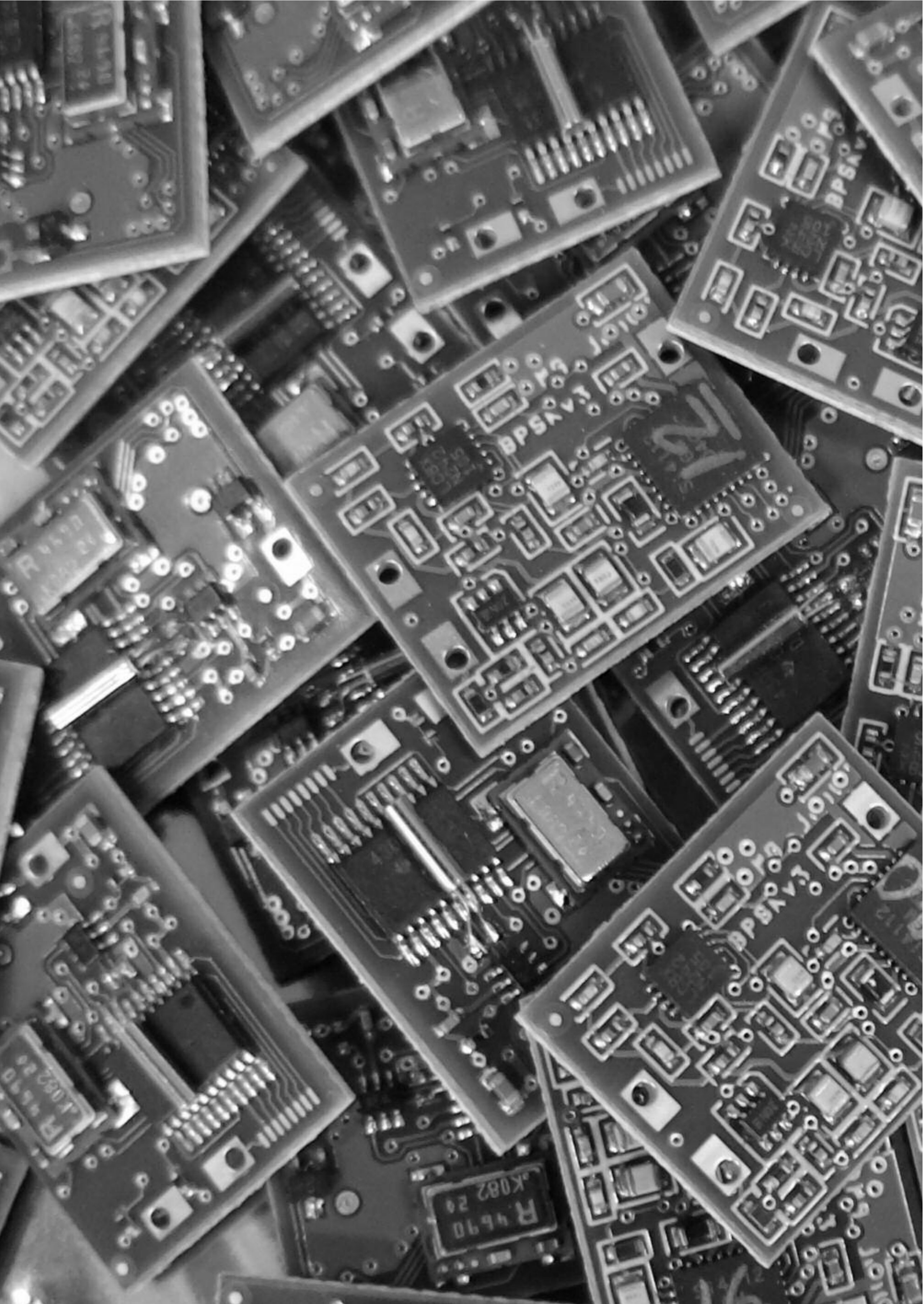
The field data used to estimate autocorrelation parameters, were not normally distributed. Nonetheless, we simulated normally distributed data and from this deduced the ideal sampling design according to the three criteria. Ideally, one would simulate data similar to the data observed. However, methods for simulating non-normally distributed data with a known autocorrelation structure are still in development (Jackson and Sellers 2008). Using simultaneously-specified models (Jackson and Sellers 2008), we explored the possibility of simulating Poisson data with a known autocorrelation structure. The general idea of this method is generating a normally distributed random vector ε with known covariance matrix, and add this to a vector of expected values (on the basis of environmental data) to create a vector X. Then a Poisson variable is generated with the exponential of X. Following this method, we experienced that the simulated autocorrelation structure of the normally distributed variable X did not show up in the autocorrelation structure of the resulting Poisson data. We recommend more work on this topic to resolve this issue for non-normally distributed data. Regardless of this practical limitation, we have no reason to believe that our results are not robust to different underlying data distributions. Even though data with different distributions will probably alter the quantitative results (i.e. absolute values of the estimates), the qualitative results (i.e. ranking of sampling designs according to the objectives) are likely to remain similar. Nonetheless, when methods become available to simulate non-normally distributed data with a specific autocorrelation structure and computationally more efficient parameter estimation methods become available, we advocate further investigation into the effects of non-normality on selecting the most appropriate sampling design.

Implications for Wadden Sea monitoring programmes

Currently, NIOZ macrobenthic monitoring programmes follow either transect sampling (Beukema 1976, Beukema and Dekker 2006, Dekker and Beukema 2007), or grid sampling with an inter-sample distance of 0.25 km (Piersma et al. 2001, van Gils et al. 2006a, van Gils et al. 2006b, Kraan et al. 2007, van Gils et al. 2009). The NIOZ monitoring programme is to be extended to cover the entire Dutch Wadden Sea for monitoring the effects of gas exploitation. This study indicates that surface-covering grid sampling with additional random sampling is the ideal sampling design for detecting temporal and spatial changes in abundances as well as mapping macrobenthic invertebrates. Given the surface area of the Dutch Wadden Sea, extending the monitoring programme at the current inter-sample distance of 0.25 km would inflate sample size to 19,000 sampling units, beyond what is feasible within seasonal and logistical constraints. We, therefore, suggest the inter-sample distance should be increased to 0.50 km (corresponding to roughly 4,700 sampling units) to allow surface-coverage of the entire Dutch Wadden Sea.

Acknowledgements

We thank all volunteers who helped collecting samples and the crew of MS *Navicula* whom provided a helpful and welcoming atmosphere on board. We thank Dick Visser for preparing the figures, Hans Malschaert and Piet Ruardij for use of the *biocluster* supercomputer, and the Nederlandse Aardolie Maatschappij (NAM) for financing AIB and JAvG. Finally, we thank the reviewers and editors for constructive comments.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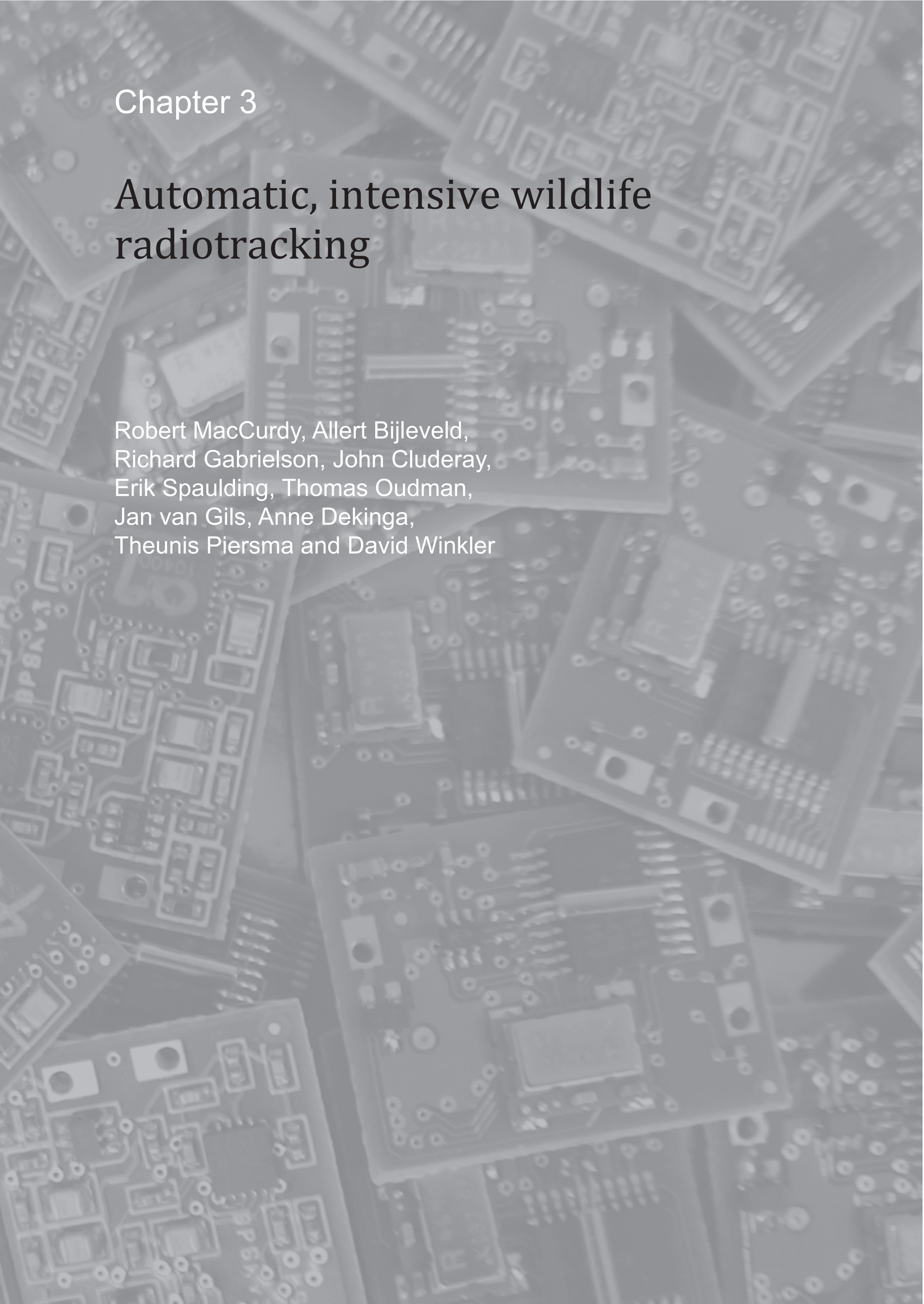


Chapter 3

Automatic, intensive wildlife radiotracking

Robert MacCurdy, Allert Bijleveld,
Richard Gabrielson, John Cluderay,
Erik Spaulding, Thomas Oudman,
Jan van Gils, Anne Dekinga,
Theunis Piersma and David Winkler

SUMMARY Recent advances in tracking technology, in part enabled by the explosion in personal wireless connectivity, have begun to give wildlife scientists the scalable tools required to monitor large numbers of individuals. Unfortunately, many of these new tools are inapplicable to many species due to mass, cost and energy constraints, leaving gaps in our understanding. Here we present a new technique, capable of automatically gathering position data with high spatiotemporal resolution for large numbers of animals over long timescales, using very small transmitters. Relative to current methods this system offers researchers unprecedented amounts of data, can be broadly applied to species that were previously too small for automated tracking systems, and reduces tracking costs. We describe the challenges encountered when tracking wildlife with existing technologies, our solution as implemented, and discuss application examples.

INTRODUCTION

Movement is fundamental to all living organisms and its study is used directly and as a proxy to quantify diverse parameters across spatial and temporal scales. The Movement Ecology field seeks to provide a unifying framework, including methods, for the long-established but often disparate practices of investigators studying organismal movements (Sugden and Pennisi 2006, Nathan et al. 2008). Researchers studying the dispersal of maple leaves, the advance of invasive insects, or the spatial resource utilization of foraging animals have traditionally developed or purchased tools specifically for their application area, with little opportunity to share these tools with groups working on different ecological systems. This practice is changing; the National Science Foundation's National Ecological Observation Network (NEON), which represents a $400 million investment over five years, is one example. NEON aims to develop ecological sensing infrastructure at 20 locations around the United States (Keller et al. 2008, Pennisi 2010), and to allow researchers to share field resources and collected data. These locations will persist for 30 years, provide year-round power, internet connectivity, and host a variety of automated and staffed sampling tools. Though its current development plan does not incorporate automated movement monitoring tools, the NEON sites, and many others around the world, present movement ecologists with an appealing opportunity: when instrumented with automated tracking tools, pervasive, persistent, coordinated and automated data collection sites have the potential to dramatically enhance our understanding of organismal movements through space and time.

We have developed a Real-Time Locating System (RTLS), based on a Time of Arrival (TOA) approach, capable of monitoring the positions of thousands of wildlife transmitters (tags) in near-real-time. This terrestrial tracking system targets regional coverage, and complements global systems like GPS by dramatically expanding the number of species that can be tracked, increasing tag lifetimes, raising location update rates, and reducing per-animal tracking costs. This method increases the number of position estimates that can be obtained from small tags by several orders of magnitude, relative to existing techniques (see Figure 3.1). In contrast to approaches that utilize existing data networks (satellite, mobile phone), by employing local point-to-point wireless connectivity, this method offers real-time position updates without recurring data costs. Since most of the system's cost is in the fixed receiver network, the incremental cost of adding additional tagged animals to the study area is extremely low, which enables large sample sizes that would be impractical or impossible via existing methods, and opens up the potential for shared tracking infrastructure.

TAG DESIGN CHALLENGES

Wildlife tracking systems that are capable of providing position information are a widely used tool; however, their application is limited by cost and mass to a relatively small number of species. To illustrate why a new tracking technology is required, the character-

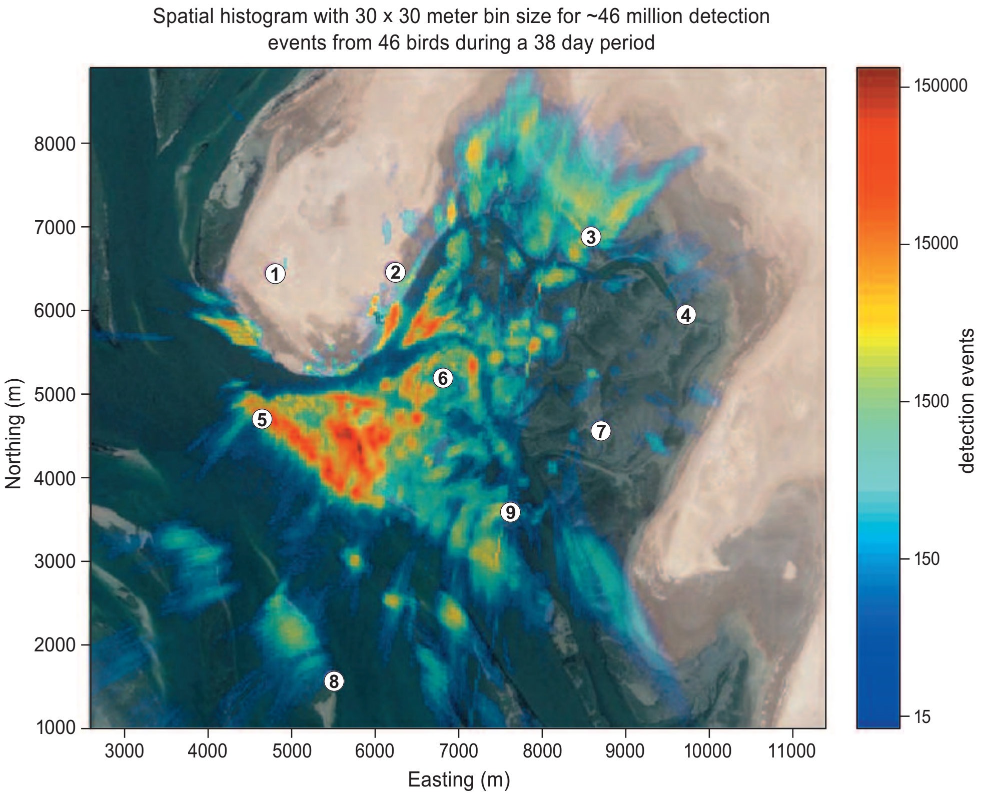


Figure 3.1 Baie d'Aouatif on the Banc d'Arguin, Mauritania with a spatial histogram showing the number of detection events in each 30x30 m cell. 46 birds were tracked over a 38 day study period producing more than 46 million position estimates. The TOA tags were configured to transmit once per second. The numbers represent the nine receiver stations.

istics of existing systems are summarized in Table 3.1. Though numerous tag sensing modalities exist, here we consider only those that provide position data. Of the parameters listed in Table 3.1, the most important is tag mass, as it determines whether a tracking methodology is suitable for any particular species. The precise amount of tag mass that a given animal can bear without adverse impacts is still unknown. Though efforts have been made to estimate the allowable load based on species-specific parameters (Caccamise and Hedin 1985), it is common practice to limit tag mass to 3–5 percent of an animal's body mass (Cochran 1972, Naef-Daenzer et al. 2001). This heuristic has a profound impact on tag design. As illustrated in Figure 3.2, tags must be lightweight if they are to be compatible with most flying vertebrates. For example, a 0.85 gram tag is light enough to be used with half of the animals included in Figure 3.2 when a 3% loading rule is enforced; for comparison the lightest Argos (Fancy et al. 1988) (satellite tracking) tag available, a 5 gram model, can be applied to fewer than 20 percent of the species presented in Figure 3.2. The increase in the number of species that can be tagged increases most rapidly for tag

Table 3.1 Comparison of different tracking technologies. All numbers represent the most favourable values currently available. NOTES:

A Tag range can be limited either by the position sensing mechanism or by the data offload system (if present). The minimum of these two is shown.

B Location Cost - total tag energy cost of each position fix. For tags that only transmit, this entry is zero. For GPS this metric is strongly dependent on the position update rate. Faster update rates use less energy per fix, but cannot use low power sleep modes, yielding greater overall energy usage than slower update rates. These data are taken from published research as well as manufacturer's data sheets; efforts have been made to provide a range from best to worst case.

C Data Transport Cost - total tag energy cost of transmitting the data or signal for each position fix. Total cost is the sum of the Location Cost and the Data Transport Cost.

D Lifetime w/ 1g battery - number of days that a tag could operate when acquiring 1 position fix per minute, using a 1 gram (35mAh) battery. For all tags that support it, this calculation includes the transport cost of sending the data back to the user, rather than storing locally on the tag, since recapture is often infeasible. The VHF calculations were done with a pulse interval of 3 seconds, which is typical for very small "Beeper" VHF tags.

E Some Argos and GPS tags are available with solar cells, which can extend their lifetime indefinitely, though the number of fixes per day is strongly linked to insolation and the strength of the GPS signal; Bouten et al. (2013) report results varying from 15 to nearly 7,000 fixes/day.

F The GPS (research) row is an estimate, based on the best recent reported results for GPS baseband and RF frontend modules.

G Conventional VHF tags usually send a simple presence/absence signal, but do not send modulated data.

	Tag Cost (USD)	Minimum Mass (g)	Range (km)$_A$	Location Error (m)	Data Back haul	Location Cost (J)$_B$	Data Transport Cost (J)$_C$	Lifetime w/ 1g battery$_D$
GPS[1]	50 - 1000	1 - 2.5	Global	1 - 50	N	0.022 - 2	0	0.58 days$_E$
GPS & Argos[2]	1500-4000	17	Global	1 - 50	Y	0.022 - 2	0.38	0.32$_E$
GPS & local wireless[3]	n/a	6 - 12	0.3 - 8.5	1 - 50	Y	3.3 - 145	n/a	n/a$_E$
Snapshot GPS[4]	3400 - 5000	39	Global	1 - 100	N	2.1	0	0.12 days$_E$
GPS(research)[5]$_F$	n/a	n/a	Global	1 - 50	n/a	0.26	n/a	1.0
Argos[6]	1300 - 4000	5	Global	250 - 1500	Y	0	0.18	1.45 days$_E$
Solar Geolocation[7]	100	0.5	Global	$50\text{x}10^3$ - $2\text{x}10^5$	N	$6.9\text{x}10^{-5}$	0	3804 days
VHF[8]	150	0.16	1 - 5	100 - 1000	Y$_G$	0	$1.0\text{x}10^{-4}$	130 days
TOA RTLS	150	0.5	5 - 10	10 - 50	Y	0	$5.0\text{x}10^{-4}$	520 days

[1] Technosmart tracking systems for animals, http://www.technosmart.eu; Lotek wireless fish & wildlife monitoring, http://www.lotek.com; Telemetry solutions, http://www.telemetrysolutions.com; Microwave telemetry, http://www.microwavetelemetry.com; Bridge et al. (2011); Edwards et al. (2013)

[2] Microwave telemetry, http://www.microwavetelemetry.com; North star science and technology, http://www.northstarst.com; Fancy et al. (1988); Bridge et al. (2011)

[3] Bouten et al. (2013)

[4] Liu et al. (2012)

[5] Tang et al. (2012); Heiberg et al. (2011)

[6] Fancy et al. (1988); Priede and French (1991); Hooijmeijer et al. (2014); Battley et al. (2012); Gill et al. (2009)

[7] Hill (1994); Afanasyev (2004); Bridge et al. (2013)

[8] LeMunyan et al. (1959); Cochran and Lord Jr (1963)

[9] MacCurdy et al. (2009, 2012); Piersma et al. (2014); Savaglio et al. (1997); *Lemnell et al. (1983)*

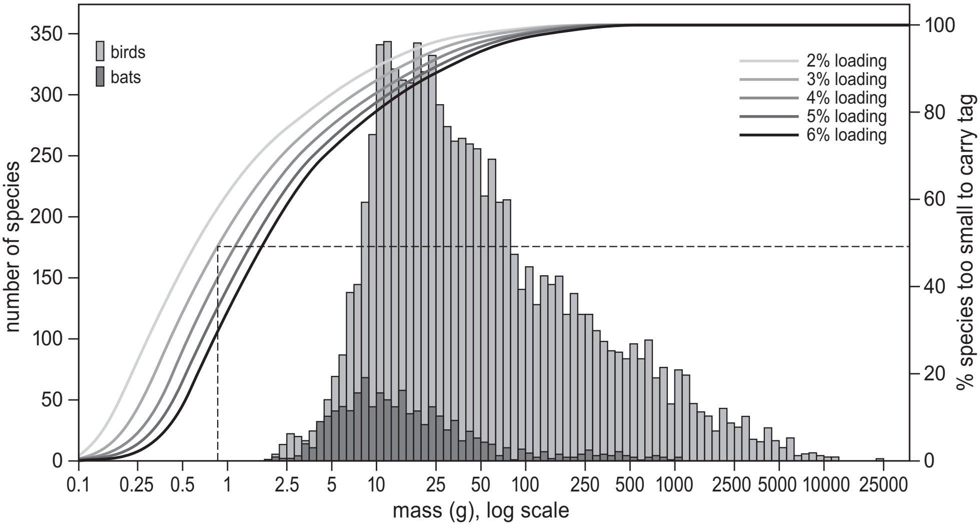


Figure 3.2 Bird and Bat mass distributions; 9278 bird species and 1067 bat species are included. Shown on the right y-axis is the percentage of birds and bats that are too small to carry a tag with a particular mass, assuming a certain maximum allowed loading. For example, the dashed lines show that 50% of birds and bats are too small to carry a 0.8 g tag, assuming 3% loading. Data are from (Smith et al. 2003, Dunning 2008).

weights between 0.5 g and 3 g; this observation motivates the design of a new class of ultra-lightweight tags.

Although we emphasize tag mass here, recent work has shown that aerodynamic drag due to tag cross-section can be significant for small birds, and should not be ignored (Bowlin et al. 2010). Nevertheless, lighter tags will generally be smaller and exhibit lower drag, so the primary focus must be to reduce the size and mass of tag components. As the largest and heaviest components, batteries dominate the mass budget of most tag designs. The energy storage capacity of any particular battery type is proportional to its mass, and steady improvements in mass-and volumetric-specific energy have enabled ever smaller batteries; however, unlike the exponential growth of transistor counts and attendant improvements in power consumption that integrated circuits have exhibited, the battery development curve over the past 20 years has shown only linear improvements (2.5x improvement) (Oudenhoven et al. 2012). Recent efforts (Chen et al. 2014) have yielded micro batteries with more than double the mass-specific energy density of comparable commercial offerings; however, if the past trend is predictive, commercial battery technology is likely to improve these metrics by only 125% over the next decade. As the three right columns in Table 3.1 reveal, this improvement will not be sufficient to allow more energy-intensive techniques like GPS to become incorporated into small tags. An improvement of more than three orders of magnitude in either circuit efficiency or energy storage will be necessary if tags that use GPS or Argos are to become both very lightweight (<1g) and long lived (100 days or more of operation).

To accommodate the limitations of current battery technology, tag designers can reduce operational lifetime, reduce the energy-intensity of the position sensing modality, or capture external energy to replenish the battery. This latter approach, utilizing photovoltaic cells, is now commonly exploited by tag designers with good results. However, the amount of incident power available to the solar array, which must be small enough to accommodate tag size and mass constraints, is insufficient to directly supply higher-power position determination schemes like GPS and Argos. For example, one of the most efficient solar cells currently available (Spectrolab tasc solar cell) has a maximum rated output of 0.027 W/cm^2, occupies 2.277 cm^2 and weighs 234 milligrams, while one of the lowest-power commercially-available GPS modules (SiRFstarIV) consumes 0.077W during acquisition. A tag using these components would require 3 cm^2 of solar cell area, weighing 300 milligrams. This is an ideal-case estimate, and the amount of solar power available is usually dramatically reduced by habitat characteristics, weather, time of day, season and component degradation, which would require a solar array at least an order of magnitude larger than this estimate. To circumvent these limitations, tags employ energy storage elements (batteries or capacitors) to accumulate solar energy over time and then rapidly discharge this energy in the position sensing circuitry. Rather than considering the power balance, tag designs must consider the daily energy balance. Solar cells can yield GPS and Argos tags that are capable of very long deployed lifetimes, but since the tag energy demands are relatively high and the external energy supply varies, these tags exhibit high variability in the number of position fixes per unit time (Bouten et al. 2013). Future GPS designs might one day improve this situation through lower power operation, though it is instructive to look at recent trends. A state of the art research (not commercialized) GPS-receiver published in 2000 (Namgoong et al. 2000) consumed 21.3 mW during the continuous tracking stage. Over a decade later, the lowest power GPS receiver demonstrated in a research setting consumed 8.7 mW (Cheng et al. 2009, Tang et al. 2012) during continuous tracking. For comparison, one of the lowest-power commercially available GPS receivers (SiRFstarIV) consumes 66 mW during continuous tracking. Decoding GPS signals is an inherently compute-intensive operation, and while the energy-intensity of GPS receivers continues to decline, it seems unlikely that energy reductions of 2 to 3 orders of magnitude will occur in the near future.

In light of these current limitations, the choice that tag users face is to trade-off tag functionality for lifetime, since tag mass is a fixed constraint for any particular species (see Table 3.1). Here, functionality could mean various things depending on the tag, including: number of position fixes per day (GPS & Argos), number of light measurements per day (Geolocators), and number of pulses per second (VHF ”beeper” tags). Reducing the number of data points gathered per day does increase the tag endurance, but at the cost of lower temporal resolution, an issue that precludes this strategy for many studies. Though they offer global coverage and high resolution, GPS-and Argos-based tags suffer from high energy consumption, requiring larger and heavier batteries. GPS receivers yield position fixes that are local to the tag, requiring additional tag energy to telemeter the position data. Geo-location tags are extremely energy-efficient and lightweight, but provide very

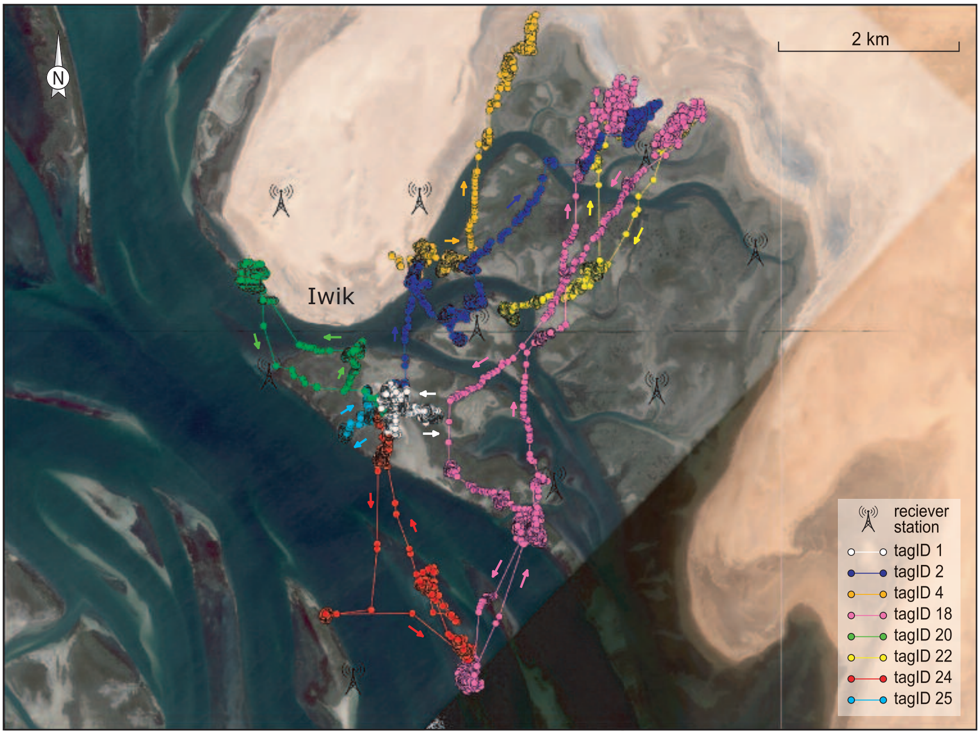


Figure 3.3 The movements of eight Red Knots (*Calidris canutus canutus*) in Baie d'Aouatif on the Banc d'Arguin, Mauritania, during a single low water period (29 January 14:52 h to 30 January 03:07 h) that show the range of individual itineraries. Connected dots indicate the measured positions and the arrows indicate the directions of movement in the course of the tide. Locations that are well separated probably indicate flight paths. This image was adapted from Piersma et al. (2014).

coarse resolution and rarely offer the capability to telemeter data. Conventional VHF tag tracking systems do not provide long tag lifetimes or offer precise position estimates. By minimizing the energy consumed per position estimate, our TOA tracking solution is able to provide remote (tag recapture is not required) position updates at high, consistent rates over long study periods using lighter tags than any other method, allowing a dramatic increase in the number of addressable species (Figure 3.3).

APPLICATIONS

Climate change, and human encroachment on critical habitat place ever-increasing pressure on wildlife, yet the evidence of specific impacts often arrives too late (Boere and Piersma 2012, Pimm et al. 2014). Multiyear monitoring of sites, chosen as gateways or hotspots, would yield precise migration timing data and individual mortality assessments. When coupled with local resource availability sampling, this system could provide an unprecedented mechanistic view into how foraging animals utilize available resources.

The high temporal resolution of TOA tracking could additionally be used to answer questions about group dynamics, collective decision making and social information use. How are movements tied to weather, climate (Lyon et al. 2008), habitat manipulation and fragmentation (Sekercioglu 2007)? What conditions dictate the range of dispersal and where do these animals go? Though current tracking tools allow coarse migratory connectivity to be studied (Webster et al. 2002, Marra et al. 2010), better spatiotemporal data could reveal how migrants utilize specific resources at each stopover point. Are there critical stopover locations without which a migratory sub-population would be expected to collapse? How might reductions in the habitat quality at a staging area impact a migratory species (Piersma 2012)? Are there thresholds below which the resource is no longer viable? Answering questions like these will require large amounts of location data with high temporal and spatial resolution; TOA tracking systems, deployed at locations of interest, will make studies like these possible. Additionally, though we have highlighted applications to small, winged species, this technology is well suited to the study of larger animals, who are capable of carrying larger conventional tracking devices: inexpensive, long-lived tags enable large numbers of individuals to be tracked, low mass offers attachment flexibility, while the recurring costs to obtain data from the system are lower than competing techniques.

METHODS

The Real-time Location System that we have built employs mobile transmitters and a fixed network of time-synchronized receivers. The receiver network continuously ’listens’ for tag transmissions and when they are detected, the arrival time is precisely measured (+/30 nanoseconds). The arrival time, a unique tag identifier code, and additional metadata about the status of the receiver are sent from each detecting receiver to a central server where they are stored in a database as an ”event”. When the server identifies groups of events that are likely to have originated from the same tag transmission, an algorithm uses the arrival times to simultaneously estimate the tag position and transmission time. This system exploits two key engineering concepts: spread spectrum signals and matched filter detection.

The term spread spectrum refers to a class of methods of expanding the amount of radio-frequency bandwidth that is used to transmit a particular signal. For example, if a spread spectrum transmitter is tasked with broadcasting a message that occupies 10 Hz of bandwidth, it might use 100 Hz of bandwidth to actually send the message. Though this might seem wasteful, spread-spectrum approaches offer several advantages relative to narrow-band methods, including increased effective signal strength, improved interference rejection, and more accurate timing resolution. Our RTLS exploits these three properties, to respectively: increase tag reception range, allow multiple tags to operate simultaneously in the same region, and precisely measure the signal propagation time.

Each tag’s transmitter performs spread-spectrum modulation by multiplying (mixing) two signals together. The first is a fixed-frequency (typically150 to 450 MHz) sinusoid,

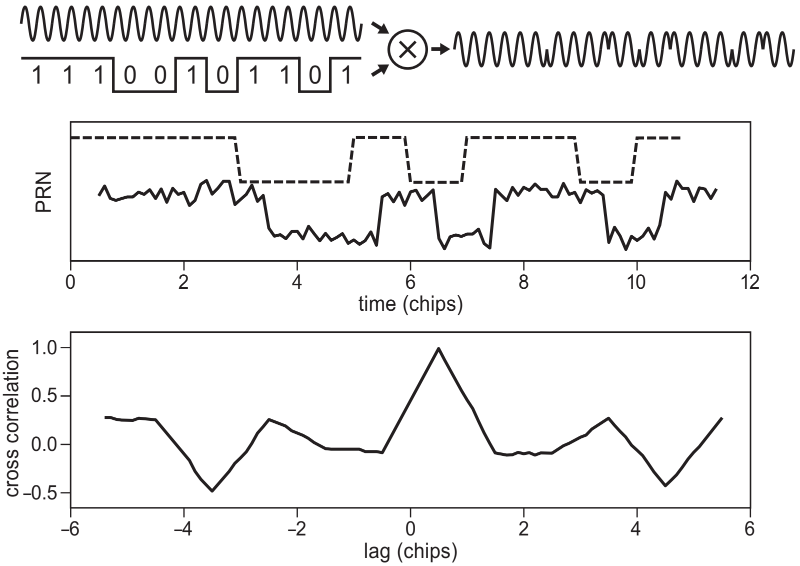


Figure 3.4 [Top]: Binary Phase-Shift Keying (BPSK) modulation of carrier by pseudo-random noise (PRN); [Middle]: PRN signal (dashed) with a noisy, delayed version; [Bottom]: Cross-correlation of the noisy delayed signal and the original PRN.

called the carrier; the second is a digital signal whose sequence of 1s or 0s is approximately random, but repeatable -a so called pseudo-random-noise (PRN) sequence; part of this sequence is common to all the tags and part of it is unique to each tag. In our tags, this multiplication has the effect of inverting the phase of the carrier in the modulated signal when a 1 is present, as illustrated at the top of Figure 3.4, a so-called Binary Phase-Shift Keying modulation scheme. This modulation is relatively easy to produce with discrete circuit building blocks (24).

$$R(l) = \sum_{m=-\infty}^{\infty} x^*(m)y(l+m) \tag{1}$$

This signal is demodulated at each in-range receiver by mixing it with another fixed-frequency sinusoid, restoring the PRN signal from the tag, albeit with additional noise. The middle chart in Figure 3.4 shows a simple example, with the dashed line representing the original PRN and the solid line representing the received PRN, corrupted by additive white Gaussian noise (AWGN) and a delay. Since the receiver knows all tag PRNs *a priori* it can search for the presence of the transmitted signal using a cross-correlation computation (equation 1). The cross-correlation R(l) of the two example signals is shown at the bottom of Figure 3.4. Notice that the domain of R(l) is the relative lag of the two signals and the range is the relative match between the two signals. The receivers use the peak cross-correlation value in combination with an adaptive threshold detection algorithm to determine that a PRN is received; the lag at that value provides an estimate of reception time.

Portability and flexibility were key design goals for this tracking system; permanently installed AC-power supplies, large fixed towers, and heavy equipment are not required. The receivers are sensitive enough to achieve 5 km reception range using 5 m telescoping pole towers with omni-directional VHF antennas. Each receiving station has a total power requirement of 25W, including secondary data radio links to communicate with the central server. This allows the receivers to be solar powered, with modest battery capacity for low-light and night-time operation.

Although each tag uses a unique orthogonal code, the current receiver design is capable of detecting only a single tag's transmission at any particular time. This causes other tag transmissions that overlap in time to be ignored (the first tag to transmit is detected). Although the tag transmissions are brief, relatively infrequent, and do not occur on exactly the same schedule (by design), if a large enough number of tags are within range of the same receiver, the receiver will inevitably fail to detect some tag transmissions. The percentage of missed tag transmissions as a function of the number of in-range transmitters and their transmission interval is shown in Figure 3.5. Note that this is not an intrinsic limitation of the method; this is a limitation of the current implementation. More powerful processors at the receivers will allow simultaneous tag detections.

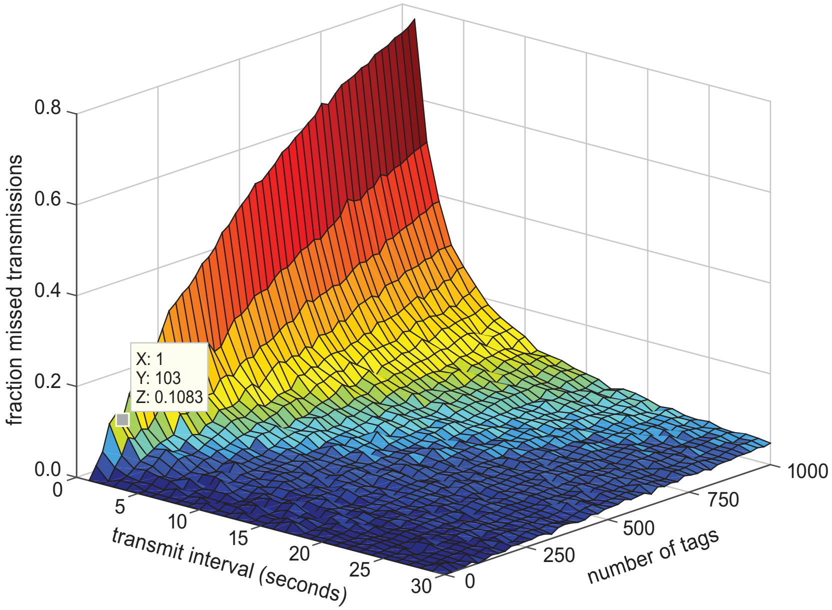
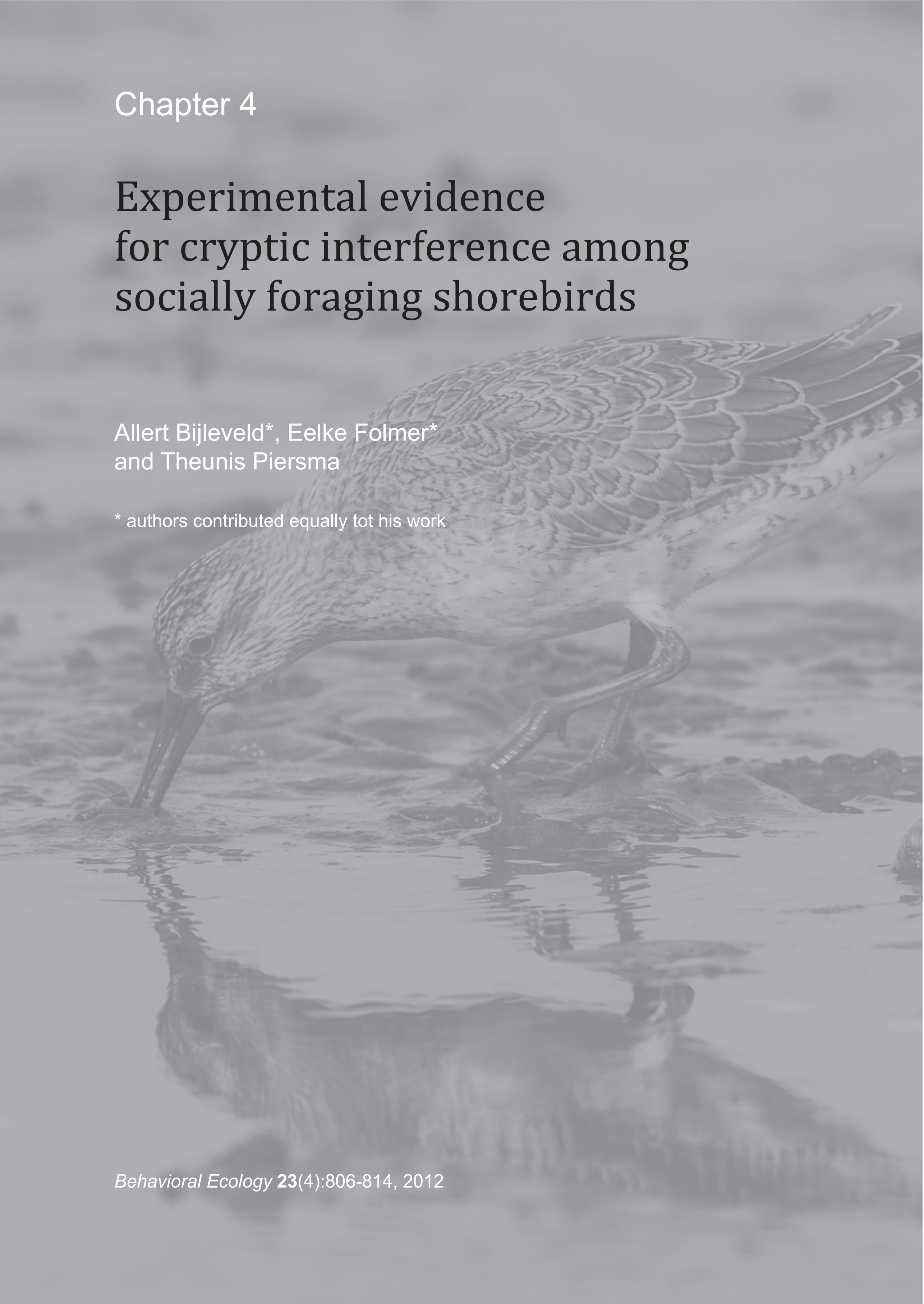


Figure 3.5 The current receiver design ignores simultaneous tag transmissions, therefore if enough transmitters are within range of a single receiver, some percentage of the total number of tag transmissions will be ignored. As the plot shows, a large number of tags can currently be accommodated even with transmit intervals shorter than half a minute. The cursor position shown corresponds to 103 in-range transmitters, each transmitting once per second. The current receivers will miss 11% of these transmissions. Future receivers, based on updated processors, will improve this capability.

When a receiver detects a tag transmission, it packages the tag id (determined by PRN number) along with the time of reception and other meta-data into a UDP datagram and sends the message via IP-radio equipment to a centralized server where the message is added to a database. Off-line operation is also possible; in this case the data from each receiver are stored locally and inserted into the database when field staff service the receiver. When the server identifies database entries from different receivers that are likely to have been from the same tag transmission event it attempts to compute a position estimate using a least-squares pseudo-range algorithm, similar to the method employed by GPS receivers. Position estimates from transmission locations within the receiver array have a 1σ error of 10 m. End-users may query the database remotely for tag position data. The frequency of position updates depends primarily on the frequency of tag transmissions, a user-specified parameter that can be traded-off against desired tag lifetime and mass to suit a particular application. Update rates as fast as 1 second are possible. Extensive technical details and performance measurements can be found in MacCurdy et al. (2008, 2009, 2012).

Section II

Sociality



Chapter 4

Experimental evidence for cryptic interference among socially foraging shorebirds

Allert Bijleveld*, Eelke Folmer*
and Theunis Piersma

* authors contributed equally tot his work

Behavioral Ecology **23**(4):806-814, 2012

SUMMARY

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 some 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. 2012). Conspecific presence can be beneficial because it provides information on food availability (Chapter 5, Krause and Ruxton 2002, Valone 2007, Danchin et al. 2008) 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. 2006b).

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. 2006b).

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. 2006b, 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. These models, however, 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). How well generalized functional response models predict intake rates and spatial distributions depend on how well these models capture essential foraging 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. 2012). 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* (hereafter called knots), 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

Knots are medium-sized shorebirds that outside the breeding season usually feed on mollusks (Zwarts and Blomert 1992, Piersma et al. 1993a, 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 light:dark) 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 breakwaters 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. 4.1). The water in the arena was

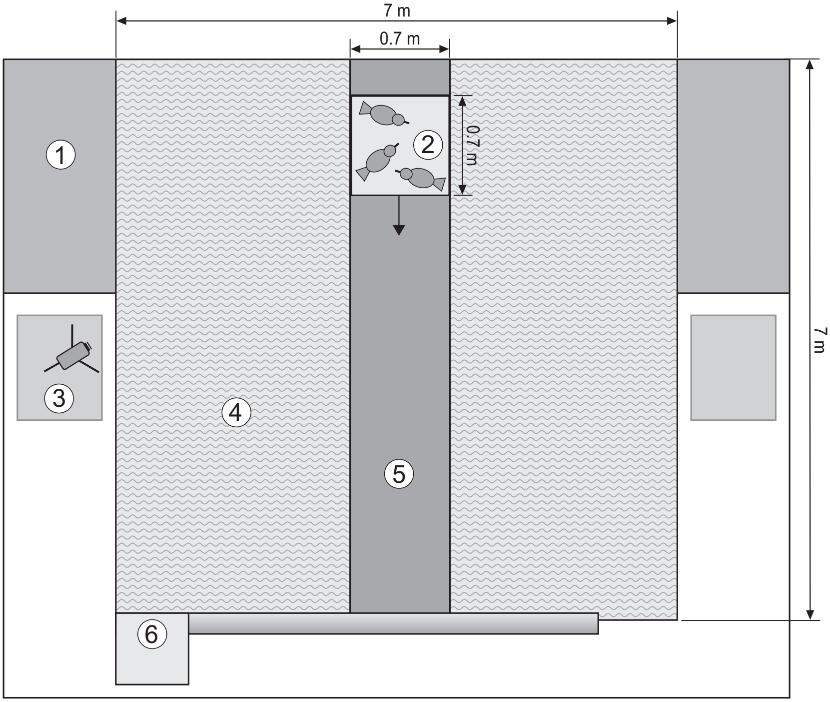


Figure 4.1 The experimental shorebird facility: 1) aviary, 2) food patch, 3) observation hide, 4) water, 5) covered lane and 6) electrical engine with beam to roll the sheet on. 2, 4 and 5 make up the experimental "arena".

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 (see Online Supplementary Material for an example trial video).

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 × 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

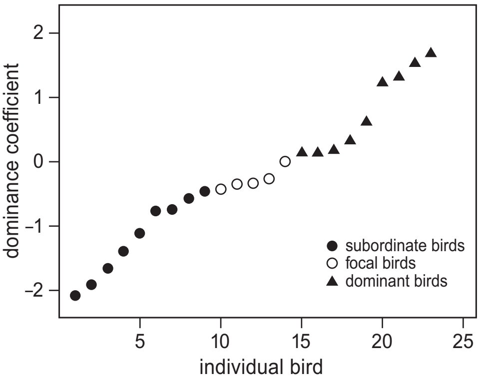


Figure 4.2 Social status of experimental birds ranked by dominance coefficients. The five intermediate birds were selected as focal birds.

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. 4.2): nine subordinates, five intermediates (focal bird group) and nine dominants. The average dominance coefficient per group was: subordinates –1.2 (SE 0.2, $n = 9$), focal birds –0.3 (SE 0.07, $n = 5$) and dominant individuals 0.8 (SE 0.2, $n = 9$) (Fig. 4.2).

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. 2005b), 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 the possibility 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 the most subordinate member of the group. Social status is potentially influenced by group size, but we rarely observed subordinate birds attacking dominants, and 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. 2005b). 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. 4.1) to acclimatize. 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 determine 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. 4.1). 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 (Aitchison 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 (Aitchison 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 2002). 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 4.1A and Figure 4.3A 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 linearly with ln(group size). The decline was approximately equal for both prey densities (–0.028 SE 0.003; Fig. 4.3A and Table 4.1A). 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 4.1B, Fig. 4.3B), but was not affected by either prey density or social status.

Table 4.1 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 (cm^2 s^{-1})	Intercept**	54.32	4.12	<0.01
		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

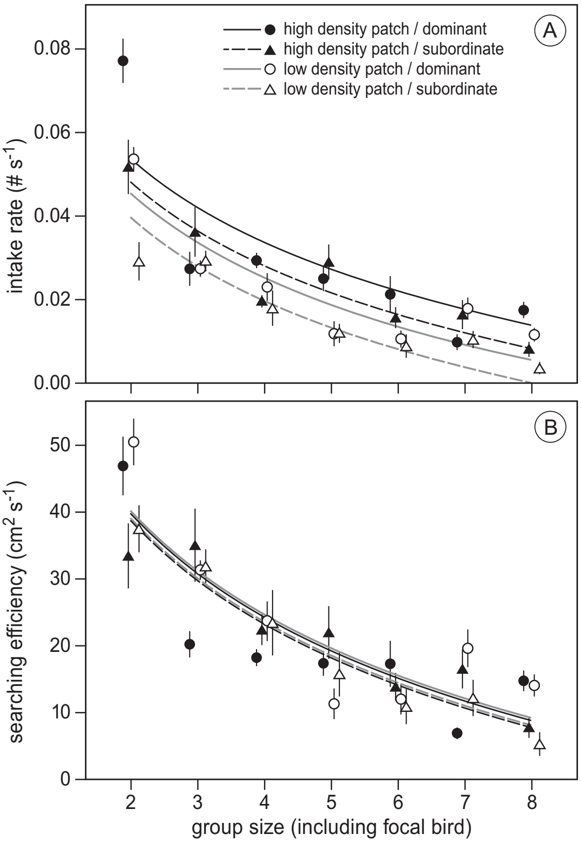


Figure 4.3 Intake rate (# s^{-1}) (panel A) and searching efficiency (cm^2 s^{-1}) (panel B) as functions of group size. The plotted lines are based on the final regression models (Table 4.2). Vertical bars denote standard errors of the means. The values on the x-axis are adjusted for graphical representation.

Time budgets

Focal birds tended to spend less time off-patch when they were in dominant positions than when they were in subordinate positions (Table 4.2A). However, the fraction of time spent off-patch did not differ by prey density or by group size.

From Table 4.2B and Figure 4.4A 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 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 4.2C, Fig. 4.4B). For

Table 4.2 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 4.1. Model estimates 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) × 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) × Group size*	-0.17	0.07	0.02
Random effects		Focal Bird	SD = 0.35		
		Residual	SD = 0.75		
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		

Table 4.2 Continued

	Behaviors	Predictors	Coefficient	SE	P
F) Fixed effects	Handling time (s)	Intercept**	-0.64	0.10	<0.01
		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 (# min^{-1})	Intercept	0.05	0.09	0.62
		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) × 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

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.

The fraction of time spent moving increased with group size (Table 4.2D, Fig. 4.4C). 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 4.2E, Fig. 4.4D). In addition, birds in dominant positions spent less time on interactions than in subordinate positions.

Table 4.2F shows that neither 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 (Table 4.2G).

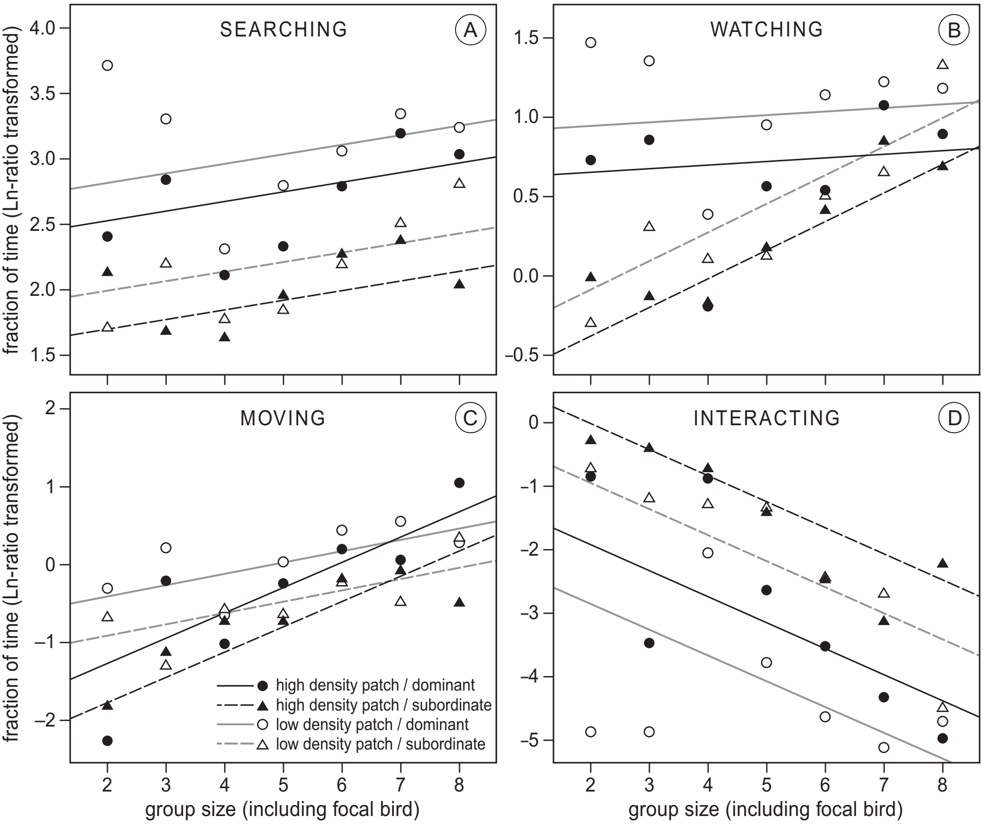


Figure 4.4 Mean transformed fractions of time spent on searching for prey (A), watching (B), moving on the food patch (C) and on interacting with conspecifics (D). The plotted lines are model estimates for prey densities and social status (Table 4.2). Note the differences in range on the vertical axes between panels. Each point in the graph represents the mean value.

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 the possibility 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 Kamil 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 efficiencies, 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 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. 2006b, 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 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 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. 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).

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Chapter 5

Beyond the information centre hypothesis

COMMUNAL ROOSTING FOR INFORMATION ON FOOD, PREDATORS, TRAVEL COMPANIONS AND MATES?

Allert Bijleveld, Martijn Egas,
Jan van Gils and Theunis Piersma

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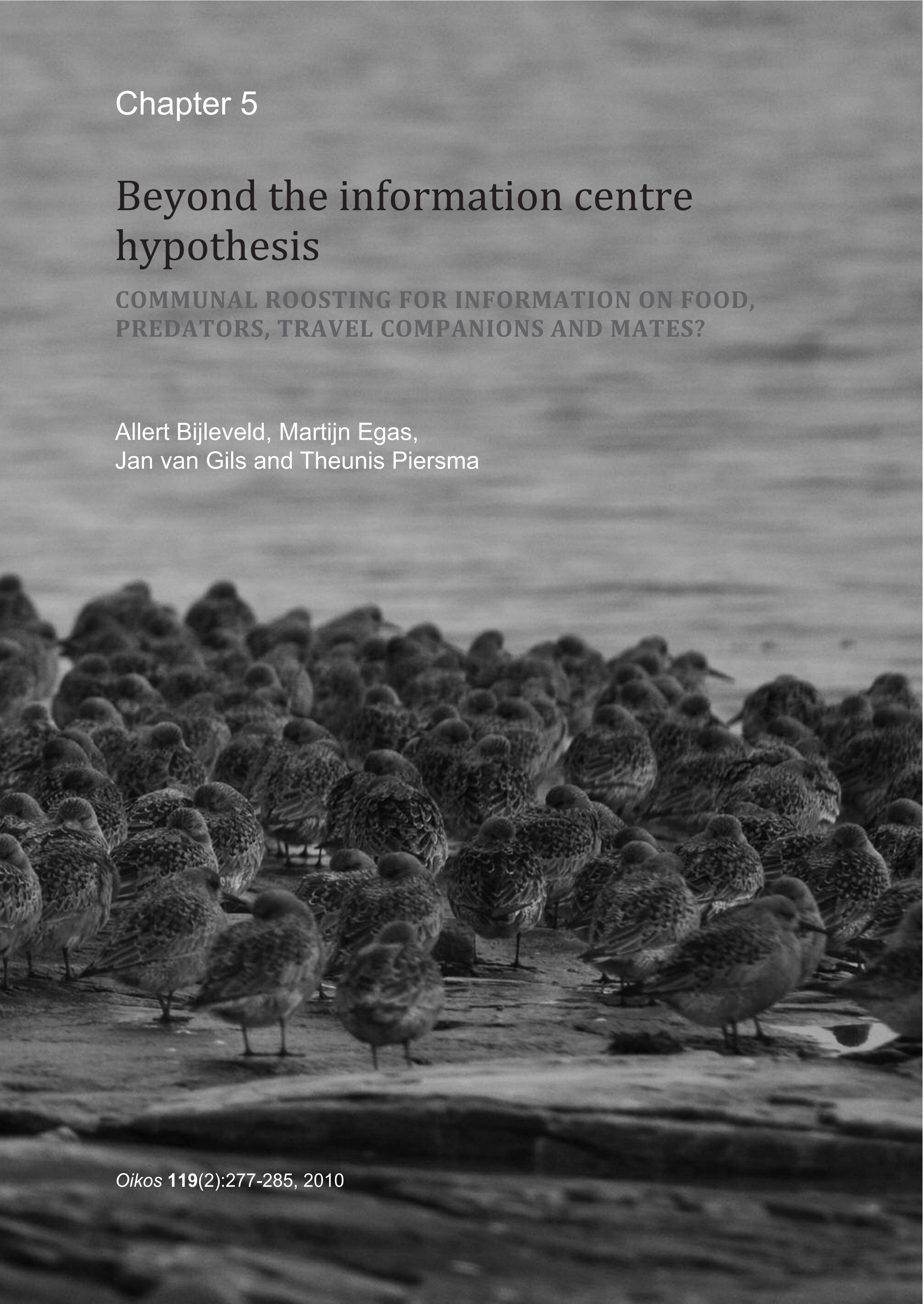

SUMMARY Communal roosting – the grouping of more than two individuals resting together – is common among animals, notably birds. The main functions of this complicated social behaviour are thought to be reduced costs of predation and thermoregulation, and increased foraging efficiency. One specific hypothesis is the Information Centre Hypothesis (ICH) which states that roosts act as information centres where individuals *actively* advertise and share foraging information such as the location of patchily distributed foods. Empirical studies in corvids have demonstrated behaviours consistent with the predictions of the ICH, but some of the assumptions in its original formulation have made its wide acceptance problematic. Here we propose to generalise the ICH in two ways: (1) dropping the assumption that information transfer must be active, and (2) adding the possibilities of information exchange on, for example, predation risk, travel companions and potential mates. A conceptual model, inspired by shorebirds arriving at roosts after foraging on cryptic prey, is proposed to illustrate how testable predictions can be generated. The conceptual model illustrates how roost arrival timing may convey inadvertent information on intake rate, prey density, forager state (i.e. digestive processing capacity) and food quality. Such information could be used by naïve or unsuccessful foragers to select with whom to leave the roost at the subsequent foraging opportunity and thus increase foraging success. We suggest that inadvertent information transfer, rather than active information exchange, predominates in communal roosts.

INTRODUCTION

Communal roosting occurs in taxa such as mammals (Lewis 1995), insects (Yackel Adams 1999) and arachnids (Grether and Donaldson 2007), but is best known from birds (Eiserer 1984). In this paper we focus on communally roosting birds and define a communal roost as a group of more than two individuals that come together to rest (Beauchamp 1999). The size of roosting groups varies from a few individuals as seen in house finches *Carpodacus mexicanus* (Dhondt et al. 2007), to roosts of several hundred-thousand individuals as in some songbirds and shorebirds (Black 1932, van de Kam et al. 2004, Winkler 2006). Within roosts, individuals can be highly site-faithful and consistently use the same resting spot (Eiserer 1984). In shorebirds, Charadrii, communal roosting sites can offer a degree of safety, if they are located in open areas with unobstructed views of their surroundings (Piersma et al. 1993a, Rogers et al. 2006, Rosa et al. 2006). In contrast, forest birds such as owls prefer concealed roosts in trees (Hayward and Garton 1984, Wijnandts 1984). Some communal roost locations can be used for many years. Some roosts of starlings *Sturnus vulgaris* have for instance existed for more than 180 years (Davis 1955). Despite extensive study and debate, the evolutionary origin of communal roosting remains unresolved (Danchin et al. 2008).

A classical way to view the evolution of communal roosting is by cost-benefit analyses. Costs associated with communal roosting can consist of increased exploitative and interference competition (Grover 1997, Keddy 2001), increased likelihood of detection by predators (Page and Whitacre 1975, Eiserer 1984), and transmission of pathogens and parasites (Moore et al. 1988, Kulkarni and Heeb 2007, Buehler and Piersma 2008). Benefits include reductions in thermoregulation costs (Brenner 1965, Wiersma and Piersma 1994, Hatchwell et al. 2009), safety by numbers from predation, as well as increased predator detection (Lack 1968, Gadgil 1972, Krebs and Davies 1993, Krause and Ruxton 2002), and increased information on foraging opportunities (Ward and Zahavi 1973).

Contradicting the main viewpoint at that time – that the evolutionary origin of communal roosting was only related to safety from predators – Ward & Zahavi (1973) argued (1) that roosts and breeding colonies could act as information centres where individuals *actively* advertise and share information on the location of patchily distributed foods, and (2) that this advantage was the *primary* evolutionary origin of communal roosting. This became known as the Information Centre Hypothesis (ICH). However inspiring, the ICH has been surrounded by controversy and objection, in particular that information benefits were the primary origin of communal roosting (e.g., Richner and Danchin 2001). To date, several studies have shown that the use of social information can promote group living (Danchin and Wagner 1997, Danchin et al. 1998, Brown et al. 2000, Wagner et al. 2000, Dall 2002, Wagner and Danchin 2003, see Danchin et al. 2008). Nonetheless, the evolutionary origin of communal roosting remains obscure, probably because there is no *single* benefit which led to the evolution of communal roosting (Crook 1965, Beauchamp 1999). The debate on the evolutionary origin of communal roosting has overshadowed the debate that communal roosts could serve as information centres. In this contribution we will focus on the information centre mechanism of communal roosting and the information benefits individuals could gain. *Information* is defined as “anything that reduces uncertainty and changes the state of the receiver in a potentially functional manner” (from Jablonka 2002, and see Danchin et al. 2004, Dall et al. 2005).

Empirical evidence for communal roosts as information centres is mostly lacking (Mock et al. 1988, Richner and Heeb 1995). Some argue that the ICH should be abandoned all together, because more parsimonious hypotheses are available (e.g., Richner and Heeb 1995, Danchin and Richner 2001) and the ICH does not describe an evolutionary stable strategy (ESS). The evolutionary maintenance of advertising foraging success to unrelated individuals can only be explained by reciprocal altruism, whereby individuals gain and lose in turn (Mock et al. 1988, Richner and Heeb 1995). This, however, is thought an unlikely condition for roosting birds, because roost composition is very dynamic (e.g., Conklin and Colwell 2008) and cheaters would be hard to identify and punish (Trivers 1971). There are several reasons, however, why communal roosts could function as information centres. Modelling studies have provided evidence that even in the presence of cheaters some individuals will always keep searching for new food patches as long as a ‘finder’s fee’ exists (Barta and Giraldeau 2001). Additionally, Lachmann et al. (2000) showed that individuals living in groups have more information available and at lower costs, and that communal roosting can be an ESS if information cannot be hidden from roost mates. If information is inadvertent, aggregations could be maintained through information-sharing mechanisms and be evolutionarily stable. On the other hand, there are cases in which information is exclusive and where the sharing of information has a cost, e.g., active information transfer by displaying. In such cases, mechanisms must operate that enable the information provider to benefit from providing information (Danchin et al. 2008), as in the two strategy hypothesis (Weatherhead 1983), or the recruitment centre hypothesis (Richner and Heeb 1995) or through kin selection (e.g., Danchin et al. 2008).

More than thirty years after publication of the ICH, its validation remains unresolved and controversial. Now, advancements in the “ecology of information” and the emergence of an information framework (e.g., Danchin et al. 2004), allow for a reconsideration of the ICH. In the present attempt, we will first review recent empirical evidence for the ICH. Second, we will generalise the ICH. Finally, we will present a framework to guide future studies of information use at communal roosts, i.e. a conceptual model that allows for testable predictions.

EMPIRICAL SUPPORT

Since Ward & Zahavi (1973), many studies have examined the possibility of communal roosts acting as information centres, but usually fail to provide convincing evidence (see Ydenberg and Prins 1984, Mock et al. 1988, Richner and Heeb 1995). Generally, local enhancement (e.g., foragers cueing in on individuals that are already foraging and visible from the roost) cannot be ruled out (Mock et al. 1988, Richner and Heeb 1995). Until recently, only two studies on breeding colonies found evidence consistent with information centre mechanisms (Brown 1986, Waltz 1987), and just one such study is available for communal roosts (Rabenold 1987). Nonetheless, several elegant and more recent studies now provide observations that are consistent with the idea that communal roosts act as information centres. Marzluff et al. (1996) experimentally made some common ravens *Corvus corax* knowledgeable by releasing them at newly created food sites, and kept others naïve by holding them captive for 2–30 days. After visiting a communal roost, dominant knowledgeable birds led roost mates to the food sources on several occasions. In another study on common ravens, Wright et al. (2003) observed that common ravens that discovered carcasses engaged in pre-roost display flights and initiated early morning departures. Successive observations suggest that information on the location of carcasses was obtained by naïve birds that roosted close to the knowledgeable birds. Communal roosts of hooded crows *Corvus corone cornix* also appear to act as information centres. Sonerud et al. (2001) created an unpredictable and ephemeral food distribution and radio-tracked 34 hooded crows. They report that naïve birds that roosted with knowledgeable birds (i.e. birds that had discovered food sites on their own) were more likely to find food sites than when no knowledgeable roost mates were present. Buckley (1997) reports that black vultures *Coragyps atratus* benefit from communal roosting because they were able to locate food by following knowledgeable conspecifics to carcasses.

GENERALISING THE INFORMATION CENTRE HYPOTHESIS

The previous section shows that empirical evidence for the ICH is available only for birds that face very patchy and temporary food conditions (i.e. carrion feeding corvids and vultures). Communal roosts as information centres might also be advantageous under less extreme foraging conditions. Moreover, the empirical evidence mostly focuses on advertent information transfer communicated through signals. For example, the aerial displays at common ravens roosts. Even if they represent advertisements of foraging opportunity, such signals might advertise individual quality and thus increase the chance of finding a high-quality mate (Marzluff et al. 1996, Wright et al. 2003). In agreement with Evans (1982) and Waltz (1982, 1987) information does not need to be actively transferred. Indeed, inadvertent information (Valone 1989, Danchin et al. 2004) might be a more general and likely source of information at communal roosts. Inadvertent information can be available as food carried in the beak or claws, distended crops, foraging frequency, and body condition (see Mock et al. 1988).

By its very nature, inadvertent information cannot be withheld by the providers and therefore its use at communal roosts can be an ESS (Lachmann et al. 2000). As long as the pay-off for roosting communally outweighs that of solitarily roosting, individuals will return to communal roosts and thereby reveal inadvertent information to the potential benefit of roost mates. Moreover, under various conditions birds may even be forced to

Table 5.1 The power of observational components to falsifying the generalised Information Centre Hypothesis based on the taxonomy proposed by Mock et al. (1988).

	ICH component	Critique	References	Essential
1	Site fidelity	Innate differences in foraging abilities, such as the efficiency in locating food sites, could exist between individuals (e.g., adults and juveniles). Unsuccessful individuals can then follow skilled individuals to increase foraging success, and thus site fidelity is not essential for an information centre mechanism.	Weatherhead (1983), Rabenold (1987)	no
2	Differential success	–		yes
3	Detection	Ward & Zahavi (1973) argue that successful foragers actively advertise their foraging success to aid detection by unsuccessful foragers. Even though differential behaviour between successful and unsuccessful individuals can facilitate information sharing, behavioural differences are not a necessary condition. An unsuccessful individual could randomly select a roost mate to follow and thus increase foraging success. In addition to active information transfer, unsuccessful roost mates could use inadvertent information.	Waltz (1982), Waltz (1987) and Mock et al. (1988)	no
4	Synchronous departure	Synchronous departures can be mitigated by weather, tidal regime, precise language, limited compass directions, variable predation risks, etc. Therefore, it is not an essential component for support nor falsification of the ICH.	Bayer (1982), Mock et al. (1988) and Richner & Heeb (1995)	no
5	Following	As opposed to strict following to the exact foraging site, the general direction that a (successful) roost mate takes can provide information on foraging success. Following should be seen more generally as adjusted behaviour.	Ward & Zahavi (1973)	maybe
6	Toleration	Competitively better foragers could use competitively inferior roost mates to locate food sites. At the foraging site the latter information suppliers could be displaced by the competitively more able followers. Such inferior individuals could keep returning to communal roosts, because roosting solitarily is more costly. Toleration at food sites is thus not an essential component of the ICH.	Weatherhead (1983)	no
7	Pay-off	The (long-term) pay-off of information use does not need to be positive for communal roosts to function as information centres. This depends entirely on the total costs and benefits of communal roosting versus those of solitary roosting. For instance, the information pay-off could be negative, but as long as the pay-off of roosting solitarily is more negative than that of communal roosting, communal roosts can exist and could possibly function as information centres.	Danchin et al. (2008)	no

return to communal roosts. In coastal areas, for example, shorebirds are forced to retreat to areas not submerged during high tide (van de Kam et al. 2004, van Gils et al. 2006b). Because information at the communal roost is inadvertent, cheating by withholding information is not possible and punishing cheaters becomes irrelevant which increases the likelihood of reciprocal behaviour. The principle holds even for large communal roosts with variable membership. Given these conditions, we suggest that the ICH should be generalised such that: (1) besides advertent information, communal roosts are information centres for inadvertent information, and (2) communal roosts can be seen as information centres on foraging opportunities, but also on other types of information (e.g., on predators, timing of migration, potential mates, etc.).

Mock et al. (1988) suggested a seven-link chain of events to falsify the ICH. Here, we argue this falsification chain should be abandoned, because most of the components do not suffice for falsifying the general concept that communal roosts act as information centres (Table 5.1). Instead, we propose two essential components which can be used for its falsification: (1) differential success and (2) adjusted behaviour. First, differential success establishes that successful individuals have information and unsuccessful individuals are in need of this information. Second, information becomes meaningful if it results in behavioural change. Therefore, unsuccessful individuals should adjust their behaviour according to the gathered information. Information transfer can be falsified if it can be shown that members of a communal roost do not comply with one of these two components. Note that the long-term pay-off (component 7, Table 5.1) for individuals in communal roosts does not need to be positive for communal roosting to be an ESS as long as the pay-off for roosting solitarily is lower.

Inadvertent social information on foraging

There are many ways in which inadvertent social information may be used by individuals to improve their foraging success. For instance, unsuccessful individuals could benefit from inadvertent social information by following the fattest roost mates to their foraging sites. Besides fatness, any other cue can be used when it is a reliable indicator of foraging success (below, we provide examples based on arrival time at the roost). Unsuccessful foragers can even follow randomly selected roost mates to increase foraging success, assuming that they have an estimate of their relative foraging success. When unsuccessful foragers decide to search for a new food patch, they face the problem that such a patch could be located in every direction from the roost. By following a random roost mate they are more likely to arrive at a food patch, while saving the costs of searching for one. Moreover, previously unsuccessful birds will have lower site-faithfulness than successful birds and departure directions would be skewed towards more rewarding food sites (Waltz 1982, 1987). Therefore, the chances of finding a better food site are larger than finding one that is worse in case an unsuccessful individual (i.e. a birds with lower than median foraging success) follows a random roost mate to its foraging area. An individual needs only a measure of median foraging success in the surrounding environment and of one's own success, which might be as simple as body condition or intake rate at the previously visited patch. It has been shown that animals are able to assess foraging success and adjust foraging decisions accordingly (Valone 1989, Galef and Giraldeau 2001, Coolen et al. 2003, van Gils et al. 2003b, Valone 2006).

Other kinds of social information

In communal roosts other kinds of social information than foraging information can be available. Here we give some examples of social information that could be available to the benefit of roost members.

As proposed for breeding colonies, communal roosts might function as "hidden leks" where extra-pair copulations could occur (Wagner 1993), and public information on the quality of mates and the distribution of potential mates can be obtained. This could increase the likelihood of choosing the best mate and thereby increase fitness (White 2004). For instance, there is evidence that communal roosting reduces costs of mating and territory acquisition in red-billed choughs *Pyrrhocorax pyrrhocorax* (Blanco and Tella 1999). Indeed, finding a mate at a communal roost might be easier than away from it (Møller 1985). After the breeding season, the proportion of juveniles within a communal roost might also provide public information on breeding habitat quality surrounding the roost. Black-legged kittiwakes *Rissa tridactyla* were able to estimate breeding habitat quality by observing breeding success of neighbours within a breeding colony (Boulinier et al. 2008). Members of a communal roost could also assess potential opponent quality (Valone and Templeton 2002). Contests might occur over food, territories, nest sites or mates. These contests can be time- and energy-consuming, and might entail a risk of injury (Krebs and Davies 1993). An individual can benefit by obtaining information on fighting ability of possible opponents by observing contests between other individuals (i.e., eavesdropping, Johnstone 2001).

Roosting communally can also provide information on the timing of migration to allow synchronised departures (Helm et al. 2006). Carefully timed migrations may decrease predation risk (Leyrer et al. 2009), and synchronous departures – enabling flight in structured flocks (Piersma et al. 1990) – may help reduce flight costs (Cutts and Speakman 1994, Weimerskirch et al. 2001). The advantages of synchronized departure and group flight during migration can also apply to commuting between roosts and food sites.

Information on the timing of moult might also provide fitness benefits through its synchronization. Mallards *Anas platyrhynchos* are stimulated to moult by the presence of moulting flock mates (Leafloor et al. 1996). Moulting reduces flight ability and thus increases the risk of predation. By moulting synchronously, an individual reduces the risk of predation compared to when moulting alone.

Selective learning may help to increase reproductive success for communally roosting birds when different types of song are available (Catchpole 1986, Hasselquist et al. 1996). Songs of male brown-headed cowbirds *Molothrus ater* differ between populations, and females are more responsive to male song from their own population than from other populations. Similarly, female cowbirds developed a preference for song types typical of their cage mates (see Galef and Laland 2005).

Information on potential predators might be available in communal roosts as well. This can be especially beneficial when a novel predator enters the habitat. Through fright behaviour from roost mates, such a predator can be identified without direct exposure (Griffin 2004).

Supply and demand of information

Within a communal roost certain members might have information that others are in need of. The supply and demand of information can vary with individual, species, time and location. During winter, information on food may be more important than information on potential mates. At the beginning of a breeding season priorities would change. Moreover, the higher the benefit of information – or the higher the costs of acquiring this information through trial and error – the higher the demand will be, and the higher the adaptive significance of communal roosts as information centres. Given the diversity in temporally fluctuating information, its sum can provide year-round information benefits in communal roosts. The available information, either advertent or inadvertent, can be used without direct benefit to the information provider. Alternatively, both the supplier and the receiver(s) of information can directly benefit from the exchange of information. In such a case communal roosts could be seen as information markets (Noë and Hammerstein 1994, Seppänen et al. 2007). For instance, successful foragers might negotiate foraging information with unsuccessful individuals for premium roosting positions (e.g., safety from predators sensu Weatherhead 1983). Or successful common ravens could negotiate a share of discovered carcasses with unsuccessful individuals in return for displacement of competitors at the carcass through group size, i.e. gang foraging (Wright et al. 2003, Dall and Wright 2009).

CONCEPTUAL MODEL: USING ROOST ARRIVAL TIMING AS INFORMATION ON INTAKE RATE, FORAGER STATE, AND PATCH AND DIET CHOICE

In this section we present a framework to guide future empirical studies on information use at communal roosts by illustrating how roost arrival timing may convey information on *where*, *with whom* and *on what* to forage. We demonstrate the framework by presenting a conceptual model based on what we already know about red knots *Calidris canutus* (hereafter called knots) in the Dutch Wadden Sea, but it is applicable to a wide range of communally roosting species.

Where to forage?

The time necessary for individuals to achieve their daily required energy intake depends on their average instantaneous energy intake rate. If we assume that knots are time-minimisers (sensu Schoener 1971, for which there is evidence as shown in van Gils et al. 2003a, van Gils et al. 2005b), aiming to collect no more than the amount of energy which they are going to spend, and that the rate of expenditure does not vary between individuals, then their daily foraging time is a good predictor of their energy intake rate.

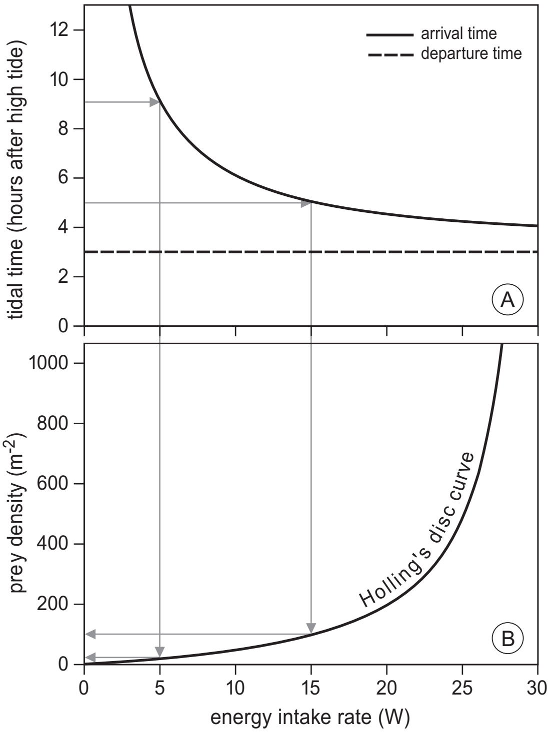

Figure 5.1 (A) Conceptual model showing how arrival time of red knot at communal roosts can give an estimate of past intake rate. Arrival time (h after high tide) can be predicted, given that knots are time-minimisers, leave the roost simultaneously 3 h after high tide, have equal energy requirements of 3.5 W (Piersma et al. 2003), and that 1.93 tidal cycles fit in 24 h. (B) Via Holling's disc equation (Holling 1959), linking intake rates to prey densities, average prey densities encountered by roost mates can be estimated using arrival times at communal roosts (see two such estimates shown as arrows going from panel A to B). The following parameters were used for Holling's functional response model: energy contents equals 300 J per prey, handling time equals 10 s, and searching efficiency equals 0.001 m^2 s^{-1}.

Furthermore assuming that all birds leave the roost together after high tide such that variation in foraging time is reflected in roost arrival times, roost arrival time becomes a direct function of intake rate (Fig. 5.1A). Individuals with high intake rates will return to the roost earlier, because they need less time to suffice their requirement. If a forager faces no other constraints on its intake rate than the rate of finding and the rate of handling food, then Holling's type II functional response (Holling 1959) couples the "expected intake rate" to an "expected prey density" (Fig. 5.1B), and thus roost arrival times can be indicators of prey density (Fig. 5.1B). A prediction resulting from this model would be that at the subsequent low tide period, unsuccessful foragers would follow individuals that had arrived at the roost early.

With whom to forage?

Currently, it is increasingly acknowledged that Holling's type II functional response model ignores an important constraint that many foragers may face. Most species are constrained by their digestive processing capacity before prey encounter rate or handling time become limiting (Jeschke et al. 2002). The red knot typically forages on molluscs buried in the sediment of intertidal mudflats (Zwarts and Blomert 1992, Piersma et al. 1993a). Once discovered, molluscs are swallowed whole and crushed in their muscular gizzards (Piersma et al. 1993b). The size of the gizzard constraints digestive processing rates (van Gils et al. 2003a, van Gils et al. 2005b), therefore, intake rate is not only a function of prey density, but also of gizzard size (Fig. 5.2A). At intermediate and high prey densities, the variation in intake rate is determined by gizzard size and not by prey density. In such cases, arrival time can give an estimate on gizzard size (Fig. 5.2B). A prediction that follows is that arrival times will be negatively dependent on gizzard sizes. Data from a radio-tracking study confirmed the presence of this negative relationship (Fig. 5.2C, based on van Gils et al. 2005b). Additionally, the birds leave the high-tide roost together, which is consistent with the assumption that knots minimise their time at the return to the roost rather than at their departure (Fig. 5.2C). For species that face a digestive constraint, information on individual state (i.e. digestive capacity) could be useful, for instance, because foraging with individuals in similar state could provide synchronization of behaviour. Given similar prey types and densities, individuals with large gizzards have higher intake rates than individuals with small gizzards. Therefore, individuals with larger gizzards satisfy their required intake quicker than individuals with smaller gizzards, and will return to the communal roost earlier (Fig. 5.2B). The consequence for an individual with a relatively small gizzard joining birds with large gizzards would be to remain on the food site alone with possible increased predation risk, or return to the roost unsatisfied. Of course, the question remains, if gizzard size and not food density determines intake rate, why different individuals go to different patches. All patches would anyhow yield the same intake rate, as determined by a bird's gizzard size. In case of the knot, the answer to this question lies in the variation in food *quality*.

On what food type to forage?

Prey can differ in quality (i.e. the amount of energy per gram indigestible shell mass) and patches of low and high quality can be found (Fig. 5.3A). Whenever high-quality prey is collected at a slower rate than low-quality prey (e.g., because densities of high quality prey are lower), this leads to gizzard-size-dependent optimal patch choice (van Gils et al. 2005b). Knots with small gizzards would maximize their energy intake rate in patches containing slowly collected high-quality prey, while birds with large gizzards would maximize their energy intake rate in patches containing rapidly collected low-quality prey (Fig. 5.3B). In such cases, gizzard-size-dependent patch choice would be expected. Indeed, published data reveal that knots with small gizzards forage on patches with high-quality prey, and knots with large gizzards forage on patches with low-quality prey (Fig. 5.3C, based on van Gils et al. 2005b). Arrival timing is a function of gizzard size, and could thus

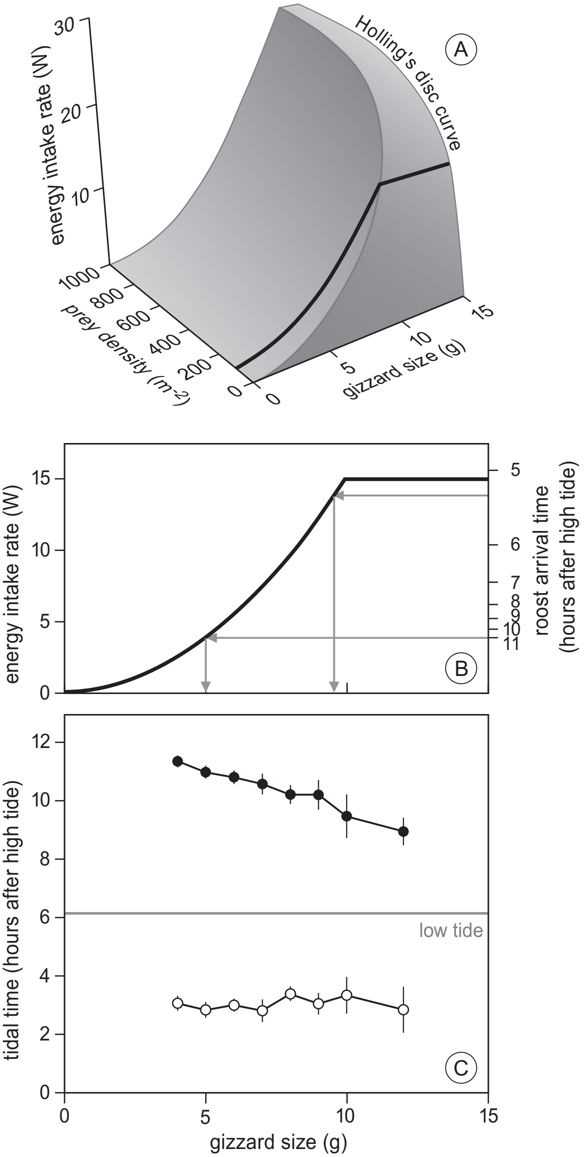

Figure 5.2 (A) The functional response taking digestive processing capacity into account. At low prey densities red knot intake rate is constrained by Holling's disc equation, but at higher prey densities by digestive processing capacity (i.e. gizzard size). The black line indicates an example intake rate as a function of gizzard mass (g) at a fixed prey density of 100 m^{-2}. (B) The black line in (A) is plotted here in a 2-D perspective. Given that individuals are digestively constrained, gizzard size determines intake rate and can be estimated from arrival times (arrows). The digestive constraint is empirically derived as: $0.05 \cdot q \cdot$gizzard mass^2 (van Gils et al. 2003a), where q denotes prey quality which equals prey energy content divided by shell content, the latter here set at 100 mg per prey, yielding a value for q of 3 J/mg. (C) Field data of red knot departure and arrival timing from their high-tide roost at Richel. Independent of gizzard mass, knots leave Richel about 3 h after high tide (open circles ± SE). Arrival times back at the roost are as predicted qualitatively (panel B): a declining function of gizzard mass (filled circles ± SE). Quantitatively there is still some mismatch between the predictions and field data, where birds with large gizzards are arriving somewhat later than predicted. Possibly this is because large gizzards incur higher metabolic costs which are not included in the simplified predictions. Data taken from van Gils et al. (2005b).

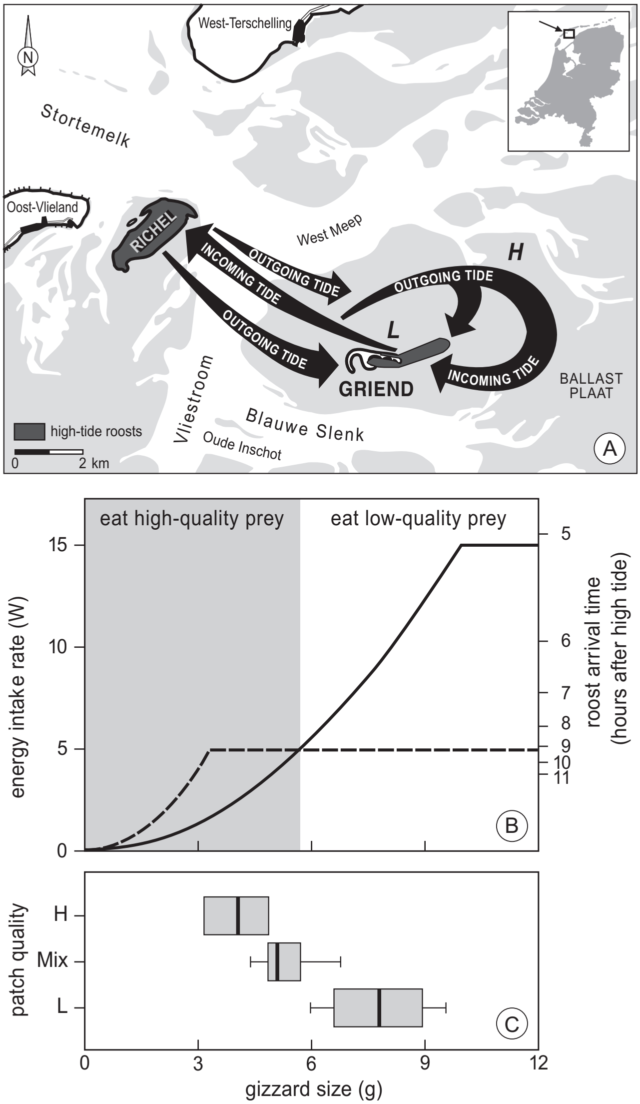

Figure 5.3 (A) Summary of typical red knot foraging itineraries in the western Dutch Wadden Sea, The Netherlands. The figure is taken from Piersma et al. (1993a). The arrows show red knot tidal movements during incoming and outgoing tides. The intertidal area is indicated by shading and bordered by the mean low-water mark at spring low tide. The two high-tide roosts on Richel and Griend are indicated in black. A patch containing low quality food (L) and a patch containing high quality food (H) are indicated based on van Gils et al. (2005b). (B) Arrival times as indicators of food quality. The predicted intake rates are given for the high quality food patch (dashed line; prey quality 9 J mg^{-1}) and the low quality food patch (solid line; prey quality of 3 J mg^{-1}). When high-quality prey occurs in lower densities than low-quality prey, rate-maximizing patch choice depends on gizzard size. In this case, knots with small gizzards (grey surface on the left) should feed at patches with low densities of high-quality prey, while knots with large gizzards (white surface on the right) should feed at patches containing high densities of low-quality prey. Arrival times can give an estimate of gizzard size and with that an estimate of food quality. (C) Field data of patch choice as a function of gizzard mass. The high quality prey patch (H) was only visited by knots with small gizzards, and the low quality prey patch (L) was only visited by knots with large gizzards. Knots with intermediate gizzards visited both patch L and H (mix). Data were taken from van Gils et al. (2005b).

give an estimate of the quality of food that roost mates encountered (Fig. 5.3B, also between years it has been found that food quality determines daily foraging times, van Gils et al. 2007). Given that individuals aim to maximise intake rate, naïve or unsuccessful knots could find the optimal prey type that matches their digestive capacity by following informed roost mates in similar state (i.e. gizzard size) during outgoing tide. A prediction would then be that knots with small gizzards follow individuals arriving at the roost late, but that individuals with large gizzards would follow individuals arriving early.

DISCUSSION

Many studies have attempted to show support for the ICH by investigating roost-departure timing (see Mock et al. 1988, Richner and Heeb 1995). The results, however, remain equivocal because firm predictions were lacking (Mock et al. 1988, Danchin and Richner 2001). Our conceptual model is oversimplified, but meets our purpose of providing a framework to study information use at communal roosts and allow for testable predictions. Some initial predictions would be that (1) a relationship exists between arrival timing and intake rate, forager state, and food quality (and prey density to a certain extent), (2) after observing arrival timing, naïve individuals will follow those individuals to food patches that have similarly sized gizzards. Our study system with knots seems well suited to test such predictions.

Our proposed framework could be applicable to other communally roosting species constrained by available foraging time. This includes corvids gathering food during daytime (Wright et al. 2003), owls hunting at night (Wijnandts 1984), grebes showing crepuscular foraging (Piersma et al. 1988), and shorebirds foraging during low tide (van de Kam et al. 2004, van Gils et al. 2005b). Roost-arrival timing is relatively easy to quantify in the field, but a major challenge will be to identify newly arrived individuals with respect to their prior knowledge and to understand how arrival timing conveys information on intake rate, prey density, forager state, food quality, etc. Another challenge will be to fit these and other kinds of information (e.g., predation risk, moult, mates and travel companions) into this framework. For instance, foraging decisions are usually state-dependent with respect to predation risk (Brown 1988, Olsson et al. 2002), and therefore arrival time at the roost and patch choice may convey information on predation risk. Under a food-safety trade-off without digestive constraints, time-minimization leads to late arrival times under a relatively low risk of predation, and early arrival times under a relatively high risk of predation. Furthermore, such information on predation risk is detectable if animals are able to judge each other's relative vulnerability to predation, e.g., body shape and condition (mass), and moult and plumage states, presumably reflecting the risk (or danger in the terminology of Lank and Ydenberg 2003) that they accepted during their foraging trips. A possible prediction would thus be that individuals in similar state follow each other. These individuals could then benefit in two main ways. First, knowledgeable individuals in a similar state (i.e. body weight) are more likely to have found the optimal food patch given the food-safety trade-off. Thus, naïve birds following knowledgeable birds can reduce the costs of finding such an optimal patch. Second, in case of a predator attack individuals with a relatively large risk of predation (e.g., relatively large body mass, advanced state of primary moult) could avoid being the least manoeuvrable in a group with increased mortality risk by foraging with individuals in similar state.

In this contribution, we have argued to move beyond the original ICH to study the ecological implications of information transfer on food, predators, travel companions and mates in communal roosts. We hope our conceptual model stimulates further development of theory (including, e.g., stochasticity of the environment), generating more quantitatively testable predictions.

Acknowledgements

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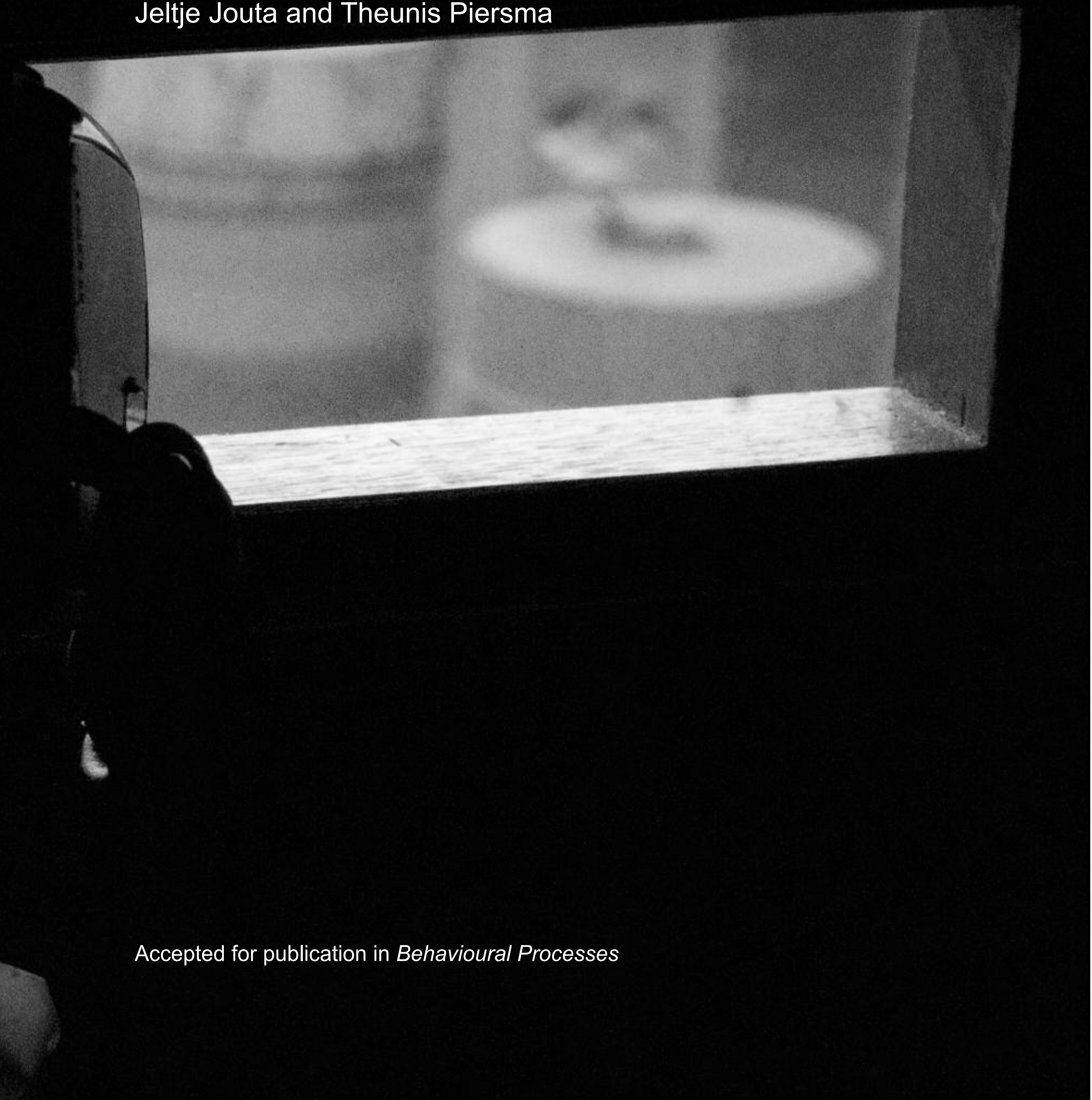
Chapter 6

Benefits of foraging in small groups

AN EXPERIMENTAL STUDY ON PUBLIC INFORMATION USE IN RED KNOTS *CALIDRIS CANUTUS*

Allert Bijleveld, Jan van Gils,
Jeltje Jouta and Theunis Piersma



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SUMMARY Social foraging is common and may provide benefits of safety and public information. Public information permits faster and more accurate estimates of patch resource densities, thus allowing more effective foraging. In this paper we report on two experiments with red knots *Calidris canutus*, socially foraging shorebirds that eat bivalves on intertidal mudflats. The first experiment was designed to show that red knots are capable of using public information, and whether dominance status or sex affected its use. We showed that red knots can detect the foraging success of conspecifics and choose a patch accordingly. Neither dominance status nor sex influenced public information use. In the second experiment, by manipulating group size, we investigated whether public information use affected food-patch discovery rates and patch residence times. We showed that the time needed before locating a food patch decreased in proportion to group size. Also, an individual's number of patch visits before locating the food declined with group size, and, to our surprise, their average patch residence time did as well. Moreover, red knots differed in their search strategy in that some birds consistently exploited the searching efforts of others. We conclude that socially foraging red knots have the potential to greatly increase their food-finding rate by using public information.

INTRODUCTION

Foraging in groups, i.e. ‘social foraging’, is a common phenomenon (Clark and Mangel 1986, Krause and Ruxton 2002, Stephens et al. 2007, Danchin et al. 2008, Sumpter 2010, Beauchamp 2014). The main cost of social foraging is competition for resources (Goss-Custard 1980, Tregenza 1995). The benefits of social foraging include increased safety from predation (Pulliam 1973), increased time that could be spent foraging rather than on anti-predation vigilance (Lima 1995), and the accessibility of public information on the availability and quality of food patches (Clark and Mangel 1984, Danchin et al. 2004, Dall et al. 2005, Valone 2007, Giraldeau and Dubois 2008). There is a growing body of literature on public information use in a range of different species (see Valone 2007, Blanchet et al. 2010, Rieucau and Giraldeau 2011). Public information was originally narrowly defined as ‘information on the quality of a food patch’ (Valone 1989). Following Wagner and Danchin (2010), we adopt the broad and intuitive definition of public information as ‘any potential information that is accessible to others’ (i.e. any information that is not private).

Public information can indicate the location of food (local enhancement, Thorpe 1956, Pöysä 1992), as well as the quality (e.g., food density) of a food patch (Valone 1989). Many different species use local enhancement to select where to eat (Galef and Giraldeau 2001). It is especially beneficial when food is clumped and patches are large enough not to be monopolized (Beauchamp 1998); if patches are small, dominant foragers can exploit food discoveries of subordinates (Vahl and Kingma 2007). Several studies have shown that the time needed to discover food patches decreases with group size (Pitcher et al. 1982, Beauchamp 1998, 2014). The slope of this relationship on a double log scale allows quantification of the effect of increased group size on food patch discovery rate (comparable to the ‘additivity coefficient’, Ranta et al. 1993). A slope of -1 indicates that the time needed to find a food patch declines proportionally to group size (full additivity). A slope between -1 and 0 indicates diminishing returns in patch-finding rate as group size increases, e.g., as group size increases foragers spend more time keeping track of the foraging success of others at the expense of finding food themselves.

Information gained from nearby foraging conspecifics can help individuals make more accurate and faster estimates of patch resource density (Clark and Mangel 1984, 1986, Valone 1989), i.e. allowing foragers to maximise energy gain by wasting less time in unprofitable patches (Charnov 1976, Templeton and Giraldeau 1996, Smith et al. 1999, Valone and Templeton 2002, van Gils et al. 2003b, Coolen et al. 2005). Foragers can optimise their patch residence times by means of Bayesian updating (McNamara et al. 2006, Valone 2006). Central to Bayesian updating is that foragers optimise their patch departure decision by combining prior information on resource density with sampling information on a patch (Oaten 1977, Green 1980, McNamara and Houston 1980, Iwasa et al. 1981, McNamara 1982, McNamara et al. 2006). By using public information, personal sampling information can be complemented to then allow faster and more accurate estimates of patch resource density (Clark and Mangel 1984, 1986, Valone 1989). Although Bayesian updating was at the core of studying public information (Valone 1989), few studies have combined the two approaches (e.g., Valone and Giraldeau 1993, Templeton and Giraldeau 1995).

Red knots *Calidris canutus* (hereafter called knots) are shorebirds that forage on patchily distributed bivalves that live burrowed in the soft sediments of intertidal mudflats (Zwarts and Blomert 1992, Piersma et al. 1993a, van Gils et al. 2005a, Kraan et al. 2009a, Kraan et al. 2009b) (reviewed in Piersma 2012). In search of their hidden prey, knots sample the mudflat by probing the sediment (Piersma et al. 1998). When a prey is detected, it is briefly handled and subtly moved into the mouth without any obvious swallowing motion (see Online Supplementary video at http://dx.doi.org/10.1016/j.beproc.2014.09.003). Previously, van Gils et al. (2003b) experimentally showed that individual knots are capable of Bayesian updating to maximise the net energy gain while exploiting patches. Knots regularly forage in groups of 4,000–15,000 individuals (Piersma et al. 1993a). Due to the large spatial extent of food patches (Kraan et al. 2009b), knots can avoid costs of interference competition in the field (Chapter 4, van Gils and Piersma 2004, Vahl et al. 2005b, van Gils et al. 2015). In combination with the cryptic nature of their buried prey, this makes knots likely candidates for using public information to increase their foraging success (Chapter 5).

In this paper we report on two complementary experiments. The first experiment was designed to show that foraging knots are capable of detecting food discoveries of group mates and use this public information to locate hidden food patches. The second experiment was designed to quantify the benefits of group size per se (i.e. public information) on patch discovery rates and patch residence times. In the first experiment we challenged knots to choose between two foraging patches in a dichotomous preference test. Both patches had two foraging knots (demonstrator birds), but only one patch contained burrowed (hidden) prey items. As dominant foragers are predicted to take advantage of public information more than subordinate foragers (Barta and Giraldeau 1998), dominance was incorporated as an explanatory variable.

In the second experiment we offered 48 patches of which only one contained hidden prey. We manipulated the level of public information by varying group size between 1 and 4. We recorded cumulative searching time and number of patches visited before finding the food patch, and calculated patch residence times. Assuming that knots search randomly between patches, we hypothesize that the number of patch visits declines proportionally to group size. Patch residence time should not be affected by group size as it depends on patch sample information (e.g., Valone 1989) that was not publicly available (each patch would accommodate one bird only). As cumulative searching time equals the number of patch visits times the average patch residence time, we hypothesize that cumulative searching times should also decrease proportionally to group size.

MATERIALS AND METHODS

Experiment 1: do knots use public information?

On 28 September 2008, 20 adult knots *Calidris canutus islandica* were caught with mist nets near the islet of Griend, The Netherlands (53°15' N, 5°15' E), and brought back to the NIOZ Royal Netherlands Institute for Sea Research, Texel, The Netherlands. The birds were housed in aviaries that were 4.5 m long, 1.5 m wide and 2.5 m high and lined with white Trespa (Trespa International BV, Weert, the Netherlands). The aviaries were equipped with running salt water along a coated concrete surface, fresh water for drinking and bathing, and a stretch of sand covered in 5 cm water to resemble the knots' natural mudflat habitat. The birds were maintained on a diet of blue mussels *Mytilus edulis*.

In order to estimate relative dominance of all birds, we recorded the number of pairwise aggressive interactions between foraging individuals, i.e. threatening, charging (moving towards conspecifics), and receding. We also scored the winners and losers of each interaction (n = 831). Individuals that retreated from an aggressive interaction were taken as losers. We observed these aggressive interactions in two 15 minute sessions each day for 10 days prior to the experiment. On the basis of these interactions, and assuming transitivity (i.e. if bird A is dominant over B and B is dominant over C, then A is dominant over C), we calculated dominance coefficients with a logistic regression (for details on the dominance hierarchy analyses see Chapter 4 and van der Meer 1992). We divided the knots into three dominance groups: five subordinates, ten intermediates and five dominants. The most and least dominant birds were 'focal birds', while the intermediate group would act as 'demonstrator birds' during the trials (Fig. 6.1).

The setup for this experiment was comparable to previous experiments on social information use (e.g., Coolen et al. 2005). We divided the indoor experimental arena (7 m × 7 m × 3.5 m) in two equal halves separated by a polyester sheet (Fig. 6.2A). In each of the two halves we placed one patch of 1 m^2 and 20 cm deep filled with wet sand. In the middle of the arena we cut a hole in the polyester sheet to fit a cubical cage (1 m^3) made of wired mesh (1 cm^2). On the two sides of the cage – facing both patches – vertical sliding doors

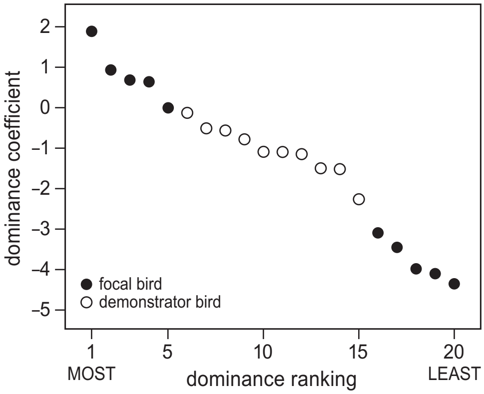

Figure 6.1 Social status of the birds in experiment 1 ranked by dominance coefficients. The five most and five least dominant birds were selected as focal birds, and the 10 intermediately dominant birds were selected as demonstrator birds.

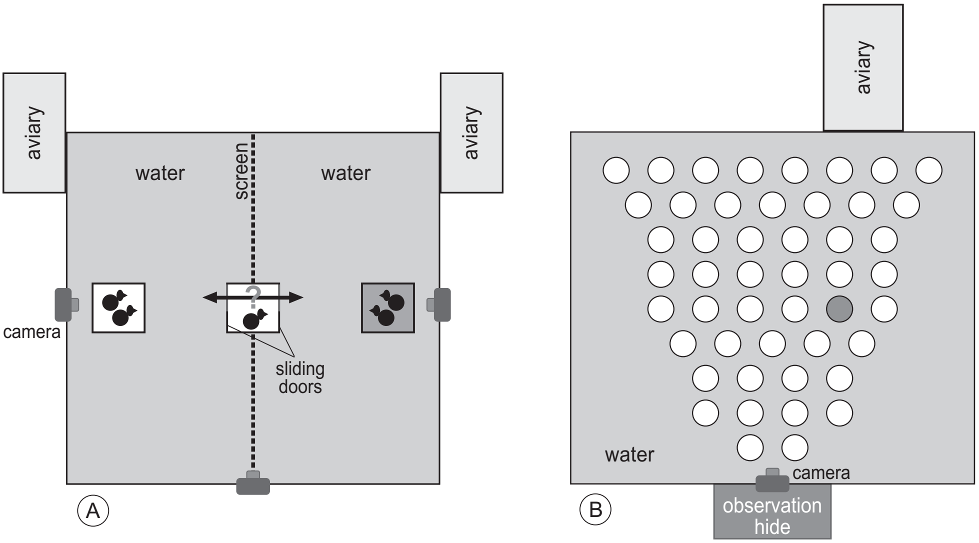

Figure 6.2 Setup for experiments 1 and 2. Panel A gives the setup for experiment 1 in which we tested the ability of knots to detect and exploit the foraging success of other knots. The shaded patch indicates the randomly assigned food patch. In panel B we provide the setup for experiment 2 in which we investigated the effect of group size on red knot food-finding rate. The shaded patch indicates the single food patch that was randomly assigned to one of the 48 patches before each trial.

were fitted that could be remotely opened simultaneously, thus providing access to the patches from the central cage. The water in the arena was kept at such a level that only the patches and cage were above water. Horizontal sliding doors on both sides connected the experimental arena to the aviaries.

Before each trial we introduced two demonstrator birds into each of both aviaries adjacent to the experimental arena to rest for a minimum of 5 min. The demonstrator birds were randomly selected from the intermediately dominant group of birds. Preferably, demonstrator birds were not used on the food patch in two consecutive trials; in 16 trials this could not be prevented given the trial schedule, but the intake rates of these birds did not differ from demonstrator birds that were not used in consecutive trials (0.002 SE 0.030, $F_{1,118} = 0.003$, $P = 0.96$).

We buried 120 blue mussels with a length of 8 (±0.5) mm at a depth of approximately 2 cm in one randomly selected patch and smoothed the patch-surface afterwards. In order to avoid leaving visible cues to the location of food burial, we applied similar treatment to the opposite patch but without actually burying prey. We then placed the focal bird in the central cage to rest for a minimum of two minutes, after which the demonstrator birds were allowed to enter the experimental arena. Two demonstrator birds would start foraging on the empty patch and two demonstrator birds would start foraging on the food patch. Birds were not able to switch between patches because of the polyester sheet. Before opening the central cage’s sliding doors allowing the focal bird access to the patches, the focal bird was able to observe the demonstrator birds for two minutes. The birds were not fed outside these trials (they obtained all the food during the trials in the experimental period lasting 10 days) and were, therefore, motivated to choose the patch with food. Once the focal bird left the central cage the doors closed and the focal bird was allowed to forage for three minutes on the patch it had chosen. Depending on the choice it made, this foraging bout was successful or unsuccessful. An edited video recording of a trial can be found in the Online Supplementary Material.

All trials were recorded on video with three cameras (one for each patch and one for the central cage). The videos were analysed with The Observer software (v4.0 Noldus Information Technology). For the minute preceding the opening of the sliding doors, we scored the time that focal birds spent on the food-patch side, or the empty-patch side of the central cage. Additionally, we counted the number of mussels eaten by the demonstrator birds before the sliding doors were opened. In these two minutes, each demonstrator bird ingested an average of 13.1 mussels (4.6 SD) on the food patch. In six trials, the demonstrator birds were able to find a stray mussel in the empty patch as well. The number of intakes on the 'empty' patch, however, was always much less than the number of intakes on the food patch. The birds, thus, never received false information and we included these trials in the analyses.

Between 19 and 28 November 2008, each focal bird was trialled 12 times making a total of 120 trials. For practical reasons we split the 120 trials into 12 blocks of 10 trials. Each block included each focal bird once, and in half of these blocks the food patch was on the left, and in the other half the food patch was in the right of the experimental arena. The order of blocks was determined by pairwise (food patch on the left or right side of the arena) random selection (Milinski 1997). To get acquainted with the experimental setup, there was a 4 week training period before the experiment. Nevertheless, sometimes the focal birds were scared of the central cage's doors opening. This especially happened when a bird was walking back and forth against one of the sliding doors at the time they were opened. The opening of the door then startled the birds which thus left the cage on the opposite side. We scored this behaviour, defined by whether focal birds jumped or ran away to the other side of the cage at the moment the sliding doors opened, from video recordings – blind to the location of the food patch – and included this as explanatory variable ('opposite') in the analyses.

Experiment 2: are food patches found faster in groups?

In this experiment we used four adult knots (also of the *islandica* subspecies) that were caught on 19 February 1999 near the island of Texel, The Netherlands (53°09' N, 4°54' E). The birds were housed in a similar fashion as explained above, and between 3 and 14 June 1999 we studied their patch finding rate as a function of group size in an experimental design comparable to that used by Pitcher et al. (1982). In an outdoor experimental arena (7 m × 7 m × 3 m), we placed 48 buckets (0.3 m in diameter) filled with wet sand in knee-deep water at a distance of approximately 0.7 m from each other such that the birds needed to make little flights in order to move between patches (similar to van Gils et al.

2003b). Patches were aligned such that a single camera covered all patches (Fig. 6.2B). Out of the 48 patches, only one contained buried prey items (approximately 240 blue mussels of a medium size class around 10 mm); the other 47 patches were empty.

Before each trial, we placed the birds that were scheduled for that specific trial in the aviary next to the arena (the other birds were kept in a box in the meantime). The opening of the door to the arena defined the start of the trial, upon which the focal birds would start searching through the patches. A trial ended when all birds had found the patch containing food.

In total, we carried out 96 trials with 24 trials per group size. In order to balance the number of trials between birds, each bird participated in 60 trials; respectively 6, 12, 18 and 24 trials for group sizes 1 to 4. This experimental design yielded a sample size of 240 estimates on behavioural variables for the statistical analyses. All trials were recorded on video and later analysed with The Observer software (v 4.0 Noldus Information Technology), allowing accurate estimation of time budgets. Our ethogram included 'searching for food', 'flying', and 'other'. We also scored the patch on which the bird was located at any given time.

Statistical analyses

We analysed all data in R v3.0.1 (R Core Team 2013). In order to control for repeated measures on focal birds, we initially analysed experiment 1 in a linear mixed-effects model with focal bird identity as a random effect. However, the estimated variance of focal bird was approximately zero (0.06, CI 95% (0; 0.50)), which simplified these analyses to a linear model. We thus analysed whether focal birds chose the food patch in a generalised linear model with binomial error structure. As explanatory variables we included 'dominance' (a factor indicating if the focal bird was dominant or subordinate), 'sex', and 'opposite' (see MATERIALS AND METHODS). In order to circumvent the experimental artefact that focal birds were sometimes startled by the opening of the sliding doors, we additionally calculated the ratio of time that focal birds spent on the food-patch side of the central cage to that on the empty-patch side. We analysed the logit of this ratio in a linear model with only an intercept.

We analysed the data from experiment 2 in general linear models with Gaussian error structure and cumulative searching times, the number of patch visits, or patch residence times (i.e. cumulative searching time per patch) as response variables. In order to control for pseudo-replication, we averaged the response variables per trial. To normalise model residuals and to account for the non-linear relationship between response variables and group size (continuous variable from 1–4), we $\log_{10}$ transformed these variables. We also investigated whether birds searched randomly between the 48 patches in experiment 2. If birds would search randomly, the number of unique patch visits is given by $48 \times (1 - \left(\frac{47}{48}\right)^{n})$, where n is the total number of patch visits including the revisits. In order to investigate individual differences in between-patch searching behaviour we additionally analysed a focal bird's contribution (%) to the total number of unique patches visited per trial. We averaged these data per focal bird and group size, and after $\log_{10}$ transforming these variables we analysed them in a linear model with Gaussian error structure, and focal bird identity, group size and their interaction as explanatory variables.

RESULTS

Do knots use public information?

Without seeing the food directly and based on the demonstrator birds' behaviour, knots were able to select the food patch in 74.6% of the trials (95% CI (62.5; 83.8%)). There was no effect of a focal bird's dominance or sex (Table 6.1A and Fig. 6.3), but focal birds had a 36.0 percentage points lower chance of selecting the food patch when they were startled by the opening sliding doors ('opposite') compared to when they were not (Table 6.1A). In the minute preceding the opening of the sliding doors, focal birds spent 67.1% of their time (95% CI (56.6; 76.1%)) on the food-patch side of the central cage as opposed to the empty-patch side (Table 6.1B), suggesting that our results are robust to the experimental artefact that focal birds were sometimes startled by the opening of the sliding doors.

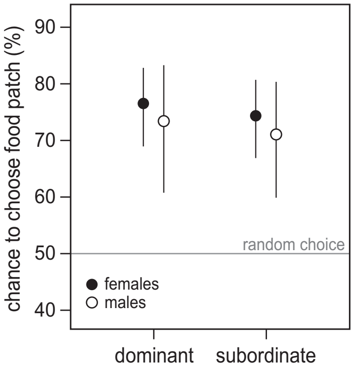

Figure 6.3 Patch choice in experiment 1: do knots use public information? The proportion of trials that focal birds selected the food patch, based on the demonstrator birds' behaviour, was 75%, and independent of sex and social dominance.

Table 6.1 Results from the statistical analyses of experiments 1: do knots use public information? In (A) the focal bird's choice of the food patch was the response variable, and as explanatory variables we included opposite (see MATERIAL AND METHODS), a focal bird's sex, and its dominance status. The intercept represents dominant females that were not startled by the opening of the sliding doors ('opposite', see MATERIAL AND METHODS). In (B) we show the results of a linear model with the ratio of time that focal birds spent on the food-patch side of the central cage to the empty-patch side. Note that the estimates are on a logit scale.

	response variable	predictor variables	estimate	SE	P
(**A**)	food-patch choice	intercept	1.18	0.39	<0.01
		opposite	-1.57	0.40	<0.01
		male	-0.16	0.50	0.74
		subordinate focal	-0.12	0.40	0.77
(**B**)	time spent near food patch	intercept	0.71	0.23	<0.01

Are food patches found faster in groups?

The between-patch searching behaviour of focal birds was approximately random, but slightly more efficient than that (Fig. 6.4). An empty patch was usually given up within a second of probing and once the first bird had encountered the food patch, the others would rapidly join. As a result the cumulative searching times until the food patch was discovered decreased with group size (Table 6.2A and Fig. 6.5A). On a log-log scale, the slope of this regression did not differ from –1 (–0.70, 95% CI (–1.29; –0.11), $t_{(94)} = -1.02$, $P = 0.31$), implying that the food finding rate was proportional to group size. The $\log_{10}$ transformed duration (s) of an individual's searching bouts increased with group size (0.65 SE 0.21, $P < 0.01$) indicating that birds searched more intermittently when alone. The number of patches visited per bird decreased with group size (Table 6.2B and Fig. 6.5B), but the slope of this relationship did differ significantly from –1 (–0.41, 95% CI (–0.80; –0.02), $t_{(94)} = -2.97$, $P < 0.01$). We did not predict an effect, but patch residence times also decreased with group size (Table 6.2C and Fig. 6.5C). A bird's contribution to the number of unique patches found declined with group size ($F_{1,4} = 837$, $P < 0.01$, Fig. 6.6), and differed significantly between focal birds both in intercept ($F_{3,4} = 59.4$, $P < 0.01$, Fig. 6.6) and in slope ($F_{3,4} = 11.1$, $P = 0.02$, Fig. 6.6).

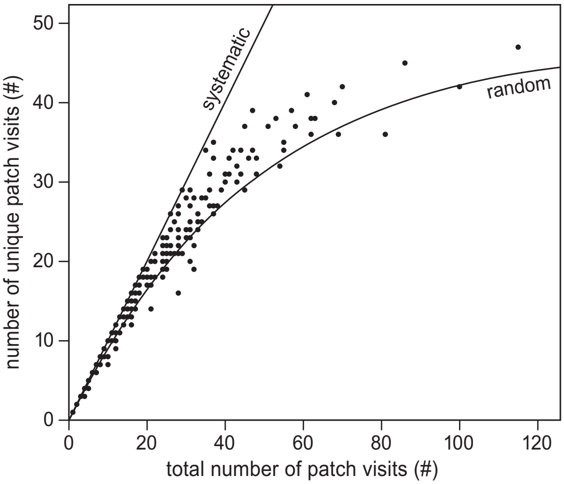

Figure 6.4 Red knot searching behaviour in experiment 2. We investigated whether birds searched randomly between the 48 patches in experiment 2. The lines represent the expectations for random searching behaviour, and for reference, also that for systematically searching foragers for which each patch visited is a new patch (y = x). Each dot represents mean values per trial and per bird.

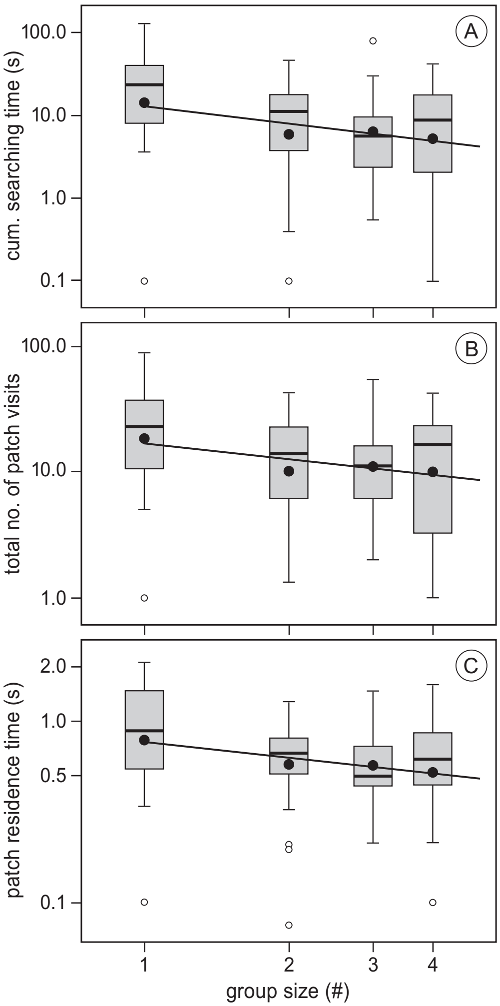

Figure 6.5 The effects of group size on different foraging behaviours in experiment 2: are food patches found faster in groups? For each bird, until it had found its first food item, we recorded the cumulative searching times (A), the number of patches visited (B), and the patch residence times (C) and analysed these variables as a function of group size. Each data point represents the mean per trial.

Table 6.2 Results from the statistical analyses of experiments 2: are food patches found faster in groups? We analysed the (A) cumulative searching times (s) and (B) number of patches visited (#) before finding the food patch, as well as (C) patch residence times (s). These behaviours, as well as group size were $\log_{10}$ transformed.

	response variable	**predictor variables**	**estimate**	**SE**	**P**
(**A**)	cumulative searching times	intercept	1.10	0.12	<0.01
		group size	-0.70	0.30	0.02
(**B**)	number of patches visited	intercept	1.22	0.08	<0.01
		group size	-0.41	0.20	0.04
(**C**)	patch residence times	intercept	0.12	0.05	0.03
		group size	-0.29	0.13	0.02

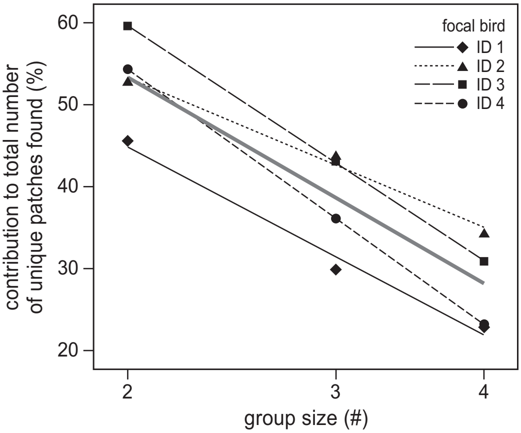

Figure 6.6 Between-individual differences in patch searching behaviour in experiment 2. We analysed an individual's average contribution to the number of unique patches searched until the food patch was found. The thick grey line indicates full proportionality to group size with a slope of -1 on a double logarithmic scale, and the other lines represent the statistical fit for each focal bird. Some focal birds (ID 2 and 3) consistently search more unique patches than others (ID 1 and 4). In the context of producer-scrounger tactics, the former can be seen as producers and the latter as scroungers.

DISCUSSION

We showed that knots detect successful foraging of conspecifics and are capable of exploiting this public information to select their food patches. Consequently, socially foraging knots can benefit from public information by a reduction of the time needed to locate food patches compared to when feeding alone. Moreover, knots differed in their search strategy in that two individuals consistently exploited the searching effort of the other two (Fig. 6.6).

Social foragers can benefit from public information, but as group sizes increase these benefits are gradually offset by increased competition for resources (Ranta et al. 1993, Beauchamp 2014). For instance, the food finding rate of greenfinches *Carduelis chloris* increased less than proportionally with group size, indicating diminishing returns of social foraging benefits (Hake and Ekman 1988). When food patches contain enough food and/or are large enough, detrimental effects of interference competition will be low and social foraging can be beneficial for an individual's long-term intake rate (Danchin et al. 2008). In our experimental setup (i.e. with respect to patch sizes, food distribution, and group sizes) knots could profit maximally from public information as evidenced by the decrease in cumulative searching times proportional to group size. The mechanism behind this proportional decrease was, however, different than we imagined beforehand. We hypothesized that this proportional decline in cumulative searching times would be caused by a proportional decline in the number of patch visits, and that patch residence times would be unaffected by group size. However, both the number of patch visits as well as patch residence times decreased less than proportionally with group size, and their combined effects resulted in a decrease in searching times proportional to group size.

The literature on public information use is growing rapidly and many species have been shown to use public information (Ranta et al. 1993, Templeton and Giraldeau 1995, Danchin et al. 1998, Smith et al. 1999, Brown and Laland 2003, van Bergen et al. 2004, Coolen et al. 2005, Sontag et al. 2006, Shrader et al. 2007, Kurvers et al. 2010b). On the other hand, there are also several experimental studies in which the use of public information could not be confirmed (see Valone 2007). Whether individuals will use public information is influence by an individual's capability to detect relevant cues, the reliability and costs of acquiring public information (Valone and Giraldeau 1993, Giraldeau et al. 2002, Valone 2007), and the reliability of personal information (Nordell and Valone 1998). For instance, foraging nine-spined sticklebacks *Pungitius pungitius* relied on public information when personal information was unreliable (van Bergen et al. 2004). Due to the random assignment of the food patch in experiment 1, the personal information that birds collected in previous trials was unreliable as indicator of the food-patch location in the current trial. Therefore, birds should maximally rely on public information.

The use of public information will also depend on the types of cues that are available. An experimental study with budgerigars *Melopsittacus undulates* did not reveal public information use (Valone and Giraldeau 1993). Perhaps handling times were too short (<1 s) to accurately acquire public information (Valone and Templeton 2002). Yet, knots have handling times <1s, and nevertheless they seem capable of using public information. Possibly, knots did not only use handling times as a cue for patch quality, but also other behaviours that correlate with foraging success. Together with an increase in the time spent handling prey, knots on the food patch in experiment 1 also searched more and moved around less than on the empty patch. Such behaviours could provide longer lasting and more accurate cues on patch quality. Similarly, in experiment 2 longer patch residence times could have provided information on the presence of food (van Gils et al. 2003b).

Social foragers can search for food themselves (producers) or search for the food discovered by others (scroungers) (e.g., Beauchamp 2014). As dominant foragers can displace subordinate foragers from food patches, dominant birds might be more likely to use public information in selecting foraging patches (Barta and Giraldeau 1998). Several studies confirm these predictions (Liker and Barta 2002, Lendvai et al. 2006). For instance, in order to increase their foraging success, dominant black-tailed godwits *Limosa limosa islandica* displaced nearby group members that had higher intake rates (Sirot et al. 2012). In our study, there was no difference between dominant and subordinate focal birds in the use of public information. Compared to the costs of aggression, perhaps dominant knots cannot benefit from aggressively displacing group members. In the field, knots forage on bivalves that are patchily distributed over what otherwise may appear like homogenous landscapes (Kraan et al. 2009a). Knots can use public information to locate such hidden food patches, yet these patches are probably large enough to avoid the costs of social foraging (Chapter 4). This large scale will particularly reduce possible benefits of monopolising food patches by dominant birds (Beauchamp 1998, Vahl and Kingma 2007).

Another benefit of social foraging is social facilitation (Zajonc 1965). Social facilitation occurs when the mere presence of other animals affects an individual's behaviour (Hoppitt and Laland 2013). In the case of foragers, an increase in the intensity of searching behaviour could stimulate this behaviour in other group members. For instance, capuchin monkeys *Cebus paella* were more motivated and successful foragers when they could see a foraging conspecific compared to when they were alone (Dindo et al. 2009). A possible benefit of social facilitation is that, as competition increases with group size, it allows foragers to scramble for the limited resources (Shaw et al. 1995, Parker 2000). Studies on social facilitation are under-represented in the literature (Dindo et al. 2009), possibly because it has been considered a process that must be ruled out when studying social learning (Hoppitt and Laland 2013). Social facilitation itself is an interesting mechanism that is capable of facilitating social learning (Galef 1993) and increasing a social forager's (short-term) intake rate (Shrader et al. 2007).

Contrary to our prediction, we found that patch residence times decreased with group size. Why we found this decrease is subject to further study, but for now we can provide four non-mutually exclusive hypotheses. First, the decline in patch residence times with group size could reflect an increase in the intensity of searching behaviour (social facilitation) due to an increase in scramble competition (Shaw et al. 1995, Parker 2000).

Second, the decrease in patch residence times could be caused by a propensity to stay together. Individuals that are left behind may be at greater risk of predation, and need to join the group to obtain the safety-benefits of social foraging (e.g., van den Hout et al. 2008). Separated individuals can more rapidly join the group by decreasing their patch residence times (Vásquez and Kacelnik 2000, Shrader et al. 2007). That knots foraged on patches close to each other is illustrated by the fact that the number of patch visits until the food was found declined less than proportionally to group size, i.e. as group size increased birds increasingly overlapped in the patches they searched.

Third, individuals in groups are able to allocate more time to foraging instead of, for example, anti-predation vigilance (Caraco 1979, Beauchamp 2014). Lone foragers are more often vigilant than foragers in groups, and their foraging bouts are more often interrupted by vigilance behaviour (Beauchamp 2014). Due to these interruptions, the searching efficiency (instantaneous area of discovery) of lone foragers could be reduced compared to individuals in groups (Dukas and Kamil 2001). As a consequence lone foragers need to search longer than when in a group to obtain similar patch sample information, i.e. have longer patch residence times. Indeed, we found that knots foraging alone had shorter searching bouts compared to when foraging in groups.

Fourth, as group size increased individuals were more often chased from their patch. Birds 'scrounged' on the information produced by others through joining them on their patch. Because the patches could accommodate one bird only, the producers would then fly off to another patch and continue searching. This behaviour increased with group size and as a consequence, patch residence times could have declined as group sizes increased.

The use of producer or scrounger tactics can differ consistently between individuals. In barnacle geese *Branta leucopsis*, for instance, producer-scrounger tactics are associated with personality variation (Kurvers et al. 2010a), and certain individuals will more readily use public information than others (Kurvers et al. 2010b). Interestingly, we also found such differences in foraging tactics between focal birds. The contribution to new patch discoveries varied consistently between focal birds meaning that certain knots scrounge on the foraging information produced by others and that public information use depends on personality (Fig. 6.6). Another study showed that certain knots are consistently more explorative with shorter patch residence times than others that were more sedentary (Chapter 7). Perhaps, these sedentary birds scrounge on the information provided by exploratory birds, but how personality relates to producer-scrounger tactics and public information use remains to be investigated.

CONCLUSION

In this study we have shown that knots are capable of detecting and using public information to increase their food-finding rate, and that knots show consistent individual differences (personalities) in public information use, i.e. producer-scrounger tactics. Dominant knots were not able to exploit public information more than subordinate birds, perhaps because in nature dominant birds cannot monopolise food due to the large patch sizes of their invertebrate prey on extensive intertidal mudflats.

Acknowledgements

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Box 6.1 Social foraging: how do humans compare to knots?

Humans are social animals that also benefit from each other to find resources. How do humans compare to knots in their capability of using the foraging success of ‘flock mates’ as a cue? Out of interest and for fun, Thomas Leerink and I repeated the ‘social information use’ experiment presented in Chapter 6 on humans during ‘open viewing days’ of NIOZ. We placed two deep trays filled with sand on either side of the experimental cage (see photo B6.1). Whereas with the experiment on knots we buried prey in one tray only, here we buried 50 marbles (with a diameter of 1 cm) in *both* trays. At the start of the trial one or two demonstrator-humans were allowed into the arena on both sides of the central cage. More or less at the same time, a focal human was released into the central cage. The humans were non-randomly selected from the group of observers. When given the green light, the demonstrator humans would start ‘foraging’ immediately, most of the time. After the focal human was able to observe the demonstrator humans for roughly 1 min, we opened the central cage’s sliding doors that allowed the focal human access to the patches. Subsequently, we counted the discovered marbles on each side. In cases that the focal human chose the side of the experimental arena where most marbles were discovered (i.e. the best food patch) his or her choice was considered successful. We carried out 186 trials. The age of demonstrator and focal humans varied between 1 and roughly 50 years, but was highly skewed to the younger individuals. Without seeing the marbles directly and based on the demonstrator humans’ success rate, the focal subjects were able to select the food patch in 67.5% of the trials (95% Confidence Interval between 58.6 and 75.3%). Knots were slightly more successful and chose the food patch in 74.6% of trials, but this difference was non-significant (Fig. B6.1).

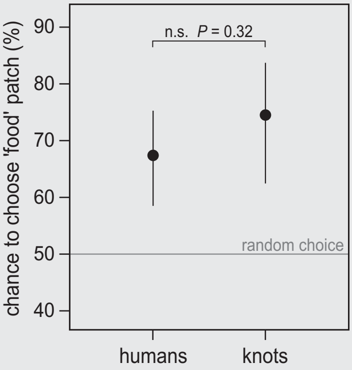


Figure B6.1 Result of the patch choice experiment on humans. The percentage of trials that focal humans selected the food patch, based on the demonstrator humans’ behaviour, was 68% for humans and 75% for knots, a difference that was non-significant.

Photo B6.1 'Testing' for social information use in an experiment on humans during the NIOZ open day 2010. Photo courtesy by Roos Kentie.

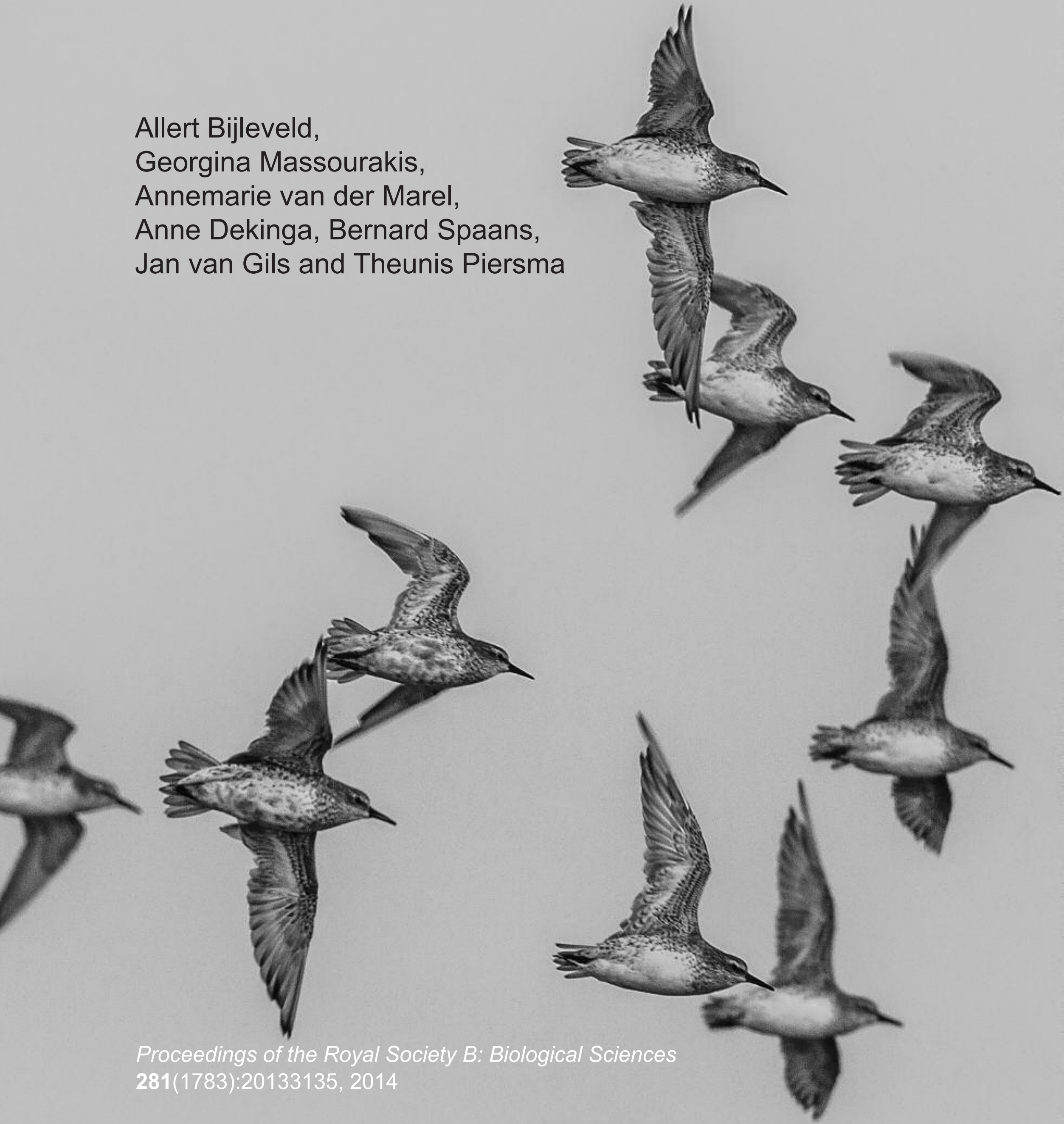
Section III

Individuality

Chapter 7

Personality drives physiological adjustments and is not related to survival

Allert Bijleveld,
Georgina Massourakis,
Annemarie van der Marel,
Anne Dekinga, Bernard Spaans,
Jan van Gils and Theunis Piersma



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SUMMARY The evolutionary function and maintenance of variation in animal personality is still under debate. Variation in the size of metabolic organs has recently been suggested to cause and maintain variation in personality. Here we examine two main underlying notions: (1) that organ sizes vary consistently between individuals and cause consistent behavioural patterns, and (2) that a more exploratory personality is associated with reduced survival. Exploratory behaviour of captive red knots (*Calidris canutus*, a migrant shorebird) was negatively rather than positively correlated with digestive organ (gizzard) mass, as well as with body mass. In an experiment we reciprocally reduced and increased individual gizzard masses and found that exploration scores were unaffected. Whether or not these birds were resighted locally over the 19 months after release was negatively correlated with their exploration scores. Moreover, a long-term mark-recapture effort on free-living red knots with known gizzard masses at capture confirmed that local resighting probability (an inverse measure of exploratory behaviour) was correlated with gizzard mass without detrimental effects on survival. We conclude that personality drives physiological adjustments, rather than the other way around, and suggest that physiological adjustments mitigate the survival costs of exploratory behaviour. Our results show that we need to reconsider hypotheses explaining personality variation based on organ sizes and differential survival.

INTRODUCTION

Animals modify aspects of their phenotype in response to changes in their environment (phenotypic plasticity, West-Eberhard 2003). Changes that are reversible within an individual's lifetime are known as phenotypic flexibility (Piersma and Drent 2003, Piersma and van Gils 2011). Animal behaviour is a classic example of phenotypic flexibility, enabling rapid and reversible responses to changes in environmental and social context (Westneat and Fox 2010). Perhaps somewhat surprisingly, given behavioural flexibility, individuals of many species have been shown to vary consistently in their behaviour across contexts, yielding the notion of 'animal personalities' (reviewed in Réale et al. 2007).

Personality refers to a suite of phenotypically or genetically correlated behavioural traits that are consistent over time or across contexts (Koolhaas et al. 1999, Sih et al. 2004b, Réale et al. 2007, Carere and Maestripieri 2013). Variation in personality is thought to be shaped by continuous interaction between genes and environment during ontogeny (Koolhaas et al. 1999, Oyama 2000, van Oers et al. 2005, Coppens et al. 2010, Duckworth 2010, Groothuis and Trillmich 2011). In recent years, considerable progress has also been made in understanding personalities from an evolutionary perspective (Réale et al. 2010a, Wolf and Weissing 2010, Dall et al. 2012). Most of the adaptive explanations involve between-individual variations in state (e.g., physiological condition, health, organ masses), in combination with positive feedback mechanisms maintaining these state variations (Dingemanse and Wolf 2010, Wolf and Weissing 2010, Dall et al. 2012). The idea is that if the state of an individual is more or less stable over time, then state-dependent behaviour will also be consistent. However, few empirical studies exist in which predictions from such state-dependent personality models have been tested (Dingemanse and Wolf 2010).

The sizes of an individual's metabolic organs (e.g., digestive organs, heart, liver) are thought to be slow-changing state variables that are *causal* to variation in personality between individuals (Careau et al. 2008, Biro and Stamps 2010, Réale et al. 2010b). This variation is thought to be maintained by a positive feedback mechanism whereby individuals with large metabolic organs behave in ways that allow for the acquisition of enough energy to sustain them. For instance, such individuals might need to be explorative, bold and/or aggressive in order to gain access to the resources necessary for the maintenance of their large organs. At the same time however, such behaviours are risky and are assumed to come attached with survival costs (Boon et al. 2008, Réale et al. 2010b). Exploratory individuals would thus lead a high-risk/high-gain lifestyle. For such behaviour to be evolutionarily stable, the associated survival costs are expected to be compensated for by correlations with particular life-history characteristics (e.g., growth, age at maturity, Stamps 2007), in line with the 'pace-of-life' concept (Réale et al. 2010b). According to the pace of life concept, metabolic costs and personality should be linked along a continuum of slow/fast life-history strategies. However, there is, as yet, little evidence to support this theory (e.g., Bouwhuis et al. 2014).

Implicit in the hypothesis that metabolic organ sizes are *causal* to personality variation, is the fact that organ sizes vary consistently between individuals allowing for consistent behaviour to develop throughout an individual's life. Organs are, however, notoriously flexible in size, reflecting changes in ecological context (Piersma 2002, Piersma and Drent 2003, West-Eberhard 2003, Piersma and van Gils 2011). Indeed, regardless of how personalities arise, it seems likely that animals with different personalities will express a preference for different environments (i.e. with respect to food type, predation risk, etc., Dall et al. 2012, Sih et al. 2012, Wolf and Weissing 2012), which may, in turn, result in specific physiological adaptations. One could thus argue that personality variation causes consistent variation in organ morphology and, consequently, in metabolic costs, rather than the other way around.

In this study we examined two critical notions underlying the hypothesis of organ-size driven personality variation: (1) that variation in digestive organ sizes cause consistent variation in behaviour, and (2) that large digestive organs and exploratory behaviour are associated with reduced survival. Our model species is the red knot *Calidris canutus* (Linnaeus, 1758, hereafter called knot), a long-distance migrating shorebird, for which contextual flexibility in organ mass has been extensively studied (Piersma 2002, Piersma et al. 2003, Piersma and van Gils 2011). Our study involved four steps. First, we experimentally determined exploratory behaviour for newly captured knots and correlated this with their digestive organ mass, i.e., the muscular stomach (gizzard). We also correlated exploratory behaviour with body mass and predicted that individuals with large body mass (i.e. large energy stores) would avoid risky behaviour and thus be less explorative (*sensu* the mass-dependent predation risk hypothesis, Witter and Cuthill 1993). Second, we manipulated gizzard mass in order to compare the effect of a small and a large gizzard on exploratory behaviour within individuals. Third, to test if the experimental quantification of exploratory behaviour is representative of this behaviour in the field, we tagged and released the experimental birds with unique combinations of colour-rings and estimated local resighting probability. We predicted that explorative birds would have a lower local resighting probability because they have larger spatial ranges than non-explorative birds. Fourth, we analysed survival and resighting probability for free-living knots, with known gizzard masses, on the basis of a sustained marking and resighting effort on free-living birds (Spaans et al. 2011).

We will show that gizzard mass, and body mass (energy stores) were negatively correlated with exploratory behaviour between individuals, and that manipulations of gizzard mass did not cause changes in exploratory behaviour. Moreover, neither gizzard mass nor exploratory behaviour, were in any way correlated with survival. We conclude that personality drives the physiological adjustments. These results call for reconsideration of hypotheses explaining personality variation on the basis of organ sizes as well as differential survival.

MATERIALS AND METHODS

Model species

Knots are long-distance migratory shorebirds that breed in the High-Arctic and spend the rest of the year along more southerly shores with extensive intertidal mudflats (Piersma 2007). The subspecies *islandica*, studied here, breeds on tundras in northern Greenland and northeast Canada and winters in northwestern Europe, including the Wadden Sea (Piersma 2007). During the nonbreeding season knots roam intertidal mudflats in large flocks in search of burrowed hard-shelled bivalves (Piersma et al. 1993a). Depending on the tides and weather conditions, the availability of the foraging grounds varies temporally and spatially as does the abundance and quality of prey (van Gils et al. 2005b, Kraan et al. 2009b).

Bivalves of suitable sizes are swallowed whole and crushed in their muscular stomach, the gizzard (Piersma et al. 1993b). The size of the gizzard sets an upper limit to the amount of shell mass that can be processed and thus limits daily intake rates (van Gils et al. 2003a). Gizzard mass is flexible within individuals and changes in response to the ratio of flesh to shell mass of their prey (prey quality) (Dekinga et al. 2001). The lower this ratio, the larger the gizzard must be to uphold energy intake rates. Gizzard mass is correlated with the mass of other digestive organs such as the intestines, liver and kidneys (Piersma et al. 1996, Piersma et al. 2003). All together, the digestive organs make up 18% of an individual's lean mass, and are a determining factor for basal and resting metabolic rates (Piersma et al. 1996, Dietz and Piersma 2007).

Twenty-three knots were caught between 17 and 20 March 2010 in the Dutch Wadden Sea (53°15'N, 5°15'E). A blood sample was taken for molecular sexing (Baker and Piersma 1999). Birds were weighed and ringed on location, where after they were transported to the experimental shorebird facility at NIOZ. Birds were housed in aviaries measuring 4 × 2 m with a height of 2.5 m and lined with white Trespa (Trespa International BV, Weert, the Netherlands). These aviaries provided running salt water along a coated concrete surface, fresh water for drinking and bathing, and a stretch of sand covered in 5 cm water to resemble the knots' natural mudflat habitat. The birds were maintained on a diet of protein-rich trout-feed pellets (Produits Trouw, Vervins, France).

Measuring organ mass

Gizzard mass was measured by AD using an ultrasound scanner (model Aquilla, Pie Medical Benelux, Maastricht, The Netherlands) as described by Dekinga et al. (2001). Two sets of measurements of gizzard width and height (cm) were taken at each measurement session. Gizzard width and height were averaged per individual, and gizzard mass (g) was derived as -1.09 + 3.78 × width × height ($r = 0.92$, $P < 0.01$; this regression was obtained with fresh gizzard masses from dead individuals). Gizzard mass was measured one day after capture (which was taken to be reflective of a birds' organ mass while free-living), and also one day before each treatment of the gizzard mass manipulation experiment.

Exploratory behaviour

We tested exploratory behaviour in a novel 'exploration arena' measuring 7 × 7 m with a height of 3 m ('novel environment' test Réale et al. 2007). The exploration arena had walls lined with white Trespa, and was filled with a layer of 30 cm seawater on top of a 50 cm deep layer of sand. Filled with only wet sand, we positioned five familiar trays (1 × 1 m, 20 cm deep) above the water surface for the birds to explore. The trays were placed approximately 90 cm from the walls and acted as foraging patches, such that the degree to which birds explored within and between patches would reflect their propensity to explore while searching for food. To further motivate the birds to search for food during the trials, familiar but empty feeders were placed at the centre of each patch. In order to induce standard hunger levels between birds, they were deprived of food for two hours prior to the experiment, periods without food that knots are accustomed to naturally as they cannot feed around high tide.

Each trial consisted of a bird being retrieved from its aviary, weighed to the nearest g, and first introduced into a familiar aviary adjacent to the exploration arena to rest for a minimum of 5 min. This aviary led into the exploration arena through a sliding door that could be remotely opened and closed via a pulley mechanism. After this door was opened, the bird was gently pushed into the exploration arena. Trials lasted 30 min. We tested 2 to 8 randomly selected birds each day between 8 and 11 June 2010, several months after capture. The procedure was repeated between 21 and 24 June 2010.

All trials were recorded on video and later analysed with The Observer XT software (v10.1 Noldus Information Technology), allowing accurate estimation of time budgets. Our ethogram included 'searching for food', 'resting', 'preening' and 'flying'. We also scored the patch on which the bird was located at any given time. The *logit* of the fraction of total time spent in search of food was positively correlated with the log-transformed number of patch visits ($r = 0.63$, $P < 0.01$). Hereafter, we will use the fraction of total time spent in search for food as the measure of exploratory behaviour.

Separating effects of body mass and energy stores on exploratory behaviour

Many species show a relationship between structural size and body mass. For knots, however, the principal component from the lengths of wing (mm), tarsus (mm), and head to bill (mm) explained only 16% of variation in body mass within the sexes (Appendix A7). In order to investigate correlations between exploratory behaviour and body mass, we analysed these variables in a bivariate mixed-effect model with individual identity as random factor (equations 7a and b in Dingemanse and Dochtermann 2013). These analyses allowed us to decompose the phenotypic (co)variance, and calculate correlation coefficients of exploratory behaviour with body mass between- and within-individuals. Between-individual and within-individual processes operate in conjunction and their separation can provide insight into the origin and maintenance of personality variation. Significant correlations between individuals would indicate that behaviour and body mass would take shape by gene-environment interactions during ontogeny, whereas significant within-individual correlations would give hints on more proximate mechanisms. For example, a negative within-individual correlation could indicate that a reduction in body mass ('hunger') motivates an individual to explore more. An in-depth discussion on the causes and consequences of between- and within-individual correlations can be found elsewhere (Dingemanse and Dochtermann 2013).

Gizzard mass treatment

Gizzard mass was manipulated by varying the quality (shell content) of the food (Dekinga et al. 2001, van Gils et al. 2003a), so that we could measure exploratory behaviour (as described previously) of the same individuals with a large and a small gizzard. To induce a relatively large gizzard we offered closed blue mussels *Mytilus edulis* that were swallowed whole. To induce small gizzards we offered only the flesh of the blue mussel, thus removing the need for shell crushing whilst keeping the digestible parts identical.

The twenty-three knots were divided into two groups of eleven and twelve individuals respectively. One group started with the large gizzard mass treatment followed by the small gizzard mass treatment, whilst the other group was simultaneously exposed to the two treatments in reversed order (a crossover-design to avoid confounding effects of time). In captivity it takes about a week for a bird's gizzard mass to match its diet (Dekinga et al. 2001). We allowed at least three weeks for the birds to increase gizzard mass after a diet switch. Trials were conducted between 21 December 2010 and 21 January 2011, after which the birds were returned to a diet of trout-feed pellets.

In order to account for variation in magnitude of gizzard mass change as well as to decompose the (co)variance into the between- and within-individual components, we analysed exploratory behaviour and gizzard mass in a bivariate mixed-effect model with individual identity as a random effect (Dingemanse and Dochtermann 2013). We did not include the initial gizzard mass measurements in this analysis, as there was no corresponding measure of exploratory behaviour at that time. The effect of the order in which birds received the gizzard manipulation was not significant (–0.19, 95%CI [–1.23; 0.77]), and for simplification we removed it from the final model. In order to test whether individuals varied consistently in gizzard mass between treatments, we calculated 'consistency repeatability' from standardised gizzard mass (Nakagawa and Schielzeth 2010).

Free-living exploratory behaviour of experimental birds

In August 2011, after the experiments had been completed, all birds (except for the two that had died) were released into the wild (53°15'N, 5°15'E). A week before their release, the birds were fed blue mussels and tagged with unique colour-coded ring combinations placed around their legs allowing for individual identification in the wild (Spaans et al. 2011). Resightings of these individuals up to March 2013 allowed us to estimate their free-living exploratory space use.

Long-term resighting analyses of free-living birds

Between 1998 and 2003, 402 *islandica* knots were captured and promptly released in the Dutch Wadden Sea after their gizzard mass had been measured, and they had been tagged with unique colour-coded combinations of rings. Resightings of these birds in the Dutch Wadden Sea (n = 1,068) were analysed over the period from capture up to March 2013 to estimate 'apparent survival' and resighting probability. Note that apparent survival includes true survival as well as permanent emigration, which cannot be separated (White and Burnham 1999). In order to correct for food type- and season induced variation in gizzard mass between and within years (van Gils et al. 2003a), we zero-centred gizzard mass for each catching event (n = 16) (van de Pol and Wright 2009).

Data analyses

For each captive individual, exploratory behaviour was measured on four occasions. Two replicates during the first quantification of exploratory behaviour, and two replicates during the gizzard mass manipulation. Fraction of time spent searching in the exploration arena (exploratory behaviour) was *logit*-transformed to conform to normality assumptions. Repeatability R in exploratory behaviour was calculated as the between-individual variance divided by the total phenotypic variance, i.e. the sum of between- and within-individual (residual) variance. Variance components were extracted from a univariate mixed-effect model with individual identity as a random effect. Confidence intervals and significance were calculated with parametric bootstrapping (Nakagawa and Schielzeth 2010). We initially included sex as fixed effect, but we removed this from the final model as exploratory behaviour did not significantly differ between males and females (0.3 SE 0.6). In order to truly capture the effect of a 'novel' environment, we correlated gizzard mass at capture to exploratory behaviour from the first replicate. Because our purpose was not to predict exploratory behaviour from gizzard mass, but only to summarise their relationship, we used standardised major axis analyses (Smith 2009).

Apparent survival and resighting probabilities were calculated from resighting histories of free-living individuals using the statistical software MARK (White and Burnham 1999). Our candidate model set included models with fixed- or residual gizzard mass dependent apparent survival and resighting probability. To account for variation in apparent survival and resighting probability between years, we additionally included models with time-dependent apparent survival and resighting probability in our candidate model set, i.e., year as factor with 15 levels. For model selection and inference we used Akaike's Information Criterion corrected for small sample size (AICc). In order to test for violations of the assumptions underlying mark-recapture analyses, we performed a goodness-of-fit test of the global model without covariates, including time effects on apparent survival and resighting probability, using the program U-CARE (Choquet et al. 2009). These results indicated that our model fitted the data adequately ($\chi^2_{(51)}$ = 60.7, P = 0.17).

Data analyses were carried out in R v2.15.1 (R Core Team 2013) with the packages 'RMark' for mark-recapture (Laake 2013), 'rptR' for univariate mixed effect repeatability (Nakagawa and Schielzeth 2010), 'smatr' for standardised major axis (Warton et al. 2012), and 'MCMCglmm' for bivariate mixed effect analyses (Hadfield 2010).

RESULTS

Exploratory behaviour

Our first set of experiments revealed that exploratory behaviour was repeatable ($R = 0.67$, 95% CI [0.38; 0.85], $P < 0.01$, Fig. 7.1A), and that it was negatively correlated with gizzard mass at capture (intercept = 5.3, 95% CI [3.0; 7.6], slope = –0.72, 95% CI [–1.06; –0.50], $r = –0.52$, $P = 0.01$, Fig. 7.1B). Within individuals, a reduction in body mass (energy stores) did not motivate birds to explore more, as the within-individual correlation of exploratory behaviour with body mass was non-significant ($r = 0.13$, 95% CI [–0.35; 0.44], Fig. 7.2). There was, however, a significant and negative between-individual correlation of exploratory behaviour with body mass ($r = –0.84$, 95% CI [–0.96; –0.45], Fig. 7.2). Body mass during these trials was correlated with body mass at capture, indicating that body mass in captivity reflects body mass while living free ($r = 0.59$, 95% CI [0.24; 0.81], $t(21) = 3.4$, $P < 0.01$).

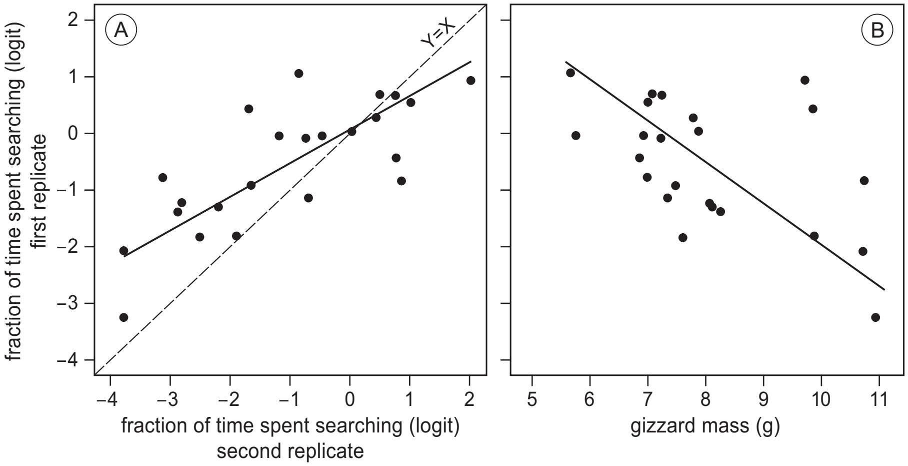

Figure 7.1 Standardised major axis regressions between the first measure of exploratory behaviour and the second (A), as well as gizzard mass (B). Gizzard mass was measured shortly after capture and is, therefore, representative for this organ mass in the wild. Exploratory behaviour was measured as the fraction of time spent searching and was *logit* transformed.

Gizzard mass treatment

Manipulating gizzard mass resulted in an average gizzard mass difference of 4.6 g between treatments (SE 0.6, ANOVA: $F_{1,44} = 66.7$, $P < 0.01$, Fig. 7.3A). An individual's exploratory behaviour did not change in response to the manipulation of gizzard mass, as evidenced by a lack of within-individual correlation of exploratory behaviour with manipulated gizzard mass ($r = –0.20$, 95%CI [–0.50; 0.11], Fig. 7.3B). Between individuals, the correlation of exploratory behaviour with manipulated gizzard mass did also not differ significantly from zero ($r = –0.40$, 95%CI [–0.90; 0.69], Fig. 7.3C). The absence of this correlation

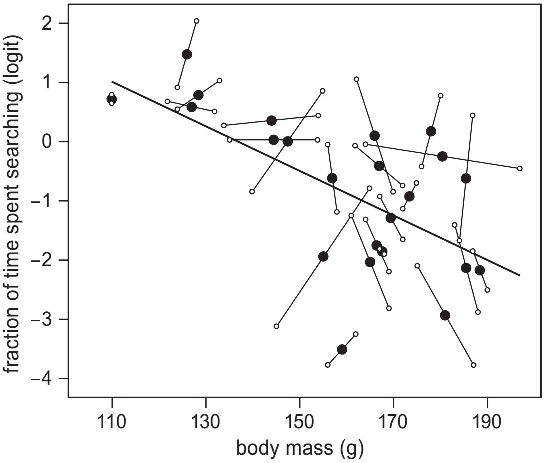

Figure 7.2 Between- and within-individual correlations of body mass with exploratory behaviour. The closed circles represent an individual's average body mass and exploratory behaviour of the first two exploration trials. The line represents the between-individual standardised major axis regression as estimated from the bivariate mixed effects model. The open circles depict an individual's body mass and exploratory behaviour at each trial. Exploratory behaviour was measured as the fraction of time spent searching and was *logit* transformed.

compared to the negative between-individual correlation we found when the birds were living free, suggests that gizzard mass is not determined by individual 'design' constraints (e.g., genetic architecture, body size), but regulated by diet. Indeed, manipulated gizzard mass (when diet was controlled for) was not repeatable ($R_{consistency}$ = 0.22, 95% CI [0.00; 0.55], P = 1.00). By contrast, exploratory behaviour in the gizzard manipulation trials was repeatable (R = 0.56, 95% CI [0.22; 0.79]) also with respect to the first measure of exploratory behaviour 6 months before (R = 0.54, 95% CI [0.21; 0.77], $P < 0.01$). Surprisingly, however, exploratory behaviour was no longer significantly correlated with gizzard mass at capture. Nonetheless, the estimated values for intercept (7.3) and slope (−0.89) were within the 95% confidence intervals ([3.9; 10.6], P = 0.24; and [−1.38; −0.57], P = 0.34 respectively) of those estimated from the correlation between the first measures of exploratory behaviour and gizzard mass at capture.

Free-living exploratory behaviour of experimental birds

Out of twenty-one experimental birds that were released in the wild, ten were resighted in the period between release and March 2013. In line with our experimental results, free-living exploratory individuals with small gizzards had a lower resighting probability than non-exploratory individuals with large gizzards. Birds that were not resighted had significantly higher exploratory behaviour scores (1.1 SE 0.4, ANOVA: $F_{1,19}$ = 7.2, P = 0.01, Fig. 7.4A) and smaller gizzard masses (−1.5 SE 0.6, ANOVA: $F_{1,19}$ = 6.0, P = 0.02, Fig. 7.4B) than birds that were resighted.

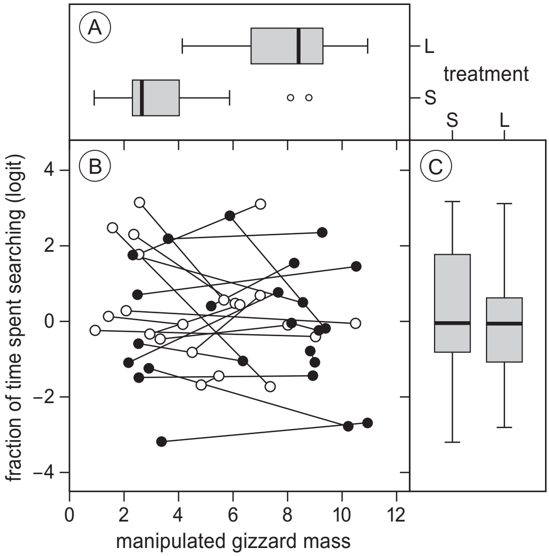

Figure 7.3 Gizzard mass and exploratory behaviour as a result of the gizzard mass manipulation. Different panels represent gizzard mass as function of treatment level (A), exploratory behaviour as a function of manipulated gizzard mass (B), and exploratory behaviour as a function of treatment level (C). Treatment level refers to the small gizzard (S) or large gizzard treatment (L). Exploratory behaviour was measured as the fraction of time spent searching and was *logit* transformed. We analysed the effect of the gizzard mass treatment on exploratory behaviour in a bivariate mixed effects model to accommodate for the differences in magnitude of gizzard mass change between individuals. Lines connect individuals between treatment levels. Closed circles in panel B represent individuals that first received the large- and then the small gizzard mass treatment; open circles represent individuals that were simultaneously given the reverse treatment order.

Long-term resighting analyses of free-living birds

Based on the analysis of our long-term resighting efforts, and in line with our independent experimental results, we found that exploratory behaviour and gizzard mass were negatively correlated in the field as well. The *logit* of resighting probability increased by 0.13 (95% CI [0.02; 0.24]) per gram of residual gizzard mass (Fig. 7.5A and Appendix Tables A7.1 and A7.2), i.e., birds with small gizzards were less often resighted in the Dutch Wadden Sea than those with large gizzards. Similarly, the average gizzard mass of individuals that were resighted outside the Dutch Wadden Sea within a year after capture was lower than that of individuals that were resighted in the Dutch Wadden Sea only (–0.80 SE 0.37, $F_{1,108} = 4.7$, $P = 0.03$, Fig. 7.5B). We did not find an effect of gizzard mass on apparent survival that averaged 0.82 (95% CI [0.79; 0.84], Tables A7.1 and A7.2 in the Appendix), suggesting that neither large metabolic machinery nor exploratory behaviour are associated with lower survival.

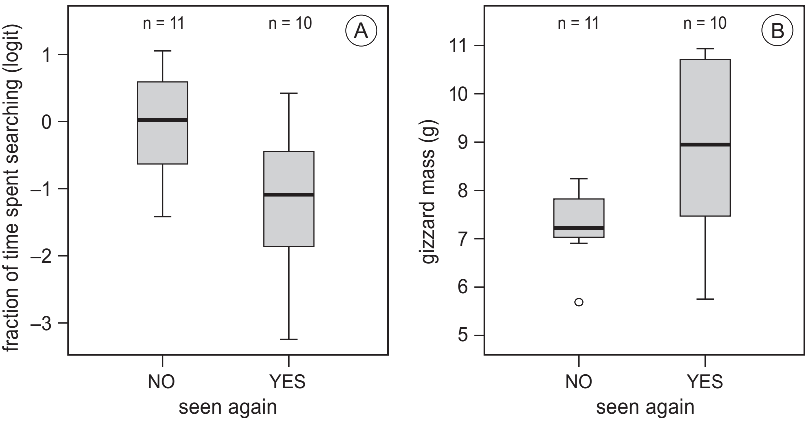

Figure 7.4 Exploratory behaviour (A) and gizzard mass (B) for knots that were, and were not, resighted in the Dutch Wadden Sea in the period between being released (August 2011) and March 2013. Exploratory behaviour was measured as the fraction of time spent searching in the first measurement of exploration and was *logit* transformed.

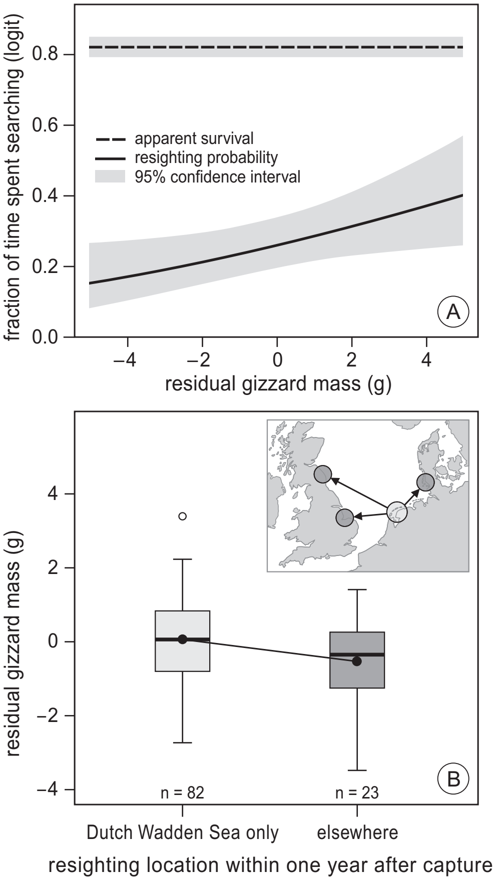

Figure 7.5 Resighting analysis of free-living knots with known gizzard mass. Apparent survival and resighting probability in the Dutch Wadden Sea as a function of residual gizzard mass at capture (A), and average residual gizzard mass for birds resighted in the Dutch Wadden Sea only and those elsewhere within one year after capture (B). Those knots that were resighted outside the Dutch Wadden Sea within a year after capture were resighted in England or Germany (see inset of panel B).

DISCUSSION

Consistent variation in (metabolic) organ mass has been hypothesised to cause variation in personality traits (Careau et al. 2008, Biro and Stamps 2010, Réale et al. 2010b). In this study we examined two critical notions underlying this hypothesis. Instead of the hypothesised *positive* between-individual correlation, we found that exploratory behaviour was *negatively* correlated with digestive organ (gizzard) mass. To examine the causality of this correlation, we manipulated gizzard mass and found that an individual's exploratory behaviour was unaffected. This led us to reject the hypothesis that variation in digestive organ size *causes* consistent exploratory behaviour within individuals. For free-living knots, we also showed that exploratory behaviour was negatively correlated with gizzard mass between-individuals, and that neither factor was associated with lower survival. Consistent variation in exploratory behaviour, or some correlated variable, seems to cause variation in digestive organ mass.

An ecology of exploratory behaviour

Consistent differences in exploratory behaviour are found in many different organisms (Réale et al. 2007). Usually, exploratory behaviour is measured in standardised experiments outside an individual's regular environment, which can be problematic for the interpretation of the trait under investigation (Carter et al. 2013). To avoid ambiguity in the measurement of personality traits, validation against behaviour in the wild is essential (Réale et al. 2007, Carter et al. 2013). Nonetheless, few studies show that small-scale exploratory behaviour in a laboratory is related to large-scale space use in the wild. In one example, after removal of a food source, non-explorative great tits *Parus major* remained close to the known feeder location, whereas explorative individuals moved further away (van Overveld and Matthysen 2010). Comparable results were found for brook charr *Salvelinus fontinalis* (Wilson and McLaughlin 2007), starlings *Sturnus vulgaris* (Minderman et al. 2010), and red squirrels *Tamiasciurus hudsonicus* (Boon et al. 2008). For knots, we now show that exploratory behaviour in a laboratory setting is also related to space use in the wild on a spatial scale of NW Europe, which is unprecedented. The experimental birds that were not resighted in the local study area after release had higher experimental exploration scores than birds that were locally resighted. The explorative individuals with small gizzards spread out on spatial scales of up to hundreds of kilometres between mudflats in England, The Netherlands, and Germany.

An individual's gizzard mass is flexible and reflects the quality of prey that it consumed over the previous few weeks (Dekinga et al. 2001). Experimental exploration scores were negatively correlated with gizzard mass in the wild, suggesting that exploratory behaviour is correlated with prey type between-individuals, either directly or indirectly, e.g., through increased access to areas where high-quality prey are available. Furthermore, the positive between-individual correlation of resighting probability with residual gizzard mass at capture was present in all years (1998-2013) after capture (between 1998 and 2003). The temporal consistency of this correlation suggests that an individual's exploratory behaviour is consistent over time and that gizzard mass is indeed behaviourally regulated.

One *could* argue that the between-individual correlation of exploratory behaviour with gizzard mass has been formed by the interaction between genetic mechanisms (e.g., coevolution, pleiotropy, linkage disequilibrium) and environmental mechanisms (e.g., permanent environmental correlations) (Dingemanse and Dochtermann 2013). The lack of repeatability in an individual's gizzard mass between the small and large gizzard mass treatment, however, does not support such an argument. Gizzard mass might still be regulated by an underlying unknown process (e.g., prey preference) that itself is correlated with exploratory behaviour. A particularly interesting mechanism which, in theory, could be capable of generating the observed correlation between exploratory behaviour and gizzard mass during ontogeny (Dingemanse and Wolf 2010, Wolf and Weissing 2010), is a positive feedback mechanism between gizzard mass and prey quality.

In the Wadden Sea, prey quality is inversely related to prey density (van Gils et al. 2005b), and the spatial extent where high-quality prey are available is limited (Kraan et al. 2009b). Because of a digestive constraint, individuals with small gizzards can only achieve sufficiently high intake rates on a diet of high-quality prey, i.e., there is positive feedback between gizzard mass and prey type (Piersma et al. 1993b, van Gils et al. 2003a, van Gils et al. 2005b). As high-quality prey are less abundant than low quality prey, it was previously thought that birds with small gizzards would have an increased starvation danger compared to birds with large gizzards (e.g., van Gils et al. 2006a). That we have now shown that there is no survival cost for having a small gizzard is at odds with this notion. Possibly, the increased starvation risk of having a small gizzard can be compensated for by being explorative, thereby allowing the discovery of high-quality prey.

Exploratory behaviour, survival, and body mass

The evolutionary origin and maintenance of phenotypic variation in animal personality is intensely debated (Dingemanse and Réale 2005, Dingemanse and Wolf 2010, Dall et al. 2012, Wolf and McNamara 2012). Recent work suggests that personality variation amongst individuals could reflect variation in adaptive specialisation to a particular life-history strategy (the 'pace of life' concept, Réale et al. 2010b). Explorative individuals are likely to incur costs associated with movement that may reduce survival, e.g. through increased metabolic costs and higher predation danger through increased exposure (Piersma et al. 2003, Boon et al. 2008). From a life-history strategy perspective, these survival costs are expected to be compensated for by increased growth, age at maturity, and reproduction if exploratory behavior is to be evolutionarily stable (a high-risk/high-gain lifestyle, Stamps 2007, Réale et al. 2010b). Empirical evidence that there are survival costs to exploratory behaviour, however, is equivocal (Smith and Blumstein 2008). Our results do not provide any evidence that exploratory behaviour is associated with reduced survival.

Other than through adaptive specialisation to a particular life-history strategy, costs of an individual's personality could be reduced through correlations with other traits such as body mass (Duckworth 2010, Westneat and Fox 2010). For instance, exploratory blackbirds *Turdus merula*, compensated for increased flight costs and predation danger by carrying smaller energy stores than more sedentary individuals, albeit at the cost of increased starvation danger (Cresswell 1999). Similarly, we found a negative correlation of body mass with exploratory behaviour between individuals. Knots show relatively small variations in structural size (van der Meer and Piersma 1994), and the observed mass differences between exploratory and non-exploratory birds (maximum of 79 g) are too large to be accounted for by differences in organ mass only (Piersma et al. 1996). Moreover, in an experimental setting, knots have been shown to actively reduce body mass in the presence of predators (van den Hout et al. 2010), allowing better escape behaviour from predators (Dietz et al. 2007). Birds with small energy stores could compensate for their increased risk of starvation by searching for higher-quality prey. Indeed, in our study lighter birds were more explorative. This effectively creates two positive feedback loops (Fig. 7.6): one between exploratory behaviour, predation danger and energy stores, and another between exploratory behaviour, prey quality and digestive organ mass. Although in our short-term laboratory study with fully mature birds we did not find a within-individual correlation between exploratory behaviour and gizzard mass, nor body mass, in the field the situation is expected to be different for two reasons. First, in the more demanding lifestyle of the wild, exploration for the sparsely distributed high-quality prey is required for individuals with small gizzards and energy stores, which are digestively constrained (Piersma et al. 1993b, van Gils et al. 2003a, van Gils et al. 2005b). Likewise, having small energy stores will increase the risk of starvation, and thus require birds to be more explorative and increase the probability of finding (high-quality) prey.

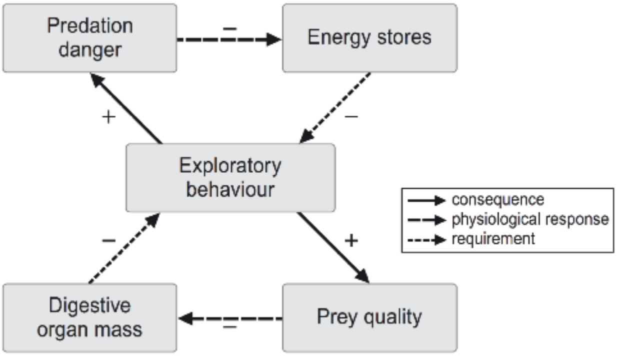

Figure 7.6 Hypothesised positive feedback loop capable of maintaining variation in exploratory behaviour between knots. The consequence of exploratory behaviour is increased predation danger, to which knots respond physiologically by having lower energy stores. Low energy stores increase starvation danger, which requires exploratory behaviour that consequently enables the discovery of high-quality prey. Digestive organ mass will be small as a physiological response to consuming high-quality prey, which in turn requires exploratory behaviour enabling the discovery of sparsely distributed high-quality prey, because birds with small gizzards can only achieve a sufficient intake rate on high-quality prey.

Second, we imagine that such feedback loops are especially important during ontogeny (either or not in interaction with genetic dispositions), after which behaviour could become fixed to some extent, i.e., consistent. Small differences in any of the variables in the hypothesized feedback loops could lead to lasting between-individual differences. For example, if by chance, a young and learning individual experiences an unsuccessful foraging bout and consequently low energy stores, it will be prompted to explore more, facing higher predation risk, and thus enforcing maintenance of lower energy stores (Witter and Cuthill 1993). At the same time, exploratory behaviour allows access to high-quality prey wherefore birds will acquire small gizzards, and thus enforcing exploratory behaviour (Fig. 7.6). The challenge is to pinpoint whether, and at what time during ontogeny, consistent variation in behaviour and physiology will start to occur. For such investigations we need to understand the key state variables involved in the trajectory towards exploratory or non-exploratory personalities. We propose that the causal framework sketched in Fig. 7.6 could be the working hypothesis upon which to build further empirical and theoretical work.

Acknowledgements

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Data accessibility

The data underlying this study is made available on Dryad (Bijleveld et al. 2014).

APPENDIX A7

Body mass, structural size and energy stores

In order to boost our sample size, we combined biometric data on our experimental birds with that on free-living knots (n = 1,453). We calculated the principal component of structural size measurements: wing length (mm), tarsus length (mm) and total head (mm, i.e. the length between the back of the head and tip of the bill). We then correlated body mass and PC1 using standardized major axis (Fig. A7.1) (Piersma 1984, van der Meer and Piersma 1994, Green 2001). In order to account for possible differences in intercept and slope between the sexes, we separated the analyses for males (n = 655) and females (n = 798). The obtained regressions were: y = 141 + 8.6x for males ($r^2 = 0.16$, $P < 0.01$), and y = 138 + 7.8x for females ($r^2 = 0.16$, $P < 0.01$).

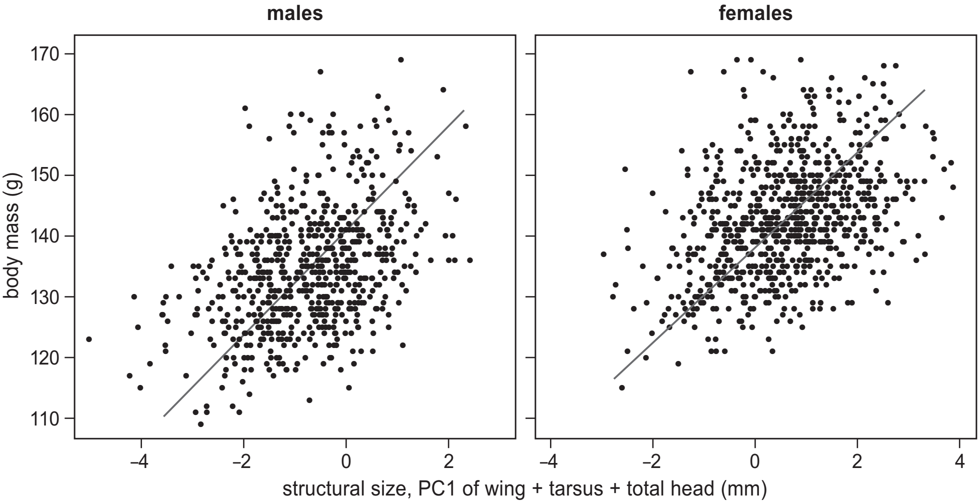


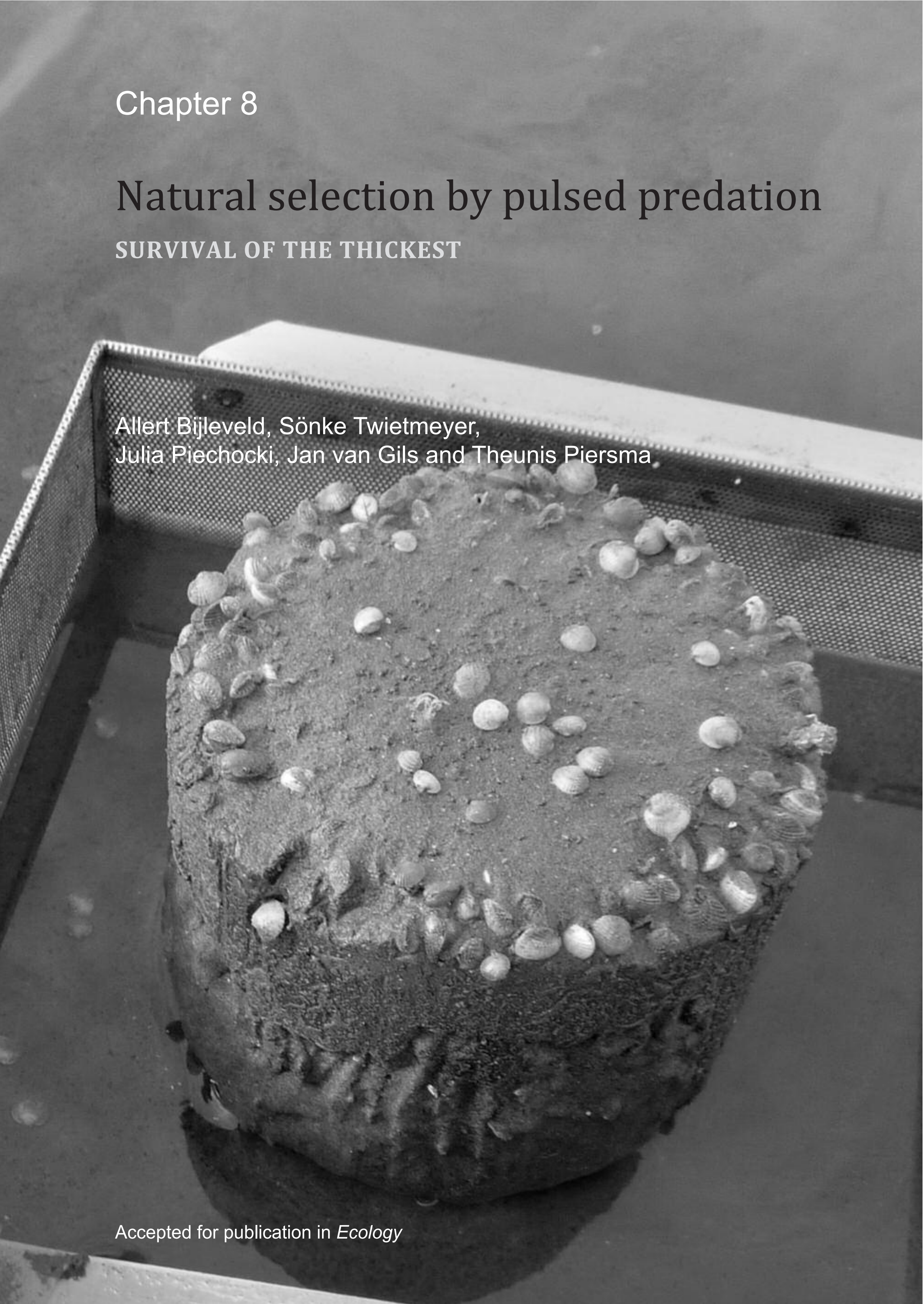
Figure A7.1 The relationship between the body mass and structural size for male and female knots. The lines represent fitted 'standardized major axis' models.

Table A7.1 Model selection results for the analyses of apparent survival and resighting probability. The models are ordered by AICc and the number of estimated parameters is given by *K*. Subscripts of apparent survival ϕ and resighting probability p indicate that they were constant (.),varied by residual gizzard mass (*gizzard*, as a covariate), or by year (*time*, as a factor).

Model	*K*	AICc	ΔAICc
$\phi_{.}\ p_{gizzard + time}$	16	2462.2	0.00
$\phi_{gizzard}\ p_{gizzard + time}$	17	2464.3	2.08
$\phi_{.}\ p_{time}$	15	2465.3	3.15
$\phi_{gizzard}\ p_{time}$	16	2466.2	4.00
$\phi_{time}\ p_{gizzard + time}$	28	2468.9	6.70
$\phi_{gizzard + time}\ p_{gizzard + time}$	29	2471.0	8.84
$\phi_{time}\ p_{time}$	27	2472.0	9.82
$\phi_{gizzard + time}\ p_{time}$	28	2472.9	10.75
$\phi_{time}\ p_{gizzard}$	16	2480.7	18.51
$\phi_{gizzard + time}\ p_{gizzard}$	17	2482.8	20.59
$\phi_{time}\ p_{.}$	15	2483.6	21.40
$\phi_{gizzard + time}\ p_{.}$	16	2484.6	22.41
$\phi_{.}\ p_{gizzard}$	3	2505.6	43.40
$\phi_{gizzard}\ p_{gizzard}$	4	2507.6	45.42
$\phi_{.}\ p_{.}$	2	2508.2	46.04
$\phi_{gizzard}\ p_{.}$	3	2509.1	46.92

Table A7.2 Parameter estimates from the best supported mark-recapture model. The estimated parameters are apparent survival ϕ and resighting probability p. Subscripts refer to effects of residual gizzard mass (*gizzard*, as a covariate) or years (as a factor). All coefficients are on a *logit* scale.

			95% confidence interval	
Parameter	**β**	**SE**	**Lower limit**	**Upper limit**
ϕ	1.52	0.09	1.35	1.69
$p_{gizzard}$	0.13	0.06	0.02	0.24
p_{1999}	-0.57	0.53	-1.61	0.46
p_{2000}	-0.91	0.59	-2.07	0.25
p_{2001}	-0.20	0.57	-1.31	0.91
p_{2002}	-0.48	0.56	-1.58	0.61
p_{2003}	-0.88	0.56	-1.97	0.22
p_{2004}	-0.38	0.55	-1.46	0.69
p_{2005}	0.45	0.55	-0.64	1.53
p_{2006}	-0.57	0.57	-1.68	0.54
p_{2007}	-0.10	0.57	-1.22	1.02
p_{2008}	-0.33	0.58	-1.48	0.81
p_{2009}	-1.53	0.65	-2.80	-0.26
p_{2010}	-1.44	0.66	-2.74	-0.14
p_{2011}	-0.17	0.64	-1.42	1.08
p_{2012}	-1.14	0.70	-2.51	0.23



Chapter 8

Natural selection by pulsed predation

SURVIVAL OF THE THICKEST

Allert Bijleveld, Sönke Twietmeyer,
Julia Piechocki, Jan van Gils and Theunis Piersma

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SUMMARY Selective predation can lead to natural selection in prey populations and may alleviate competition among surviving individuals. The processes of selection and competition can have substantial effects on prey population dynamics, but are rarely studied simultaneously. Moreover, field studies of predator-induced short-term selection pressures on prey populations are scarce. Here we report measurements of density dependence in body composition in a bivalve prey (edible cockle, *Cerastoderma edule*) during bouts of intense predation by an avian predator (red knot, *Calidris canutus*). We measured densities, patchiness, morphology, and body composition (shell and flesh mass) of cockles in a quasi-experimental setting, i.e. before and after predation in three similar plots of 1 ha each, two of which experienced predation, and one of which remained unvisited in the course of the short study period and served as a reference. An individual's shell and flesh mass declined with cockle density (negative density dependence). Before predation, cockles were patchily distributed. After predation, during which densities were reduced by 78% (from 232 m^{-2} to 50 m^{-2}), the patchiness was substantially reduced, i.e. the spatial distribution was homogenized. Red knots selected juvenile cockles with an average length of 6.9 mm (SD 1.0). Cockles surviving predation had heavier shells than before predation (an increase of 21.5 percentage points), but similar flesh masses. By contrast, in the reference plot shell mass did not differ statistically between initial and final sampling occasions, while flesh mass was larger (an increase of 13.2 percentage points). In this field-study, we show that red knots imposed a strong selection pressure on cockles to grow fast with thick shells and little flesh mass, with selection gradients among the highest reported in the literature.

INTRODUCTION

Predation is a key process in the ecology and population dynamics of prey (Vermeij 1987, Krebs and Davies 1997), and selective predation is an important agent of natural selection due to the removal of specific classes of prey (Endler 1986, Wade and Kalisz 1990), leading to the evolution of predator defense mechanisms (Caro 2005). Furthermore, when prey suffer from density-dependent processes, by thinning prey densities, predation can alleviate competition between surviving individuals (de Roos and Persson 2013). For instance, if individual growth is negatively density-dependent, predation reduces competition and enhances the growth of surviving individuals. Predation can thus have a major influence on densities, patchiness, size structure, body composition and potentially the reproductive output of prey at the population level (Gurevitch et al. 2000, de Roos and Persson 2013).

Although predator-prey interactions have been studied for a long time (Verhulst 1838, Krebs and Davies 1997, Caro 2005), studies that quantify the short-term selection pressures by predators on prey populations are rare, especially in the wild (Endler 1986, Calsbeek and Cox 2010). Here, we report on natural predation by red knots (*Calidris canutus*, hereafter called knots) on edible cockles (*Cerastoderma edule*) burrowed at shallow depths in temperate intertidal mudflats without experimental artefacts resulting from predator exclosures. In fact, we utilized the spatial unpredictability in the occurrence of flocks of foraging knots (Folmer et al. 2010) to provide us with predation plots as well a reference plot without predation. We quantified densities, patchiness, and external morphology (shell length, width and height), as well as body composition (shell and flesh mass) of cockles in their natural environment. We were able to quantify these variables before and after a two-week pulse of intense predation by knots, as well as in a situation without predation; the latter served as a reference. The comparison of cockles between the predation and the reference plots enabled us to study effects of predators on their prey in this quasi-experimental natural setting. Note that we consider it a *quasi*-experiment because we did not control where the birds foraged. We will show that the cockles suffered from intra-specific competition (negative density dependence), and that knots can have profound effects on the length distribution of cockles, as well as their density, patchiness, and body composition. We calculated selection gradients that were among the highest reported in the literature, and showed that knots imposed strong selection on cockles to grow fast with thick shells and little flesh mass.

METHODS

Background

Knots are medium-sized shorebirds that during the non-breeding season live in tidal areas (Piersma 2007, 2012). They are social and foraging groups of up to several thousand individuals are common (Piersma et al. 1993a). Over short time-scales (weeks) their foraging locations tend to be unpredictable, which is attributed to their strong social attraction

(Folmer et al. 2010), mobility (van Gils et al. 2005b), and the large spatial extent of foraging opportunities (Kraan et al. 2009a). Within each low-tide period, knots fly tens of kilometers across exposed mudflats in search of buried hard-shelled mollusks such as edible cockles (Piersma et al. 1993a, van Gils et al. 2005b). Because they swallow their prey whole, knots are limited to ingesting cockles smaller than 16 mm (Zwarts and Blomert 1992, Piersma et al. 1993a) and constrained by the amount of shell material that they can process (van Gils et al. 2003a). Due to this digestive constraint, knots maximize their energy intake rates by selecting individual cockles with large flesh mass compared to their shell mass (van Gils et al. 2005a).

Cockles are suspension feeding bivalves that are commonly found in the Dutch Wadden Sea (Beukema et al. 1993). Their spatial distribution is widespread (Kraan et al. 2009a), and they can be found in densities of up to several thousand individuals m^{-2} (Jensen 1993). Cockle population size as well as recruitment greatly varies between years (Beukema et al. 1993). They spawn between May and August leading to distinct year classes (Beukema et al. 2001). After a planktonic phase of several weeks, they settle on mudflats when they are approximately 0.3 mm long (e.g., De Montaudouin and Bachelet 1996). Cockles live in mudflats with inundation times ranging from 2 to 12h and sediment grain sizes ranging from 75 to 275 μm (Kraan et al. 2010). Nonetheless, cockles, prefer mudflats with inundation times between 6 and 8h (Kraan et al. 2010). Due to short siphons, they are limited in their burying depth and are found within a few cm of the surface (Zwarts and Wanink 1989). Living close to the surface and within reach of predators, e.g., knots with their 4 cm long bills, cockles rely on predator defenses such as shell thickness (armor). Cockles can grow to a maximum of 50 mm, and generally don't live longer than 5 years (Beukema et al. 1993).

Study design

Our study site was located in the Dutch Wadden Sea on the tidal flats near the uninhabited islet of Griend (53°14.615'N, 5°15.219'E, Appendix Fig. A8.1). Griend is surrounded by extensive intertidal mudflats that stretch for tens of kilometers. Near Griend, we selected three plots (plots A, B and C) of 100 × 100 m each where knots were previously seen foraging on cockles. All plots were visually identical, located at similar distances from Griend (590, 660 and 520 m for plots A, B and C, respectively), and had similar inundation times (7.6, 7.7 and 6.7 hours for plots A, B and C, respectively) and sediment grain sizes (182, 182 and 185 μm for plots A, B and C, respectively) (see Compton et al. 2013). Given the wide range of inundation times (from 2 to 12h) and sediment structures (from 75 to 275 μm) that cockles occur at (Kraan et al. 2010), the differences in habitat characteristics between the plots are actually small. In fact, all plots fall within the preferred habitat range of cockles (Kraan et al. 2010). Due to difficulty in predicting where knots would forage within a tide (Folmer et al. 2010), we did not know beforehand at which plot, if any, knots would forage. Two of the three plots were visited by knots (plots A and B), and even though we had seen foraging knots there as well, plot C was not visited by knots during our measurement interval. This allowed us to study the effect of knot predation on cockles in comparison to a reference plot without predation, i.e., a before-after control-impact design. All three plots were sampled intensively over a relatively large spatial scale (1 ha).

Sampling the prey

On 12 and 18 August and on 4 September 2010 we sampled cockle densities in plots A, B and C, respectively. On 26 August, knots gave up foraging in plots A and B. On 26 August, 2 and 9 September we resampled cockle densities in plots A, B and C, respectively. Although ideally, we should have sampled all plots simultaneously, logistical limitations prevented us from doing so. Nonetheless, the sampling dates were relatively close together and we have no reason to suspect that factors that vary over time have influenced our results (Zwarts 1991). At each plot we sampled 150 stations of which 100 sampling stations were placed 10 m apart on a systematic grid, and the remaining 50 sampling stations were randomly placed on grid lines (Chapter 2). This sampling design allowed for precise estimation of mean densities, as well as spatial autocorrelation parameters that were necessary for estimating patchiness and accurate spatial interpolations of cockle densities (Chapter 2).

We marked sampling stations with color coded PVC tubes (Ø 20 mm) reaching 20 cm above the mudflat. We avoided resampling the exact locations by initially sampling east and finally sampling 10 cm west of the marker. At each sampling station we collected one core (1/56 m^2) to a depth of 20–25 cm, which we rinsed over a 1-mm mesh sieve. We collected and froze all cockles before taking them to the laboratory where their lengths, widths and heights (as defined by Zwarts and Blomert 1992) were measured to the nearest 0.1 mm. From a subsample of 115 sampling stations (1,094 individuals), we determined an individual's body composition by measuring dry mass of the shell (DM_{shell}) and ash-free dry mass of the flesh ($AFDM_{flesh}$) according to the procedure described by Piersma et al. (1993a). These body compositional samples were unevenly distributed between plots and sampling occasions. For the first and second sampling occasion we sampled 21 and 0 individuals from plot A, 186 and 72 individuals from plot B, and 214 and 601 individuals from plot C. In order to correct for this uneven distribution, we analyzed the data in mixed-effect analyses with sampling station as random effect (see Data analyses).

Spatially autocorrelated cockle densities

Often, animal densities are positively correlated over small distances, and the further apart, the weaker this correlation. A spatial autocorrelation function describes how spatial autocorrelation changes with distance, and can be used for estimating the average patch size (e.g., Kraan et al. 2009a), or for spatial interpolations (Cressie 1993). In order to investigate the effect of predation on the patchiness of cockles, as well as to visualize their spatial distributions, we calculated spatial autocorrelation functions and interpolated cockle densities across each plot. Per sampling core, we counted the number of cockles that were suitable for knots to swallow (smaller than 16 mm). We normalized model residuals by transforming the numbers of suitable cockles with the common logarithm ($\log_{10}$). To avoid taking the logarithm of zero, we added one before the data transformation. We calculated a correlogram based on the (transformed) numbers of suitable cockles per sampling core for each plot with a spatial lag of 3 m. We then fitted several commonly used spatial autocorrelation functions to the correlograms and selected the exponential spatial autocorrelation function (Chapter 2, van der Meer and Leopold 1995) that had the lowest Akaike Information Criterion between all plots.

In order to estimate the average cockle patch size within plots, we calculated at what distance the autocorrelation reached the arbitrary value of 0.1 (Kraan et al. 2009a). In the presence of spatial autocorrelation, we estimated mean cockle densities and their standard errors with generalized least squares (Cliff and Ord 1981), otherwise we used ordinary least squares analyses (Chapter 2). For each plot, we spatially interpolated cockle densities with 'kriging' (Cressie 1993). For representation purposes, we back-transformed the density estimates with their 95% Confidence Interval (CI) and divided these by the surface area of the sampling core to obtain cockle densities in numbers m^{-2}. Note that as a result of the logarithmic transformations, model results represent geometric means instead of arithmetic means. In order to correct for this bias and obtain the arithmetic means, we multiplied the back-transformed estimates by the antilog of $0.5 \times \log_e(10) \times \sigma^2$ (Rothery 1988).

Sampling predator abundances

In order to estimate densities of foraging knots in the study plots, we video-recorded each plot, in good weather at daytime, during low tide for as long the plot was studied (between the initial and final prey sampling of each plot). By slowly moving the camera from left to right, each plot could entirely be captured by one camera. In total we video-recorded knots for 15 and 22 hours in plots A and B, and for 0 hours in plot C as there were no knots present during the short study-period. Based on these recordings we estimated that an average of 74 (4.9 SD) knots per plot were present in plots A and B for an average duration of 2 hours per tide and none in plot C.

Data analyses

Due to non-linearity and heteroscedasticity, the allometric relationships between body composition and length are usually analyzed with linear regressions on a log-log scale. However, due to remaining nonlinearity, we modelled an individual's DM_{shell} and $AFDM_{flesh}$ with length on a log-log scale using non-linear local regression models (LOESS with local quadratic fitting, Appendix Fig. A8.2) (for the R-script see Bijleveld et al. 2015). LOESS is flexible and follows the data regardless of any non-linear patterns. To compare DM_{shell} and $AFDM_{flesh}$ between differently sized cockles, we extracted an individual's residual from the non-linear LOESS fits, which reflects their relative DM_{shell} and $AFDM_{flesh}$. For representation purposes, we back transformed these residuals into ratios representing an individual's body composition relative to the expected value for that length. Note that even though shell length is a one-dimensional measure of body size, our results were similar to analyses with three-dimensional measures of size (length × width × height). Because length is a more intuitive measure of size than the three-dimensional multiplication and has been used in bivalve studies before (e.g., Armonies 1992, Zwarts and Blomert 1992, Piersma et al. 1995, van Gils et al. 2005b), all our analyses are based on length. In order to select the smoothing parameter of the LOESS fits, we inspected the pattern of model residuals with length. A smoothing parameter of 0.5 gave the smoothest fits (i.e. removed the size-dependence) while still following the structural features of our data (Jacoby 2000). In order to assess the goodness-of-fit, resembling the coefficient of determination r^2, we calculated the ratio of the sum of squares in the LOESS fitted values to the total sum of squares in the dependent variable (Jacoby 2000). The calculated ratios for DM_{shell} and $AFDM_{flesh}$ were 0.99 and 0.98, but note that, in comparison to r^2 values, the interpretation of these ratios is not straightforward (Jacoby 2000).

For the density dependence analyses we included cockles from all plots, but excluded those samples from the final sampling occasions in the predation plots. Density dependence is a result of intra-specific competition that is not limited to specific size classes, i.e., size classes that knots can swallow. We, therefore, included cockles of all lengths (between 3.6 and 41.6 mm) in the analyses of density dependence. With this subset of data we calculated an individual's relative DM_{shell} and $AFDM_{flesh}$ as described previously, and analyzed these traits in linear mixed-effect models with sampling station as a random effect, and shell length (mm) plus log_{10}-transformed cockle density (m^{-2}), and their interaction, as explanatory variables. A significant interaction between length and density on an individual's relative DM_{shell} or $AFDM_{flesh}$ would indicate that cockles of different lengths are differentially affected by density dependence (intra-specific competition). In order to avoid computational issues due to collinearity between predictors, we centered length and log_{10}-transformed density by subtracting their means (12.9 mm and 3.07, respectively). By parametric bootstrapping (n = 1,000), we calculated significance under the null hypothesis that the estimated coefficients are zero.

To analyze the effects of knot predation on an individual's relative DM_{shell} and $AFDM_{flesh}$, we selected cockles from all plots and sampling occasions, but only those of suitable sizes for knots to swallow (length < 16 mm, n = 887). With this subset of data we calculated an individual's relative DM_{shell} and $AFDM_{flesh}$ as described above, and analyzed these traits in linear mixed-effect models with sampling station as a random effect, and 'sampling occasion' (a factor coding for either initial or final sampling) plus 'predation' (a factor coding for either the predation or reference plots), and their interaction, as explanatory variables. Due to the positive correlation between an individual's relative $AFDM_{flesh}$ and DM_{shell} ($r = 0.29$, $P < 0.01$), we also analyzed these data in bivariate mixed-effect models, i.e., a model with $AFDM_{flesh}$ and DM_{shell} simultaneously as response variables. These results were, nevertheless, similar to univariate analyses and for brevity we present the univariate mixed-effect models. We additionally investigated the effect of predation on the shape of cockle shells by calculating the ratio of both shell height and shell width to length. We analyzed these ratios in mixed-effect models as explained above, but included cockle length (centered by subtracting its mean) as an explanatory variable in the analyzes of the ratio of width to length to correct for its linear increase with shell length (0.008 SE 0.001, $P < 0.01$). By parametric bootstrapping (n = 1,000), we calculated significance under the null hypothesis that the estimated coefficients are zero.

We calculated linear and nonlinear selection gradients (Lande and Arnold 1983, Endler 1986) on length and body composition with multivariate models following Johnson et al. (2012). As collinearity between variables can make these multivariate analyses unreliable, we calculated selection gradients for length in a multivariate model with an individual's relative $AFDM_{flesh}$ and DM_{shell}. The condition numbers of the resulting variance-covariance matrices indicated no problems with collinearity for neither the predation ($\kappa = 2.4$) or the reference plot ($\kappa = 1.5$). By parametric bootstrapping ($n = 1{,}000$), we calculated standard deviations and significance of the selection gradients under the null hypothesis that they are zero.

All data analyses were carried out in R v3.1.0 (R Core Team 2013) with the packages 'ncf' for calculating correlograms, 'fields' for spatial interpolations, and 'lme4' for mixed-effect model analyses.

Table 8.1 Mixed-modelling results for the effects of cockle lengths and densities on their relative body composition.

Response variables	Random effects	Predictors	Estimates	SE	*P*
(**A**) relative DM_{shell}		intercept	-0.000	0.004	1.00
		length	-0.000	0.000	0.69
		density	-0.031	0.011	<0.01
		length × density	-0.002	0.001	0.08
	sampling station		0.023	0.003	<0.01
	residual		0.063	0.001	<0.01
(**B**) relative $AFDM_{flesh}$		intercept	-0.002	0.008	0.82
		length	0.001	0.000	0.16
		density	-0.057	0.018	<0.01
		length × density	0.006	0.001	<0.01
	sampling station		0.053	0.005	<0.01
	residual		0.063	0.001	<0.01

Note: The mixed-modelling results for the effects of cockle length (mm) and density (m^{-2}) on an individual's relative (A) dry mass of the shell (DM_{shell}), and (B) ash-free dry mass of the flesh ($AFDM_{flesh}$). Cockle density was $\log_{10}$-transformed. In order to avoid computational issues due to collinearity, covariates were centered with their mean length (12.9 mm) and $\log_{10}$-transformed density (3.07). The random effect estimates refer to standard deviations. Note that these data included cockles of all lengths (3.6 - 41.6 mm) and excluded data from the final sampling occasions in the predation plots.

RESULTS

Density dependence

A cockle's relative shell mass (DM_{shell}) and flesh mass ($AFDM_{flesh}$) declined with cockle density (Table 8.1 and Fig. 8.1). The interaction between length and density on relative DM_{shell} was nonsignificant (Table 8.1 A). For relative $AFDM_{flesh}$ this interaction was significantly positive (Table 8.1 B), indicating that smaller cockles were proportionally more affected by intra-specific competition than larger ones.

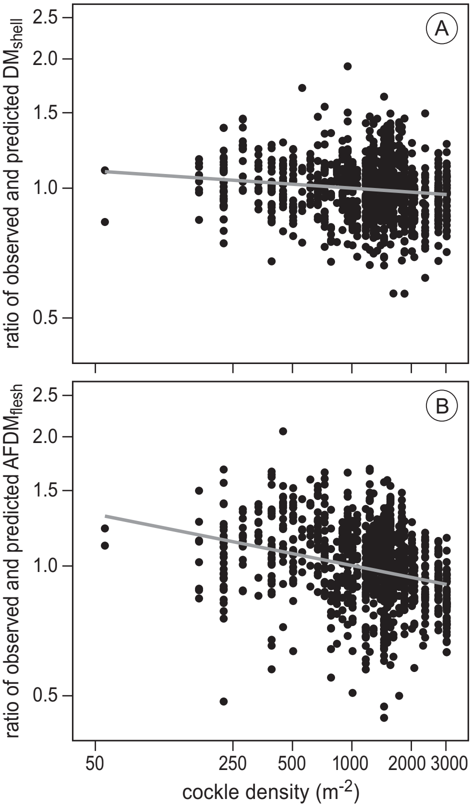


Figure 8.1 Negative density dependence in body composition of cockles. An individual's relative (A) dry mass of the shell (DM_{shell}) and (B) ash-free dry mass of the flesh ($AFDM_{flesh}$) were plotted against cockle densities (m^{-2}). For representation purposes, we back transformed relative body composition into ratios representing an individual's body composition relative to the expected value for that length. Note that these data included cockles of all lengths (3.6 – 41.6 mm) and excluded data from the final sampling occasions in the predation plots. The slope of the regression between relative $AFDM_{flesh}$ and cockle density in panel (B) decreased with cockle length as indicated by the significantly positive interaction between cockle length and density (Table 8.1). Therefore, the regression presented in panel (B) shows the decline in an individual's relative $AFDM_{flesh}$ with cockle density for 6.9 mm long cockles (i.e. mean cockle length eaten by knots).

Predation and the patchiness of prey

Before predation the cockles (length < 16 mm) were patchily distributed (Fig. 8.2 A, C, and E). This was evidenced by the significant positive autocorrelation at distance zero (b_0) and the decline of autocorrelation with distance (b_1) that we measured in plot A (b_0 = 0.47 SE 0.05, $P < 0.01$, and b_1 = –0.05 SE 0.01, P < 0.01), plot B (b_0 = 0.54 SE 0.12, $P < 0.01$, and b_1 = –0.07 SE 0.02, $P < 0.01$), and plot C (b_0 = 0.35 SE 0.10, $P < 0.01$, b_1 = –0.05 SE 0.02, $P = 0.03$) (Fig. 8.3 A, C, and E). The distance at which autocorrelation dropped below 0.1 (the average patch size) was 31 m for plot A, 25 m for plot B, and 24 m for plot C. Initial cockle densities were on average 186 m^{-2} (95% CI [119; 278]) in plot A, 277 m^{-2} (95% CI [210; 362]) in plot B, and 1,230 m^{-2} (95% CI [1,037; 1,457]) in plot C.

Knot predation reduced cockle densities by 72% in plot A and 83 % in plot B to 52 (95% CI [42; 62]) and 48 m^{-2} (95% CI [38; 59]) respectively (Fig. 8.2 A-D). After predation, the patchiness in cockle densities was substantially reduced (homogenized), as shown by the nonsignificant spatial autocorrelation parameters after predation for both plot A (b_0 = 0.13 SE 0.22, $P = 0.56$, and b_1 = 0.29 SE 0.63, $P = 0.66$) and plot B (b_0 = –0.06 SE 0.15, $P = 0.68$, and b_1 = –0.07 SE 0.23, $P = 0.77$) (Fig. 8.3 B and D). Compared to the initial sampling, mean cockle density in the reference plot was similar to the final sampling (1,280 m^{-2}, 95% CI [1,030; 1,587], Fig. 8.2 E and F). There were some differences in the spatial density distribution between the initial and final sampling in the reference plot (Fig. 8.2 E and F), but these probably reflect sampling error. The autocorrelation parameters (b_0 = 0.41 SE 0.14, $P < 0.01$, b_1 = –0.06 SE 0.03, $P = 0.04$), as well as the average patch size (24 m), were similar to those at initial sampling (Fig. 8.3 E and F).

Selective predation and phenotypic traits of the prey

The differences in length distribution and body composition of cockles, before and after predation, were pronounced. Before predation, the mean length of suitable cockles (length < 16 mm) in both plots A and B was 7.4 mm (2.4 SD), whereas after predation the mean length increased to 10.4 mm (2.9 SD, Fig. 8.4 A and B). Subtracting the frequency distributions of suitable cockles before and after predation suggests that knots had selected cockles with a mean length of 6.9 mm (1.0 SD). The length distribution of suitable cockles in the non- predation reference plot C did not differ between the initial (10.9 mm 1.8 SD) and final sampling (11.1 mm 1.8 SD, Fig. 8.4 C).

Predation had no effect on the shape of cockle shells as neither did the ratio of width to length before predation (0.65 SD 0.07) differ with that after predation (0.66 SD 0.08), nor did the ratio of height to length differ between before (0.90 SD 0.05) and after predation (0.91 SD 0.07). In reference plot C, the ratio of cockle width to length did differ significantly (0.01 SE 0.005, $P = 0.01$) between the initial (0.66 SD 0.07) and final sampling (0.67 SD 0.05), as did the ratio of height to length differ significantly (0.01 SE 0.003, $P < 0.01$) between initial (0.89 SD 0.05) and final sampling (0.90 SD 0.04). The changes in shell shape between initial and final sampling in the reference plot were small and similar to the predation plots, as neither did the changes in height-to-length (–0.004 SE 0.007, $P = 0.53$),

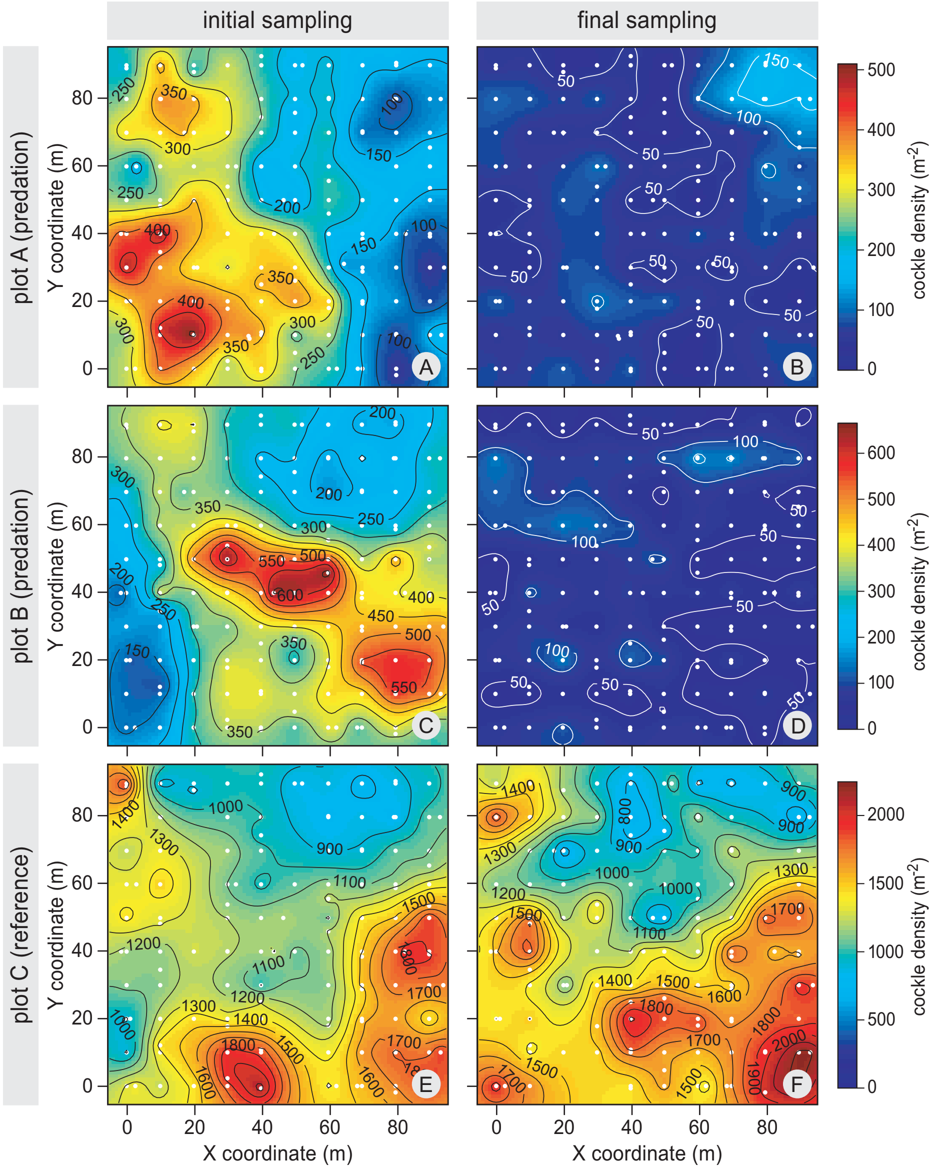


Figure 8.2 Spatial density distributions of cockles (length < 16 mm). Rows represent the different plots (respectively plots A, B, and C), and the columns represent the sampling occasion with the initial sampling shown on the left (panels A, C and E), and the final sampling shown on the right (panels B, D and F). The top two rows (panels A-D) show the plots where cockles were fed upon by knots, and the third row (panels E-F) show the reference plot where knots were not observed foraging. For the spatial representation of final densities (panels B and D) we spatially interpolated densities with the autocorrelation function estimated from the initial sampling. White dots show the sampling stations and the colors represent cockle densities in numbers per m^2. Note that the density scales differ between plots.

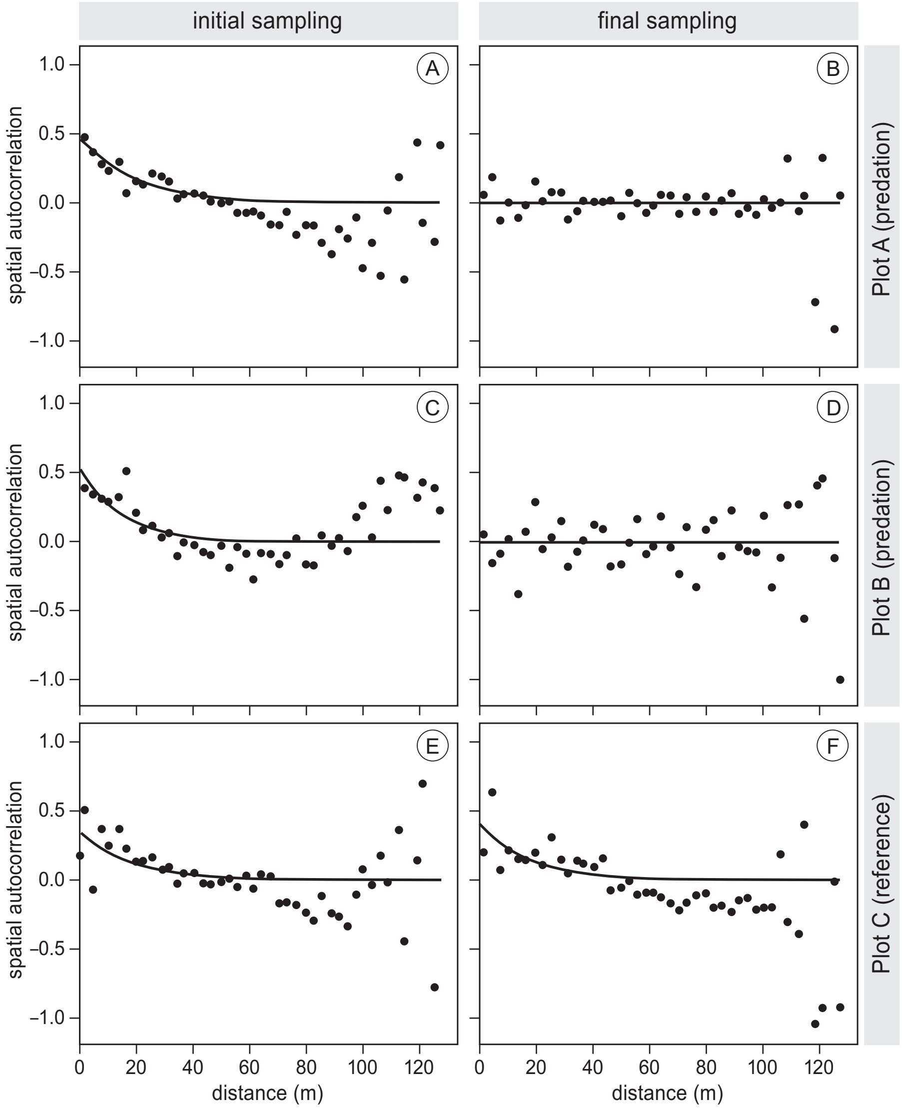
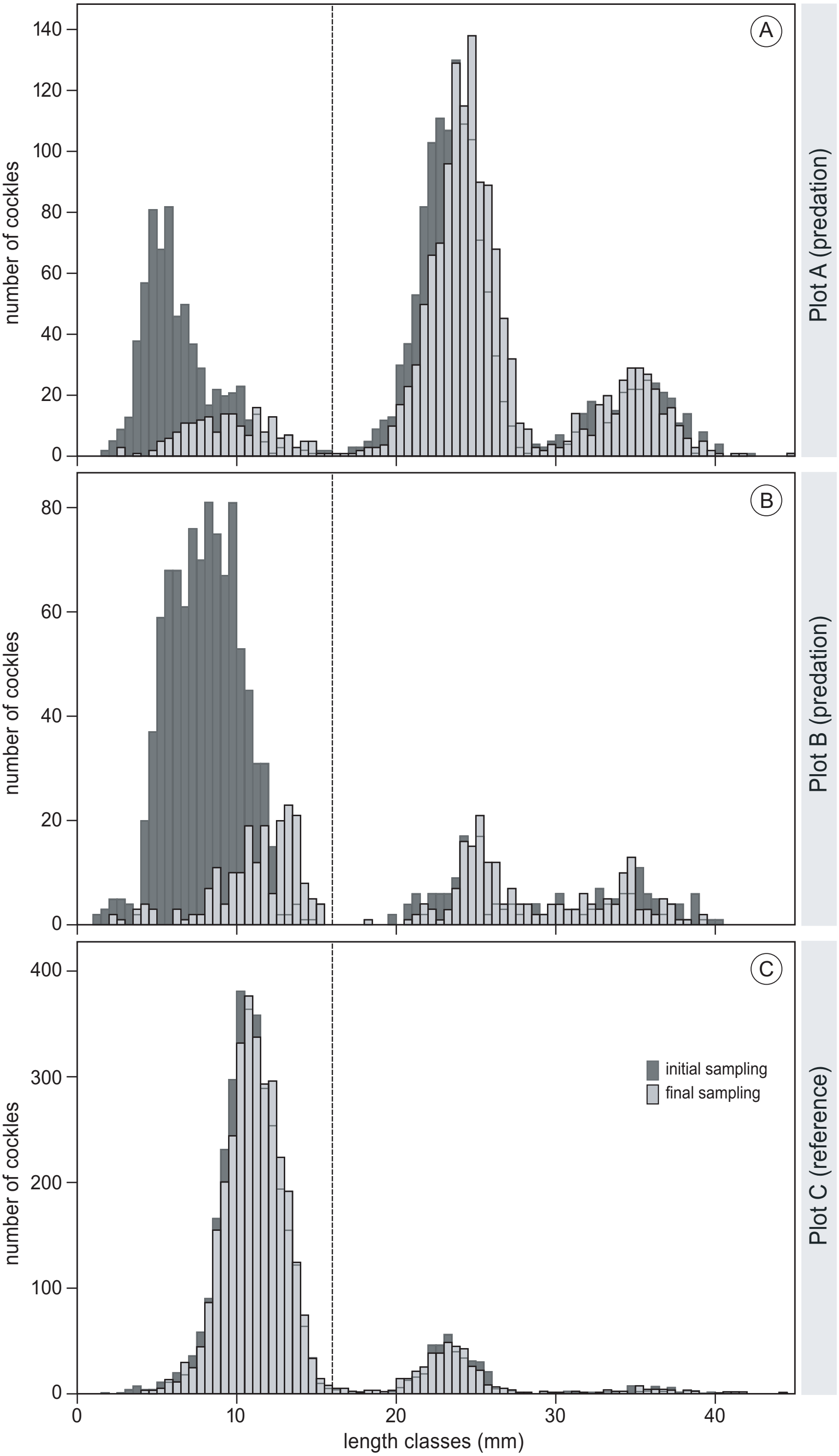


Figure 8.3 Spatial autocorrelation functions of the transformed numbers of suitable cockles (length < 16 mm) per sampling core. The rows represent the different plots (respectively plots A, B, and C), and the columns represent the sampling occasion with the initial sampling shown on the left (panels A, C and E), and the final sampling shown on the right (panels B, D and F). Plots A and B were visited by foraging knots, and plot C was a reference plot without knot predation. The initial autocorrelation functions are given by: $y = 0.47e^{-0.05x}$ for plot A, $y = 0.54e^{-0.07x}$ for plot B, and $y = 0.42e^{-0.06x}$ for plot C. The final autocorrelation function for plot C was $0.41e^{-0.06x}$.

Figure 8.4 (Right) Effects of predation on the length distribution of cockles. We present the length distributions of cockles at initial and final sampling for predation plot A (A), predation plot B (B), and for the reference plot without predation (C). The vertical lines indicate the upper limit (16 mm) of cockles that knots are able to swallow. Note the different scales of the y-axis.


A
B
C
Plot A (predation)
Plot B (predation)
Plot C (reference)
number of cockles
number of cockles
number of cockles
0
20
40
60
80
100
120
140
0
20
40
60
80
0
100
200
300
400
0
10
20
30
40
length classes (mm)
initial sampling
final sampling

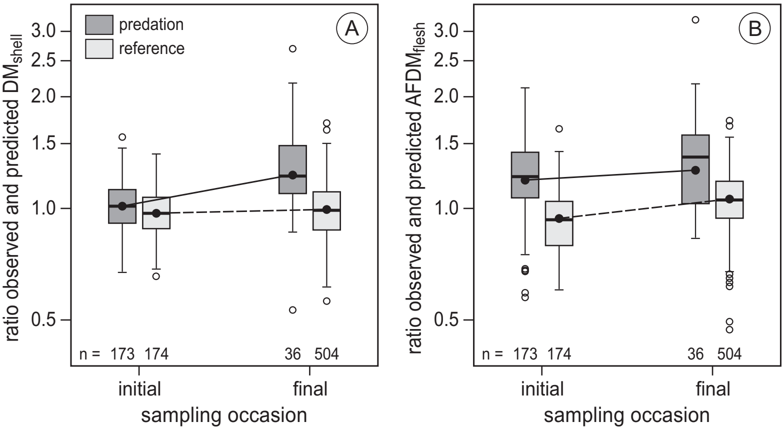


Figure 8.5 Effects of predation on cockle body composition. We present an individual's relative (A) dried shell mass (DM_{shell}), and (B) ash-free dry mass of the flesh ($AFDM_{flesh}$) at the initial and final sampling occasion and separated for the predation plots and reference plot. For representation purposes, we back transformed relative body composition into ratios representing an individual's body composition relative to the expected value for that length. Note that these data were limited to cockles that knots were able to swallow (lengths < 16 mm). The boxes indicate the inter quartile range, the horizontal lines in the boxes indicate the median, the whiskers indicate the 95% data range, and the points indicate the <5% data range. The circles represent model estimates from Appendix Table A8.1, which are connected within the predation treatment (solid lines) and reference treatment (dotted lines).

Table 8.2 Cockle selection gradients imposed by knot predation.

selection gradient	trait	predation			reference			difference		
		est.	SE	*P*	est.	SE	*P*	est.	SE	*P*
linear (β)	length	1.39	0.28	<0.01	0.40	0.09	<0.01	1.00	0.29	<0.01
	DM_{shell}	1.41	0.33	<0.01	0.02	0.09	0.82	1.39	0.34	<0.01
	$AFDM_{flesh}$	-0.41	0.26	0.12	0.65	0.10	<0.01	-1.07	0.28	<0.01
nonlinear (γ)	length	3.48	1.11	<0.01	0.28	0.20	0.16	3.21	1.13	<0.01
	length × DM_{shell}	0.97	1.25	0.44	-0.05	0.15	0.75	1.02	1.26	0.42
	length × $AFDM_{flesh}$	-2.11	0.96	0.03	0.64	0.19	<0.01	-2.75	0.98	<0.01
	DM_{shell}	4.77	1.76	<0.01	0.36	0.18	<0.05	4.41	1.77	0.01
	DM_{shell} × $AFDM_{flesh}$	-0.06	1.10	0.96	0.12	0.16	0.44	-0.18	1.11	0.87
	$AFDM_{flesh}$	1.44	0.82	0.08	0.38	0.26	0.14	1.06	0.86	0.22

Note: We estimated cockle selection gradients for the predation and reference plot, and we show their differences. The traits refer to a cockle's length in mm, as well as its relative dry mass of the shell (DM_{shell}), and relative ash-free dry mass of the flesh ($AFDM_{flesh}$). Note that we limited these analyses to cockles that knots could ingest (lengths <16 mm).

nor the changes in width-to-length ratios (0.02 SE 0.010, $P = 0.14$) differ significantly between the predation and reference plots.

Individuals surviving predation had heavier shells, an increase of 21.5 percentage points (95% CI [12.4; 31.2], $P < 0.01$, Appendix Table A8.1, and Fig. 8.5 A), than before predation, indicating that predation affected cockle shell thickness. An individual's relative $\text{AFDM}_{\text{flesh}}$ did not differ between the initial and final measures (6.4 percentage points higher, 95% CI [–5.1; 19.1], $P = 0.26$, Appendix Table A8.1, and Fig. 8.5 B). In reference plot C, we observed no significant difference in an individual's relative DM_{shell} between initial and final sampling (2.4 percentage points, 95% CI [–3.3; 8.4], $P = 0.42$, Appendix Table A8.1, and Fig. 8.5 A). However, we did observe that an individual's relative $\text{AFDM}_{\text{flesh}}$ was 13.2 percentage points larger in the final sample compared to the initial sample (95% CI [2.6; 25.1], $P = 0.02$, Appendix Table A8.1, and Fig. 8.5 B).

Selection gradients

In the predation plots, we observed positive linear selection gradients on cockle length and relative DM_{shell}, but we did not find this for an individual's relative $\text{AFDM}_{\text{flesh}}$ (Table 8.2). The nonlinear (quadratic) selection gradients on length, and relative DM_{shell} were also significantly positive, and we found that natural selection favored combinations of large lengths and small relative $\text{AFDM}_{\text{flesh}}$ (Table 8.2). In the reference plot, we did not find a significant linear selection gradient on an individual's relative DM_{shell}, but those on length and relative $\text{AFDM}_{\text{flesh}}$ were significantly positive (Table 8.2). In addition, the nonlinear selection gradient on DM_{shell} was significantly positive, and natural selection favored combinations of large lengths and large relative $\text{AFDM}_{\text{flesh}}$ (Table 8.2).

The significantly positive linear selection gradients on length, and $\text{AFDM}_{\text{flesh}}$ in the reference plot indicated growth between the initial and final sampling period. In order to account for such growth and investigate the net effect of predation on natural selection, we subtracted the linear selection gradients of the reference plot from those of the combined predation plots. These adjusted selection gradients confirmed that predation generated a positive selection gradient on cockle length, a positive selection gradient on relative DM_{shell}, but also revealed a negative selection gradient on relative $\text{AFDM}_{\text{flesh}}$ (Table 8.2).

DISCUSSION

The processes of selection and competition are rarely studied together, and field studies of predator-induced short-term selection pressures on prey populations are scarce. In this quasi-experimental field study, we showed that cockles suffered from intra-specific competition, and that selective predation by knots has profound effects on the density, the patchiness, as well as the length distribution and body composition of their cockle prey. Knots ate small cockles with thin shells and proportionally large flesh content imposing a strong selection pressure on cockles to grow fast and have thick shells with little flesh mass. Before discussing the ecological implications of our study, we will first address possible caveats in our study design.

Study design and robustness of results

The nature of our field-study suggested some problems of sampling design. The predation and reference plots were sampled in sequence (the reference plot was sampled 2–3 weeks after the predation plots). The difference in depletion between the predation and reference plots could therefore be confounded by some (environmental) variable that changed over time causing differential natural mortality or emigration between the predation and reference plots. We do not think this is a realistic concern as in August-September the environmental conditions in the Wadden Sea, and indeed cockle body condition, tend to be stable (Zwarts 1991). Parada and Molares (2008) estimated the natural mortality of cockles at 0.01 day^{-1}, which, in our study, would translate into a density reduction of 7 % over the course of 14 days. Thus, natural mortality alone cannot explain the observed density changes.

Also cockle emigration rates seem too low to account for the observed density reduction. Only spat up to a size of 3.5 mm is capable of migration in the water column over large distances (Armonies 1992). Larger cockles are capable of crawling over the surface at speeds of 0.6 cm day^{-1} (Flach 1996), but speeds of 50 cm day^{-1} have also been reported (Mouritsen 2004). Such speeds will correspond to an average linear movement of 0.08 m, and 7 m at the most, during our short study period. These distances fall comfortably within the 1 ha scale of our plots. Like natural mortality, emigration does not seem capable of reducing cockle densities by 72–83%.

In fact, the numbers of knots that we observed in the predation plots are capable of causing the observed depletion. In our plots, knots foraged on average for 2 hours per tide, and selected 6.9 mm long cockles with an average of 1.9 mg AFDM$_{\text{flesh}}$ (Appendix Fig. A8.2). In order to maintain their energy balance, knots require an intake rate of 0.3 mg AFDM$_{\text{flesh}}$ s^{-1} (Piersma et al. 1995). The average difference of 182 cockles per m^2 before and after predation would thus be capable of sustaining 69 knots per tide throughout our study period of 24 low tides. This estimate is similar to the 74 (4.9 SD) knots that we observed per tide, which shows that knot predation would indeed cause a depletion of 72–83%.

The absence of true replication of the reference plot leads to the question whether this is a sufficient reference. We argue that the large spatial spread (across 1 ha) of the samples taken within the reference plot should be seen as replication. Nevertheless, there were differences between the predation and reference plot, e.g., cockle abundance, size distribution. In ideal circumstances the two treatments should only differ in predation level. For a field-study like this, the habitat differences (e.g., in inundation time, sediment structure) between the predation and reference plot were actually very small (Kraan et al. 2010, but see Methods). In fact, the reference and predation plots were all in the preferred habitat range of cockles (Kraan et al. 2010), and all plots contained cockles of suitable sizes to knots. There is nothing to suggest that the differences in depletion between the predation and reference plots would be caused by something else than predation. Moreover, the presence of foraging knots in the reference plot, before and after the experimental observation period, indicated its potential suitability to knots.

The timing between resampling the predation and reference plots was different (14 days for the predation and 5 days for the reference plot). That exposure to potential predation was smaller, does not make the unvisited reference plot less of a valid reference for lack of predation. Nonetheless, the difference in timing might affect the comparison of selection gradients between the predation and reference plots (i.e. the net selection gradients, Table 8.2). We would argue, however, that our results are robust to this difference in sampling interval for the following reasons. As a consequence of the shorter sampling interval, we underestimated the increase in mean length in the reference plot and consequently overestimated the net selection gradient on length. However, the increase in length due to growth (over 14 days) was small compared to the increase in mean length due to the selective removal of small size classes (Fig. 8.4 A and B). The selection gradient for relative flesh mass was also robust to the difference in sampling interval, in fact, the estimate is conservative. Since the selection gradient on flesh mass in the reference plot would have been larger when given more time, subtracting this from the selection gradient in the predation plot would have resulted in a stronger (more negative) net selection gradient. Note that the selection gradients resulting from predation are as expected based on knot foraging behavior (e.g., van Gils et al. 2003a, van Gils et al. 2005a).

Density dependence in the prey

Predation can have profound influences on the population dynamics of species, especially when population processes are density dependent (Gurevitch et al. 2000). For example, by reducing prey numbers predation can reduce competition and enhance growth (van Gils et al. 2012). This has a major influence on size structure, and potentially on reproductive output at the population level (Beukema et al. 2001, de Roos and Persson 2013). Initially there was debate on whether bivalve suspension feeders, such as cockles, can show negative density dependence, as they are hypothesized to be less susceptible to intra-specific competition for resources (Levinton 1972). However, later empirical studies showed that suspension feeding bivalves are actually susceptible to competition for space and/or for food at even quite low densities (Peterson and Andre 1980, Jensen 1993, Kamermans 1993). In particular, cockle growth (De Montaudouin and Bachelet 1996), flesh content (Sutherland 1982a), reproductive success (Beukema et al. 2001), and survival (Parada and Molares 2008) have been shown to decrease with increased cockle densities. Here, we additionally demonstrate declines in the relative shell and flesh mass of cockles with density. We also show that the smallest cockles were most susceptible to intra-specific competition on flesh mass (as indicated by the significant interaction between length and density on $AFDM_{flesh}$, Table 8.1 B).

Depletion of cockle densities and community effects

Predators may substantially impact the densities of their prey. Over the course of 4 months, for instance, common eiders *Somateria mollissima* consumed between 48 and 69% of their bivalve prey in an area of 6.7 ha (Guillemette et al. 1996). In a study on knots, it was shown that during single low-tide periods they were able to take 25% of the bivalve stock (in this particular case represented by *Mya arenaria*) in small areas (100 m^2) (van Gils et al. 2003b). Among the most substantial prey depletion reported in literature is that of a combination of different wader species foraging on Chironomid larvae in 100 m^2 plots decreased in density by 87% over the course of 13 days (Székely and Bamberger 1992).

Prey depletion is often studied by means of predator exclosures (Sih et al. 1985), artifacts that in intertidal soft-sediment systems tend to alter the physical environment and affect prey behavior, growth, etc. (Wilson 1991). Predator exclosures also suffer the problem of a mismatch of scale between the area covered by exclosures (several m^2) and the much larger extents over which predators forage (Thrush 1999). This study is quite unique in its ability to estimate depletion on a relatively large, and ecologically relevant, spatial scale without experimental artifacts.

The arms race between predators and prey

Natural selection by selective removal of prey can have a profound influence on prey behavior, morphology and physiology (Genovart et al. 2010, Benkman et al. 2013, Vedder et al. 2014). Under the selection pressures imposed by predators, prey continuously evolve behavioral, morphological, and physiological defense mechanisms (Dawkins and Krebs 1979). In the case of bivalves, they can reduce predation risk either by burrowing deeper into the sediment (Zwarts and Wanink 1989), building armor (Vermeij 1987), or quickly attaining a refuge in size (Paine 1976). Cockle burying depth is limited by their short siphons and they are found within a few cm of the surface (Zwarts and Wanink 1989). This excludes the option to reduce risk via burrowing deeper and hence cockles need to rely on predator defenses such as fast growth and/or shell thickness (armor). Cockles longer than 16 mm cannot be ingested by knots (Zwarts and Blomert 1992, Piersma et al. 1993a) and thus attain a refuge in size (Paine 1976). Indeed, we found that knots mainly foraged on juvenile cockles of 7 mm in length. Cockles that survived predation by knots had heavier shells indicating that knots selectively fed upon cockles with a light shell. Alternatively, the observed increase in shell mass might have been an induced predator response (Harvell 1990). Indeed, the intra-specific competitive release due to knot predation could have accelerated a predator-induced increase in shell mass. Nevertheless, given published shell accumulation rates (e.g., Smith and Jennings 2000), the magnitude of the observed increase within two weeks in shell mass, with 21.5 percentage points, seems too large to be accounted for by a plastic predator-induced response alone. Furthermore, due to their digestive constraint, knots are expected to selectively feed upon on cockles with little shell mass and large flesh mass thus maximizing their energy intake rates (van Gils et al. 2003a). Our data does suggest that knots are capable of selecting those individuals with little shell mass and large flesh mass (Table 8.2).

The strength of natural selection

Estimates of natural selection gradients on morphological traits are common, but few are available for body compositional traits (Kingsolver et al. 2012). Compared to the standardized selection gradients reported in the literature (Lande and Arnold 1983, Endler 1986), the ones we found in the present study rank among the highest (Siepielski et al. 2009, Kingsolver and Diamond 2011a). For example, more than 99% of the linear selection gradients reported in literature are smaller than the ones we found on cockle length and shell mass in the predation plots (Kingsolver and Diamond 2011b). The fact that we observed such strong (nonlinear) selection gradients implies that individual cockles have the potential to increase fitness quite substantially. That this has not happened on the population level (assuming that the traits have a heritable component, e.g., Luttikhuizen et al. 2003), suggests that cockles are limited in their evolutionary response by, for instance, trade-offs between fitness components, or temporal and spatial fluctuations in natural selection (Kingsolver and Diamond 2011a, Kingsolver et al. 2012). We have investigated survival without taking reproduction into account. Perhaps, increased survival from predation (investing in armor) comes at the cost of reproduction and competitive ability, thus reducing total fitness. Interestingly, and perhaps indicative of a trade-off between investing in armor or flesh mass, the selection gradients when predators are present show that cockles invested in armor, but when predators were absent cockles invested more in incorporating flesh mass (Table 8.2). Indeed, it has been found that a large flesh mass increases reproduction in bivalves (Honkoop et al. 1999, Beukema et al. 2001). The population response to selection is an average over space and time (Siepielski et al. 2009). As shown by the fact that only two of the three plots were experiencing predation in this study, knot predation pressure will vary in both space and time (Folmer et al. 2010) and thus create temporal and spatial fluctuations in the direction and strength of natural selection.

Acknowledgments

We thank Ewout Adriaans for transport to Griend, Dirk de Boer and Peter van Tellingen for provisioning us on Griend, and 'Natuurmonumenten' for allowing us access to Griend. Anne Dekinga and Jan Drent provided valuable advice on the fieldwork, and Patrick Leven helped carrying it out. Lisanne Derksen, Patrick Leven, and Jeremy Smith took measurements of the thousands of cockles in the laboratory. Dick Visser prepared the figures, Sander Holthuijsen prepared Appendix Fig. A8.1, and Jan Drent and Tanya Compton gave valuable comments on previous drafts. We also like to thank A. Richard Palmer and Lindsey R. Leighton for their valuable feedback on the manuscript. Our work was supported by core funding of NIOZ to TP, a grant from the Waddenfonds to TP ('Metawad', WF 209925) and a NWO-VIDI grant to JAvG (no. 864.09.002).

Data accessibility

The data underlying this study is made available on Dryad (Bijleveld et al. 2015).

Box 8.1 Is there ‘emergent facilitation’ between knots and larger shorebirds?

Especially when population processes are density dependent and predation is limited to specific life stages (de Roos and Persson 2013), the effects of depletion by predation can affect the species community and composition (Terborgh and Estes 2010). Juvenile cockles are eaten by knots (Piersma et al. 1993a), whereas adult cockles are eaten by oystercatchers *Haematopus ostralegus* (Sutherland 1982b). This size selectivity of two predators on a shared prey species could lead to what de de Roos et al. (2007) called ‘emergent facilitation’ (Fig. B8.1, Zwarts and Wanink 1984).

Because of negative density-dependence among cockles (Chapters 8 and 9), reductions in densities allow remaining cockles to increase flesh mass. In Chapter 8, we show that knot predation alleviated competition among cockles by reducing densities from an average of 232 to 50 m^{-2}. Supporting the idea of emergent facilitation (T. van Kooten and J. A. van Gils, unpublished manuscript), oystercatchers tend to maximize energy intake rates at these reduced densities (Sutherland 1982b, a). Moreover, as a large flesh mass is linked to increased individual reproductive capacity (Honkoop et al. 1999, Beukema et al. 2001), knots could enhance the size of their own food stocks after the next cockle spawning event. Whether ‘emergent facilitation’ occurs in the field and whether its effect is of significance to the ecology and population dynamics of knots and oystercatchers remains to be investigated.

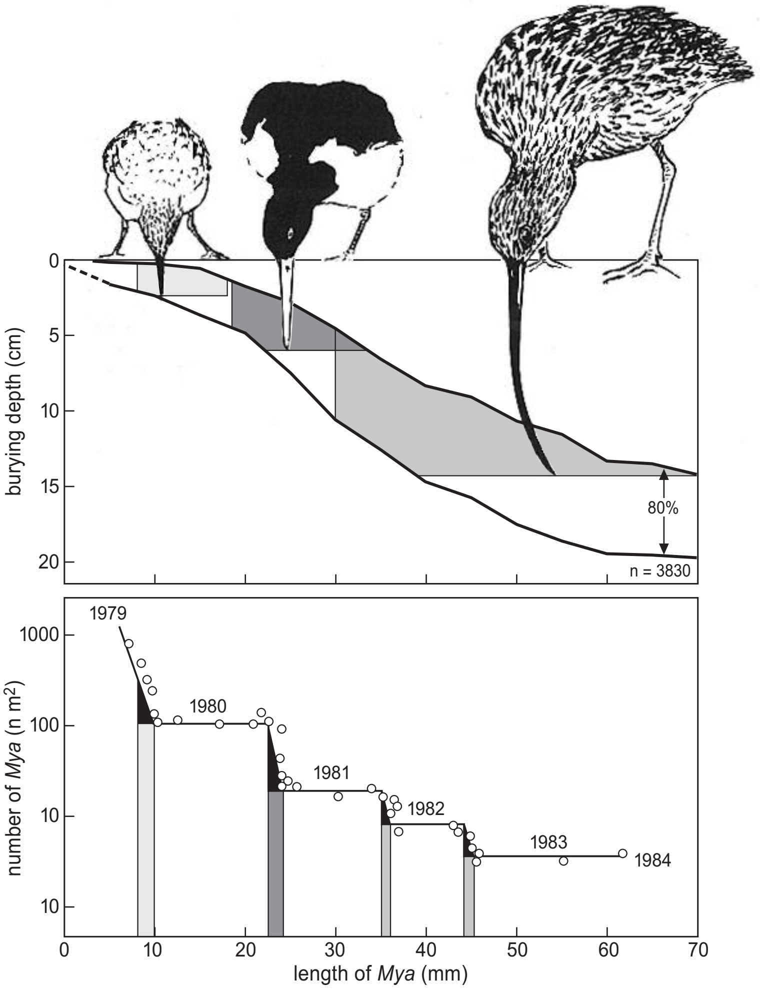


Figure B8.1 An early example of successive predation that could lead to 'emergent facilitation' between knots, oystercatchers (*Haematopus ostralegus*) and curlews (*Numenius arquata*). Panel (A) shows the range of burying depth of the soft-shell clam (*Mya arenaria*). The shaded areas show the size selection of accessible prey for the three bird species. Panel (B) shows the decline in soft-shell clam numbers as well as the growth in shell-length of the particular cohort from 1979. The vertical bars represent predation events. This figure is copied from Zwarts (1997, page 18).

Box 8.2 Can knots somehow sense the relative body composition of individual cockles?

Knots maximise their energy intake rate by feeding on cockles with large flesh mass and little shell mass (van Gils et al. 2003a). In Chapter 8 we show that, due to selective predation by knots, average cockle flesh mass decreased and average shell mass increased between initial and final sampling (Fig. 8.5). These data suggest that knots are capable of selecting cockles that have large flesh mass and little shell mass.

Due to a very successful spawning event in 2011, cockle densities were high (see Chapter 9). Consequently, knots could easily find cockles and permitted themselves the luxury of rejecting some of their discovered prey. On 25 September, we were observing two large flocks of foraging knots, which numbered 4,000 and 7,000 birds, respectively. The moment that these groups had flown off, we collected 94 rejected cockles from the mud surface. Two days later, we collected 199 reference cockles from 21 sampling stations near the location where we had collected the rejected cockles. In order to test whether the rejected cockles were of lower quality than the reference cockles, we brought them back to the laboratory and measured their ash-free dried flesh mass ($AFDM_{flesh}$) and dried shell mass (DM_{shell}). Similar to the procedure describe in Chapter 8, we then calculated their relative body composition.

We tested body composition in bivariate mixed effect models with sampling station as random effect. The only explanatory variable was a factor with two levels ('reference' or 'rejected'). This analysis revealed that, compared to reference cockles, the relative $AFDM_{flesh}$ of rejected cockles was 11.8 percentage points lower (95%CI [2.9; 19.6], $P < 0.01$), whereas DM_{shell} did not differ between the groups (–1.6 95%CI [–5.1; 1.8], $P = 0.33$, Fig. B8.2).

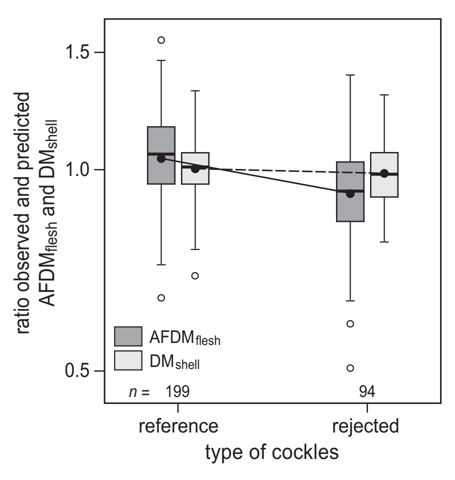
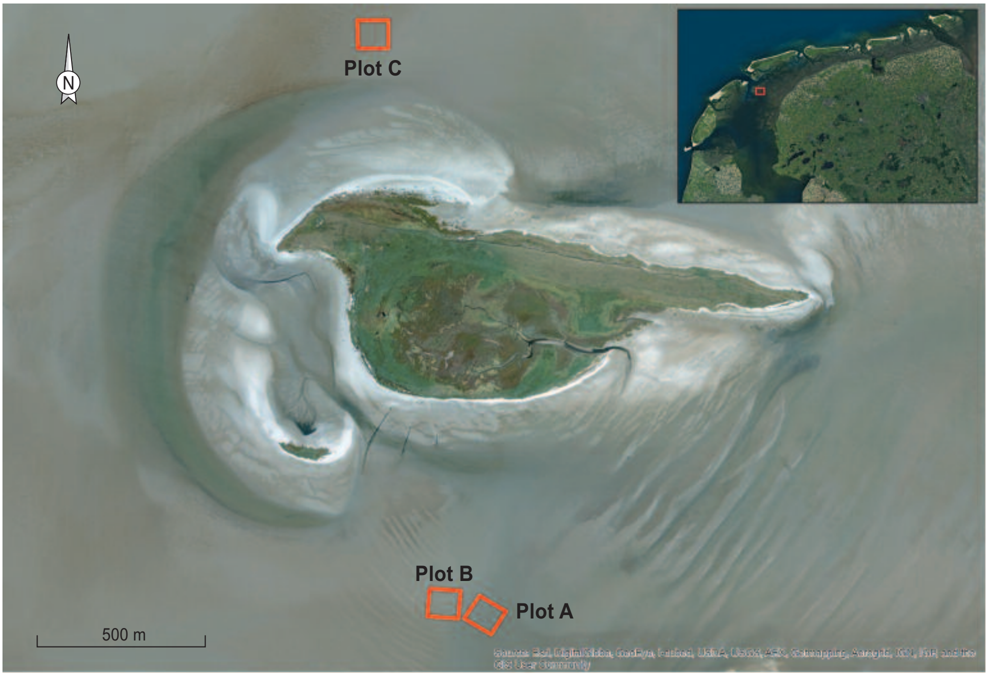


Figure B8.2 Do knots select individual cockles based on their relative flesh and shell mass? We sampled rejected cockles from the surface and reference cockles from sites nearby. To compare cockles from these two groups, we calculated their relative flesh mass ($AFDM_{flesh}$) and shell mass (DM_{shell}).

In line with our earlier results (Fig. 8.5), these findings suggest that knots appear capable of selecting individual cockles based on their relative flesh mass. In contrast to our previous results, knots did not select their prey according to cockle shell mass. However, because these data were gathered opportunistically without a solid experimental design, we should be careful to draw conclusions from the present analysis. One drawback of our data collection method could, for instance, be that we collected cockles that were unable to bury fast due to reduced condition (reflected by lower flesh mass). Even though we were quick to collect the cockles after knots were gone, our sample could, nonetheless, be biased towards reduced flesh masses in rejected cockles. Whether knots indeed have sophisticated sensory capabilities necessary for detecting variation in flesh mass and shell mass relative to a cockle's length needs to be explicitly tested, for instance, by offering knots choices between manipulated cockles with enlarged and reduced relative flesh masses and shell masses.

APPENDIX A8



Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, and the GIS User Community

Figure A8.1 Map of the study area. Our study area was situated near the islet of Griend in the Dutch Wadden Sea (53°14.615'N, 5°15.219'E). The three study plots of 100 × 100 m are outlined in red.

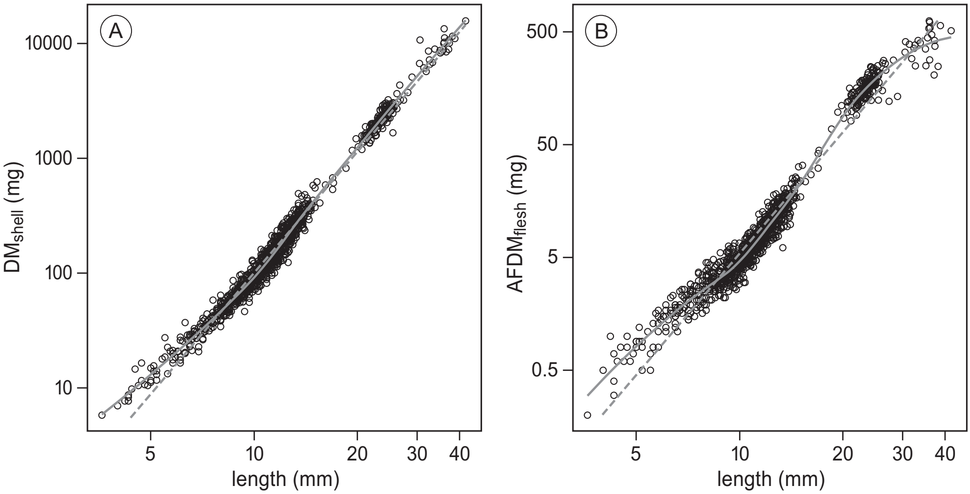
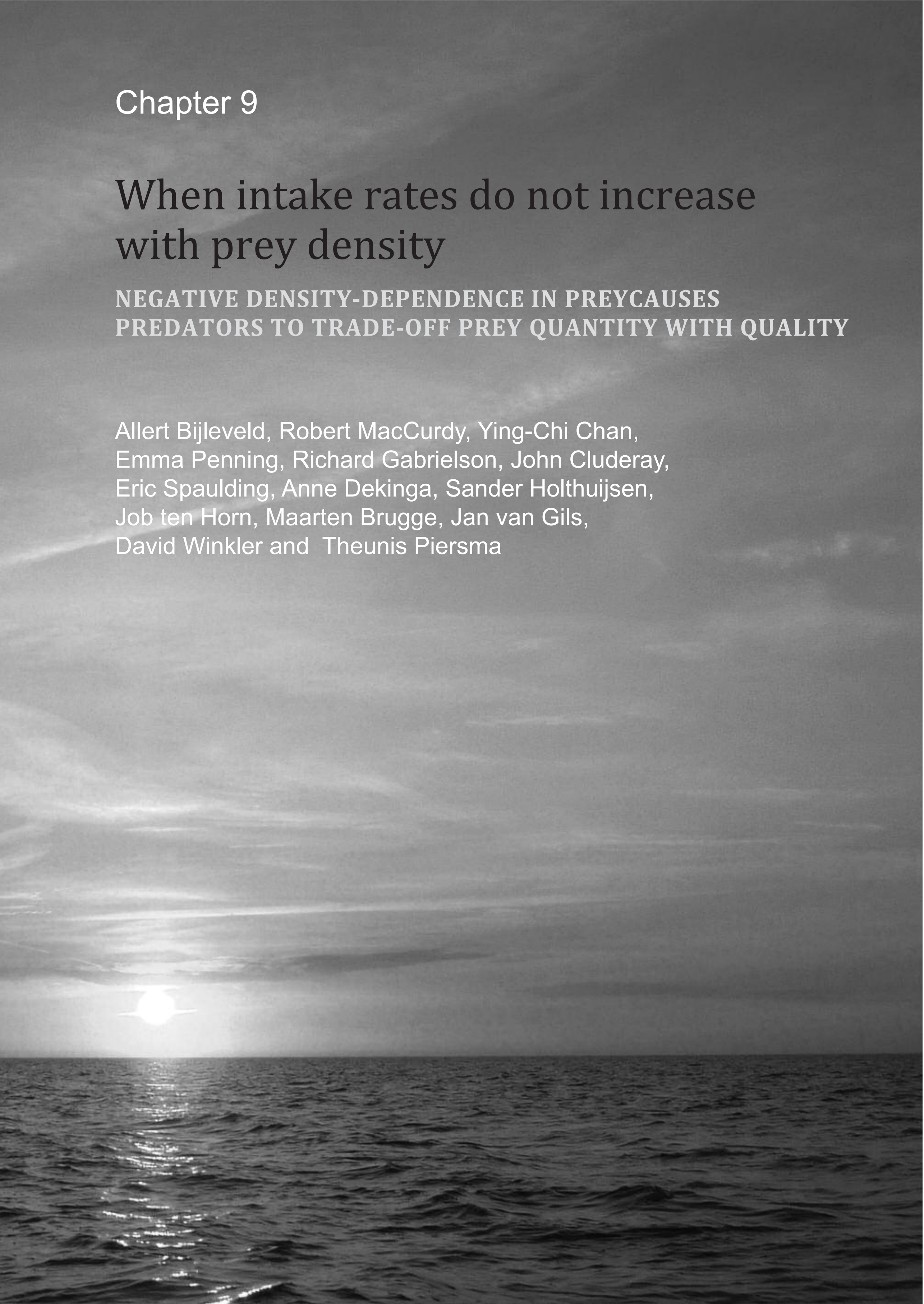


Figure A8.2 Allometric relations between cockle length and body composition. Normally, allometric relationships are analyzed with linear regression on a log-log scale (dashed lines). Because of remaining non-linearity in these allometric relationships, we fitted non-linear local regression models (LOESS, solid lines). We obtained an individual's relative body composition by extracting its residual from these regressions for (A) dry mass of the shell (DM_{shell}), or (B) ash-free dry mass of the flesh ($AFDM_{flesh}$) with length on a log-log scale.

Table A8.1 Mixed-modelling results for the effects of predation on a cockle's relative body composition.

Response variables	Random effects	Predictors	Estimates	SE	*P*
(**A**) relative DM_{shell}		intercept	-0.01	0.01	0.23
		final sampling	0.01	0.01	0.47
		predated	0.02	0.01	0.18
		final sampling × predated	0.07	0.02	<0.01
	sampling station		0.03	0.00	<0.01
	residual		0.07	0.00	<0.01
(**B**) relative $AFDM_{flesh}$		intercept	-0.05	0.02	0.01
		final sampling	0.05	0.02	0.01
		predated	0.10	0.02	<0.01
		final sampling × predated	-0.03	0.03	0.42
	sampling station		0.06	0.01	<0.01
	residual		0.07	0.00	<0.01

Note: The mixed-modelling results for the effects of predation on an individual's relative (A) dry mass of the shell (DM_{shell}), and (B) ash-free dry mass of the flesh ($AFDM_{flesh}$). The predictor 'intercept' refers to the mean values at the initial sampling occasion in the reference plot. The other predictors give the difference of the intercept with the final sampling in the reference plot ('final sampling'), the initial sampling in the predated plots ('predated'), and the final sampling in the predated plots ('final sampling × predated'). The random effect estimates refer to standard deviations. Note that we limited these analyzes to cockles that knots are able to ingest (lengths < 16 mm).



Chapter 9

When intake rates do not increase with prey density

NEGATIVE DENSITY-DEPENDENCE IN PREYCAUSES PREDATORS TO TRADE-OFF PREY QUANTITY WITH QUALITY

Allert Bijleveld, Robert MacCurdy, Ying-Chi Chan,
Emma Penning, Richard Gabrielson, John Cluderay,
Eric Spaulding, Anne Dekinga, Sander Holthuijsen,
Job ten Horn, Maarten Brugge, Jan van Gils,
David Winkler and Theunis Piersma

SUMMARY Density dependence is generally studied within trophic levels, but may also impact higher trophic levels. Without density dependence, a predator's intake rate increases with prey density. Thus, large prey densities should attract many predators. Here, we sampled the density and quality of bivalve prey (edible cockles *Cerastoderma edule*) across 50 km^2 of mudflat, and simultaneously, with novel time-of-arrival methodology, tracked their avian predators (red knots *Calidris canutus*). We showed that, due to negative density-dependence in the quality of cockles, the intake rates of red knots declined at high prey densities. Resource-selection modelling revealed that red knots selected areas of intermediate cockle densities where they maximised energy intake rates given their phenotype-specific digestive constraints (indicated by gizzard mass). Because negative density-dependence is common for many different prey species, we oppose the current consensus and suggest that hump-shaped functional responses are widespread. Prey density alone may thus be a poor predictor of intake rates, carrying capacity and spatial distributions of predator populations.

INTRODUCTION

Density dependence has mainly been studied within trophic levels in the context of population regulation (Sutherland 1996, Turchin 1999, Sinclair and Krebs 2002, de Roos and Persson 2013). As density increases, survival and reproduction decrease to a point that mortality and reproduction are at equilibrium (i.e. demographic carrying capacity, Sutherland 1996, Sinclair and Krebs 2002). Negative density-dependent survival and reproduction are population processes mediated by the frequency distributions of individual states (e.g., body mass, Sæther 1997, Turchin 1999). As population size increases, intra-specific competition increases and individual body masses decrease, which reduces reproductive output and survival probability (Paine 1976). An ignored aspect of these well-studied processes within trophic levels has been the possibility that individual states (body masses) have implications for higher trophic levels as well (Fig. 9.1).

A key concept linking two trophic levels is the ‘functional response’, a function that describes how a predator’s per capita intake rate varies with prey density (Holling 1959). The functional response is fundamental to spatial distribution modelling (Fretwell and Lucas 1970, Sutherland 1996), the estimation of carrying capacity (Sutherland and Anderson 1993, Goss-Custard et al. 2002), and the analysis of population dynamics in predator-prey systems (de Roos and Persson 2013). In almost all published functional response models, predator intake rates increase with prey density (type I, II or III, Jeschke et al. 2002). Among predators, the most widespread is Holling’s type II functional response (also known as Holling’s disc equation), where intake rate increases with prey density towards an asymptote that is set by handling time (Jeschke et al. 2002). In few cases intake rates decline at high prey densities, which results in a hump-shaped functional response (a type IV functional response, Holling 1961). The decline in intake rate at high prey densities has been attributed to a decrease in predator searching efficiency (e.g., due to increased predator detection, confusion, mobbing), and an increase in associated foraging costs (e.g., due to the accumulation of toxic prey substances, an increased risk of injury, etc.) (see Jeschke et al. 2002 and references therein). These processes are specific to particular predator-prey systems. Instead, a more general phenomenon is negative density-dependence (Gurevitch et al. 1992) that, via a reduction in the prey’s energy state, can also cause a declining energy intake rate to predators at high prey densities.

The consequence of negative density-dependence is that predators are faced with a trade-off between the quantity and quality of their prey (Sutherland 1982a). At low prey densities, predators have difficulty finding prey, but those prey have a relatively large energy content. At high densities prey are easier to find, but have relatively low energy content. Indeed, herbivores have been shown to select foraging locations of intermediate biomass density, thereby maximizing energy intake rate (Wilmshurst et al. 1999, Fryxell et al. 2004, van Beest et al. 2010). Conversely, there is a vast literature of ecological theory resting upon the type II functional response model (Skalski and Gilliam 2001), and predators (consumers of herbivores and animals of higher trophic levels, Fig. 9.1) are

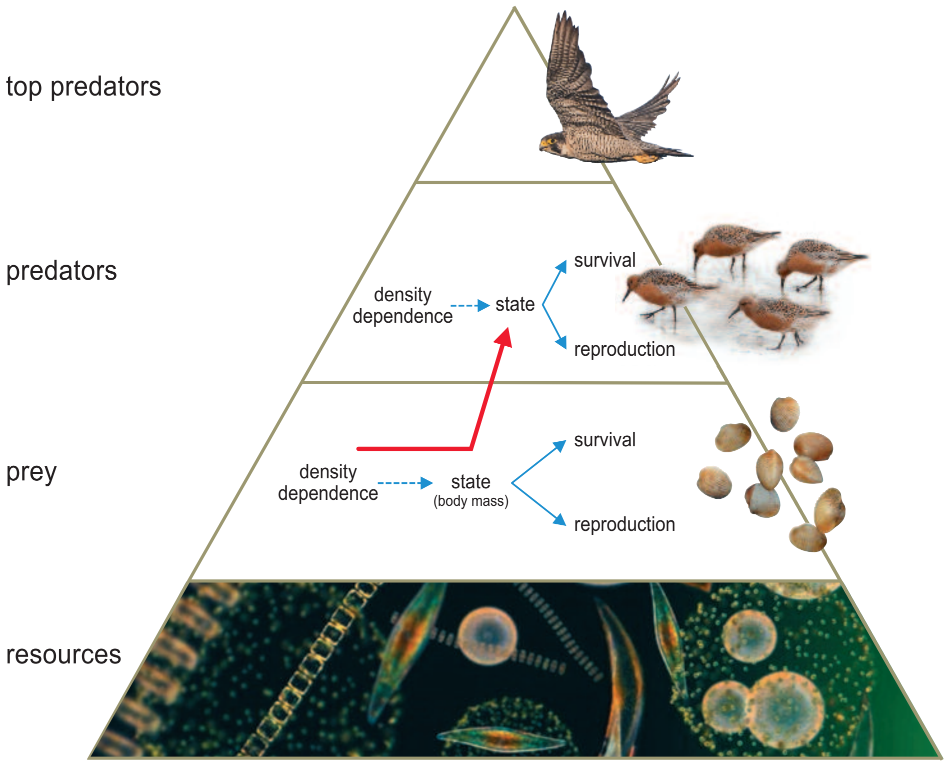


Figure 9.1 A trophic pyramid for our study system. Within trophic layers negative density-dependence has been studied in the context of population regulation. For instance, as population size increases an individual's state (e.g., body mass) decreases, which negatively affects their reproductive output and survival probability. Here, we focus on the effects that negative density-dependence among prey has on their predators. Negative density-dependence occurs within all trophic levels. Likewise, the effects of density dependence occur between all trophic levels. Dashed lines represent negative interaction pathways, and solid lines represent positive interaction pathways. The red arrow represents the focus of this study, i.e. the between trophic-level effect of density dependence. Photo courtesy: Jan van de Kam (*Falco peregrinus* and *Calidris canutus*), Allert Bijleveld (*Cerastoderma edule*), and http://seahack.org (several phytoplankton species).

generally assumed to maximise energy intake rates at the highest prey densities (Stephens and Krebs 1986, Sutherland 1996, Stephens et al. 2007, Westneat and Fox 2010).

In this field study, we aimed to understand, and predict, the spatial foraging distribution of avian predators (red knots *Calidris canutus islandica*, hereafter called knots) based on the spatial distribution in quantity and quality of their bivalve prey (edible cockles *Cerastoderma edule*) (Fig. 9.1). We measured the densities (quantity) and relative flesh masses (quality) of cockles over a large intertidal area of 50 km^2. We found that with an increase in cockle density, a cockle's relative flesh mass declined (negative density-dependence). From these data, we calculated a hump-shaped functional response and predicted that knots would maximise their energy intake rate on intermediate cockle densities. Because knots are digestively constraint by the amount of shell material they can process (van Gils et al. 2003a) and they vary in their processing rate (indicated by gizzard mass), knots maximize their intake rates at different cockle densities. In order to test whether knots maximised their intake rates at intermediate cockle densities, we tracked the positions of knots with a novel automated tracking methodology (MacCurdy et al. 2012, Piersma et al. 2014) providing high spatial resolution (37 m) and temporal resolution (1 Hz) in the position fixes.

MATERIALS AND METHODS

Study area and background

Our study site was located in the western Dutch Wadden Sea near the uninhabited islet of Griend (53°15'N, 5°15'E). Griend is surrounded by extensive intertidal mudflats where, during low tide in the non-breeding season, large flocks of knots can be found foraging. In one tidal cycle, knots often fly tens of kilometres in search of buried hard-shelled bivalves or gastropods (*Hydrobia ulvae*) (Piersma et al. 1993a, van Gils et al. 2005b). Due to low densities of alternative prey (Appendix Fig. A9.1), knots in our study area and period mainly foraged on cockles. In 32 droppings containing 272 ingested prey items, 82% were cockles, 17% *H. ulvae*, and the remaining 1% were *Macoma balthica*, *Mytilus edulis* or *Ensis directus*. In terms of flesh mass, cockles contributed to 99% of ingested biomass. Consequently, we focus on the interaction between knots and cockles.

Cockles can be found in densities of up to several thousand individuals m^{-2}, and it has been shown that their quality declines with increasing density (negative density-dependence, Chapter 8). Knots swallow their prey whole, which limits the size of ingestible cockles to those smaller than 16 mm in length (Piersma et al. 1993a). Additionally, their intake rate is constrained by the rate of processing ingested shell materials (van Gils et al. 2003a). Due to this digestive constraint, knots maximise their energy intake rates by selecting individual cockles with large flesh mass compared to their shell mass (van Gils et al. 2003a).

The predators

Between 2 August and 18 September 2011, we tracked 47 knots with the novel and prototype version of the Time-Of-Arrival (TOA) tracking system (MacCurdy et al. 2012, Piersma et al. 2014). We released all birds between 2 and 5 August 2011, after gluing a 7 g tag (<5 % of body mass) to their rump with cyanoacrylate (Appendix Fig. A9.2A). Nineteen of these birds had been captured on Griend in March 2010 and were released after 1.5 years in captivity, and the other 28 were caught on the nearby islet of Richel (53°17’N, 5°07’E, Appendix Fig. A9.2B) between 2 and 4 August 2011. Before releasing the birds, we measured the size of their muscular stomach (gizzard) with ultrasound (Dekinga et al. 2001) as described in detail in Chapter 7. The average gizzard mass was 7 g (2.0 SD) ranging between 4.0 and 10.4 g.

The tags emitted a radio signal each second, which could be received by nine stations that were set up at fixed locations in the study area (Appendix Fig. A9.2B). If at least three of the receiver stations registered the tag signal, the position of the bird was estimated based on the arrival times of the signal and locations of the receiver stations (Fig. 9.2). In order to reduce measurement error, we median-filtered the positioning data with a 7-points sliding window. Because birds moved out of the area and because of technical issues inherent to the use of prototype systems, we lost reception of many tags in the course of our study. Therefore, we restrained our statistical analyses to the period between 12 August and 26 August 2011, and to the area surrounding Griend, i.e. the period and area with the most regular tracking data and the most knots. During this period, we collected a total of 1,341,438 estimated positions for 19 different knots. Compared to alternative tracking methodologies, this volume of positions estimates is unprecedented (Chapter 3).

In order to identify intensively used areas and to reduce the computational issues associated with this large data set (e.g., time-consuming calculations, serial autocorrelation, Aarts et al. 2008), we summarised our tracking data as 'residence patches'. We divided all individual tracks into sections between two consecutive high tides and calculated resi-

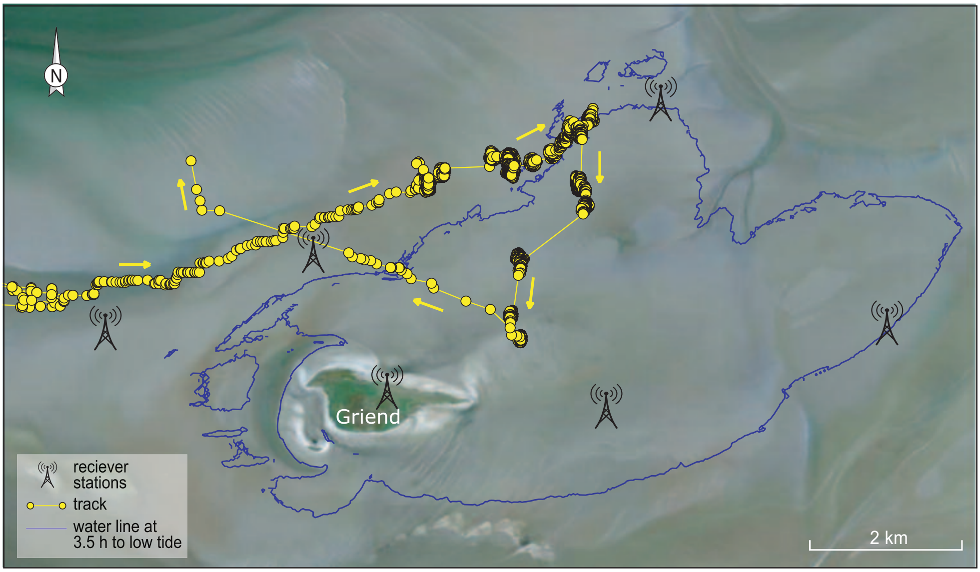


Figure 9.2 A characteristic knot movement pattern around low tide (this one was measured on 15 August 2011). The dots represent estimated positions that are connected by lines, and the arrows indicate the direction of movement. After roosting nearby on Richel (see Appendix Fig. A9.2B) and by the time the receding water level had exposed suitable foraging grounds, the bird arrived on the mudflats north of Griend and carried on towards the northeast. With the incoming tide, it moved to the elevated mudflats northeast of Griend before flying back to Richel. The underlying satellite imagery was obtained from Bing in the QGIS OpenLayers plugin.

dence times for successive positions within these tidal periods (Barraquand and Benhamou 2008). For calculating residence times, we used a time window of 3 h and a patch diameter of 250 m reflecting the scale of sampling cockles. Following Lavielle (2005), we segmented these residence time data automatically and we refer to Barraquand and Benhamou (2008) for details. To exclude the position fixes of flying birds as well as infrequently used areas, we disregarded segments with a residence time < 10 min (n = 165). For each segment we extracted the median coordinate and residence time. We will refer to each segment as a 'residence patch' indicating both the location and the time spent there.

The extent of available mudflat area is restricted by the tide that forces birds to move during parts of the tidal cycle. Because we were interested in foraging behaviour and resource selection without tidal forcing, we restricted our residence-patch data to 3.5 h before and 2.5 h after low tide (see Appendix Fig. A9.3). Additionally, we restricted our analyses to individuals with 5 or more calculated residence patches. In total, this procedure resulted in data from 13 individuals with 365 residence patches ranging in duration from 10 min to 4.7 h (using 558,781 estimated locations).

The prey

Between 15 and 19 July 2011, we sampled cockle density and body composition (flesh and shell mass) on a 250 m sampling grid, complemented by an additional 20% sampling stations randomly placed on the grid lines (Appendix Fig. A9.2B). This composite sampling design allowed for accurate spatial interpolations of cockle density and body composition (Chapter 2), necessary for predicting these variables at locations where knots were recorded foraging. In order to reduce laboratory time, we measured body composition of cockles on roughly 25% of the sampling stations (i.e. on 500 m grid spacing). During high tide, sampling sites were accessed by rubber boats, during low tide by foot. At each sampling site, when travelling by boat, we collected two sampling cores of 1/128 m^2. When travelling by foot, we collected one core of 1/56 m^2. We rinsed the samples over a 1-mm mesh sieve and collected the cockles. Judging their length in the field, we stored cockles < 8 mm in a 4% formaldehyde solution, and froze larger cockles (Compton et al. 2013). In the laboratory, we measured their lengths to the nearest 0.1 mm. For estimating body composition, we measured ash-free dry mass of the flesh ($AFDM_{flesh}$) and dry mass of the shell (DM_{shell}) according to the procedure described by Piersma et al. (1993a). Often, cockles were too small to separate their flesh from their shell. In those cases, we measured ash-free dry mass of whole individuals ($AFDM_{total}$). In order to acquire $AFDM_{flesh}$ for these individuals, we subtracted ash-free dry mass of the shell ($AFDM_{shell}$) from $AFDM_{total}$. Following Zwarts (1991), we estimated $AFDM_{shell}$ in mg from length as $0.0047 \times mm^{2.78}$. To reduce measurement error in $AFDM_{flesh}$ of small cockles, we pooled similarly sized cockles and calculated average $AFDM_{flesh}$. Overall, we sampled 854 stations and collected 15,874 individual cockles. In total, we obtained 663 estimates for $AFDM_{flesh}$ from 1,721 individuals that we collected from 120 sampling cores. For analysing DM_{shell} we collected data of 82 individuals from 33 sampling stations.

$AFDM_{flesh}$, DM_{shell} and their variances increase with cockle length. In order to compare body composition between differently sized cockles, we therefore calculated an individual's relative body composition by dividing its measured $AFDM_{flesh}$ or DM_{shell} by the average (predicted) length-specific body compositional trait (Chapter 8). To predict average body composition, we fitted non-linear local regression models (LOESS with local quadratic fitting) between $AFDM_{flesh}$ or DM_{shell}, and length on logarithmic scales (Appendix Fig. A9.4). For representation purposes, we back-transformed these residuals to reflect an individual's relative deviation in body composition compared to the average cockle of identical length.

For each sampling stations, we calculated cockle density by counting the number of cockles knots can swallow (length < 16 mm) and dividing that by the surface area of a sampling core. In order to normalise model residuals, we transformed these counts with the common logarithm ($\log_{10}$). To avoid taking the logarithm of zero, we added one before the data transformation.

We analysed the density dependence on relative $AFDM_{flesh}$ and DM_{shell} in linear mixed-effect models with sampling station as a random effect and cockle density (m^{-2}) as an explanatory variable. We also investigated effects of length and the interaction of length and density on both relative $AFDM_{flesh}$ and DM_{shell}. Density dependence is not limited to specific size classes, therefore, we included cockles of all lengths (between 1.0 and 41.1 mm). We centred length and $\log_{10}$-transformed density by subtracting their means of 8.9 mm and 3.14 respectively. By parametric bootstrapping (n = 1,000), we calculated significance under the null hypothesis that the estimated coefficients are zero.

Interpolating resource landscapes

In order to calculate resource landscapes for foraging knots, we spatially interpolated cockle density and $AFDM_{flesh}$ across the study area. Because of low sample sizes, this was not possible for DM_{shell}. In order to interpolate cockle density and relative $AFDM_{flesh}$, we calculated correlograms and fitted exponential spatial autocorrelation functions (Appendix Fig. A9.5) (Chapters 2 and 8). To reduce prediction error in interpolating $AFDM_{flesh}$, we included interpolated cockle densities as a covariate.

We interpolated cockle densities and relative $AFDM_{flesh}$ on spatial grids with a resolution of 25 by 25 m. For each grid cell we predicted the knot's energy intake rate by multiplying the numerical functional response (type II) by the density-dependent energy content of cockles: $IR = [\ (a \times N)\ /\ (1 + a \times N \times T_h)\ ] \times e(N)$, where IR is the energy intake rate (mg $AFDM_{flesh}$ s^{-1}), a is searching efficiency (m^2 s^{-1}), N is interpolated cockle density (m^{-2}), T_h is handling time (s), and e(N) is density-dependent $AFDM_{flesh}$ (mg) of cockle prey. We used a searching efficiency of 6.4 cm^2 s^{-1} (Piersma et al. 1995), and a handling time of 4.0 s (SD 1.7) that we estimated from video recordings of 23 tagged birds handling 637 cockles. In order to convert relative $AFDM_{flesh}$ to absolute flesh mass e_N, we assumed that knots fed on cockles of 7 mm long, which is the size that knots preferentially selected in this area the previous year (Chapter 8). Consequently, we multiplied the spatially interpolated relative $AFDM_{flesh}$ by 1.7 mg (the average $AFDM_{flesh}$ of 7 mm cockles, Appendix

Fig. A9.4A). The resulting predicted intake rate (IR) in mg AFDM$_{flesh}$ s^{-1} scales to intake rate in Joule s^{-1} by multiplying it with 22 J mg^{-1} (the average energy density of cockle flesh mass, Zwarts and Wanink 1993).

We calculated a bird's digestive constraint on shell mass intake rate (c, mg s^{-1}) as q × 0.05 × G^2 (van Gils et al. 2005b), where q is the ratio of AFDM$_{flesh}$ to DM$_{shell}$, and G is an individual's gizzard mass (g). Because the sample size was inadequate for spatially interpolating DM$_{shell}$, we predicted relative DM$_{shell}$ from interpolated densities with the density-dependent model presented in Appendix Table A9.1B. To get absolute shell masses, we multiplied relative DM$_{shell}$ by 24.3 mg (the average DM$_{shell}$ for cockles of 7 mm, Appendix Fig. A9.4B). We then calculated a bird's gizzard-mass-dependent intake rate as the minimum of its predicted intake rate without a digestive constraint (IR) and its digestive constraint c (van Gils et al. 2005b). We predicted gizzard-mass-dependent intake rate for an average gizzard mass (7 g, IR$_{avg.gizzard}$), and for each individual's measured gizzard mass (IR$_{ind.gizzard}$). In order to compare IR$_{ind.gizzard}$ between birds (Appendix Fig. A9.6), we standardised IR$_{ind.gizzard}$ by subtracting an individual's mean IR$_{ind.gizzard}$ and dividing it by its standard deviation. Thus, large values of IR$_{ind.gizzard}$ reflect areas where individuals would achieve a large intake rate given their gizzard mass.

Resource selection analyses

Within a used-availability design (Manly et al. 2002), we modelled variation in knot location density as a function of prey-related covariates (i.e., cockle density, relative cockle AFDM$_{flesh}$, predicted intake rates). The values of covariates at the bird's residence patches (used points) are contrasted with those that were available to them (availability points). The null model is that resources are selected proportional to their availability, and that deviations from proportionality indicate avoidance or preferential selection. We complemented each residence patch with 15 availability locations resulting in a sample size of 5,475 (see Appendix Fig. A9.7). At each used and availability location, we extracted from the resource landscapes: cockle density, cockle quality (relative AFDM$_{flesh}$), and predicted intake rates without a digestive constraint (IR), with an average digestive constraint (IR$_{avg.gizzard}$), and with an individual-specific digestive constraint (IR$_{ind.gizzard}$). We analysed the used (1) and availability (0) data in mixed-effect logistic regression models, thus correcting for variation among individuals. In order to avoid biased estimates of the resource selection functions, we applied infinitely weighted logistic regression by weighing used locations by 1 and availability locations by 1000 (Fithian and Hastie 2013). We additionally weighted our used locations by their residence time (h). The resource selection function is defined as the exponent of the predictors of the logistic regression model ignoring the intercept, which is proportional to the density of knot locations. For representation purposes, we scaled the resource selection functions between zero and one.

We calculated a null-model (intercept only) for the used-availability data. For each of the five explanatory resource-related covariates, we fitted two additional models with: (1) an intercept and linear predictor, and (2) an intercept, a linear, and a quadratic predictor.

The quadratic term can capture possible trade-offs between resources, e.g., between cockle density and relative $AFDM_{flesh}$. High residual spatial and temporal correlation within location observations could lead to overly complex models. We, therefore, used likelihood-based cross validation (Aarts et al. 2013) for selecting between the shapes of resource selection models (i.e. a null-, linear-, or quadratic), see Appendix Table A9.2.

We analysed our data in R v3.1.0 (R Core Team 2013) with the packages 'ncf' for calculating correlograms, 'fields' for spatial interpolations, 'lme4' for mixed-effect model analyses, and 'adeHabitatLT' for calculating residence times. We additionally used the packages 'RODBC', 'PBSmapping', 'spatstat', 'sp', 'raster', 'rgdal', for working with the (spatial) data. For plotting the spatial data we used QGIS v2.2.0 (http://qgis.osgeo.org). We segmented residence time data with Matlab (code available from http://www.math.u-psud.fr/~lavielle/programmes_lavielle.html).

RESULTS

Negative density-dependence in the prey

Both the relative flesh mass ($AFDM_{flesh}$) and shell mass (DM_{shell}) of cockles declined with their density (Fig. 9.3A, and Appendix Table A9.1). Neither length, nor its interaction with density, significantly affected a cockle's relative body composition. The decline in relative $AFDM_{flesh}$ was stronger than the decline in relative DM_{shell}. For this reason, the ratio of flesh to shell mass (digestive quality) also declined with cockle density. Because of the negative density-dependence among cockles, the functional response of knots is hump-shaped (Fig. 9.3B).

Interpolated resource landscapes

With interpolated cockle densities (Fig. 9.4A) and relative $AFDM_{flesh}$ (Fig. 9.4B), we predicted a knot's intake rate landscape without a digestive constraint (IR, Fig. 9.4C), with an average digestive constraint ($IR_{avg.gizzard}$, Fig. 9.4D), and with an individual-specific digestive constraint ($IR_{ind.gizzard}$, Fig. 9.5). As can be seen from Fig. 9.5, birds with different gizzard masses maximise their intake rates at different locations.

Resource selection

The resource selection modelling (Appendix Tables A9.2 and A9.3) showed that knots preferentially selected locations of intermediate cockle densities (Fig. 9.6A). At these locations, the birds encountered cockles with intermediate relative $AFDM_{flesh}$ (Fig. 9.6B). Likewise, they encountered intermediate predicted intake rates when ignoring the digestive constraint (IR, Fig. 9.6C) and when considering an average digestive constraint ($IR_{avg.gizzard}$, Fig. 9.6D). When we incorporated an individual-specific digestive constraint, we found that knots had selected those locations where they maximised their individual gizzard-mass-dependent energy intake rate ($IR_{ind.gizzard}$, Fig. 9.6E).

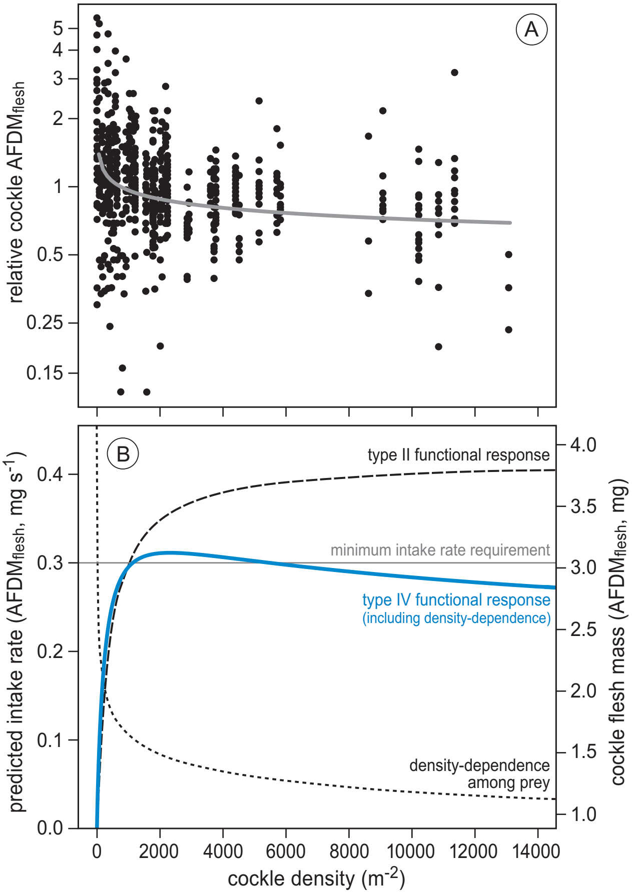


Figure 9.3 Negative density-dependence in body composition of cockles caused a hump-shaped functional response for knots. (A) A cockle's relative ash-free dry mass of the flesh ($AFDM_{flesh}$) plotted against cockle density (m^{-2}). The regression line reflects the statistical model presented in Appendix Table A9.1A. (B) The predicted energy functional responses of knots (solid blue line) including the negative density-dependence in flesh mass for 7 mm long cockles (dotted line with the units on the right y-axis). We also plotted the type II functional response without the negative density-dependence among cockles (dashed line). For reference, we included the threshold intake rate that knots need to acquire energy balance (grey horizontal line, Piersma et al. 1995).

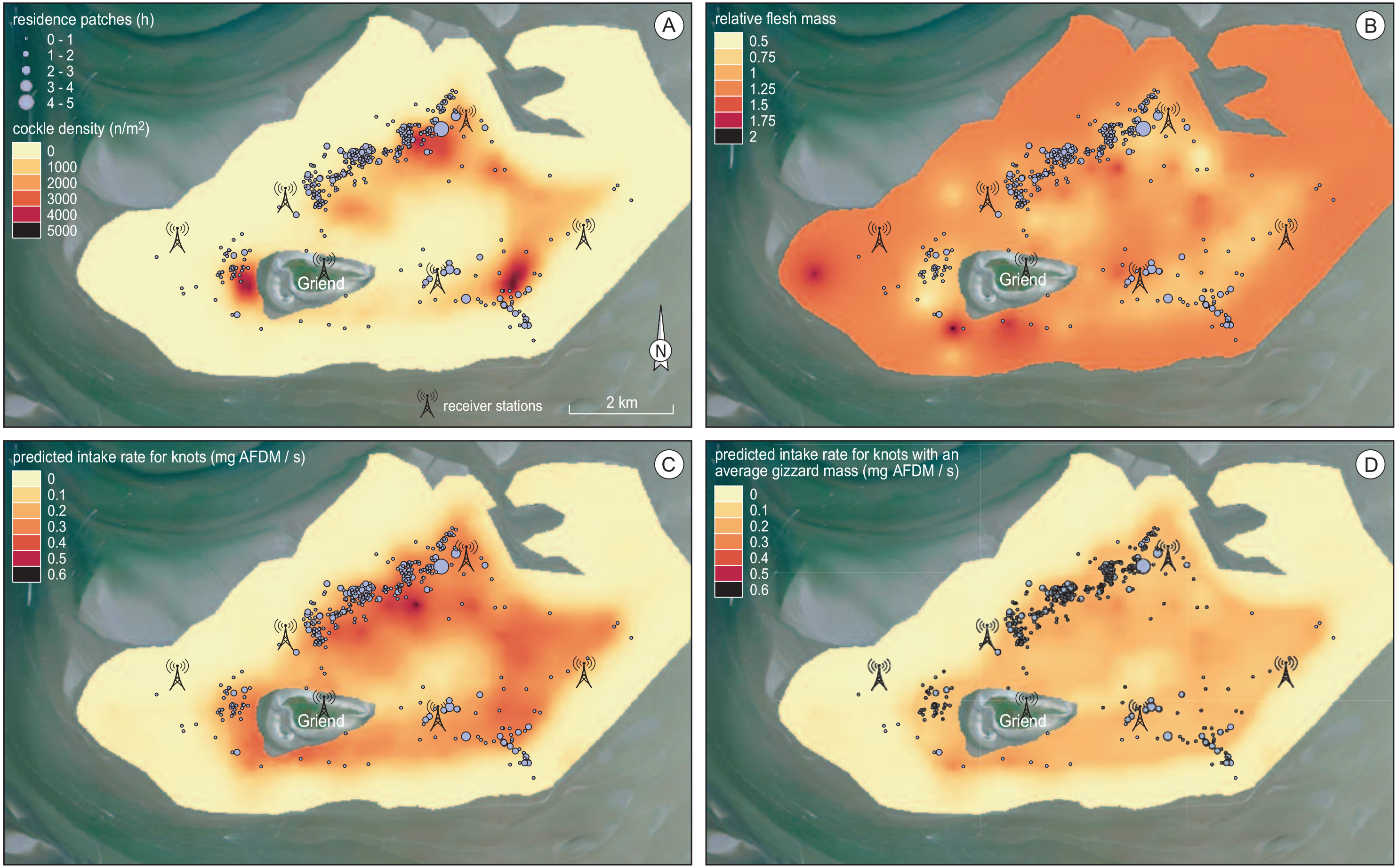


Figure 9.4 Resource landscapes with the low-tide distribution of knots. The panels show interpolated (A) cockle densities (m^{-2}), (B) relative flesh masses of cockles (AFDM$_{flesh}$), (C) predicted intake rates of knots (IR, mg AFDM$_{flesh}$ s^{-1}), and (D) average gizzard-mass-dependent predicted intake rates (IR$_{avg.gizzard}$, mg AFDM$_{flesh}$ s^{-1}). The panels additionally show the residence patches of all tagged knots. The sizes of these symbols indicate how long a bird had spent in that particular location ranging from 10 min to 4.7 h. The underlying satellite imagery was obtained from Bing in the QGIS OpenLayers plugin.

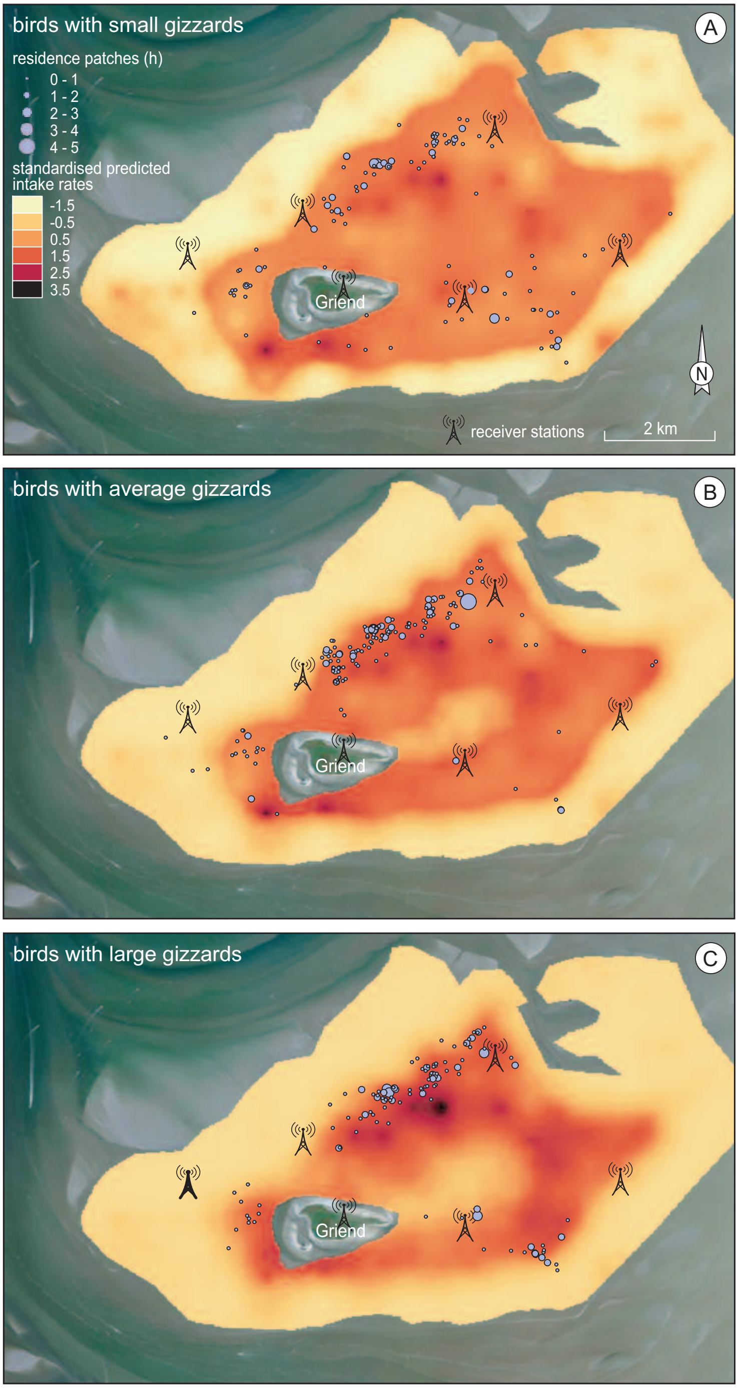


Figure 9.5 Resource landscapes of an individual's gizzard-mass-dependent predicted intake rates ($IR_{ind.gizzard}$, standardised). We plotted the standardised $IR_{ind.gizzard}$ landscape for three hypothetical birds: (A) a bird with a small gizzard (4 gram), (B) an average gizzard (7 gram), and (C) a large gizzard (10 gram). We superimposed the residence patches of the tagged birds with (A) gizzards < 6 g, (B) gizzards > 6 g and < 8 g, and (C) gizzards > 8 g. The sizes of these residence-patch symbols indicate how long a bird had spent in that particular location ranging from 10 min to 4.7 h. Note that the resource landscape in panel B is the standardised resource landscape of Fig. 9.4D. The underlying satellite imagery was obtained from Bing in the QGIS OpenLayers plugin.

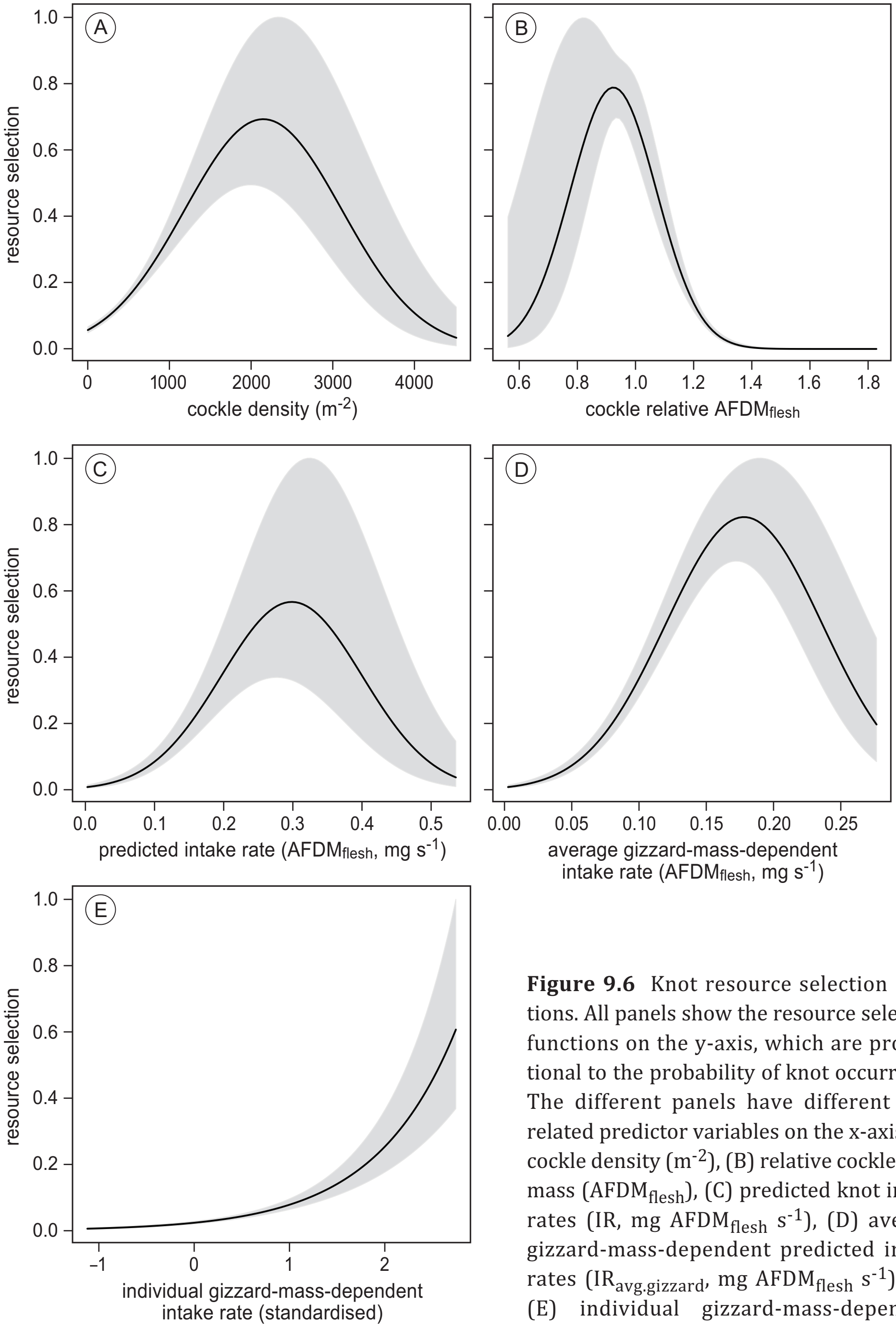


Figure 9.6 Knot resource selection functions. All panels show the resource selection functions on the y-axis, which are proportional to the probability of knot occurrence. The different panels have different prey related predictor variables on the x-axis: (A) cockle density (m^{-2}), (B) relative cockle flesh mass (AFDM$_{flesh}$), (C) predicted knot intake rates (IR, mg AFDM$_{flesh}$ s^{-1}), (D) average gizzard-mass-dependent predicted intake rates (IR$_{avg.gizzard}$, mg AFDM$_{flesh}$ s^{-1}), and (E) individual gizzard-mass-dependent predicted intake rates (IR$_{ind.gizzard}$, standardised). Note that these resource selection functions are the exponent of fitted logistic regression models excluding the intercepts (Appendix Table A9.3). As a result, for instance, the linear model in Appendix Table A9.3E becomes curved in (panel E).

DISCUSSION

We have shown that negative density-dependence within a trophic level can directly affect higher trophic levels. In particular, we found that negative density-dependence among prey presented their predators with a trade-off between prey quantity and quality. Instead of the general simplification that energy intake rates increase with prey densities, the functional response of knots feeding on cockles was hump-shaped. Resource selection modelling confirmed that knots in the wild preferentially selected locations with intermediate cockle densities and flesh masses. In fact, knots selected foraging locations where they could maximise their energy intake rates given their phenotype-specific digestive constraint (gizzard mass).

How do knots accomplish gizzard mass dependent intake rate maximisation?

In behavioural ecology, the classical view is that animals optimally adjust their behaviour to the environment while accounting for their physiological constraints (e.g., Stephens and Krebs 1986). Consequently, this view assumes that an animal's proximate cause of behaviour is equal to its ultimate cause (Tinbergen 1951, Kennedy 1992, Hogan 2014), which requires animals to have some sort of internal representation of the fitness maximisation that they aim to achieve, i.e. that animals possess 'goal-directedness' (*sensu* MacFarland 1989). Goal-directedness is of course one possibility, but requires cognitive capabilities that need to be examined (Barnard 2004). Until such capabilities are confirmed, we perhaps better adhere to more parsimonious causation (McNamara and Houston 2009, Hogan 2014).

Outside migratory periods, knots are 'time-minimisers' (Box 9.1) and aim to achieve an average intake rate that matches their daily energy expenditure (van Gils et al. 2003a). Knots have been hypothesized to actively adjust their behaviour based on their digestive constraint that is determined by gizzard mass (e.g., van Gils et al. 2003a, van Gils et al. 2005b). For instance, van Gils et al. (2005b) suggested that, in order to maximise intake rate, knots choose their foraging locations (prey qualities) based on their gizzard mass, i.e. have goal-directedness. They also argued that, as knots have small gizzards during migration, the large between-individual variation in gizzard mass reflects variation in arrival date. In spite of these suggestions, there is no evidence for goal-directedness in knots and gizzard mass also varies between individuals outside the migration period (Battley and Piersma 2005). As we will argue next, this makes 'reversed causality' the more parsimonious explanation. That is: knots attain a gizzard mass that matches the average prey qualities they have ingested (or will ingest) at their foraging locations.

Gizzard mass is flexible and, over the course of several weeks, reflects the quality of the diet. Birds feeding mainly on high-quality prey maintain small gizzards, while birds mainly feeding on low quality prey maintain large gizzards (Dekinga et al. 2001). Because of large metabolic maintenance costs, knots may try to maintain the smallest possible gizzard mass (Piersma et al. 2003). If we assume, for illustrative purposes, that all knots have similar metabolic requirements and consequently aim for similar levels of absolute daily energy intake, then the gizzard-mass-dependent intake-rate maximisation that we observed in the field (Fig. 9.6E and Appendix Table A9.3E) reflects gizzard mass minimisation together with consistent between-individual variation in ingested prey qualities. More explicitly, because of the maintenance costs of the gizzard (Piersma et al. 2003), we suggest that knots will maintain the smallest gizzard mass that their required intake rate allows while feeding on particular prey qualities. The large variation in gizzard mass at a given moment in time can then be explained by variation in ingested prey qualities. Note that while knots are time-minimisers, differences in metabolic requirements are probably reflected by differences in the time spent foraging instead of by differences in their gizzard mass (Box 9.1, Zwarts et al. 1990, van Gils et al. 2005b).

Individual differences in prey selection and foraging distributions

In the past decade, research on consistent individual differences in behaviour (animal personality) has gained momentum (Verbeek et al. 1994, Gosling and John 1999, Sih et al. 2004b, Réale et al. 2007, Dall et al. 2012). Animal personality has been shown to correlate with individual resource specialisation (Dall et al. 2012), and may drive spatial distributions (Boon et al. 2008, Minderman et al. 2010). In knots, personality variation was recently shown to correlate with the scale of their spatial distribution (Chapter 7). Moreover, gizzard mass was found to be behaviourally regulated, i.e. knots differed consistently in the average prey quality they ingested. Likewise, our present results showed that habitat selection by knots correlated with their gizzard mass, which also suggests that they consistently ingest particular prey qualities. To guide potential future research, we will provide three non-mutually exclusive hypotheses that could explain why knots differ in the prey quality they ingest.

(1) At large spatial scales, knots might select foraging locations based on habitat characteristics such as prey density, inundation time, and/or predation danger. If knots differ in their preference for certain habitat and if these habitat characteristics are correlated with prey quality (as they often are, e.g., Beukema and Dekker 2006), knots could consistently ingest particular prey qualities.

(2) At small spatial scales, the birds could differ in their diet specialisation, which has been shown to explain consistent variation in other behaviour (Marchetti and Price 1989, Dall et al. 2012). The experience that a knot gathers as a result of feeding on high-quality prey could make it easier for this animal to specialise its feeding on high quality prey (Bergmüller and Taborsky 2010, Sih et al. 2015). For instance, it could learn about their distribution, or adapt its physiology to increase processing efficiency for high-quality prey. In order to specialise on a particular prey quality, knots need to be able to sense quality variation between cockles. A previous study, in which cockle body composition was measured before and after predation by knots, shows that cockles that survived predation had relatively little flesh mass and large shell mass (Chapter 8). Knots thus appear able to somehow sense the quality of an individual cockle (Box 8.2).

(3) In line with diet specialisation, consistent prey quality ingestion could also originate from competition avoidance (Bergmüller and Taborsky 2010, Dall et al. 2012). Knots

are known to avoid interference competition (Chapter 4) and, when given a choice between equally accessible and available prey types, they prefer high quality prey (van Gils et al. 2005a). As prey density and quality are often inversely related (Fig. 9.3A), birds compete over the less abundant high-quality prey. As a result, competitively dominant birds would forage in areas with high-quality prey, while competitively subordinate birds would forage in areas with low-quality prey.

Whether knots consistently differ in habitat choice and diet selectivity, and whether these differences are driven by social dominance, are questions that remain to be studied. Nevertheless, they certainly seem promising ways to gain an understanding of the mechanisms causing spatial distributions of foragers in the field.

Mechanistically understanding spatial distributions

Movement ecology has become a large field (Nathan et al. 2008, van Gils et al. 2015), but the mechanisms underlying movement and spatial distributions based on resource landscapes remain elusive (see Fryxell et al. 2004). Probably, this is due to the considerable logistical difficulties of sampling resource landscapes at appropriate spatial scales (Wilmshurst et al. 1999, Fryxell et al. 2008). If we would have been ignorant of digestive constraints and individual gizzard masses (Fig. 9.6E), we would have erroneously concluded that knots do not maximise their energy intake rates (Fig. 9.6C and D). This shows that in order to understand spatial distributions of predators it is important to measure both predator and prey phenotypes on relevant spatial scales. Adequately understanding the mechanisms of resource selection is essential to conservation science, e.g., for predicting predator distributions in novel or dynamic environments (Babin et al. 2011).

How common is a hump-shaped functional response?

The functional response of herbivores is hump-shaped because the digestive quality of forage decreases with an increase in biomass and age (Fryxell 1991). Herbivores have been shown to select foraging locations of intermediate biomass density where they maximise energy intake rates (Wilmshurst et al. 1999, Fryxell et al. 2004, van Beest et al. 2010). For foragers at higher trophic levels ('predators'), the common assumption is that they maximise energy intake rates by foraging at the highest prey densities (Fretwell and Lucas 1970, Sutherland 1996). Here, we have shown that negative density-dependence among prey can result in a hump-shaped functional response for predators as well. As negative density-dependence is commonly found in many different species (Gurevitch et al. 1992), do predators then commonly face a hump-shaped functional response? First of all, this is determined by the strength of negative density-dependence among prey, and second, by how fast a predator's prey consumption levels-off with prey density. Handling and digestion times are inversely related to the rate at which prey consumption levels off. In the presence of negative density-dependence among prey, predators with considerable handling or digestion times are thus likely to face a hump-shaped functional response. Given that most predators are either handling or digestion limited (Jeschke et al. 2002), we predict that most predators will actually be faced with hump-shaped functional responses.

Consequences of hump-shaped functional responses

Foraging distribution models assume that predators aggregate where predicted intake rates are highest (Fretwell and Lucas 1970, Sutherland 1996). The shape of the functional response, therefore, directly determines where predators will aggregate. By wrongly assuming a continually increasing, rather than hump-shaped, functional response, the number of predators at high density patches will be overestimated. For instance, when ignoring density dependence among cockles, the carrying capacity (i.e. the surface area of suitable knot habitat where predicted intake rates were above a knot's minimum requirement, Fig. 9.3B) was overestimated by 12.4%. This overestimation of carrying capacity can have consequences for conservation strategies (Sutherland and Anderson 1993, Goss-Custard et al. 2002).

For barnacle geese *Branta leucopsis*, it has been hypothesized that grazing by foraging flocks stimulated renewed protein-rich grass growth, thereby providing opportunity for future foraging on high quality vegetation (Drent and Swierstra 1977). Indeed, without lowering biomass, grazing improved the vegetation quality and attracted foraging geese (Ydenberg and Prins 1981). Furthermore, brent geese *Branta bernicla* are hypothesized to adopt a cyclic grazing pattern that optimizes their protein intake between locations (Drent & Van der Wal 1999). We can speculate about this "grazing optimization hypothesis" in the context of our study. Thinning of cockle densities reduces competition among cockles and allows the surviving cockles to accumulate flesh mass. Even though it is highly speculative, knots may optimise energy intake rates by 'gardening' their cockle prey. However, opposite to grazers, predators kill their prey and reduce their density, which thereby become difficult to find (Chapter 8), which in turn reduces the benefit from such 'gardening'. One way to investigate this 'gardening hypothesis' is to determine whether knots, after thinning cockle densities, allow time for their prey to increase in body mass before revisiting these locations (Drent and Van der Wal 1999).

Conclusion

We showed that due to negative density-dependence in the quality of prey predators were faced by a hump-shaped functional response. Indeed, knots selected locations of intermediate prey densities where they maximised their predicted energy intake rates given their individually varying digestive capacity. This shows that in order to understand spatial distributions of predators it is important to measure both predator and prey phenotypes on relevant spatial scales. Because negative density-dependence is common among many prey species, we propose that, contrary to the literature, hump-shaped functional responses are widespread among predators.

Acknowledgements

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Box 9.1 Time-minimisers and energy-maximisers are both rate maximisers

In most (optimal) foraging models it is assumed that the currency that foragers maximise is the rate of net energy gain (Pyke et al. 1977, Stephens et al. 2007). One of the most important assumptions in foraging theory is that a high rate of energy gain is beneficial to foragers (i.e. it increases fitness) (Stephens and Krebs 1986). Foragers could either aim to obtain as much energy as possible (i.e. be 'energy maximisers'), or to acquire a given amount of energy in the shortest time possible (i.e. be 'time minimisers') (Schoener 1971). Time minimisation is beneficial if fitness doesn't increase continuously with total energy gained and if the time spent on other activities, such as fighting, fleeing, and body care also increase fitness.

Whether foragers maximise their total energy gain or minimise their active foraging time, they all aim to maximise their *rate* of energy gain (Hixon 1982). Energy maximisation and time minimisation represent the endpoints of a continuum of foraging strategies. Furthermore, this continuum represents a gradient of temporal scales over which energy intake is measured (Bergman et al. 2001), i.e. all foragers will be energy maximisers if the measurements have been obtained over small enough time scales. The crucial difference between the contrasting foraging strategies is that a time minimiser stops foraging after obtaining some net energy requirement, while an energy maximiser continues to forage throughout the entire period (Hixon 1980). Depending on the seasonally varying food conditions and energy requirements, individuals will vary in the proportion of time spent foraging (Zwarts et al. 1990) and thus vary along the continuum of time-minimising and energy maximising.

APPENDIX A9

Table A9.1 Mixed-modelling results for density dependence in cockle relative body composition. We analysed the effects of cockle density (m^{-2}) and length (mm) on an individual cockle's relative (A) ash-free dry mass of the flesh ($AFDM_{flesh}$), and (B) dry mass of the shell (DM_{shell}). Cockle density was log_{10}-transformed, and covariates were centred on their mean length (8.9 mm) and log_{10}-transformed density (3.14). The random effect estimates refer to standard deviations.

Response variables	Random	Predictors	Estimates	SE	*P*
(**A**) relative $AFDM_{flesh}$		intercept	-0.03	0.02	0.16
		density	-0.12	0.02	<0.01
		length	-0.00	0.00	0.52
		density × length	0.00	0.00	0.25
	sampling station		0.15		
	Residual		0.16		
(**B**) relative DM_{shell}		intercept	-0.01	0.02	0.75
		density	-0.06	0.03	0.04
		length	-0.00	0.00	0.97
		density × length	0.00	0.00	0.38
	sampling station		0.04		
	residual		0.04		

Table A9.2 Model selection results for the shape of resource selection functions. We analysed the same response variable with different types of prey related explanatory variables (resource landscapes): (A) cockle density (m^{-2}), (B) relative cockle ash-free dry mass of the flesh ($AFDM_{flesh}$), (C) predicted intake rates (IR, mg $AFDM_{flesh}$ s^{-1}), (D) average gizzard-mass-dependent predicted intake rates ($IR_{avg.gizzard}$, mg $AFDM_{flesh}$ s^{-1}), and (E) individual gizzard-mass-dependent predicted intake rate ($IR_{ind.gizzard}$, standardised). In order to analyse the shape of knot resource selection functions (RSF), we compared linear and quadratic models to the null model (intercept only). We avoided collinearity between the linear and quadratic terms by calculating orthogonal polynomials. To compare the different shapes of RSF, we calculated the log-likelihood of models by cross validation as follows (Aarts et al. 2013). We treated the 13 individuals as independent sampling units, and by excluding one individual at a time, fitted the resource selection model to this training data. With this fitted model, we predicted the response of the excluded individual and calculated the log-likelihood in comparison to its observed response data. We repeated this procedure for all individuals and summed their log-likelihoods. The null-model with only an intercept had a log-likelihood of -1365.3. Comparing the log-likelihoods revealed that (as indicated in bold) the quadratic resource selection function was the best model for cockle density, relative $AFDM_{flesh}$, IR, as well as $IR_{avg.gizzard}$. Conversely, the linear model described the $IR_{ind.gizzard}$ resource selection function best. Note that the linear and quadratic terms were also imposed on the random effects (random slopes mixed-effect modelling).

	Resource landscapes	RSF shape	Log-Likelihood
(**A**)	cockle density (m^{-2})	linear	-1272.0
		quadratic	-1208.7
(**B**)	relative cockle $AFDM_{flesh}$	linear	-1257.2
		quadratic	-1208.0
(**C**)	predicted intake rate	linear	-1178.0
	(IR, mg $AFDM_{flesh}$ s^{-1})	**quadratic**	-1123.3
(**D**)	average gizzard-mass-dependent	linear	-1175.6
	intake rate ($IR_{avg.gizzard}$, mg $AFDM_{flesh}$ s^{-1})	**quadratic**	1137.9
(**E**)	individual gizzard-mass-dependent	**linear**	-1171.1
	intake rate ($IR_{ind.gizzard}$, standardised)	quadratic	-1184.5

Table A9.3 Parameter estimates of the best supported resource selection functions. (A) cockle density (m^{-2}), (B) relative cockle ash-free dry mass of the flesh ($AFDM_{flesh}$), (C) predicted intake rates (IR, mg $AFDM_{flesh}$ s^{-1}), (D) average gizzard-mass-dependent predicted intake rates ($IR_{avg.gizzard}$, mg $AFDM_{flesh}$ s^{-1}), and (E) individual gizzard-mass-dependent predicted intake rates ($IR_{ind.gizzard}$, standardised). We provide the fixed-effect estimates that represent the average response, and random-effect estimates that represent the individual variation in responses. Note that the estimates of the random effects are given in standard deviations.

	Resource landscape	Model part	Predictors	Estimates	SE
(**A**)	cockle density (m^{-2})	fixed	intercept	-9.4	0.05
			linear	53.3	6.04
			quadratic	-33.1	3.45
		random	intercept	0.0	
			linear	19.1	
			quadratic	7.6	
(**B**)	relative cockle $AFDM_{flesh}$	fixed	intercept	-9.8	0.07
			linear	-98.9	5.21
			quadratic	-59.8	11.87
		random	intercept	0.0	
			linear	5.3	
			quadratic	38.0	
(**C**)	predicted intake rates (IR, mg $AFDM_{flesh}$ s^{-1})	fixed	intercept	-10.2	0.17
			linear	122.8	14.56
			quadratic	-43.9	3.63
		random	intercept	0.5	
			linear	46.7	
			quadratic	2.9	
(**D**)	average gizzard-mass-dependent predicted intake rates ($IR_{avg.gizzard}$, mg $AFDM_{flesh}$ s^{-1})	fixed	intercept	-10.2	0.12
			linear	136.1	9.43
			quadratic	-36.4	4.26
		random	intercept	0.0	
			linear	16.7	
			quadratic	6.9	
(**E**)	individual gizzard-mass-dependent predicted intake rates ($IR_{ind.gizzard}$, standardised)	fixed	intercept	-9.7	0.09
			linear	91.1	7.92
		random	intercept	0.2	
			linear	23.1	

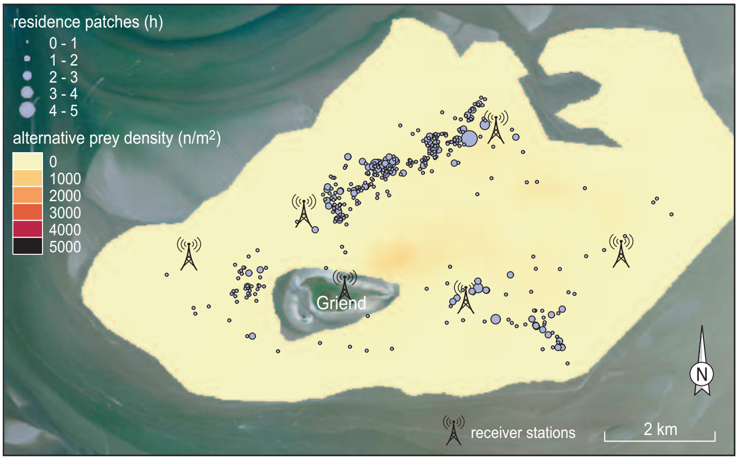


Figure A9.1 The spatial distribution of alternative prey densities. The average density of alternative prey was 33 m^{-2} (95%CI [9.6; 63.7]) and low compared to those of edible cockles (Fig. 9.4A). Of the prey occurring in our sampling cores, knots are known to forage on balthic tellins (*Macoma balthica*), sand gapers (*Mya arenaria*), and *Abra tenuis*. We selected individuals of these species, which knots could swallow (length < 18 mm, Piersma et al. 1993a), summed the numbers of individuals per sampling core, and calculated densities as described in the Methods for edible cockles (*Cerastoderma edule*).

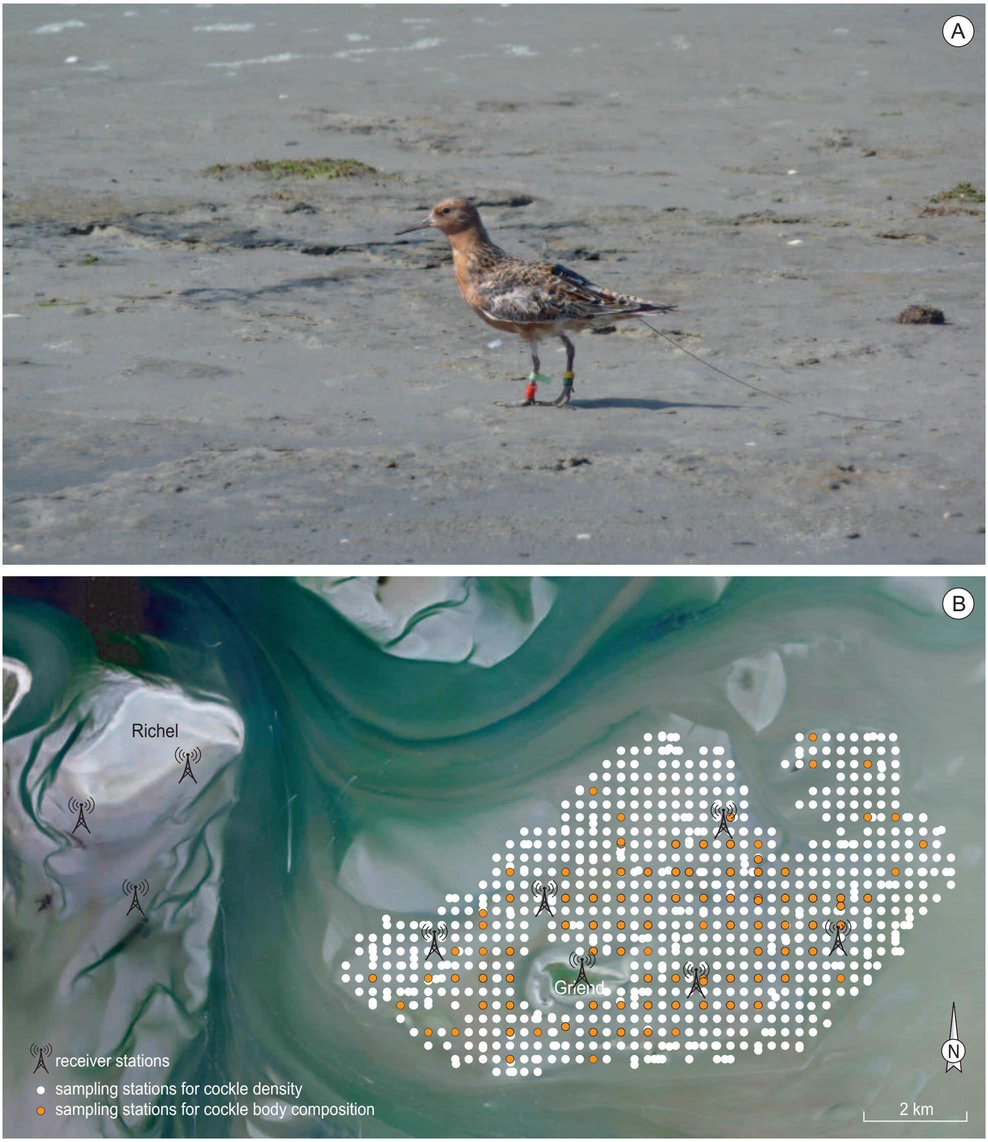


Figure A9.2 (A) Photo of a tagged knot moments after its release, and (B) an overview of the study area with the array of (9) receiver stations and sampling stations. We calculated cockle densities for all sampling stations, and when cockles were found we also measured their lengths. From a subset of sampling stations, we additionally measured cockle body composition. These stations are indicated in grey. The underlying satellite imagery was obtained from Bing in the QGIS OpenLayers plugin.

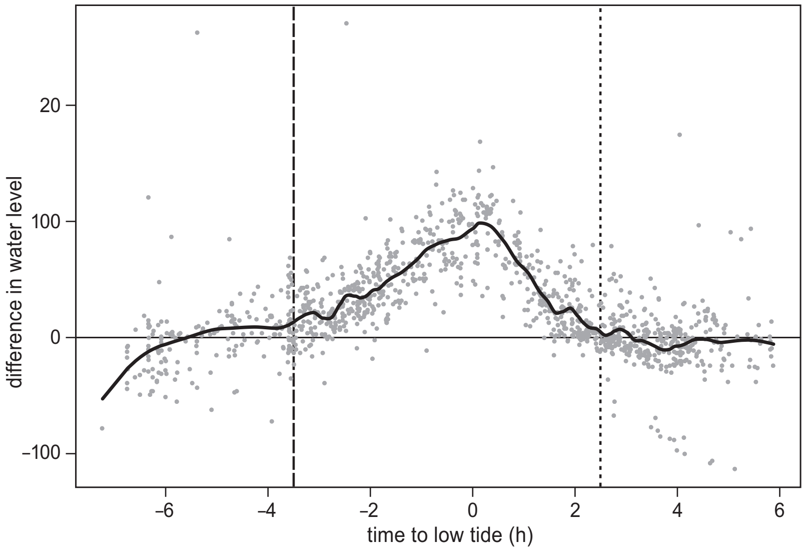


Figure A9.3 Tidal forcing on knot spatial distributions. Each dot represents a residence patch. The y-axis shows the difference (cm) between the water level and the height of the mudflat where the birds were located (residence patches). A positive difference indicates that birds were located on exposed mudflat. Negative values indicate that birds were standing in the water. The time to low tide (h) is shown on the x-axis. Between the dashed and dotted line there was minimal tidal forcing and the birds were more or less free to choose where to forage. The tidal data were collected by Rijkswaterstaat at West-Terschelling (53°21.45'N, 5°13.13'E) at an interval of 10 min (http://www.rijkswaterstaat.nl). The heights of the mudflats were obtained from Rijkswaterstaat as well and were collected between 2003-2008.

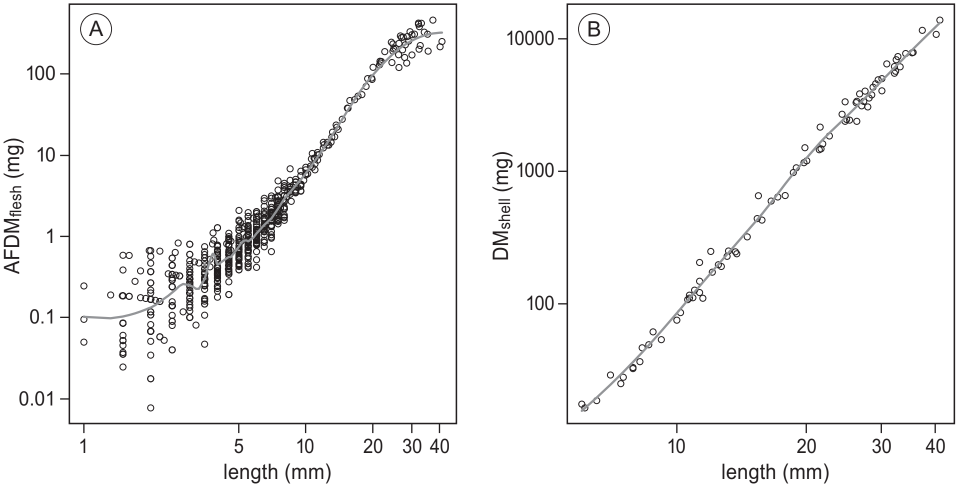


Figure A9.4 Allometric relations for cockle (A) ash-free dry mass of the flesh ($AFDM_{flesh}$), and (B) dry mass of the shell (DM_{shell}). We fitted non-linear local regression models (LOESS, grey lines) to body compositional traits and length on log-log scales (Chapter 8). We used smoothing parameters of 0.2 and 0.5 for the LOESS models visualized in respectively panels A and B.

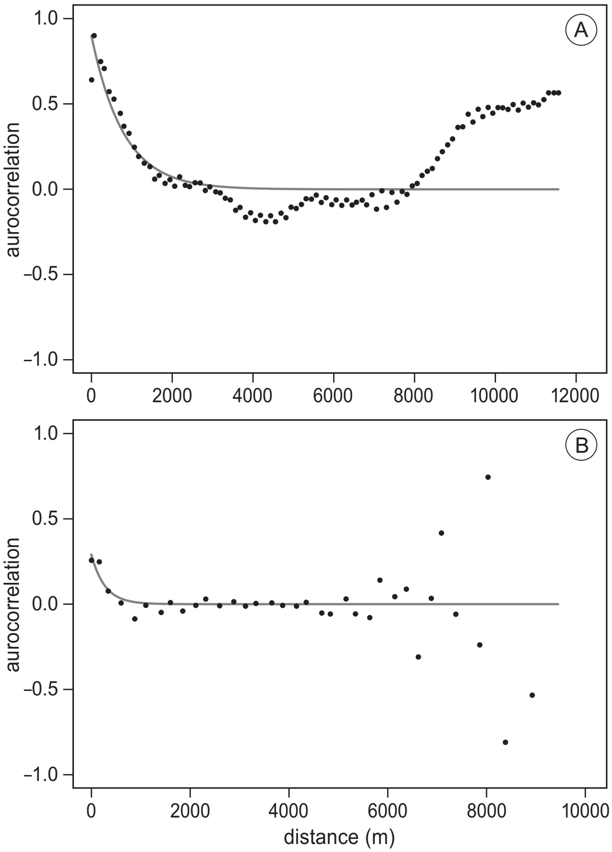


Figure A9.5 Spatial autocorrelation functions (correlograms) underlying the resource landscapes. In (A) we present the correlogram for cockle density. In (B) we present the correlogram of a cockle's relative ash-free dry mass of flesh ($\mathrm{AFDM}_{\mathrm{flesh}}$). The spatial autocorrelation function for density is given by $y = 0.90e^{-0.001x}$, and for relative $\mathrm{AFDM}_{\mathrm{flesh}}$ by $y = 0.29e^{-0.004x}$. For calculating the correlograms, we chose a spatial lag of half that of the inter-sampling distance, i.e. 125 m for interpolating densities and 250 m for interpolating relative $\mathrm{AFDM}_{\mathrm{flesh}}$.

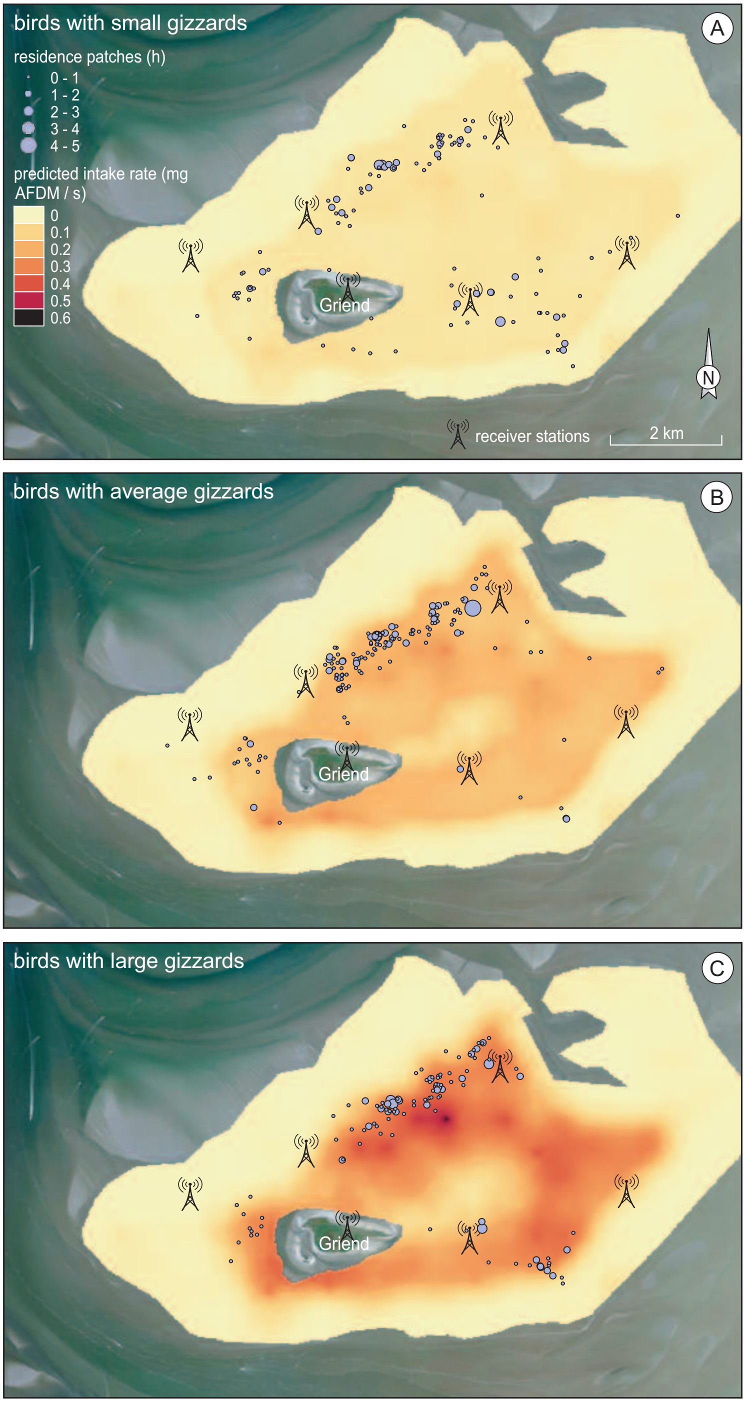


Figure A9.6 Individual gizzard-mass-dependent predicted intake rates ($IR_{ind.gizzard}$). We plotted the $IR_{ind.gizzard}$ landscapes for three hypothetical birds: (A) a bird with a small gizzard (4 gram), (B) an average gizzard (7 gram), and (C) a large gizzard (10 gram). In order to visualise the difference in predicted intake rates between birds with differently sized gizzards, we used the same colour scaling between panels. We additionally plotted the residence patches of the tagged knots with (A) gizzards < 6 g, (B) gizzards > 6 g and < 8 g, and (C) gizzards > 8 g. The sizes of these residence patch symbols indicate how long a bird had spent in that particular location ranging from 10 min to 4.7 h. Note that the resource landscape of panel B is identical to Fig. 9.4D. The underlying satellite imagery was obtained from Bing in the QGIS OpenLayers plugin.

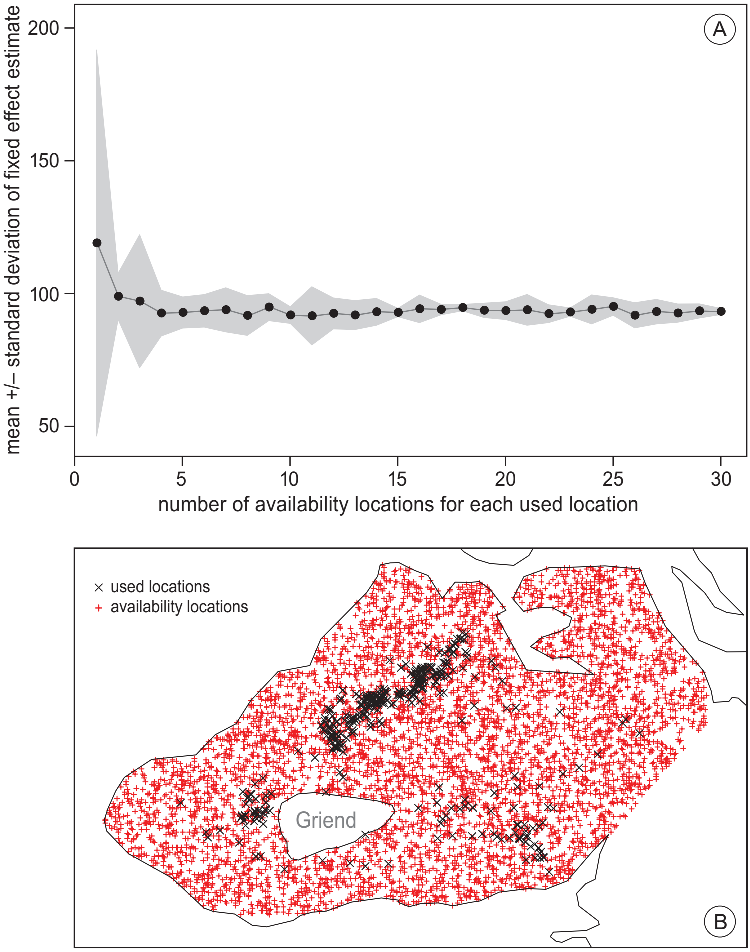


Figure A9.7 Methodology of the used-availability analyses. In order to determine the number of randomly selected availability locations, we conducted a sensitivity analysis on the fixed-effect parameter estimates. (A) An example of the sensitivity analyses on resource selection modelling. Here, we show the standard deviation (based on 5 estimates) of the linear fixed-effect estimate of the individual-gizzard-mass dependent predicted intake rate model ($IR_{ind.gizzard}$). The x-axis gives the number of availability locations for each used location. The mean of the fixed-effect and its standard deviation levelled off with the ratio of availability for each used location. We selected a ratio of 15 availability locations to each used location providing reliable model estimates. (B) Map of the used and availability locations underlying our resource selection analyses.

Section IV

General discussion

Chapter 10

The many dimensions of knots

THE INTEGRATION OF A PHENOTYPE

Allert Bijleveld

The main goal of the research presented in this thesis was gaining a deeper understanding of the spatial distribution of social predators. Questions that we asked were: Do knots use public information to find their hidden food? Do individuals differ in the way they search for food? Can we predict the spatial distribution of knots based on the spatial distribution of their prey? Do individual knots have distinct 'personalities' with reference to movement and foraging decisions, and if so, can we explain how and why they consistently differ in behaviour?

In this final chapter, I will highlight some of our findings and at the same time seek directions for future studies. In line with the thesis structure, I have divided this general discussion into different sections. First, I will briefly discuss sampling methodology and the importance of estimating spatial autocorrelation functions for understanding spatial distributions. Second, I consider the sociality of knots. In this section I will reflect on the information benefits of social foraging and communal roosting, as well as the interference-costs that are associated with social foraging and how these relates to spatial distribution modelling. Third, I will discuss individuality. In particular how differences between individuals may drive spatial distributions, and the ecology and evolutionary background of animal personalities. Fourth, I will tie the knot together and propose an ecological-evolutionary framework for the development of personality differences between knots. Finally, I will briefly summarise our main findings and suggest some future research directions.

SAMPLING METHODOLOGY

Quantifying the spatial distribution of species is essential to understand the underlying mechanisms (Thrush 1991, Legendre et al. 1997). One way to quantify the spatial distribution of a species is by estimating how spatial autocorrelation varies with distance, the so-called spatial autocorrelation function. For bivalves, few studies investigate the spatial autocorrelation function explicitly (e.g., Thrush et al. 1989, Hewitt et al. 1996, Hewitt et al. 1997a, Hewitt et al. 1997b, Legendre et al. 1997, Kraan et al. 2009a, Kraan et al. 2009b). Studies that investigate spatial autocorrelation in combination with predation are especially rare (e.g., Boldina and Beninger 2013).

The novel sampling design that we propose in Chapter 2 allowed for accurately estimating spatial autocorrelation. Even though the finding itself is not novel (e.g., Huxham and Richards 2003, Kraan et al. 2009a, Boldina and Beninger 2013), by estimating the spatial autocorrelation function we revealed that cockles cluster in patches both at small spatial scales (Fig. 8.2 and 8.3), as well as large spatial scales (Fig. 9.4 and Appendix Fig. A9.5). What is more novel is our use of the spatial autocorrelation function to demonstrate that predation by knots substantially homogenized the spatial distribution of cockles (Fig. 8.3).

The spatial autocorrelation function can also be used to predict (map) the spatial distribution of prey. These maps can, for instance, be used to understand the distribution of predators (Chapter 9). For the predators, spatial autocorrelation might convey information to find their prey more efficiently (Nolet and Mooij 2002, Klaassen et al. 2006a, van Gils 2010). For instance, if knots are unsuccessful in finding prey, large spatial autocorrelation implies that they also won't be more successful nearby; they better move elsewhere. To maximise the probability of finding prey, they should move at least a distance equal to the spatial range of the autocorrelation function (Klaassen et al. 2006a), i.e. the distance at which the autocorrelation reaches zero (Fig. 8.3 and Appendix Fig. A9.5). Moreover, positive spatial autocorrelation in prey abundance (i.e. patchiness) allows knots to benefit from the sampling behaviour of others, for instance, through local enhancement (Chapter 6, Pöysä 1992, Danchin et al. 2008, Beauchamp 2014).

SOCIALITY

Information benefits of social foraging

Animals live in uncertain and variable environments in which information on resources can increase foraging success and efficiency (Stephens and Krebs 1986, Dall et al. 2005, Stephens et al. 2007, Danchin et al. 2008). Especially for foragers that have a limited time window to gather their food, such as tidal foragers, information on prey distributions can be important for survival. Foragers could gather such information by trial and error (e.g., by sampling the environment) or by monitoring the behaviour of others, i.e. by using public information (Valone 1989, Valone and Templeton 2002, Danchin et al. 2004, Valone 2007, Danchin et al. 2008). Public information covers all information that is not private and thus accessible to others (Chapter 6, Wagner and Danchin 2010). Animals from a wide range of species are reported to use public information and the literature on public information use is still growing (see Valone 2007, Blanchet et al. 2010, Rieucau and Giraldeau 2011).

Public information use

Mudflats appear, at first glance, uniform and featureless. To estimate local densities of their buried prey, knots need to probe and sample the mudflat. Due to spatial heterogeneity in elevation of food patches and variation in the timing and level of low water, the availability of food patches is variable (e.g., van Gils et al. 2005b, Piersma 2012). Hence, socially foraging knots are likely candidates for using public information to increase foraging success. Knot distributions in the field were found consistent with the assumption of 'ideal free distribution' models that foragers have complete information on the possible intake rates at different locations (van Gils et al. 2006b). The question remained whether knots can acquire such information socially.

In Chapter 6 we show that knots can indeed monitor the foraging success of their flock mates, and that they choose their foraging locations accordingly. By incorporating pubic information a knot's intake rate increased proportionally with group size.

Socially foraging individuals can search for food themselves (so-called producers) or search for the food discovered by others (so-called scroungers) (Barnard and Sibly 1981, Barnard 2004, Beauchamp 2014). In Chapter 6 we also show that the use of producer or scrounger tactics differs consistently between individuals: some knots searched for prey, while others exploited these efforts. Similar findings were reported for barnacle geese *Branta leucopsis*. Barnacle geese differed in their use of public information, which was negatively correlated with their boldness, i.e. their readiness to explore novel objects (Kurvers et al. 2010a, Kurvers et al. 2010b). Until recently, the use of public information in relation to personality has received little attention (Kurvers et al. 2010b). In fact, at the time of the public information experiments we were unaware that knots consistently differed in their exploratory behaviour (Chapter 7). We believe that future investigations on links between exploratory behaviour and information use will clarify spatial foraging distributions of knots and of social foragers in general.

Public information on communal roosts

Communally roosting birds are spectacular to watch, especially their seemingly coordinated flights and sudden drops towards the ground. Communal roosting has also stimulated spectacular scientific debates (e.g., Mock et al. 1988, Richner and Heeb 1995). Particularly on the idea that information benefits provide the primary evolutionary origin and maintenance of communal roosting (Ward and Zahavi 1973). Four decades after publication, the Information Centre Hypothesis remains controversial.

In Chapter 5 we show that there is empirical support for communal roosts as information centres. Whether this is the primary evolutionary cause driving communal roosting is a question that is hard to answer. Because many species roost communally, we think it is particularly interesting to focus on the information benefits that individuals could gain from roosting communally. The original information centre hypothesis states that information transfer must be active. We suggest that inadvertent public information is widely available at communal roosts and this is a more likely source of information. The information conveyed inadvertently is acquired at lower costs compared to trial-and-error sampling, and might even be unavailable when roosting solitary.

The difficulty of unequivocally testing hypotheses on information use at communal roosts probably reflects their controversy. Especially in the field, it is difficult to identify whether individuals have used information from each other on a roost. However, the ongoing developments of small tracking devices that are capable of collecting high resolution spatial and temporal data (Chapter 3, Bouten et al. 2013, Klaassen and Reneerkens 2014) could provide a means to study information use at communal roosts.

Cultural evolution

Natural selection acts through the interaction of an organism with its environment (West-Eberhard 2003, Duckworth 2009, Piersma and van Gils 2011, Odling-Smee et al. 2013). Through so-called ‘niche construction' (Odling-Smee et al. 2013), individuals can to some extent control the environment that they encounter, which feeds back on their fitness (Laland et al. 2013, Laland 2014). By roosting communally, knots create their own environment in which different types of public information are available. In a group, the sum of information as well as traditions can be defined as culture (Danchin et al. 2004). I like to propose that through public information use, communal roosting may allow cultural evolution (Laland et al. 2000).

Slowly the similarities between cultural and genetic transmissions are becoming recognised (Mesoudi et al. 2004, Jablonka et al. 2005). Culture consists of non-genetic, heritable differences among populations and requires overlapping generations that allow transmission of phenotypic traits (Danchin et al. 2004). The main difference between cultural and genetic selection is that cultural traits have the property to be passed on between unrelated group members.

Within communal roosts many types of information are available (Chapter 5). The spread of this public information might lead to a roost culture and perhaps eventually to cultural evolution. For instance, through public information use, free-living great tits (*Parus major*) acquired novel foraging techniques that rapidly spread through the whole population (Aplin et al. 2014). A study on communally breeding northern gannets (*Morus bassanus*) revealed that competition in combination with public information on foraging locations probably caused segregation in foraging area use between nearby colonies (Wakefield et al. 2013). Likewise, public information on communal roosts could drive spatial segregation on foraging areas and consequently drive cultural evolution. Note that the socially acquired behaviour is not necessarily the most optimal or adaptive behaviour, i.e. informational cascades (Giraldeau et al. 2002). An ‘informational cascade’ occurs when an individual’s decisions are predominantly based on the behaviour of others instead of its own. Therefore, through informational cascades, cultural evolution might not always select for beneficial traits.

Interference and spatial distribution modelling

When resources are distributed in patches, as they frequently are (Levin 1992), behavioural ecologists often use ideal free distribution models to predict foraging distributions across these patches (Goss-Custard 1980, Sutherland 1983, Ens and Goss-Custard 1984, Holmgren 1995, Moody and Houston 1995, Tregenza 1995, Stillman et al. 1996, van Gils and Piersma 2004, Smallegange and van der Meer 2009, van der Meer and Smallegange 2009, Quaintenne et al. 2011). In order to get realistic predictions on spatial distributions, the choice of the interference model should have a strong biological underpinning. Especially because subtle differences in the selected interference mechanisms result in qualitatively different predictions of the spatial distribution of foragers (van der Meer and Ens 1997). Understanding the mechanisms of interference competition is therefore of paramount importance (Skalski and Gilliam 2001, Vahl et al. 2005b, Smallegange 2007, Folmer 2012).

In Chapter 4 we show that the intake rates of knots decline with group size, but that the common mechanisms of interference competition also declined or were virtually absent. We found that the main mechanism of interference was due to avoiding encounters with conspecifics, so-called ‘cryptic interference’. Note that cryptic interference is more than a state of avoidance behaviour that reduces the available searching time (Stillman et al. 1997, Smallegange and van der Meer 2009). With increasing group size, knots increasingly divert their attention between searching for prey and avoiding interactions with conspecifics, which additionally reduces their searching efficiency (Goss-Custard 1976, Cresswell 1997, Dukas and Kamil 2001, van Gils et al. 2015).

Interference models that are based on behaviour (so-called mechanistic interference models) are preferred from a scientific point of view (van der Meer and Ens 1997). However, if they don't incorporate the key interference behaviour, the resulting aggregative response will be flawed. Perhaps phenomenological interference models (that are based on a statistical fit between intake rate or searching efficiency, and competitor density) are not so bad after all *because* they fit the data and don't assume and possibly miss underlying behaviours (Sutherland 1983). Even though there has been substantial progress since Fretwell and Lucas (1970) proposed the 'ideal free distribution' as a null model, there is no grand unified theory to predict forager distributions based on the distribution of food and basic foraging behaviour. Ecology is a much less deterministic science than chemistry or physics. The interactions between an individual and its environment are determined by a wealth of different state dependent behaviours. Perhaps, therefore, a 'grand unified theory' is not possible (Tregenza 1995). Moreover, mechanistic 'ideal free distribution' models assume that all individuals are 'aimless billiard balls' and equal which is obviously not true. They thus are best seen as helpful null-models to come to grips with distributional problems (e.g., Bautista et al. 1995, van Gils et al. 2006b, Leyrer et al. 2012).

INDIVIDUALITY

All individuals are equal but some are more equal than others

Within species, individuals differ in their morphology and behaviour, which can both affect foraging decisions and spatial distributions (Parker and Sutherland 1986, le V. dit Durell 2000). For instance, morphology (e.g., bill length) affects the costs and benefits that are associated with a particular behaviour, which will affect where individuals will forage (Mathot et al. 2007, Catry et al. 2012, Duijns et al. 2014). How behaviour affects the spatial distribution of foragers has also been investigated, but only for the limited number of behaviours that were thought to directly affect fitness, e.g. dominance (Réale et al. 2007). A well-known example is the phenotype-limited distribution introduced by Parker and Sutherland (1986). They altered the assumption of 'ideal free distribution' models that all individuals should be equal and allowed individuals to vary in their susceptibility to interference. The prediction is that intake rates can differ between patches and that competitively dominant individuals should be found on the highest quality territories. Such phenotype-dependent spatial distributions can have important consequences for population dynamics (le V. dit Durell 2000, Bolker et al. 2003). In addition to dominance, animals differ in many more behaviours that could affect their spatial distribution.

Animal personalities

The study of animal personalities (i.e. consistent among-individual differences in behaviour) has become popular among ecologists and evolutionary biologists. Probably because personalities are commonly found among many different species across the animal kingdom (Verbeek et al. 1994, Gosling and John 1999, Gosling 2001, Sih et al. 2004b, Réale et al. 2007, Bell et al. 2009). The ecological implications of personality can be substantial (Wolf and Weissing 2012). For instance, animal personality can affect species interactions and population dynamics (Bolnick et al. 2003), and habitat use (Werner et al. 1981, Boon et al. 2008, Minderman et al. 2010). Populations composed of a diversity of personality types should also be less vulnerable to (human induced) environmental changes (Bolnick et al. 2011, Sih et al. 2012, Wolf and Weissing 2012). The presence of animal personality signifies that behavioural flexibility is limited and that, when the context changes, individuals may not always behave optimally (Sih et al. 2004a, Sih et al. 2004b). Because natural selection favours optimal behaviour, a major puzzle in evolutionary and behavioural ecology is how and why animal personalities persist over evolutionary time.

In recent years, there has been substantial progress to explain animal personalities from proximate as well as ultimate points of view (e.g., Koolhaas et al. 1999, Dall et al. 2004, Koolhaas et al. 2007, Wolf et al. 2007, Biro and Stamps 2008, Careau et al. 2008, McNamara et al. 2009, Bergmüller and Taborsky 2010, Dingemanse and Wolf 2010, Réale et al. 2010b, Wolf and Weissing 2010, Wolf and McNamara 2012, Carere and Maestripieri 2013). As discussed in Chapter 7, most of the adaptive (ultimate) explanations of behavioural consistency involve between-individual variations in state. State is defined as any feature of an individual that affects the cost and benefits of its behaviour (Houston and McNamara 1999). State variables that underlie consistent among-individual differences in behaviour may be fixed (e.g., structural body size in adults), but they may also be flexible (e.g., body mass). Provided that among-individual differences in state are maintained via positive feedback between an individual's state and their state-dependent behaviour (e.g., Dingemanse and Wolf 2010, Wolf and Weissing 2010, Sih et al. 2015). Positive feedback mechanisms combine proximate (e.g., neurophysiology, hormone concentrations, maternal effects, social interactions) with ultimate explanations (fitness consequences) to understand the maintenance of animal personality (Sih et al. 2015).

Because the densities of high quality prey are low, competition for high quality prey could force individual knots to feed on particular resource qualities (Chapter 9, Van Valen 1965, Bolnick et al. 2003, Araújo et al. 2011). Positive feedback between an individual's resource specialisation, experience, and physiology could then account for consistency in their behaviour (Bergmüller and Taborsky 2010, Dall et al. 2012). For instance, an individual that feeds on high quality prey learns about their scattered distribution, and adapts its gizzard mass to increase processing efficiency. Both factors make it easier for this animal to continue to forage on high quality prey (e.g., Marchetti and Price 1989). Such positive feedbacks would then reinforce an individual's resource specialisation and exploratory behaviour.

An animal's personality develops during ontogeny by continuous interactions between the environment (e.g., climate, competition, predation pressure, resource availability, and resource quality), genes, and prior phenotypic expression itself (Koolhaas et al. 1999, Turner 2009, Stamps and Groothuis 2010a, Groothuis and Trillmich 2011). Individuals have the capacity to develop in a variety of different ways that can have a profound influence on how they respond to conditions later in life (e.g., Bateson 2005). Under variable but predictable conditions, an animal's phenotype can thus be well adapted to the local environment.

During ontogeny initial differences in state interact with the environment. These interactions can have cascading effects on other parts of an animal's phenotype and drive consistent adaptive behaviour (West-Eberhard 2003, Stamps and Groothuis 2010a, Stamps and Groothuis 2010b, Groothuis and Trillmich 2011). Natural selection and phenotypic plasticity can thus reduce costs associated with an individual's behaviour enforcing correlations between behaviour, physiology and morphology (Chapter 7, Dingemanse et al. 2007, Sih et al. 2010, Carere and Maestripieri 2013). For instance, exposure to predation generated a correlation between aggression and exploration in sticklebacks *Gasterosteus aculeatus* (Bell and Sih 2007). We found that exploratory knots were smaller and had larger flight capabilities than non-exploratory knots (Box 10.1), which could reduce an individual's costs associated with an exploratory lifestyle (e.g., metabolic costs of flight, exposure to predation, see Chapter 7).

From an adaptive (ultimate) perspective the ontogeny of animal personality has so far received little attention (but see Stamps and Groothuis 2010a, Stamps and Groothuis 2010b). Perhaps, this is because of the complexity in disentangling the continuous interactions and feedbacks between developing phenotypic traits and environments. Nonetheless, to aid our understanding of the ecology and evolution of animal personalities, we need to study the interactions between the environment and phenotypic traits during ontogeny together with their fitness consequences (Groothuis and Trillmich 2011, T. Piersma pers. comm.).

RETYING THE EXPLORATORY KNOT

In the past decades, our research group has gathered a wealth of information on the evolutionary ecology of knots and the interaction with their environment (e.g., Piersma 1994, Zwarts 1997, van Gils 2004, Vahl 2006, Reneerkens 2007, Buehler 2008, Kraan 2010, van den Hout 2010, Leyrer 2011, Piersma and van Gils 2011, Folmer 2012, van der Geest 2013). This provides us with a unique opportunity to use the knot as a model species and synthesize an empirically-based evolutionary-ecological conceptual framework for the development and maintenance of personality variation. Though this conceptual framework is speculative, it may aid future studies on knot personalities and perhaps provide some interesting thoughts for animal personality research in general.

Integrating knot personality development with adaptive evolutionary ecology

During ontogeny, the interaction between an individual's genes and the environment result in an adaptive phenotype (Monaghan 2008). Animals have different ways of responding to environmental variation. Based on the speed of this response, we have characterized three adaptive trait categories (Fig. 10.1): 'behavioural', 'physiomorphic', and

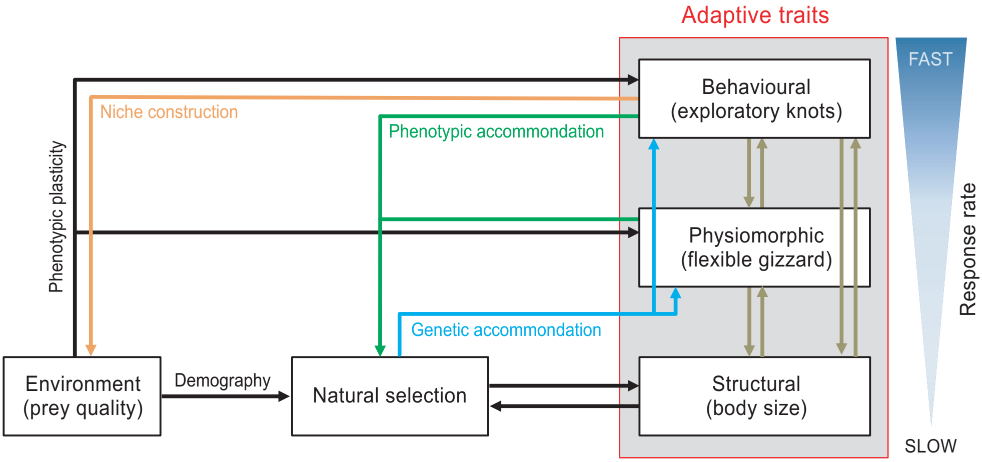


Figure 10.1 Evolutionary-ecological framework of personality development between knots. The grey area highlights the combinations of '*adaptive traits*' that depict a knot's phenotype. Note that with the term '*physiomorphic*' we indicate physiological traits, as well as flexible morphological traits such as gizzard mass, body mass, etc.. Through '*phenotypic plasticity*', variability in the environment will induce an adaptive phenotypic response that can be immediate ('*behavioural*'), or requires time ('*physiomorphic*'). The slowest adaptive response to environmental change is via structural traits such as body size ('*structural*'). For a structural phenotypic response, the environment is a direct agent of natural selection through mortality and reproduction, i.e. '*demography*'. An individual's adaptive phenotypic response can also feed back to the environment, i.e. '*niche construction*' or niche picking. An explorative knot, for instance, explores large areas in search of high food quality thus creating its own prey quality environment. An individual's adaptive phenotypic response will affect whether an individual will survive in its environment ('*phenotypic accommodation*'). If this phenotypic variance is partly due to genetic variation among individuals, phenotypic accommodation can lead to '*genetic accommodation*'. This conceptual framework expands on the positive feedback that we introduced in Chapter 7 (Fig. 7.6). In this feedback loop, capable of maintaining personality variation, exploratory behaviour allows access to high-quality prey through niche construction. Therefore, exploratory birds will acquire small gizzards through phenotypic plasticity, which enforces exploratory behaviour through their digestive constraint, i.e. they require high quality prey to achieve a sufficiently high intake rate. This illustration was inspired by Fig. 1 in Lister (2014).

'structural'. The 'physiomorphic' category includes physiological traits (e.g., hormone levels, immunity, crushing power by gizzards, digestive enzymes), as well as flexible morphological traits (e.g., fat stores, muscle and gizzard sizes, Piersma and van Gils 2011). Through day-to-day decisions, behaviour allows the fastest response to the environment (Duckworth 2009). Physiomorphic traits have an intermediate response rate, e.g., the gizzard mass of knots take one to two weeks to adjust to a change in diet (Dekinga et al. 2001). The 'structural' category refers to traits that, compared to a behavioural response, are thought to be more fixed throughout an adult's life, such as body size. For a structural response, the environment acts as a direct agent of natural selection through demographic rates (reproduction and survival) (e.g., Kraan et al. 2009b, Kentie et al. 2013, Lok et al.

2015, Rakhimberdiev et al. 2015). Those individuals that survive will live to reproduce and their phenotypic traits will increase in (gene) frequency. The combinations of all three trait categories depict a knot's adaptive phenotype (the grey area in Fig. 10.1).

The negative correlation that we found between exploratory behaviour and gizzard mass (Fig. 7.1B) suggests a trade-off between an individual's behavioural and physiomorphic response (Fig. 10.2A). Moreover, both an individual's exploratory behaviour and gizzard mass were correlated with structural traits (i.e. body size, Box 10.1), which suggests that an individual's structural traits mediate behavioural and physiomorphic responses (Fig. 10.1). A proximate explanation for such trade-offs could be that large non-exploratory knots with large gizzards have reduced flight capacity (Box 10.1) and probably increased travelling costs that are associated with exploratory behaviour (Piersma et al. 2003). Likewise, small knots with small gizzards could experience increased risk of starvation due to the digestive constraint that is associated with small gizzards (van Gils et al. 2003a).

In Chapter 7 we show that exploratory behaviour does not correlate with survival probability, which suggests that combinations of exploratory behaviour, gizzard mass, and body size reflect alternative strategies with equal fitness, i.e. the combined phenotype is an adaptive response to the environment (Fig. 10.2B). Whether it is exploratory versus non-exploratory behaviour, a small gizzard versus a large gizzard, or small bodies versus large bodies, these contrasts may all reflect extreme phenotypes on a continuum of combinations between behavioural, physiomorphic, and structural responses to environmental conditions. The levels of an individual's behavioural, physiomorphic and structural response depend on the exact costs and benefits of the combined responses, which will change continuously in interactions with the environment (Bateson 2005). Small differences in any of the traits could ultimately lead to lasting personality variation (Sih et al. 2015).

Across generations, a species will evolve towards having combinations of behavioural, physiomorphic, and structural traits that are the most adapted to the past environment. On the shorter timescales within an individual's lifetime, phenotypic plasticity can drive combinations of these traits and allow knots, during their ontogeny, to maintain their adaptive response to their experienced environment (phenotypic accommodation, Fig. 10.1). Phenotypic accommodation (through physiomorphic as well as behavioural traits) may well precede changes in gene frequencies (Wcislo 1989, West-Eberhard 2003, Jablonka et al. 2005, Duckworth 2009, Piersma and van Gils 2011). If the degree or pattern of phenotypic accommodation is partially genetically coded and if there is variation among individuals, natural selection can enforce changes in frequencies of the relevant genes ('genetic accommodation', West-Eberhard 2003, West-Eberhard 2005).

Phenotypic plasticity itself may also be reflected in the genotype. Genetic variation for plasticity has been demonstrated, which suggests that adaptive phenotypic plasticity can evolve through natural selection (West-Eberhard 2003). In unpredictable environments, natural selection may favour phenotypic plasticity, including phenotypic flexibility (e.g., Moran 1992, Piersma and Drent 2003, Piersma and van Gils 2011). There may, however,

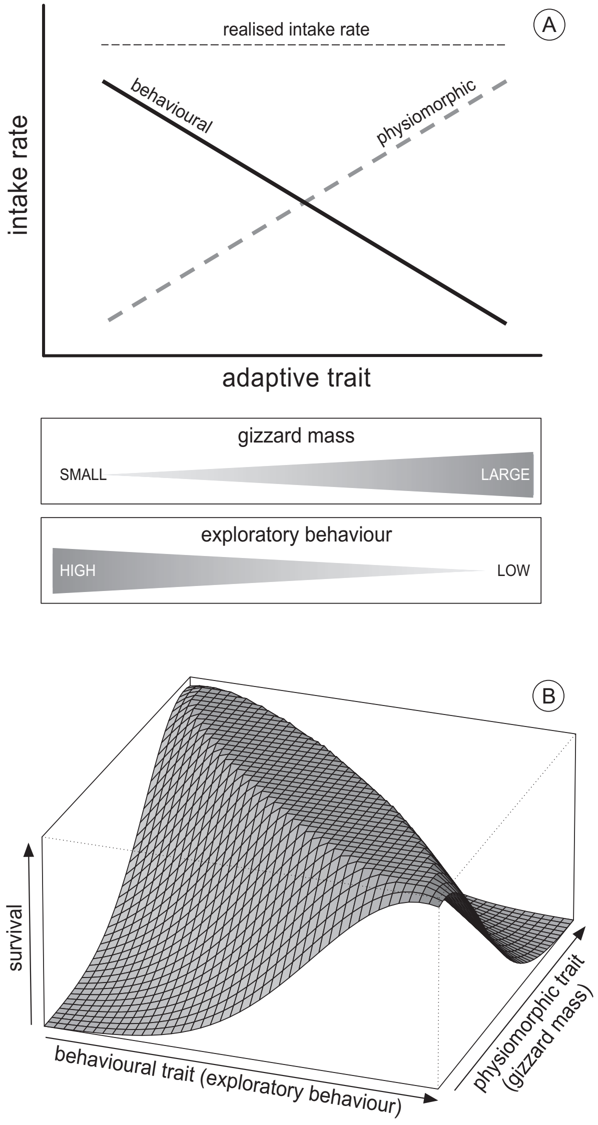


Figure 10.2 Trade-offs between adaptive traits. The negative correlation that we found between gizzard mass and exploratory behaviour (Fig. 7.1B) suggests a trade-off between an individual's physiomorphic and behavioural traits. In panel (A), we represent this trade-off. For the sake of argument, we assume that all knots aim for the same intake rate. In order to realise this intake rate, knots can permit different combinations of gizzard mass and exploratory behaviour. In panel (B), we schematically show how the trade-off between physiomorphic and behavioural traits result in equal survival (fitness) that is shown on the z-axis.

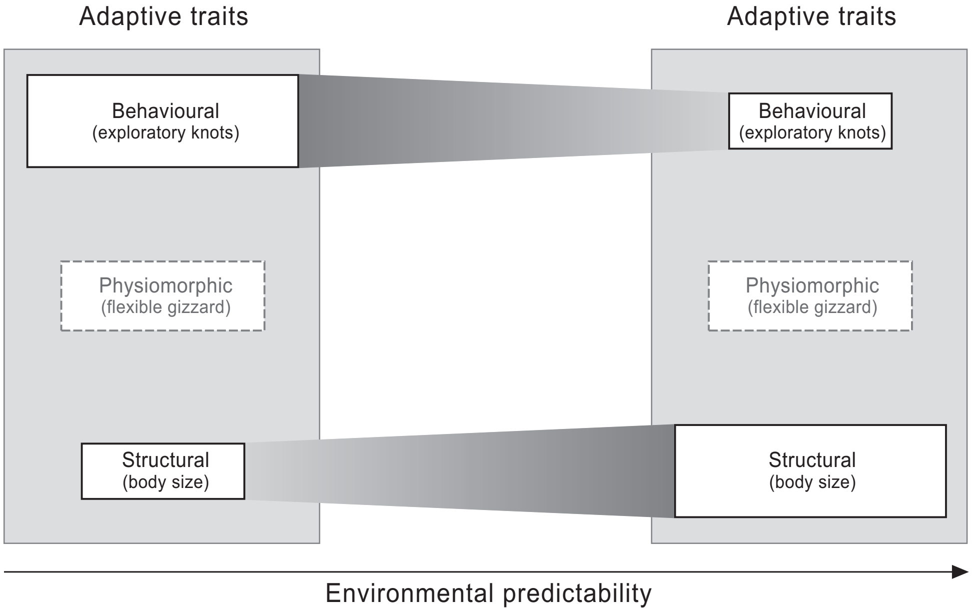


Figure 10.3 The hypothesized effect of enviromental predictability on the adaptive response of an individual. Here we built on Fig. 10.1 and added an axis of environmental predictability. Assuming that phenotypic plasticity has some cost, we examplify the extremes of an individual's adaptive response to the environment, i.e. a behavioural and structural response. The box-size of an individual's behavioural and structural traits reflect their relative weight in either an unpredictable (left) or predictable environment (right). Unpredictable environments will favour adjustments based on phenotypic flexibility rather than based on the natural selection of structural traits, and *vice versa*.

also be costs associated with phenotypic plasticity (Bateson 2001, Dall et al. 2004). Once a phenotype is 'fully' formed, during a change in local conditions it may be difficult and costly to switch to another, better adapted, phenotype (Bateson 2001). The predictability of the environment in combination with the costs of behavioural, physiomorphic, and structural plasticity will therefore determine whether such adaptive traits become genetically accomodated (Baldwin 1896, Crispo 2007). Assuming that plasticity has some cost, individuals living in predictable environments will adapt with structural traits that are more or less fixed during a lifetime. Likewise, individuals living in unpredictable environments will adapt with the more plastic physiomorphic and behavioural traits (Fig. 10.3).

THE ENDLESS KNOT

The work presented in this thesis provides us with a better understanding of the spatial distribution of knots. We have established that knots use public information to find their hidden prey, which increases their foraging success. Even though knots rarely fight and are seemingly peaceful birds, we found that knots do engage in serious forms of interference. Interference that is not clearly expressed and thus ‘cryptic’. Currently, models to predict the spatial distributions of foragers do not incorporate such interference mechanisms.

In the field, we have shown that knot predation can have substantial influence on cockle densities, and that, by selecting high quality cockles, knots exert strong selection pressures on cockles to defend themselves and have thick shells. In fact, these selection pressures are amongst the highest reported in the literature. By measuring individual prey as well as predator characteristics, we found that knots maximise their energy intake rates at intermediate prey densities. This makes prey density alone a poor predictor of intake rates, a statement that counters most of what you would read in the pertinent literature. It is an important finding as it affects how we model spatial distributions and carrying capacity. Another noteworthy finding was that knots have personalities too, i.e. they consistently differ in their exploratory behaviour. Even though a knot’s gizzard is flexible, it is behaviourally constrained due to consistent prey ingestion. Knots with different exploratory behaviour and gizzard masses have equal survival. These traits thus reflect different foraging strategies that result in equal fitness.

As usual each answer leads to new questions. We found that knots consistently differed in their social foraging tactics. Some knots consistently exploited the searching efforts of others. Public information use in relation to personality differences has, so far, received little attention in the literature. A promising next step could be to investigate whether non-explorative birds rely on the searching effort of exploratory birds. In the field, it is difficult to identify whether individuals use public information while foraging or roosting. Hopefully, further technological advances could provide a means to study information use in the wild. Studies on the ecological implications of animal personality in the wild are currently rare. Especially, studies that combine ecological feedbacks with the ontogeny of animal personalities are lacking. They are, nonetheless, necessary to gain a thorough understanding on the evolutionary origin and maintenance of personality variation. Rather than to only focus on the evolution of personality, we need to understand the proximate ecological mechanisms as well. Perhaps the framework we proposed that centres on the whole organism (Fig. 10.1) can aid future research. Disentangling the continuous interactions and feedbacks between phenotypic traits and the environment is, however, no easy task, as it requires the disentangling of an endless knot.

Box 10.1 Exploratory birds are smaller and have larger flight capacity than non-exploratory birds

In Chapter 7 we found that exploratory birds have smaller body masses than non-exploratory birds. This was partly due to the fact that they had smaller energy stores, but also because they were structurally smaller: exploratory behaviour was negatively correlated with the first principal component of body-size traits (intercept = −0.64, 95% CI [−1. 26; −0.02], slope = −1.08, 95% CI [−1.61; −0.72], $r = -0.42$, $P = 0.046$, Fig. B10.1A). With ultrasound, we also measured the (transversal) height of an individual's pectoral muscle (Dietz et al. 1999). We did this one day after capture, which therefore reflected the birds' muscle mass while free-living. The mass of the pectoral muscle relates to an individual's flight capacity (Dietz et al. 2007). Following Dietz et al. (1999), we derived its weight (g) as −10.9 + 31.7 × transversal height (cm). We found that pectoral muscle mass was not correlated with exploratory behaviour ($r = 0.23$, $P = 0.31$). However, because total body mass was negatively correlated with exploratory behaviour, an individual's flight capability (i.e. the pectoral muscle as fraction of total body mass) was positively correlated with exploratory behaviour (intercept = −1.25, 95% CI [−1.34; −1.16], slope = 0.16, 95% CI [0.11; 0.24], $r = 0.47$, $P = 0.03$, Fig. B10.1B).

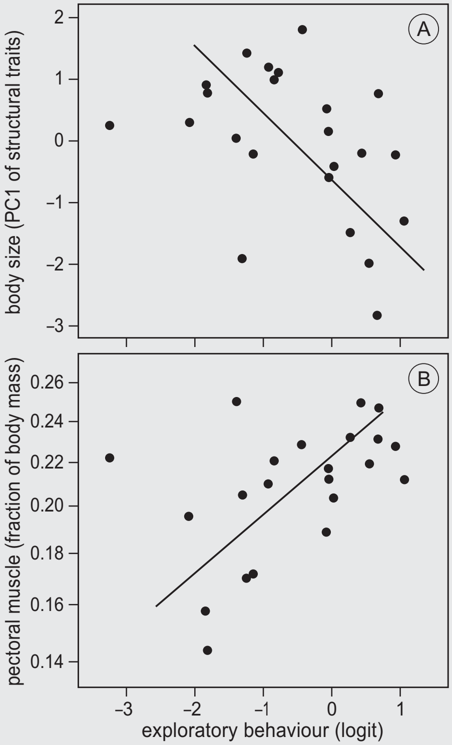
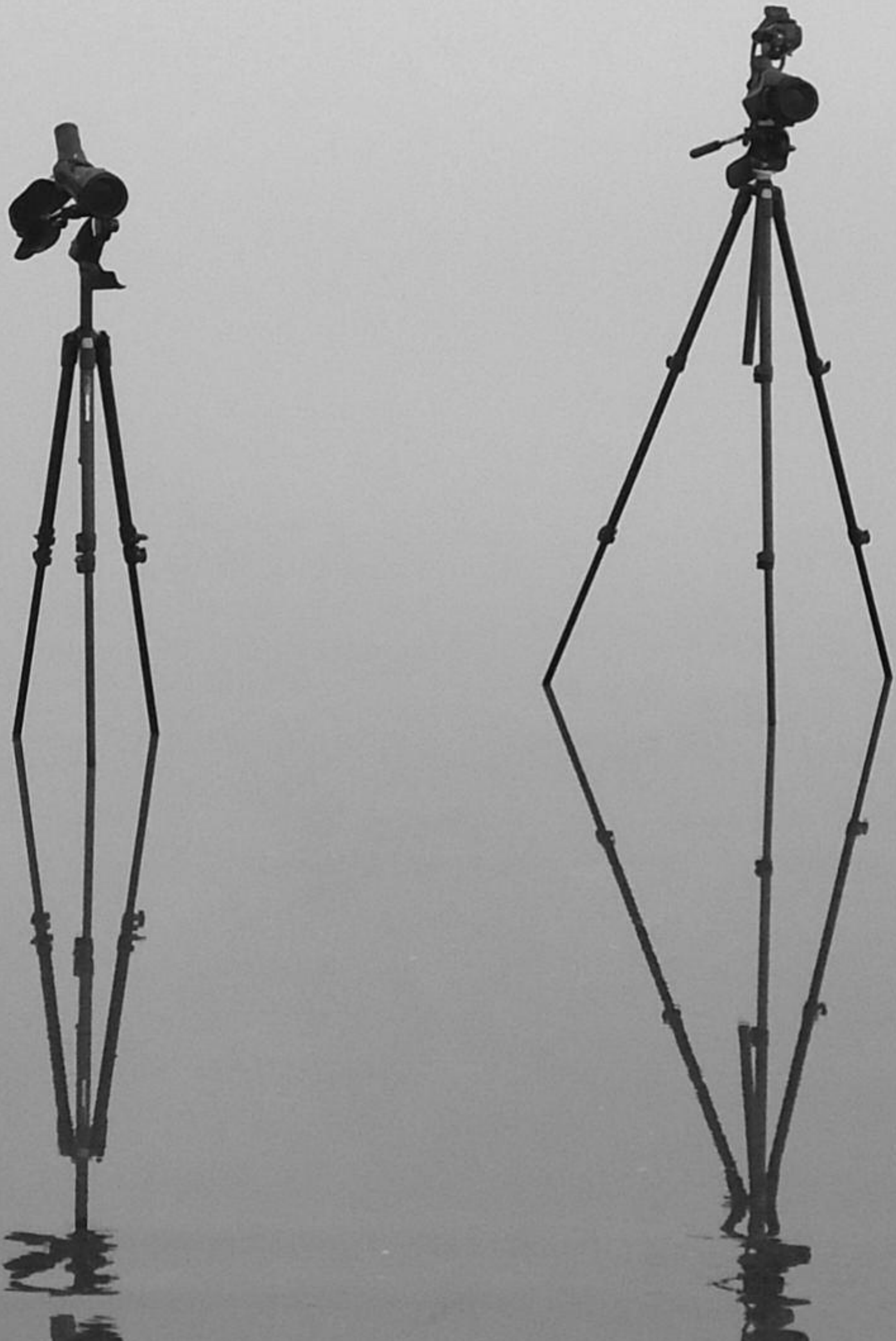


Figure B10.1 Standardised major axis regressions of an individual's exploratory behaviour with (A) body size, and (B) relative pectoral muscle mass. Exploratory behaviour is the logit of the fraction of time spent searching (see Chapter 7). Body size was estimated by extracting the first principal component of wing length (mm), tarsus length (mm) and total head (mm, i.e. the length between the back of the head and tip of the bill) (see Appendix of Chapter 7). Relative pectoral muscle mass was calculated as the fraction of an individual's body mass. Note that we analysed logit-transformed relative pectoral muscle masses.



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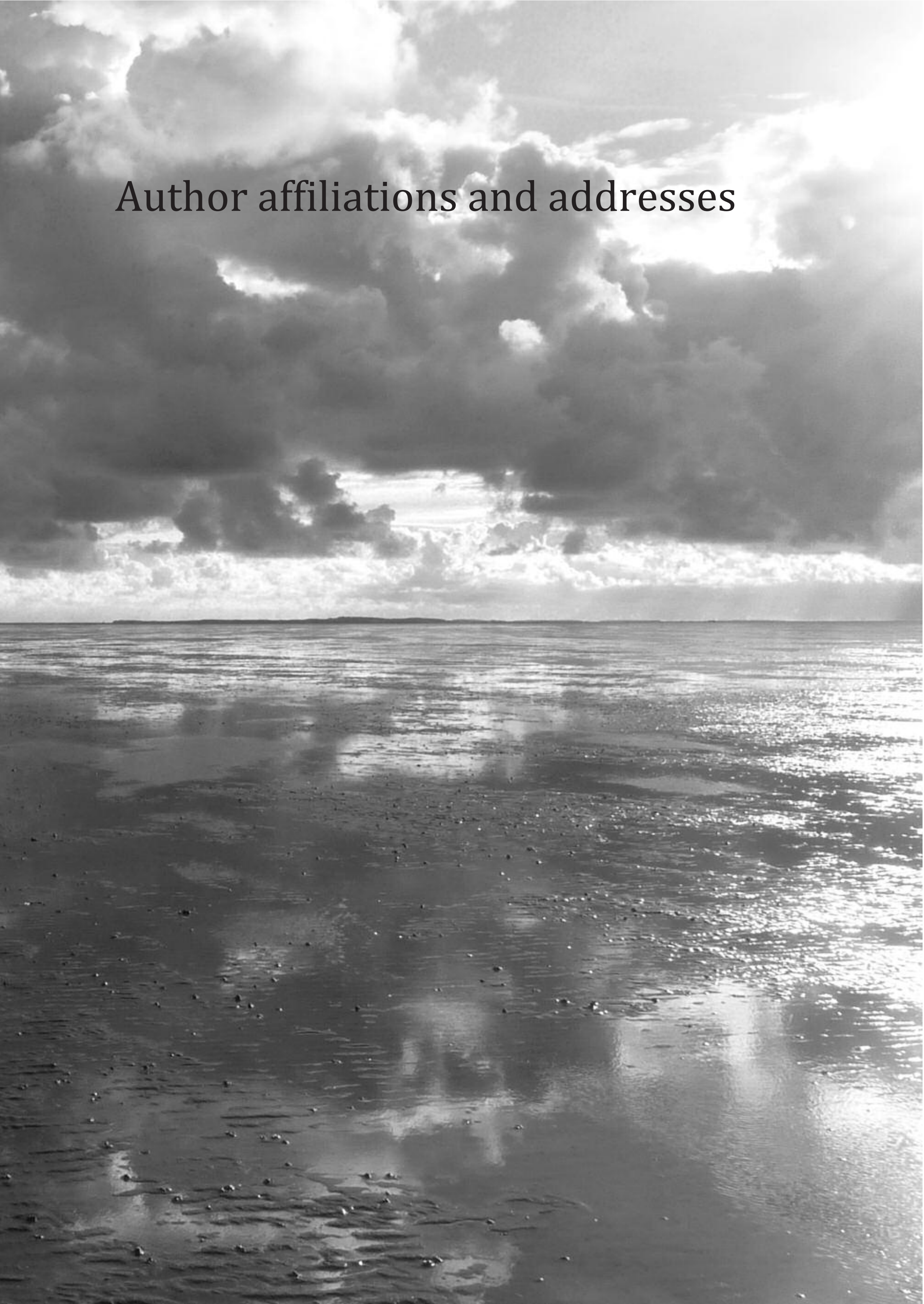

Author affiliations and addresses

Allert I. Bijleveld
Email address: allert.bijleveld@gmail.com
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Maarten Brugge
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Ying-Chi (Ginny) Chan
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

John Cluderay
Marine Technology Electronics, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Anne Dekinga
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Martijn Egas
Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam,
P.O. Box 94248, 1090 GE Amsterdam, the Netherlands

Eelke O. Folmer
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Richard M. Gabrielson
Bioacoustics Research Program, Cornell Laboratory of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA, *and* Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853, USA

Jan A. van Gils
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Sander Holthuijsen
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Job ten Horn
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Jeltje Jouta
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Casper Kraan
National Institute of Water and Atmospheric Research, P.O. Box 11-115, Hillcrest, Hamilton 3251 New Zealand

Robert B. MacCurdy
Department of Mechanical and Aerospace Engineering, Cornell University, Ithaca, NY 14853, USA

Annemarie van der Marel
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Georgina Massourakis
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Jaap van der Meer
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Emma Penning
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Julia Piechocki
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Theunis Piersma
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands, *and* Chair in Global Flyway Ecology, Animal Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, the Netherlands

Bernard Spaans
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

Eric L. Spaulding
Bioacoustics Research Program, Cornell Laboratory of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA

Sönke Twietmeyer
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands, *and* Department of Biogeography, Trier University, Universitätsring 15, D-54296 Trier, Germany

Henk W. van der Veer
Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

David W. Winkler
Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853, USA

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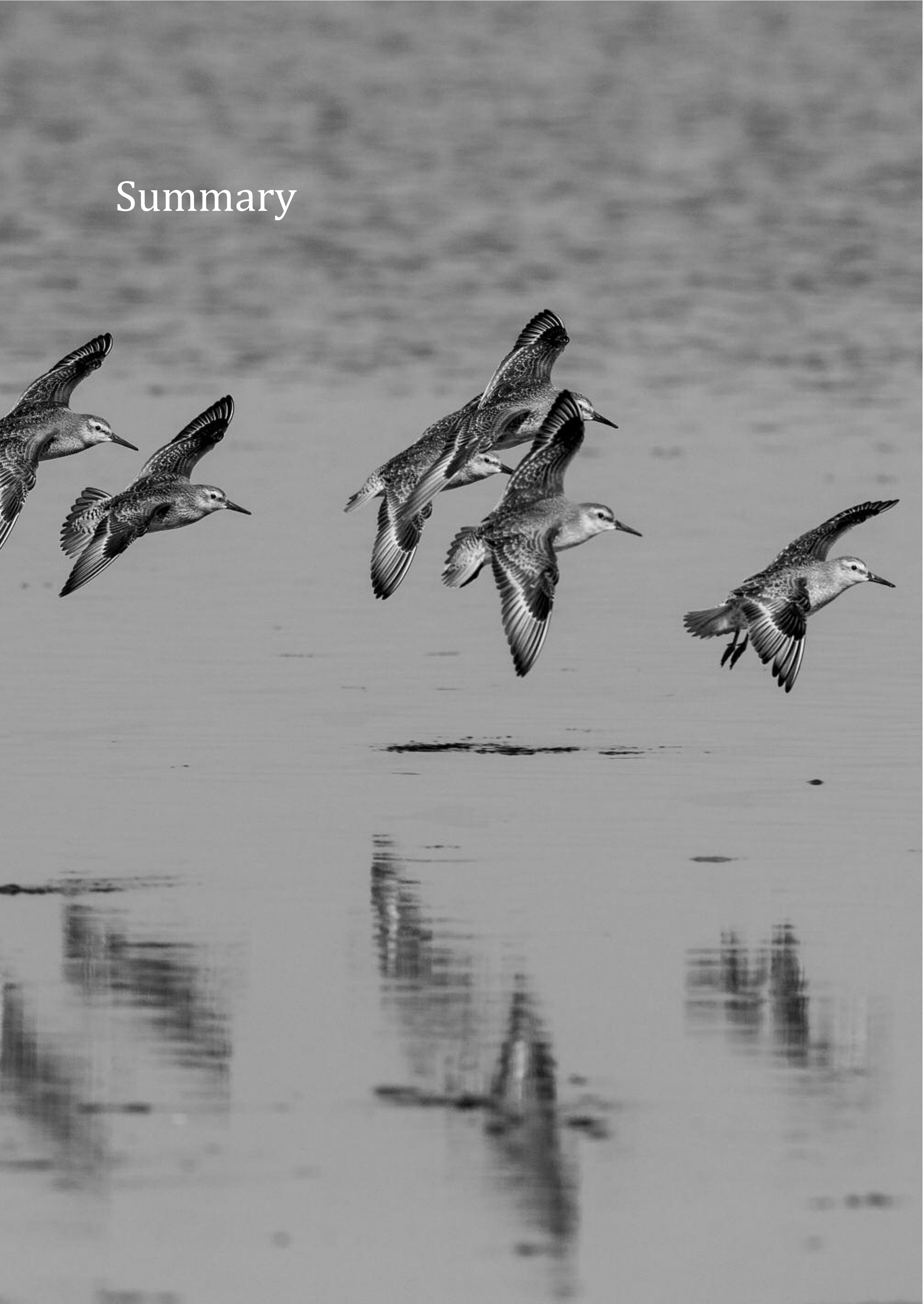
Summary



The main goal of the research presented in this thesis was to gain a deeper understanding of the spatial distributions of social predators. In order to gain such understanding, I built on three decades of research on red knots (*Calidris canutus islandica*, hereafter called knots). Knots are medium-sized shorebirds that feed on hard-shelled molluscs living in intertidal mudflats. Even though this research mainly concerns knots, the understanding that we have gained is certainly not limited to this single species. In fact, knots could serve as a model for a wider range of species, perhaps including humans.

Questions that we asked are: Do knots use public information to find food? Can we predict the spatial distribution of knots based on the spatial distribution of their prey? Do individuals differ in the way they search for food? Do individual knots have distinct 'personalities' with reference to movement and foraging decisions, and if so, can we explain how and why they consistently differ in behaviour?

We studied knots outdoors on the intertidal mudflats of the Dutch Wadden Sea as well as indoors, i.e. under captivity in the unique experimental shorebird facility at NIOZ Royal Netherlands Institute for Sea Research. These experiments in artificial, controlled conditions allowed disentangling the mechanisms that drive their behaviour. Their decisions in the wild are what we finally try to comprehend. In order to gain an understanding of the mechanisms that drive the spatial distributions of social predators, one needs to combine both methods.

My thesis is divided into four sections that I will summarise consecutively. For the study of interactions between prey and predator their abundances need to be sampled. In the first section we develop a methodology for sampling both prey and predator distributions. In the second section we study aspects of behaviour between knots (their so-called sociality). Here we untie the effects that conspecifics have on an individual's foraging success. Then we switch to individuality. In this third section we show how individual variation in knots is crucial for understanding their foraging decisions. We also show that the spatial distribution of knots can be explained by individual differences in prey. In the fourth section I tie the knot together by discussing some of our findings in a broader context and suggest directions for further research.

SAMPLING METHODOLOGY

Sampling spatial and temporal distributions of a species is central to ecologists, as well as to conservation biologists that are concerned with advising policy makers. In order to maximize effectiveness at minimal costs, these sampling efforts should be optimised.

In **Chapter 2** we develop an optimal sampling design for monitoring programmes with objectives that have conflicting demands on the sampling design. These objectives were: (1) estimate changes in abundance, (2) predict abundances at unsampled locations, or (3) estimate spatial autocorrelation model parameters. With Monte-Carlo simulations, we compared five popular sampling designs: simple random sampling, grid sampling, two types of transect sampling, and our novel grid sampling design with additional random sampling stations. We compared these sampling designs at four levels of naturally occurring spatial autocorrelation, i.e. the level of spatial clustering. Grid sampling with a number of random samples placed on gridlines catered best for all three objectives combined, and can therefore be widely applied.

Knots feed on hard-shelled molluscs buried in the sediment, e.g., Baltic tellins (*Macoma balthica*) and edible cockles (*Cerastoderma edule*). Having developed a sampling design that allows accurately mapping prey densities, we also needed a new methodology to sample spatial distributions of knots. The miniaturisation of tracking technology proceeds at a high speed and has begun to provide tools to ecologists that require the monitoring of large numbers of individuals. Unfortunately, many of these new tools are inapplicable to many species due to mass, cost and energy constraints, leaving gaps in our understanding.

In **Chapter 3** we present a new technique with small transmitters, which is capable of automatically gathering position data for large numbers of animals over long timescales. Relative to current methods, this technique offers ecologists unprecedented amounts of data with accurate position estimates at a high frequency (every second). Moreover, it can be broadly applied to species that were previously too small for automated tracking systems, and due to reduced tracking costs, the numbers of individuals that can be tracked is large.

SOCIALITY

When resources are distributed in patches, as they frequently are, behavioural ecologists often use ideal free distribution models to predict foraging distributions across these patches. When predators aggregate in the best food patches, they increasingly interfere with each other. Consequently, they suffer reduced intake rates. When predators aggregate even more, their intake rate drops below the intake rate that they could have acquired on a different patch with lower food density but also with less competition.

Understanding how intake rate decreases as a function of the number of competitors is of paramount importance to predicting spatial distributions of foragers. Especially because subtle differences in these interference functions may result in qualitatively different predictions. Moreover, resource competition and interference competition are hard to separate as both their negative effects increase with an increase of group size. In an attempt to exclude resource depletion and study interference competition in isolation, we designed an experimental setup with moving patches. Because of the moving patches, new prey became available and prey density remained constant.

In **Chapter 4** we show that the intake rates of knots declined with group size, but surprisingly the common interference mechanisms also declined or were virtually absent. The main mechanism of interference competition among knots is avoiding encounters with conspecifics, so-called ‘cryptic interference’. Cryptic interference reduces the available searching time and, because knots divert their attention between searching for prey and avoiding interactions with conspecifics, reduces their searching efficiency. To accurately predict intake rates and model foraging distributions, we need to account for the possibility of cryptic interference.

Foraging together can also be beneficial to individuals. These benefits include increased safety in numbers, increased time that could be spent foraging rather than on anti-predation vigilance, and the accessibility of foraging information. In 1973 Peter Ward and Amotz Zahavi proposed that communal roosting (the grouping of more than two individuals resting together) evolved primarily as centres where individuals *actively* advertise foraging information such as the location of patchily distributed foods. Their proposal has stimulated fierce debates and has not been widely accepted.

In **Chapter 5** we review this controversial 'information centre hypothesis' and summarize studies that demonstrate behaviours consistent with the predictions of the hypothesis. Whether actively sharing foraging information is the primary evolutionary cause driving communal roosting is a question that is hard to answer. Because communal roosting is widespread, we think it is particularly interesting to focus on the information benefits that individuals could gain from roosting communally. We suggest that inadvertent information transfer, rather than active information exchange, predominates in communal roosts. To illustrate how testable predictions can be generated, we propose a conceptual model on communally roosting knots. In particular, we illustrate how roost arrival timing may convey inadvertent information on intake rate, prey density, forager state (i.e. digestive processing capacity) and food quality. Unsuccessful foragers could use such information in order to select with whom to leave the roost at the subsequent foraging opportunity. Thus increasing their foraging success.

Information gained from others can help individuals to make better estimates of patch resource density enabling foragers to increase their intake rate, e.g., by wasting less time searching for food in unprofitable patches. The presence of other foragers can also indicate the location of food, so-called local enhancement, which is commonly used by many species.

In **Chapter 6** we show that socially foraging knots also use public information. By monitoring the foraging success of their flock mates they were able to find food faster. In fact, the time needed to locate a food patch decreased proportionally to group size.. Another interesting finding was that knots differed in their search strategy: some individuals consistently exploited the searching efforts of others.

INDIVIDUALITY

Individuals of many species have been shown to vary consistently in their behaviour across contexts. This variation is referred to as 'animal personality'. Animal personality indicates that behavioural flexibility is limited and that, when the context changes, individuals may not always behave optimally. Because natural selection favours optimal behaviour, a puzzle in evolutionary and behavioural ecology is how and why animal personality persists over evolutionary time. Most of the adaptive (ultimate) explanations of behavioural consistency involve between-individual variations in state. An individual's state is defined as any feature of an individual that affects the cost and benefits of its behaviour. Recently, variation in the size of metabolic organs has been suggested to cause and maintain variation in personality. Large metabolic organs require bold and explorative behaviour that allow for the acquisition of large amounts of energy necessary to sustain these metabolically expensive organs.

In **Chapter 7** we examine this hypothesis. We showed that exploratory behaviour of captive knots was negatively rather than positively correlated with digestive organ (gizzard) mass. In a follow-up experiment we reciprocally reduced and increased an individual's gizzard mass and found that its exploratory behaviour was unaffected. Few studies show how personality traits measured under controlled environments in the laboratory relate to behaviour in the wild. In order to test whether the experimental quantification of exploratory behaviour was representative of this behaviour in the field, we tagged and released the experimental birds with unique combinations of colour-rings and estimated local resighting probabilities. Birds that were not resighted locally, over the 19 months after release, had higher exploration scores than birds that were resighted. Moreover, a long-term mark-recapture effort on free-living knots with known gizzard masses at capture confirmed that local resighting probability (an inverse measure of exploratory behaviour) was correlated with gizzard mass without detrimental effects on survival. We conclude that personality drives physiological adjustments, rather than the other way around, and suggest that physiological adjustments mitigate the survival costs of exploratory behaviour. Our results show that we need to reconsider hypotheses explaining personality variation based on organ sizes and differential survival.

From individual variation among knots we then switch to individual variation among their prey, the cockles. Selective predation can lead to natural selection in prey populations and may also alleviate competition among surviving individuals. The processes of selection and competition can have substantial effects on prey population dynamics, but are rarely studied simultaneously.

In **Chapter 8** we study the processes of selective predation and competition in the wild. We measured densities, patchiness, morphology, and body composition (shell mass and flesh mass) of cockles before and after predation in three similar plots of 1 ha each. Two of these plots experienced predation, and one plot remained unvisited in the course of the short study period and served as a reference. We showed that predation by knots substantially reduced cockle densities and homogenised their spatial distribution. Moreover, knots selected those individual cockles that allowed them to maximise their energy intake rates, i.e. juvenile cockles with large flesh mass and little shell mass. By this selective predation knots imposed a strong selection pressure on cockles to grow fast with thick shells and little flesh mass. The calculated selection gradients are among the highest reported in the literature. We also found that cockle body composition declined with cockle density (negative density-dependence) possibly through intra-specific competition.

The effects of density dependence are generally studied within trophic levels. However, density dependence within a trophic level may also have implications for higher levels. Until now the idea is that a predator's intake rate always increases with prey density. Large prey densities should thus attract many predators. However, the presence of negative density-dependence among prey challenges this prediction.

In **Chapter 9** we investigate negative density-dependence among cockles and its implications for the energy intake rate of knots. With the method that we present in Chapter 2, we sampled the density and quality of cockles across 50 km^2 of mudflat. Simultaneously, we tracked the spatial distribution of knots with the novel time-of-arrival methodology that we introduce in Chapter 3. We show that, due to negative density-dependence in the flesh mass of cockles, knots are faced with a trade-off between prey quantity and quality. At low prey densities predators have difficulty finding prey, but those prey have relatively large energy content. At high densities prey are easier to find, but have relatively low energy content. Contrasting the current viewpoint, knots do not necessarily maximise their energy intake rates at the highest prey densities. Resource-selection modelling revealed that the tagged knots indeed avoided areas with the highest cockle densities. They preferred foraging on areas with intermediate cockle densities where they could maximise energy intake rate given their phenotype-specific digestive constraints (as indicated by gizzard mass).

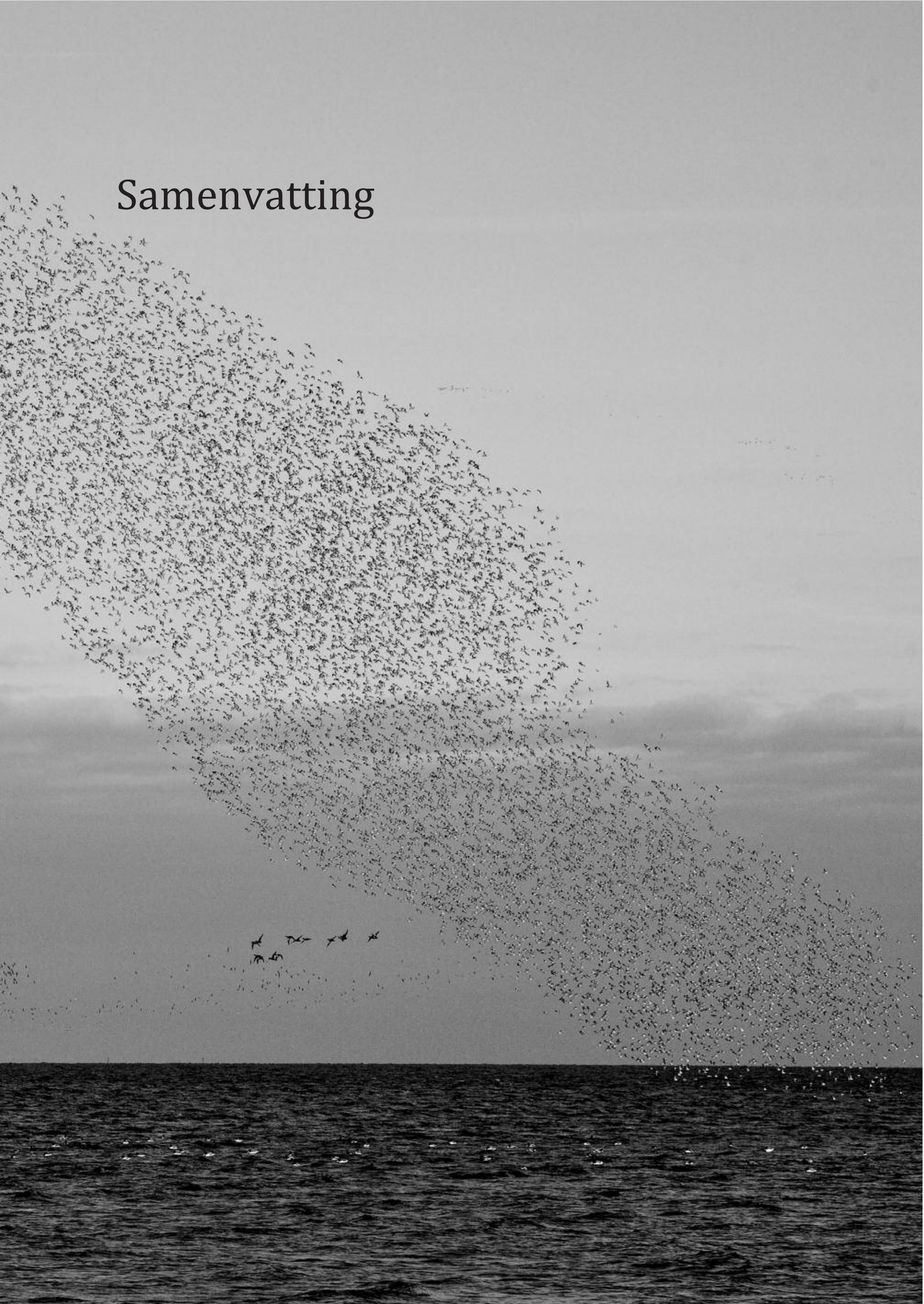
Because negative density-dependence is common for many different (prey) species, we oppose the current consensus and suggest that predators will often maximise their energy intake rates at intermediate prey densities. Prey density alone may thus be a poor predictor of intake rates, carrying capacity and spatial distributions of predator populations.

RETYING THE KNOT

The work presented in this thesis provides us with a better understanding of the spatial distribution of knots. The mechanisms that we unraveled can be relevant for studies on foragers in general.

In **Chapter 10** I highlight some of our findings and discuss them in a broader context. Such as the importance of estimating spatial autocorrelation functions for understanding spatial distributions, the possibility of cultural evolution at communal roosts, how 'cryptic interference' relates to spatial distribution modelling, how consistent differences between individuals may drive spatial distributions, and the phenomenon of animal personality. Finally, I propose a framework for the development of adaptive personality differences between knots. This framework may contribute to future studies on knot personality and provide some interesting thoughts for animal personality research in general.

Samenvatting



Het belangrijkste doel van het in dit proefschrift gepresenteerde onderzoek is om beter te begrijpen wat de ruimtelijke verspreiding van groepsdieren bepaalt. Ik bouwde voort op drie decennia onderzoek aan kanoeten (*Calidris canutus islandica*). Kanoeten zijn steltlopers die zich voeden met schelpdieren die in de droogvallende platen van de Waddenzee leven. Hoewel dit onderzoek zich toespitste op kanoeten, is het inzicht dat we hebben verkregen zeker niet beperkt tot deze soort. Kanoeten dienen als model om algemene biologische principes te begrijpen, mogelijk dezelfde principes als die bij mensen een rol spelen.

Voorbeelden van vragen aan het begin van mijn promotietraject waren: Gebruiken kanoeten elkaar om verborgen voedsel te vinden? Kunnen we op basis van de ruimtelijke verspreiding van prooien de ruimtelijke verspreiding van kanoeten voorspellen? Verschillen individuen van elkaar in de manier waarop ze voedsel zoeken? Hebben kanoeten ‘persoonlijkheden’ met betrekking tot hun gebiedsgebruik en foerageerbeslissingen, en zo ja, kunnen we begrijpen hoe en waarom ze structureel verschillen in gedrag?

We bestudeerden kanoeten buiten op de wadplaten van de Nederlandse Waddenzee, maar ook binnen. Dat wil zeggen: in gevangenschap in de unieke experimentele Wadvogelunit bij het NIOZ Koninklijk Nederland Instituut voor Onderzoek der Zee op Texel. Dit soort experimenten in kunstmatige en gecontroleerde omstandigheden maken het mogelijk om de onderliggende mechanismen van gedrag te ontdekken. Het is echter hun gedrag in het wild waar we uiteindelijk in geïnteresseerd zijn. Daarom is het van belang om beide soorten onderzoek toe te passen om tot ecologisch relevant begrip te komen.

Mijn proefschrift is verdeeld in vier secties die ik achtereenvolgens zal samenvatten. Om de interacties tussen prooi en predator zoals de kanoet te bestuderen, is het belangrijk om hun dichtheden en ruimtelijke verspreiding te bemonsteren. In het eerste deel van mijn proefschrift bespreken we daarom de ontwikkeling van zulke bemonsteringmethodes. In het tweede deel van mijn proefschrift onderzoeken we de socialiteit van kanoeten. Hierin proberen we de invloeden die soortgenoten hebben op het foerageersucces van individuele kanoeten te ontrafelen. Vervolgens schakelen we in het derde deel over op individualiteit. We laten zien hoe individuele verschillen tussen kanoeten van cruciaal belang zijn voor het begrijpen van hun foerageerbeslissingen. Ook laten we zien dat de ruimtelijke verdeling van kanoeten deels bepaald wordt door individuele verschillen binnen een prooitype. Het vierde en laatste deel van mijn proefschrift bevat de algemene discussie waarin ik het gedrag van kanoeten ontrafel. Hiermee plaats ik onze bevindingen in een bredere context en suggereer ik mogelijkheden voor vervolgonderzoek.

BEMONSTERINGSMETHODIEK

Het bemonsteren van soorten om hun verspreiding, in zowel ruimte als tijd, te kunnen bepalen is centraal voor ecologen, maar ook voor biologen die zich inzetten voor natuurbehoud en natuurbeleid. Omdat de middelen voor bemonsteringprogramma’s beperkt zijn moeten deze om een zo hoog mogelijke effectiviteit te behalen geoptimaliseerd worden.

In **Hoofdstuk 2** ontwikkelen we een bemonsteringsprogramma waarbij de onderliggende doelstellingen andersoortige eisen stelden aan de methode. De verschillende doelstellingen waren: (1) het schatten van abundantie, (2) het voorspellen van abundantie op niet gemonsterde locaties, of (3) het nauwkeurig schatten van de ruimtelijke parameters van autocorrelatie. Aan de hand van Monte-Carlo-simulaties vergeleken we vijf populaire bemonsteringmethodes: een aselecte steekproef, een raster, twee soorten lijnbemonsteringen, en onze nieuwe bemonsteringsmethode waarbij een raster aangevuld wordt met aselect gekozen bemonsteringslocaties. We vergeleken deze methodes op vier niveaus van natuurlijk voorkomende ruimtelijke autocorrelatie (een maat voor samenklontering van dieren). De rasterbemonstering met een percentage aselect gekozen bemonsteringslocaties leverde het beste resultaat op voor de drie gecombineerde doelstellingen en kan dus breed ingezet worden.

Kanoeten voeden zich voornamelijk met schelpdieren, zoals nonnetjes (*Macoma balthica*) en kokkels (*Cerastoderma edule*), die in de bodem van getijdengebieden leven. Nu we een methode hebben ontwikkeld om dichtheden van deze schelpdieren nauwkeurig te kunnen bepalen, hebben we ook een methode nodig om de ruimtelijke verspreiding van kanoeten te bemonsteren. De miniaturisatie van zendertechnologie is heel snel gegaan en op dit moment komen de middelen beschikbaar waarmee ecologen grote aantallen individuen kunnen volgen. Maar vanwege hun nog steeds grote gewicht kunnen deze hulpmiddelen nog niet worden toegepast op verreweg de meeste soorten. Hierdoor beperkt onze kennis zich tot de grotere soorten.

In **Hoofdstuk 3** presenteren we een nieuwe techniek die met behulp van kleine zenders automatisch positiegegevens verzamelt. Door de korte tijdsduur van een seconde tussen opeenvolgende posities kunnen er grote hoeveelheden gegevens verzameld worden. Posities die met een hoge nauwkeurigheid worden berekend. Biologen kunnen deze techniek inzetten voor onderzoek aan soorten die eerder te klein waren voor automatische volgsystemen. Bovendien zijn de zenders binnen dit volgsysteem stukken goedkoper waardoor grote aantallen individuen kunnen worden gevolgd.

SOCIALITEIT

Als prooien samenklonteren in zogenaamde voedselpatches, zoals ze vaak doen, grijpen gedragsecologen over het algemeen naar ‘ideaal-vrije-verdelings’-modellen om de ruimtelijke verspreiding van foeragerende predatoren te voorspellen. In eerste instantie kiezen predatoren een voedselpatch met de hoogste prooidichtheid. Door daar samen te klonteren zitten ze elkaar fysiek in de weg (interferentiecompetitie) en concurreren ze om het aanwezige voedsel (voedselcompetitie). Beide vormen van competitie verminderen de voedselinnamesnelheid. Bij een bepaalde groepsgrootte zal de voedselinnamesnelheid gedaald zijn tot onder het niveau dat ze zouden kunnen behalen op een andere voedselpatch met een lagere voedseldichtheid, maar ook met minder competitie.

Kennis over hoe de voedselinnamesnelheid afneemt als gevolg van interferentiecompetitie is van groot belang voor het voorspellen van de ruimtelijke verspreiding van predatoren. Vooral omdat subtiele verschillen in de vorm van deze interferentiefunctie tot kwalitatief verschillende voorspellingen kan leiden. In experimenten zijn voedselcompetitie en interferentiecompetitie helaas moeilijk van elkaar te scheiden. In een poging om voedselcompetitie uit te sluiten en interferentiecompetitie in afzondering te bestuderen, ontwierpen we een experimentele opstelling met bewegende patches. Door het bewegen van de patches kwamen er steeds nieuwe prooien beschikbaar waardoor de voedseldichtheid constant bleef.

In **Hoofdstuk 4** laten we zien dat de voedselinnamesnelheid van kanoeten afneemt met toenemende groepsgrootte (competitie), maar merkwaardigerwijze dat de gangbare mechanismen van interferentiecompetitie ook afnamen of vrijwel afwezig waren. Het belangrijkste mechanisme van afname in voedselinnamesnelheid is het vermijden van ontmoetingen met groepsgenoten, de zogenoemde ‘cryptische interferentie’. Cryptische interferentie is niet alleen een verlies aan tijd die besteed had kunnen worden aan het zoeken naar voedsel. Ook moeten kanoeten hun aandacht verdelen tussen het zoeken naar prooien en het vermijden van interacties met soortgenoten waardoor hun zoekefficiëntie afneemt. Om in het vervolg de ruimtelijke verspreiding van foeragerende predatoren goed te kunnen voorspellen, moeten we in de modellen rekening houden met cryptische interferentie.

Naast de bovengenoemde nadelen heeft het foerageren in groepen ook voordelen. De voordelen zijn onder meer: 1) veiligheid in aantallen, 2) meer tijd die besteed kan worden aan het zoeken naar voedsel in plaats van waakzaamheid, en 3) toegang tot sociale informatie. In 1973 hebben Peter Ward en Amotz Zahavi de zienswijze geïntroduceerd dat gemeenschappelijk slaapplaatsen op de eerste plaats zijn geëvolueerd als centra waar dieren *actief* informatie delen over bijvoorbeeld de locatie van voedselpatches. Deze zienswijze heeft tot heftige discussies geleid.

In **Hoofdstuk 5** hebben we deze controversiële ‘*information centre hypothesis*’ herzien en vatten we studies samen waar de resultaten overeenkomen met de voorspellingen van deze hypothese. Of informatieoverdracht werkelijk de belangrijkste reden is geweest voor de evolutie van gemeenschappelijk slaapplaatsen is moeilijk vast te stellen. Aangezien gemeenschappelijke slaapplaatsen zo algemeen zijn, denken wij dat het interessanter is om te onderzoeken welke informatie individuen tot hun beschikking hebben op gemeenschappelijke slaapplaatsen. Wij opperen de hypothese dat onbedoelde informatieoverdracht, in plaats van actieve uitwisseling van informatie, domineert.

Om te illustreren hoe toetsbare voorspellingen kunnen worden gegenereerd stellen we een conceptueel model voor dat gebaseerd is op het gedrag van kanoeten op gemeenschappelijk hoogwatervluchtplaatsen (slaapplaatsen). In het bijzonder illustreren we hoe aankomsttijden op een slaapplaats onbedoeld informatie verschaffen over voedselinnamesnelheid, prooidichtheid, prooikwaliteit, maar ook over de fysiologie van soortgenoten (bijvoorbeeld de grootte van hun spiermaag). Onsuccesvolle dieren kunnen dergelijke informatie gebruiken om hun foerageersucces te verhogen. Bijvoorbeeld door op basis van deze informatie te kiezen wie ze de daaropvolgende foerageergelegenheid zullen volgen.

Informatie die via anderen verkregen is kan individuen helpen om nauwkeuriger en sneller de voedseldichtheid van een plek in te schatten. Hierdoor verspillen dieren minder tijd aan zoeken in onrendabele voedselpatches waardoor ze in staat zijn hun voedselinname te verhogen. Sociale informatie kan ook helpen om voedsel te vinden. Dit noemt men '*local enhancement*'. Het is wijd verspreid onder uiteenlopende diersoorten. *Local enhancement* is vooral gunstig wanneer prooien samenklonteren en de voedselpatches groot genoeg zijn om niet te kunnen worden gemonopoliseerd door individuen.

In **Hoofdstuk 6** laten we zien dat kanoeten door informatie van hun soortgenoten te gebruiken inderdaad hun voedsel sneller kunnen vinden. Het bleek dat de tijd die nodig was voor het lokaliseren van voedsel proportioneel afnam met groepsgrootte. Bovendien verschilden individuele kanoeten in hun zoekstrategie. Sommige kanoeten bleken structureel de zoekinspanningen van anderen uit te buiten.

INDIVIDUALITEIT

Het is aangetoond dat individuen van vele soorten *structureel* verschillen in gedrag waarbij het begrip 'dierenpersoonlijkheid' gehanteerd wordt. Dierenpersoonlijkheden impliceren dat de flexibiliteit in gedrag beperkt is. Dat wil zeggen dat wanneer de leefomgeving verandert, individuen zich niet altijd optimaal kunnen aanpassen. Als gevolg hiervan is het ontstaan en blijven bestaan van persoonlijkheden een evolutionair raadsel. De meeste adaptieve verklaringen voor verschillen in persoonlijkheid hebben betrekking op consistente verschillen in 'toestand'. Een individu zijn 'toestand' wordt gedefinieerd als een eigenschap die de kosten en baten van zijn gedrag beïnvloedt. Een recente hypothese is dat variatie in orgaangrootte verschillen in persoonlijkheid veroorzaakt en handhaaft. De gedachte is dat individuen met grote organen doortastend en exploratief gedrag moeten vertonen om het mogelijk te maken de grote hoeveelheden voedsel te verwerven die nodig zijn om deze energetisch dure organen te onderhouden.

In **Hoofdstuk 7** rapporteren we over de toetsing van deze hypothese. We tonen aan dat het exploratiegedrag van kanoeten in gevangenschap juist omgekeerd, dus negatief, gecorreleerd was aan hun orgaangroottes (hun spiermaag). In een vervolgexperiment, waarbij we kanoeten hun spiermaag door middel van een aangepast dieet konden verkleinen en vergroten, vonden we dat exploratiegedrag niet werd beïnvloed door de grootte van de spiermaag. Slechts enkele studies laten zien hoe persoonlijkheidskenmerken gemeten in het laboratorium overeenkomen met hun gedrag in het wild. Om dit te onderzoeken hebben we de kanoeten losgelaten met unieke combinaties van kleurringen om zo hun plaatstrouwheid te kunnen bepalen. Of deze vogels lokaal werden teruggezien gedurende de 19 maanden na hun vrijlating was negatief gecorreleerd met hun exploratiegedrag in de eerdere experimenten. Bovendien konden we aan de hand van een lange termijn veldinspanning laten zien dat de lokale terugziekans van vrij levende kanoeten (wat als het ware een 'omgekeerde' maat voor exploratiegedrag is) positief gecorreleerd was aan de grootte van hun spiermaag. Bovendien was er geen verschil in overleving tussen individuen die verschilden in de grootte van hun spiermaag. Onze resultaten laten zien dat we de hypothese om verschillen in persoonlijkheid te verklaren aan de hand van verschillen in orgaangroottes moeten herzien. Wij concluderen dat persoonlijkheid orgaangrootte stuurt, in plaats van andersom, en suggereren dat dit soort fysiologische verschillen aanpassingen zijn om de kosten van (exploratie)gedrag te compenseren.

Van individuele verschillen tussen kanoeten stappen we vervolgens over op individuele verschillen binnen een prooitype. Selectieve predatie kan leiden tot natuurlijke selectie binnen prooien. Bovendien kan predatie de competitie tussen overlevende individuen verlichten. Natuurlijke selectie en competitie kunnen belangrijke gevolgen hebben voor de populatiedynamica van prooien, maar zijn zelden gelijktijdig bestudeerd.

In **Hoofdstuk 8** hebben we aantallen, samenklontering, morfologie, en lichaamssamenstelling (schelpmassa en vleesmassa) van kokkels gemeten in drie gelijke percelen van 1 ha. Op twee van deze percelen hebben in de loop van onze korte studieperiode kanoeten gefoerageerd en het derde perceel zonder kanoetenpredatie diende als referentie. Door kanoetenpredatie waren de kokkeldichtheden aanzienlijk verminderd en hun ruimtelijke verspreiding gehomogeniseerd. Kanoeten selecteerden individuele kokkels waarmee ze hun energie-innamesnelheden konden maximaliseren. Dat wil zeggen: kleine kokkels met veel vleesmassa en weinig schelpmassa. Door deze selectieve predatie legden kanoeten een grote selectiedruk op aan kokkels om snel te groeien met dikke schelpen en weinig vleesmassa. De gemeten selectiedruk behoorde tot de hoogste waarden ooit gerapporteerd in de literatuur. De schelpmassa en vleesmassa van kokkels nam bovendien af met kokkeldichtheid (negatieve dichtheidsafhankelijkheid), waarschijnlijk door onderlinge competitie om de beschikbare middelen. Hierdoor kan predatie de competitie onder overlevende kokkels verlichten.

De effecten van dichtheidsafhankelijkheid worden over het algemeen bestudeerd binnen trofische niveaus. Dichtheidsafhankelijkheid kan echter ook een rol spelen tussen trofische niveaus. Tot nu toe dacht men dat de voedselinnamesnelheid van predatoren altijd toeneemt met een toename in prooidichtheid. In dit geval verwacht men dat een hoge prooidichtheid veel predatoren zal aantrekken.

In **Hoofdstuk 9** analyseren we dichtheidsafhankelijkheid van kokkels in relatie tot de energie-innamesnelheid van kanoeten. De dichtheid en vleesmassa van kokkels over 50 km^2 van het droogvallende wad wordt gerelateerd aan de verspreiding van kanoeten. Op de bemonstering van kokkels en kanoeten passen we de nieuwe methode toe, zoals gepresenteerd in respectievelijk Hoofdstuk 2 en Hoofdstuk 3. We tonen aan dat, als gevolg van negatieve dichtheidsafhankelijkheid in de vleesmassa van kokkels, kanoeten een afweging moeten maken tussen de kwantiteit en kwaliteit van prooien. Dat wil zeggen dat kokkels bij een hoge dichtheid makkelijker te vinden zijn, maar dat hun vleesmassa lager is. En omgekeerd hebben kokkels bij een lage dichtheid een hogere vleesmassa, maar zijn ze moeilijker te vinden. In tegenstelling tot de huidige gedachte maximaliseren kanoeten hun energie-innamesnelheid dus niet per se op de hoogste prooidichtheid. Met behulp van zogenaamde '*resource-selection*'-modellen konden we aantonen dat de gezenderde kanoeten inderdaad gebieden met de hoogste kokkeldichtheid meden. Ze hadden een voorkeur voor plekken waar ze, gegeven de grootte van hun spiermaag, hun energie-innamesnelheid konden maximaliseren. Dat wil zeggen dat ze kozen voor gebieden met intermediaire kokkeldichtheid.

Omdat negatieve dichtheidsafhankelijkheid een veelvoorkomend verschijnsel is onder (prooi)dieren, suggereren wij dat in tegenstelling tot de literatuur veel meer predatoren hun energie-innamesnelheid zullen maximaliseren op intermediaire prooidichtheden. Prooidichtheid alleen kan dus een slechte voorspeller zijn van de energie-innamesnelheden, draagkracht en de ruimtelijke verspreiding van predatoren.

HET ONTRAFELEN VAN DE KANOET

Het in dit proefschrift gepresenteerde onderzoek geeft ons een beter begrip van de ruimtelijke verspreiding van kanoeten. Daaraan liggen mechanismen ten grondslag die ook bij andere groepsdieren een rol kunnen spelen.

In **Hoofdstuk 10** bespreek ik een aantal van onze bevindingen in een bredere context. Zoals het belang van het meten van ruimtelijke autocorrelatie voor een beter begrip van de ruimtelijke verspreiding van dieren, de mogelijkheid van culturele evolutie op gemeenschappelijke slaapplaatsen, hoe 'cryptische interferentie' betrekking heeft op het modelleren van ruimtelijke verspreidingen, hoe consistente verschillen tussen individuen (dierenpersoonlijkheden) verschillen in ruimtelijke verspreiding bepalen, en de ecologische en evolutionaire achtergrond van dierenpersoonlijkheden. Tot slot stel ik een ecologisch-evolutionair kader voor om de ontwikkeling van verschillen in persoonlijkheid tussen kanoeten beter te kunnen begrijpen. Met dit kader hoop ik interessante richtlijnen te bieden voor toekomstige studies aan persoonlijkheden bij kanoeten, maar hopelijk ook voor onderzoek van dierenpersoonlijkheid in zijn algemeenheid.

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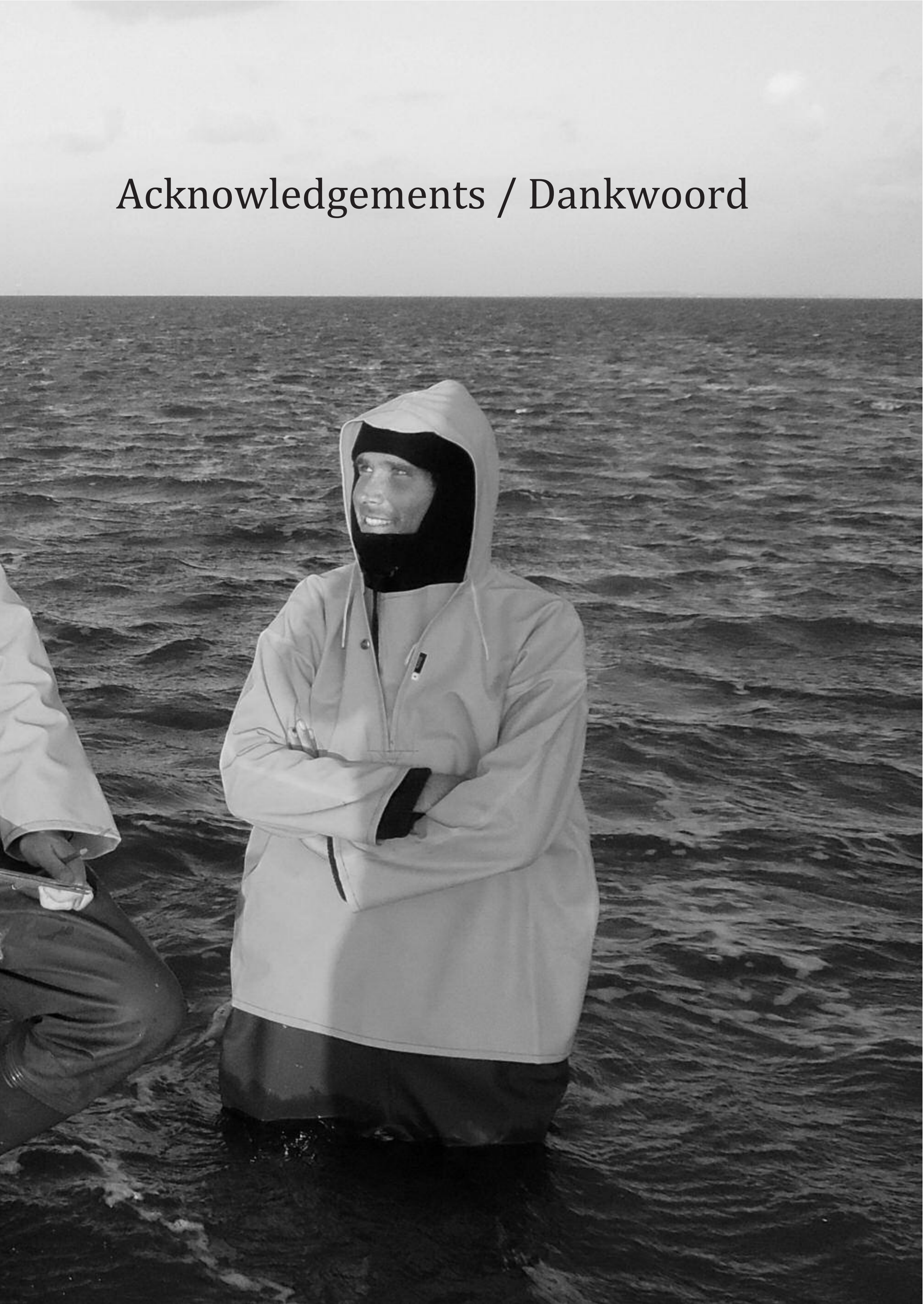

Met dit proefschrift sluit ik zes hele leuke en bijzondere jaren van mijn leven af. Van een stadsjongen ben ik een eilander geworden. Van een student doctor. Althans, bijna. Al het werk dat ik hier gepresenteerd heb is tot stand gekomen met de hulp van veel mensen. In de 'acknowledgements' van de verschillende hoofdstukken bedank ik veel van hen. Hier wil ik een aantal mensen in het bijzonder bedanken.

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I also would like to thank "the old" super KNIOZ football team: Craig, Pedro, Maarten, Cees, Matthijs. You guys are great! I treasure all of our memories together as well as our European Championship League. I, the student, am the last one living on Texel. All of you are now living spread out over Europe (and Houten). It is so special and valuable to me that wherever one of us lives, we fly in and play a football game against a local team. Who will we play after our game in Montpellier this fall? Our meetings are not only fun and games. Once, something scientific has come out of our get-togethers. Cees, thank you for suggesting the title of my thesis!

Another group of friends that has spread out over the world are the Popjes: Alex, Sara, Marieke, Vicencio, Nick, Anne, Peter, Femke, Jurgen, Nellie, Bart, Catarina, Jessica, Erik, Laurens, and Rosanne. Guys, thank you so much for being my friends. We have known each other for a long time now and even though we live far apart (like Texel-Amsterdam) we see each other on a regular basis. And whenever we see each other it is a lot of fun.

Dan mijn paranimfen. Het nu al magische duo Matthijs en Roeland. Dank jullie wel! Ik zie er naar uit om jullie in een pinguïnpak te zien. Roeland, ik had me geen betere kamergenoot kunnen wensen dan jij. We hebben vaak kleine dingetjes aan elkaar gevraagd en grotere dingen besproken. Gelukkig had ik uiteindelijk geen reden om jaloers te worden op een ander die met je zou gaan voetjevrijen. Ik zal het missen om ons kantoor binnen te lopen en je halfnaakt en bezweet te 'betrappen'. Naast het werk hebben we, samen met Maaike en Roos, een mooie vriendschap opgebouwd. We mochten een week op jullie Vuurtoreneiland passen wat een prachtige ervaring was. Volgens mij kijkt Jasmijn nooit meer hetzelfde naar vuurtorens. Jullie zijn hele speciale en warme mensen. We zullen zeker contact houden en jullie zijn altijd welkom waar we dan ook wonen.

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Groningen. Wat een bijzonder moment. Je bent een fantastische gozer! Tamar, jij ook. Je bent geweldig. Jullie zijn heel warm liefdevol, zorgzaam en altijd in voor een geintje. We kunnen altijd alles tegen elkaar zeggen en onze harten luchten over incidenten op het werk en vraagstukken in de wetenschap. Ik realiseer me vaak dat het bijzonder is wat wij met onze gezinnetjes hebben. Samen hebben we zulke mooie dingen meegemaakt. Waaronder een geweldige vakantie naar Mallorca, een sprookjesachtig ITGWO op Vlieland, een ontroerend concert van Pearl Jam en tot diep in de nacht smallville spelen. Onze kinderen zijn samen op Texel opgegroeid. Wat een goed begin van hun leven. Dat neemt niemand ze meer af. Ook al wonen jullie nu in Frankrijk, jullie houden allemaal een speciale plek in onze harten. Veerle et Ravi, comment ça va? Hebben jullie al veel Franse vriendjes? Veerle, bevalt het paardrijden? Ravi, caca! Wij missen jullie. Gelukkig zien we elkaar snel weer.

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