

Red knot habits

*an optimal foraging perspective on
intertidal life at Banc d'Arguin*



Thomas Oudman

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An optimal foraging perspective on intertidal life
at Banc d'Arguin, Mauritania



Royal Netherlands Institute for Sea Research

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Red knot habits

An optimal foraging perspective on intertidal life
 at Banc d'Arguin, Mauritania

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Chapter 1

General Introduction

Thomas Oudman

"I will not attempt any definition of instinct. A little dose [...] of judgement or reason often comes into play, even in animals very low in the scale of nature."

Charles Darwin in *On the Origin of Species* (1859)

In recent history many animal species, if not most, have been facing rapid changes in their environment by habitat destruction, exploitation of their resources, climate change, or a combination (Tilman *et al.* 2001; Butchart *et al.* 2010; Leadley *et al.* 2010). Currently, human-induced environmental change proceeds at unprecedented rates (e.g. IPCC 2014). To develop adequate measures that help existing ecosystems to prosper, a deeper understanding of how populations react to changing circumstances is needed more than ever.

The connection between populations and their environment is shaped by evolution through natural selection (Darwin 1859). The phenotype adjusts to environmental change by selection of adaptive variation over generations, but also by plastic (West-Eberhard 2003) and flexible (Piersma & van Gils 2011) development of the individual phenotype. This can be any phenotypic trait, but the most directly observable interaction with the environment, in many organisms, is through behaviour. Behavioural choices influence whether the individual thrives or dies, which in turn is a basic ingredient of natural selection. Many different approaches are being used to study the relationship between populations and the environment, all uncovering different aspects of its stunning complexity. This thesis contains five studies from a behavioural perspective, which I hope will contribute as well, if only a bit.

Using behaviour to study ecological interactions: the optimality approach

Conventional wisdom has it that, contrary to humans who make conscious decisions, other animals simply act by ‘instinct’. It implies that animal habits are the expression of a genetically orchestrated behaviour, whereas humans at least to some extent have the ability to anticipate and to choose rationally. However, there is no biological evidence for any such distinction. As implied in the above quote by Darwin, it should always be considered that behaviour involves decision making. Animals must make decisions whenever alternatives appear (McFarland 1977). When and where to breed, where and when to forage, what food to search for, all must be decided. What sources are used to inform these decisions, and how they are judged, has been shaped by evolution. It cannot be expected that animals measure all available information, that they necessarily measure it correctly, or even that the best decision is always made when all information is measured. But it is to be expected that animal senses have evolved to gather available information that is necessary to choose the fitness-maximizing option (Schmidt, Dall & van Gils 2010). That implies that fitness questions can be investigated by asking which information influences animal decisions, and how this information is perceived. This is the basis of ‘optimality models’ (reviewed in McNamara, Houston & Collins 2001). Optimality models provide a way to generate quantitative hypotheses on how animals will respond to changes in environmental variables; behaviourally, developmentally and evolutionarily.

In search of a population with an easy fitness currency

A considerable difficulty in the application of optimality models has been the search for a ‘currency’ in which fitness consequences should be measured, on the basis of which to compare alternative options (Stephens & Krebs 1986). Animals must consume enough of the right nutrients, reproduce, avoid to be consumed or to fall ill, and provide the best

possible circumstances for their offspring to do the same. All these factors may influence what is the best option, but not all are always relevant (Owen-Smith 1993). For example, the life cycle of migratory birds includes the distinction between the breeding season and the non-breeding season. Especially in species that do not provide parental care outside the breeding season, the main determinant of fitness then is to survive, and to be ready for the next breeding season. The important decisions then primarily concern habitat selection and diet selection. Although a crude simplification, the animal's habitat selection may be understood by assuming that the animal needs to consume a certain daily amount of energy, and that it will choose its foraging location such that it is able to reach these requirements, at the least possible risk of mortality. At this location, its general diet selection may be understood by assuming that it chooses to forage on that mix of resource types that offer the highest intake rate of the necessary nutrients, thereby minimizing the time needed for foraging. We have now entered the realm of 'optimal foraging theory' (MacArthur & Pianka 1966; Stephens & Krebs 1986; Piersma & van Gils 2011).

RED KNOTS

This thesis is concerned with the foraging behaviour of red knots *Calidris canutus* during the winter season. Red knots are medium sized migratory shorebirds that breed in the High Arctic and spend the winter in temperate and tropical regions (Fig. 1.1), where they fully rely on intertidal mudflats and forage mainly on small mollusc prey during the low tide (Piersma & Davidson 1992). They ingest their prey whole, and digest them in their specialized muscular stomach, the gizzard (Piersma, Koolhaas & Dekinga 1993). In the breeding area they feed mostly on insects, but regularly also include plant material in their diet (leaves and berries; J.A. van Gils and J. Wilson, personal communication). Also during staging, red knots occasionally forage on plant material (e.g. in Gdańsk Bay, J.A. van Gils, personal communication). At Banc d'Arguin, red knots feed on seagrass rhizomes at a rate that has been increasing in recent years (van Gils *et al.* 2016), acting as a secondary resource when mollusc availability is low (van Gils *et al.* in prep). Six subspecies are distinguished worldwide (Buehler, Baker & Piersma 2006), all threatened in their existence by climate change in the breeding areas and destruction of the intertidal areas that they rely on during migration and in the winter (Piersma 2007; Ma *et al.* 2014; Piersma *et al.* 2016; van Gils *et al.* 2016).

Wintering red knots are particularly suited for the study of behaviour under natural conditions with the use of optimal foraging theory, for several reasons. Firstly, their wintering range is confined to a well-defined, accessible and readily observable habitat: intertidal mudflats (Piersma 2012). The mollusc prey that they forage on are largely sessile, and can be sampled and quantified accurately through time and space using specialized sampling methods (Beukema 1976; Piersma, de Goeij & Tulp 1993; Bijleveld *et al.* 2012). Secondly, red knots comprise one of the few vertebrate species that are still being found in their natural habitat, with much of the food web complexity that it had in pre-industrial times, even in Western Europe. This offers the possibility to study the intricate

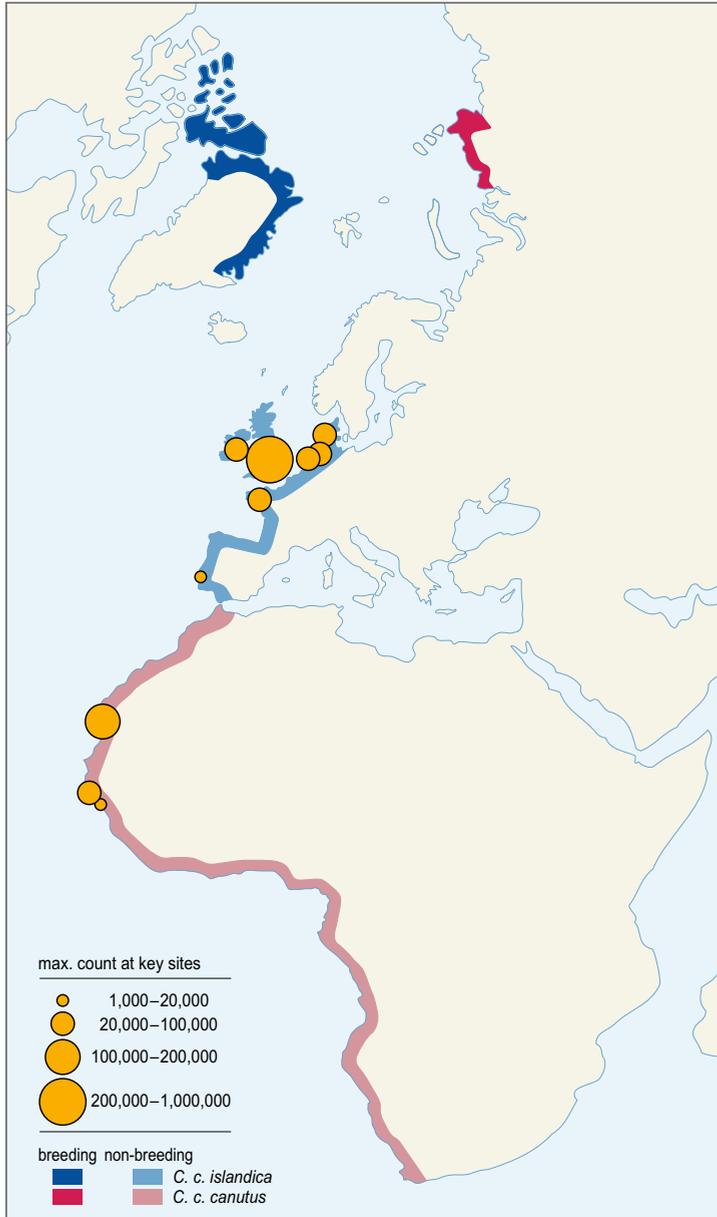


Figure 1.1 Winter distribution of red knots *C. c. islandica* and *C. c. canutus*. The red knot subspecies *islandica* (in blue) breeds in N Greenland and NE Canada, and winters along the W European coast, mainly the Wadden Sea. Subspecies *canutus* (in red) breeds in N Siberia, and winters on the W African coast, and mainly Banc d'Arguin. *Canutus* red knots stage in the Wadden Sea during migration, where they then co-occur with the *islandica* red knots. Nonetheless, individuals virtually never switch migration scheme. Shown are the estimated red knot numbers in the period 2010–2014 (van Roomen *et al.* 2015). Breeding and non-breeding areas reproduced from Davidson & Piersma (2009) and Bijleveld (2015).

behavioural responses that red knots have evolved in interaction with the ecologically highly complex environment that they inhabit. Thirdly, red knots show not only highly variable habits across the world and even within populations (van Gils *et al.* 2005a; van Gils *et al.* 2006; Piersma 2007), but also a highly flexible physiology that closely interacts with behavioural variability (Dekinga *et al.* 2001; Piersma 2002). This enables the study of individual variation in (non-)behavioural traits, and the interactions between behavioural decisions and the environment.

Last, but certainly not least, red knots are a superb study species because so many studies have already been performed, and much of their basic ecology, the important physiological parameters and behavioural details have been uncovered. Worldwide logistics are currently in place that allow an active international research community to study their wintering and staging areas worldwide, especially in the subspecies *C.c. islandica*, *C.c. canutus* and *C.c. rufa* (Piersma 2007).

Red knots wintering in the Wadden Sea

Red knots wintering in the Wadden Sea belong to the subspecies *C.c. islandica*, maintaining a migratory connection via Iceland with their breeding grounds in N Greenland and NE Canada (Fig. 1.1; Davidson & Wilson 1992). This population has received by far the most attention of all. No fewer than 12 PhD theses involving red knot foraging behaviour have been defended at the University of Groningen (all listed in Bijleveld 2015, except the newest; de Fouw 2016). The current thesis draws heavily on them all, and particularly on the first, the third and the eleventh (Piersma 1994; van Gils 2004; Bijleveld 2015). Piersma (1994) provided the ecological foundation, describing general basic foraging ecology and diet of the red knot, the significance of its migration, energetic bottlenecks and physiology, with particular attention to the gizzard and its relation to the diet. Van Gils (2004) provided a solid basis for the use of optimal foraging theory and diet choice experiments to clarify the functional relationship between the observed variability in gizzard mass and the diet and habitat selection of red knots in the Wadden Sea. Bijleveld (2015) introduced the study of consistent individual variation in physiology and habitat- and diet selection, focussing on personality differences as a cause rather than an effect of physiomorphic differences. In addition, it provided the ins and outs of radio tracking red knots, with a spatially explicit resource sampling scheme underlying it.

Red knots wintering at Banc d'Arguin

The work in this thesis focusses on the red knot subspecies *C. c. canutus*, wintering at the other major wintering site along the East Atlantic flyway, the Banc d'Arguin in Mauritania (Fig. 1.1). In a practical sense, this work comprises not much more than previously successful research techniques in the Wadden Sea, applied to the red knots at Banc d'Arguin. These red knots breed in Siberia and meet the *islandica* subspecies in autumn during stopover in the Eastern Dutch and German Wadden Sea and the Baltic coast, before continuing to the wintering grounds of W Africa, and mainly the Banc d'Arguin (Dick, Piersma & Prokosch 1987). The total population size there was estimated reliably for the first time in 1980 and estimated at 350,000 individuals (Altenburg *et al.* 1982). Since then,

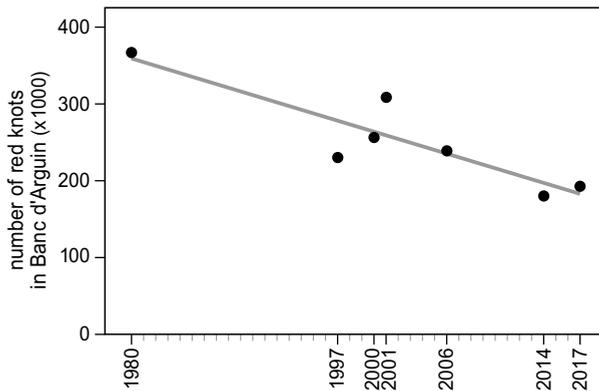


Figure 1.2 The number of red knots counted in all complete winter counts of Banc d'Arguin. Grey line shows the linear regression ($F_{1,5} = 20.3$, $R^2 = 0.76$, $p = 0.004$). Counts were performed in January or early February. Data by courtesy of Parc National du Banc d'Arguin, SOVON, Birdlife International and Wetlands International.

the population has been showing a significant decline that seems to be continuing to this day (Fig. 1.2), with the current best estimate being 200,000 (van Roomen *et al.* 2015, Oudman *et al.* 2017). The causes are probably multiple. A decline in resource availability in the Wadden Sea, the main important stopover area during migration, may have contributed in the recent past (van Gils *et al.* 2009; Kraan *et al.* 2010). Reasons may also be found in the Arctic. There, rising spring temperatures are causing a mismatch between egg-hatching and the peak in insect abundance potentially causing high mortality in juveniles during migration and on the wintering grounds, where bivalve availability to juveniles is lower, presumably due to shorter bills (van Gils *et al.* 2016). Changes in red knot habitat also take place at Banc d'Arguin, which can be explained by cyclical ecosystem dynamics, but do point out a high sensibility to ecosystem disturbance (de Fouw *et al.* 2016). Disturbance is indeed taking place, e.g. by the recent increase in the harvesting of several ray species (mainly Lusitanian cownose ray *Rhinoptera marginata* and blackchin guitarfish *Rhinobatos cemiculus*; Sidi Yahya Cheikhna Lemrabott, personal communication), whose population sizes have been greatly reduced by intense harvesting in the 1980s and 1990s.

Hence, *canutus* red knots face environmental change in all the ecosystems that they connect. This provides an important practical purpose for investigations on their ecology. It also provides a highly appealing ecological study system: what are the complex behavioural mechanisms that have allowed them to persist until now?

STUDY OUTLINE

The studies in this thesis are specifically aimed at a further understanding of the foraging decisions of *canutus* red knots wintering at Banc d'Arguin, taking the foraging decisions of *islandica* red knots in the Wadden Sea as a reference. In **Chapter 2** we set out to deter-

mine the factors that influence red knot diet composition, focusing on the two main prey types of red knots in Banc d'Arguin, *Loripes lucinalis* and *Dosinia isocardia*. Based on knowledge from the Wadden Sea red knots, we expected that Banc d'Arguin red knots would ignore any other food type than *Loripes*. This prediction highly contrasted the actual diet, a mix of *Loripes* and other mollusc species. We hypothesized that this discrepancy is a consequence of the peculiar metabolism of *Loripes*, involving sulfide-oxidizing bacteria and causing a toxic effect due to the ingestion of sulphur compounds. This hypothesis was tested in an experiment with captive red knots in Mauritania. In **Chapter 3** we extend the diet choice predictions of Banc d'Arguin red knots to the field, by implementing the toxin constraint into the digestive rate model, which was previously designed to test diet choice of Wadden Sea red knots (Hirakawa 1995; van Gils *et al.* 2005b). We tested whether this addition is necessary to explain winter survival of red knots, based on annually measured winter densities of *Loripes* and *Dosinia*. In **Chapter 4** we perform another diet experiment to test another expected consequence of the toxin constraint, which is that a larger gizzard mass should increase the maximum intake rate of non-toxic *Dosinia*, but not of toxic *Loripes*. This has the implication that individuals with larger gizzards are expected to prefer a lower proportion of *Loripes* in the diet. In **Chapter 5**, we put the consequently expected causal relation between individual gizzard mass and diet preferences to the test in the wild, using an automated radio tracking system to record patch residence times (MacCurdy, Gabrielson & Cortopassi 2012; Piersma *et al.* 2014; Bijleveld *et al.* 2016). In **Chapter 6** we use the obtained residence patch locations to compare space use of tagged red knots to similarly tagged conspecific counterparts in the Dutch Wadden Sea (Bijleveld *et al.* 2016). Based on two extensive benthos sampling schemes, we tested whether red knots adjusted the degrees of aggregation and site fidelity to differences in the resource landscape. In **Chapter 7**, I place the implications of these studies in a broader context. I emphasize the potential role that the observed behavioural decision processes may have on population dynamics and the development of the individual phenotype. This is of immediate relevance for an understanding of the evolutionary forces that shape the red knot and the intricate relationship with its environments; environments that it shares with us.





Chapter 2

Digestive capacity and toxicity cause mixed diets in red knots that maximize energy intake rate

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Theunis Piersma
Jan A. van Gils

ABSTRACT

Among energy-maximizing animals, preferences for different prey can be explained by ranking them by their energetic content. However, diet choice also depends on characteristics of the predator such as the need to ingest necessary nutrients, and the constraints imposed by digestion and toxins in food. In combination, these factors can lead to mixed diets in which the energetically most profitable food is not eaten exclusively even when it is abundant. We studied diet choice in red knots (*Calidris canutus canutus*) feeding on molluscs at a West African wintering site. At this site, the birds fed primarily on two species of bivalves, a thick-shelled one (*Dosinia isocardia*) that imposed a digestive constraint, and a thin-shelled one (*Loripes lucinalis*) that imposed a toxin constraint. The latter species is toxic due to its symbiotic association with sulphide-oxidizing bacteria. We estimated experimentally the parameters of a linear programming model that includes both digestive and toxin constraints, leading to the prediction that red knots should eat a mixture of both mollusc species to maximize energy intake. The model correctly predicted the preferences of the captive birds, which depended on the digestive quality and toxicity of their previous diet. At our study site, energy maximizing red knots appear to select a mixed diet as a result of the simultaneous effects of digestive and toxin constraints.

INTRODUCTION

Understanding the mechanisms that govern diet preference is a fundamentally important issue in ecology, as these mechanisms will determine habitat selection, predator-prey interactions, and overall population dynamics (e.g. Holt and Kotler 1987; Duffy 2003; Finke and Denno 2004; Piersma 2012). In ecology, diet selection questions are often interpreted in the light of optimal foraging theory (MacArthur and Pianka 1966; Stephens and Krebs 1986). Energy-maximizing animals must ingest diets that maximize energy intake without stepping out of the bounds imposed by nutritional, digestive, and toxin constraints (Westoby 1974; Pulliam 1975; Jeschke *et al.* 2002; Piersma and van Gils 2011). We used a linear programming model (Westoby 1974; Belovsky 1978) in which energy intake rate is maximized but digestive and toxicity constraints are also recognized to explain the diet selection of red knots (*Calidris canutus*). We parameterized and tested the model on the subspecies *C. c. canutus* (Buehler and Piersma 2008) in the birds' main wintering area, Banc d'Arguin in Mauritania, West Africa (Leyrer *et al.* 2006).

Red knots are shorebirds that feed on molluscs and commonly face a digestive constraint (van Gils *et al.* 2003a; Piersma 2007; Buehler and Piersma 2008). They are known to select thin-shelled prey, thereby minimizing ballast intake and, thus, processing time (van Gils *et al.* 2003a; van Gils *et al.* 2005b; Quaintenne *et al.* 2010). In Banc d'Arguin, red knots forage on the extensive intertidal seagrass beds, where the bivalve *Loripes lucinialis* (Lucinidae, Bivalvia) is their most abundant prey, followed by the bivalve *Dosinia isocardia* (Veneridae, Bivalvia) (van der Geest *et al.* 2011; van Gils *et al.* 2012; Ahmedou Salem *et al.* 2014). Together, *Loripes* and *Dosinia* constitute most of the potential prey available (Honkoop *et al.* 2008; Chapter 4). If their diet of red knots were indeed governed by the ballast-processing constraint, then the birds should be eating the thin-shelled *Loripes* and ignoring the thicker-shelled *Dosinia*. They are not. Field studies show that a large part of the diet consists of prey other than *Loripes*, while densities are high enough to provide a pure *Loripes* diet (Chapter 4; van Gils *et al.* 2012; Onrust *et al.* 2013). Thus, Banc d'Arguin red knots seem to actively select a mixed diet of *Loripes* and other prey species, in contrast to what would be predicted by the customary foraging models.

Mixed diets can result from different nutritional requirements (Westoby 1974; Pulliam 1975; Simpson *et al.* 2004), but the flesh of different mollusc species are nutritionally similar (e.g. Zwarts and Wanink 1993). Alternative explanations for mixed diet selection include the need to regularly sample the quality of different prey types and the inability of a forager to distinguish between prey types (e.g., McNamara and Houston 1987). These arguments cannot, however, explain the consistently low fraction of *Loripes* in the red knots' diet when availability is high.

Here we study the hypothesis that a toxin in *Loripes* causes red knots to prefer a mixed diet. Captive red knots on a *Loripes* diet developed diarrhea within an hour after ingestion (T. Oudman, personal observation). Two captive red knots maintained on a *Loripes* diet for two weeks showed reduced feeding rates, low body mass, improper preening, ruffled feathers, drooping wings, and docile behaviour (M. V. Ahmedou Salem and J. A. van Gils, unpublished data). This toxicity is most likely the result of the peculiar metabolic system

of *Loripes*, which is largely dependent on the nutrients synthesized by symbiotic sulphide-oxidizing bacteria (van der Geest *et al.*, 2014). A consequence of this symbiosis is the presence of sulfur-rich granules in the gills (Cary *et al.* 1989; Anderson 1995); in fact, van der Heide *et al.* (2012) found a relative sulfur content of 2–4% (of total body dry flesh mass). Although monogastric animals are less susceptible to sulfur toxicity than ruminants (microbes in the rumen convert sulfur to toxic sulfide), high sulfur doses are toxic across species, resulting in diarrhea, dehydration and lower feeding rates (Hall 2007). However, the precise physiological mechanism that causes *Loripes* to be toxic to red knots remains to be studied.

Belovsky and Schmitz (1994) argue that mixed diets can be optimal for herbivores when the intake rates on different food types are limited by different constraints, including feeding time (the sum of searching and handling times), digestion time, and toxicity (see Ritchie 1988 for an empirical example). Toxicity can play a decisive role in diet selection by herbivores (Johnson *et al.* 1993; Schmidt *et al.* 1998; Marsh *et al.* 2006) as well as other animals (Toft and Wise 1999; Skelhorn and Rowe 2007; Barnett *et al.* 2012). Hence, a combination of digestive and toxicity constraints might explain mixed diet selection in red knots.

A linear model with a digestive and a toxicity constraint

We assume that a red knot has unlimited access to *Dosinia* and *Loripes* of fixed sizes, with negligible search times. Furthermore, we assume that all *Loripes* contain a fixed amount of toxin and *Dosinia* contain no toxin. Following Belovsky and Schmitz (1994), a digestive constraint (c , maximum processing rate of ballast dry mass DM_{shell} in mg s^{-1}) is defined as

$$r_d k_d + r_l k_l \leq c, \quad (2.1)$$

where r_d and r_l are the intake rates (number of prey s^{-1}) on *Dosinia* and *Loripes* respectively, k_d and k_l are the ballast masses of their respective individual prey in milligrams. Similarly, the toxin constraint (q , maximum intake of toxin s^{-1}) is defined as

$$r_d s_d + r_l s_l \leq q \quad (2.2a)$$

We scale the unit of toxin to the toxin content of *Loripes*, so the toxin content of *Loripes*, s_l , is 1 (unitless). Since *Dosinia* is not toxic, s_d is 0, and the toxin constraint simplifies to

$$r_l \leq q. \quad (2.2b)$$

Defining e_d and e_l as the ash-free dry flesh masses $AFDM_{\text{flesh}}$ (scaling linearly with caloric content, see van Gils *et al.* 2005b) per individual *Dosinia* and *Loripes*, respectively, then total energy intake rate (Y , $\text{mg AFDM}_{\text{flesh}} \text{s}^{-1}$) is defined by

$$Y = r_d e_d + r_l e_l. \quad (2.3)$$

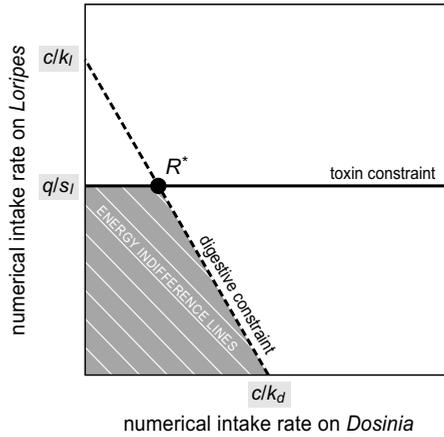


Figure 2.1 Optimal diet (R^*) under a digestive constraint (c , dashed line) and a toxin constraint (q , solid line). The gray area represents all possible combinations of intake rates on *Dosinia* (d) and *Loripes* (l), and the white lines are energy indifference lines that connect points of equal energy intake rate, with energy intake increasing towards the upper right corner of the diagram. Value k represents the ballast mass of individual prey.

The constraints limit the combinations of r_d and r_l that are possible for the forager (constraint lines in Fig. 2.1). The optimal diet is thus the combination of intake rates that maximizes Y while obeying both constraints, denoted as $R^* = (r_d^*, r_l^*)$.

Partial preferences are predicted when $r_d^* > 0$ and $r_l^* > 0$. Figure 2.1 shows that this is always and only true when the constraint lines cross and the slope of the energy indifference lines (lines that connect points of equal energy intake rate) is intermediate to the slopes of both constraint lines. In practice, this means that the prey type that is the higher quality prey type with respect to one constraint should be the poorer quality prey type with respect to the other constraint. If these conditions are satisfied, then R^* is calculated by equating both constraints (eqq. 2.1, 2.2b):

$$R^* = (r_d^*, r_l^*) = \left(\frac{c - qk_l}{k_d}, q \right). \quad (2.4)$$

Model parameterization and testing

When using linear programming models, each constraint line must be estimated with data from a setting where the constraint is actually effective (Hobbs 1990; Owen-Smith 1993, 1996). To this end, the constraint lines were each determined independently in a separate experiment before being tested in another experiment whether they could explain the observed diet selection by red knots. In this first experiment, we separately measured maximum long-term intake rates of *Loripes* and *Dosinia*, the latter being a suspension-feeding bivalve that does not have a sulfur-based metabolism. Thus, the long-term maximum intake rate on *Dosinia* gives us an estimate of c , the digestive constraint (van Gils *et al.* 2005b). If the *Loripes* intake rate is limited by a toxin constraint, then the

maximum ballast mass intake rate should be lower than c . The measured maximum intake rate on *Loripes* then provides an estimate of the toxin constraint, q . Other necessary parameters (k_d , k_l , e_d and e_l) were directly measured on individual *Loripes* and *Dosinia*.

In a second experiment, we analysed diet preferences of captive red knots with different dietary histories. For a period of 3 h, *ad libitum* amounts of either *Loripes* or *Dosinia* were offered to single birds, and directly afterward both prey types were offered simultaneously to give a choice between the two. Results from this experiment are compared with the predictions of the linear programming model. To evaluate the necessity of accounting for *Loripes* toxicity when predicting diet choice by red knots, models with and without a toxin constraint are considered.

The effect of water availability on the proposed constraints

High temperatures and a lack of freshwater in Banc d'Arguin impose physiological stress on red knots with respect to water balance and salt excretion (Klaassen and Ens 1990; Verboven and Piersma 1995; Gutiérrez *et al.* 2011b). Given the diarrhetic effect of *Loripes*, its toxicity may (partially) lie in its negative effect on water balance. In that case, the maximum ingestion rate of red knots on *Loripes* should be dependent on water salinity and availability. We tested for this by including three different water treatments in the first experiment, offering the birds either freshwater, seawater or no supplementary water at all.

ANIMALS, MATERIALS AND METHODS

The birds

Experiments were carried out in January/February 2011 at the Iwik research station of Parc National du Banc d'Arguin, Mauritania, West-Africa (lat. 19°53'N, long. 16°17'W). Six red knots were caught locally with mist nets, individually colour-ringed for identification (for procedures see Leyrer *et al.* 2006, 2013) and placed indoors in a 1.5 × 1.0 × 0.5 m holding pen under temperatures varying between 18° and 24°C. Three birds were juvenile (i.e. in their 2nd calendar-year, half a year old), and the other three were in their third calendar-year or older.

For the experiments the holding pen was divided into six transparent compartments of 0.5 × 0.5 m to isolate each bird. *ad libitum* access to freshwater was given between experimental trials. Outside of the experiments, staple food consisting of live molluscs (mainly *Loripes lucinalis* and *Dosinia isocardia* but also, e.g., *Senilia senilis*, *Bittium reticulatum*, and *Abra tenuis*) was offered throughout the day. At night, the birds were offered the flesh of large *S. senilis* and trout pellets (Trouvit, Produits Trouw, Vervins, France).

Prey were collected daily in the field by sieving mud over a 2-mm sieve and were kept fresh by storing them in a refrigerator at 7°C the day before use. Birds were offered only live prey rinsed with seawater. To ensure a rate-maximizing feeding strategy during the foraging trials, the total amount of food was adjusted to maintain a constant low, but not unnatural, body mass (90 – 110 g; Leyrer *et al.* 2012). All birds were weighed every morning to the nearest gram, and their health status was monitored throughout each day.

Parameterization of prey characteristics

We separated the flesh and shell material of 200 *Dosinia* and *Loripes* individuals of variable lengths. By measuring shell length (to the nearest 0.1 mm) and separately drying (3 days at 60°C), weighing (to the nearest 0.1 mg), incinerating (5 hrs at 560°C), and weighing again, we determined ballast dry masses, DM_{shell} , and ash-free dry flesh masses, $AFDM_{\text{flesh}}$. Based on data presented by Zwarts and Wanink (1993) it is reasonable to assume that metabolizable energy density in the flesh is similar in different prey species and sizes (estimated as 15.95 kJ/g in van Gils *et al.* 2005b). We therefore used $AFDM_{\text{flesh}}$ as our measure of energy content. The relationships between lengths and masses were used to estimate average DM_{shell} and $AFDM_{\text{flesh}}$ of 8–9 mm *Dosinia* (k_d and e_d , respectively, in eqq. 2.1-2.4) and 8–9 mm *Loripes* (k_l and e_l , respectively).

Experiment 1: parameterization of digestive and toxin constraints

Individual birds that had been withheld food for 6 h were offered *Dosinia* (4–14 mm) or *Loripes* (4–11 mm) in separate trials *ad libitum* for 6 h. All prey items were counted before and after each trial to determine the number of prey items consumed. The lengths of subsamples were measured before and after each trial to infer size distributions. Both measures were combined to estimate total DM_{shell} intake in each trial and divided by the total time of the trial to arrive at long-term DM_{shell} intake rates.

The digestive constraint c equals the best estimate of the long-term DM_{shell} intake rate on *Dosinia*. The long-term DM_{shell} intake rate on *Loripes* is expected to be lower due to its toxicity. Then, because toxicity is measured in units of an individual *Loripes* of 8–9 mm, toxin constraint q equals the estimated long-term DM_{shell} intake rate on *Loripes*, divided by k_l .

To get the birds accustomed to captivity a habituation period of 6 days preceded the experiment. In each trial, either *Loripes* or *Dosinia* was offered, combined with one of three drinking water regimes; *ad libitum* freshwater, *ad libitum* seawater (salinity ≈ 40 ‰, Wolff and Smit 1990), or no water. First, all birds performed each combination of diet and water treatment once, resulting in 36 trials (6 birds \times 2 prey types \times 3 water treatments). Additionally, 10 randomly chosen trials were repeated (not all trials were repeated due to time limitations). Two trials where all prey items were eaten were removed from the analysis because this would give an underestimation of maximum intake rate. These trials were repeated on another day with more food. This resulted in a total of 46 trials for intake rate analysis (*Loripes*: 8 with freshwater, 7 with seawater and 8 without water; *Dosinia*: 8 with freshwater, 8 with seawater and 7 without water) performed on 12 different experimental days, with a day of rest between each experimental day.

Water intake was measured in each trial by subtracting evaporated water in a reference water bowl (either freshwater or seawater) from water that disappeared from the water bowl in the trial. Seven trials involving 3 different birds were removed from the analysis because birds were observed bathing in the water bowl, resulting in 24 trials for water consumption analysis (*Loripes*: 5 with freshwater and 6 with seawater; *Dosinia*: 7 with freshwater and 6 with seawater).

Experiment 2: state-dependant preference test

Either *Loripes* (4–11 mm) or *Dosinia* (4–14 mm) were offered *ad libitum* to a single bird for 3 h, preceded by 6 h of food deprivation. Directly afterwards, a preference test was carried out in which the bird was simultaneously offered 40 *Loripes* and 40 *Dosinia* individuals, all of the same length (8–9 mm) and arranged in separate piles on a white plastic tray (0.25 × 0.30 m, with three high edges of 0.2 and one low edge of 0.05 m). The bird had to step over the low edge to reach the prey items, each an equal distance away. The species of each ingested prey item was recorded. The tray was removed after 20 ingestions or after 1 h (one case, 13 ingestions). Each of the six birds was exposed to both treatments twice, yielding a total of 24 trials carried out over 4 days (in between the last four experimental days of experiment 1).

Statistical analyses

Generalized linear mixed model selection was performed in R using the function `lmer` from library `lme4` in R, version 3.0.1 (R Development Core Team 2013) to test the effect of treatments in both experiments. Bird ID and trial number (experiment 2 only) were included as random variables. For both experiments, a set of candidate models, including all combinations of explanatory variables and their second-order interactions, was ranked according to the likelihood of each model. Rank was determined by calculating the Akaike weight of the model, using second-order corrected Akaike Information Criterion (AICc) for small sample sizes (Burnham and Anderson 2002). We tested for the potential effect of treatment on the previous day by adding previous day treatment as a fixed factor and comparing the calculated AICc values.

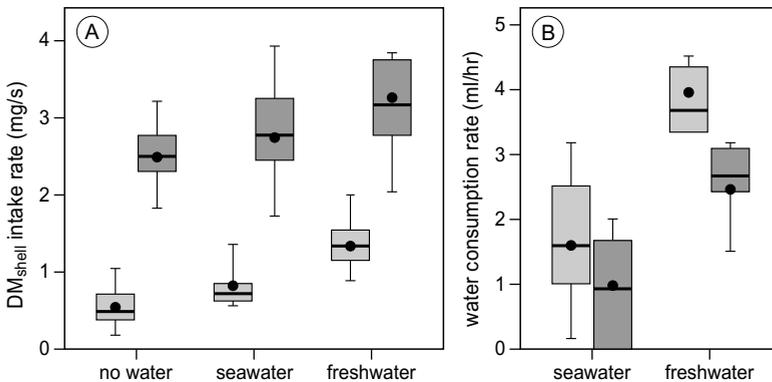


Figure 2.2 Long-term intake rate (A) and water consumption rate (B) of red knots feeding on *Loripes* (lightly shaded boxes) or *Dosinia* (darkly shaded boxes). Whiskers indicate the most extreme data points. The birds had *ad libitum* access to either freshwater or seawater or were provided no water at all. Circles reflect the values as estimated by the best statistical models based on these data (model 1a.4 in A, model 1b.4 in B, see Table 2.1). Ballast dry masses (DM_{shell}) intake rates on seawater are used to parameterize the diet selection model.

RESULTS

Verifying the presence of a toxin constraint

In red knots, maximum DM_{shell} intake rate depends on gizzard size (van Gils *et al.* 2003a). However, measured DM_{shell} intake rates on diets of either *Dosinia* or *Loripes* were found to be distinctively different from each other (Fig. 2.2A, model 1a.4 in Table 2.1; data deposited in the Dryad Digital Repository: <http://10.5061/dryad.5fp4g> [Oudman *et al.* 2014]). The *Dosinia* DM_{shell} intake rate resembled the expected intake rate of a digestively constrained red knot with a gizzard of 7.7 g (see van Gils *et al.* 2003a for calculations), which is 1.4 g lower than the mean gizzard mass found in free-living birds in the same period (A. Dekinga, unpublished data). The DM_{shell} intake rate of *Loripes* was only 30% of the average DM_{shell} intake rate on *Dosinia*, which shows that a factor other than shell-mass processing limited the intake rate of *Loripes*. Without exception, birds suffered from

Table 2.1 Model selection to find the best fits to the data obtained in each experiment, by comparing weighted corrected Akaike Information Criterion (AICc) values.

Model ^a	Fixed effects ^b	K ^c	$\Delta AICc$	AICc Weight	Cumulative Weight	LL ^d
Experiment 1: Long-term DM_{shell} intake rate:						
1a.4	Diet + water	6	0	0.93	0.93	-28.16
1a.5	Diet + water + diet : water	8	5.14	0.07	1	-27.86
1a.2	Diet	4	11.78	0	1	-36.64
1a.1	1	3	76.53	0	1	-70.21
1a.3	Water	5	77.37	0	1	-68.17
Experiment 1: Long-term water consumption:						
1b.5	Diet + water + diet : water	5	0	0.70	0.70	-67.54
1b.4	Diet + water	4	2.11	0.24	0.94	-70.09
1b.3	Water	3	5.04	0.06	1	-72.92
1b.2	Diet	3	53.68	0	1	-97.24
1b.1	1	2	55.20	0	1	-99.26
Experiment 2: Prey preference:						
2.5	Number + diet + number : diet	6	0	1	1	-220.30
2.4	Number + diet	5	21.88	0	1	-232.27
2.2	Number	4	34.46	0	1	-239.58
2.3	Diet	4	39.32	0	1	-242.01
2.1	1	3	52.29	0	1	-249.51

^a Models 1a use the normal distribution; models 1b use the Poisson distribution. Both contain bird ID as a random factor. Models 2 are binomial and contain both bird ID and trial number as random effects.

^b Diet refers to a diet of either *Dosinia* or *Loripes*, water refers to the different water treatments, and number refers to the choice number (1–20) in experiment 2.

^c Number of parameters in the model.

^d Log likelihood.

^e Ballast dry mass.

diarrhea once being given a diet of only *Loripes*; they recovered within an hour after being offered different foods.

The effect of water availability

DM_{shell} intake rates for *Dosinia* and for *Loripes* were highest when freshwater was provided as drinking water (estimate \pm SE; 3.3 ± 0.14 mg/s and 1.34 ± 0.09 mg/s, respectively); lower when seawater was provided (2.75 ± 0.14 mg/s and 0.82 ± 0.1 mg/s, respectively); and lower still when no water was provided (2.49 ± 0.14 mg/s and 0.56 ± 0.09 mg/s, respectively). However, the availability of freshwater did not release birds from a toxin constraint, as the intake rate of *Loripes* was still lower than that of *Dosinia* (Fig. 2.2A). Birds drank more when *Loripes* rather than *Dosinia* was on offer and also drank more when freshwater was provided (2.88 ± 0.14 and 2.60 ± 0.14 mL/hr on *Loripes* and *Dosinia*, respectively) rather than seawater (1.19 ± 0.16 and 0.90 ± 0.17 mL/hr, respectively), as shown in figure 2.2B (see also models 1b in Table 2.1). A comparison of these results with the long-term food intake rates shows that an increased food intake (be it *Dosinia* or *Loripes*) coincides with increased water intake.

Parameterization of the diet selection model

The DM_{shell} of 8–9 mm *Dosinia*, k_d , was 102.7 ± 18.2 mg (mean \pm SD), and the DM_{shell} of 8–9 mm *Loripes*, k_l , was 69.6 ± 14.2 mg. $AFDM_{\text{flesh}}$ of 8–9 mm *Dosinia*, e_d , and *Loripes*, e_l , was 5.7 ± 1.1 mg and 9.7 ± 1.8 mg, respectively (see also Table 2.2). We parameterized the digestive and toxin constraints based on the estimated values with seawater (the only source of water for red knots on Banc d'Arguin). Digestive constraint c equals the maximum long-term DM_{shell} intake rate on *Dosinia* (2.75 mg/s), leading to an energy intake rate of 0.15 mg $AFDM_{\text{flesh}}$ /s. Long-term maximum DM_{shell} intake rate on *Loripes* (0.82 mg/s) was divided by k_l to arrive at a toxin constraint q of 0.012 individual *Loripes* per second, equivalent to an energy intake rate of 0.12 mg $AFDM_{\text{flesh}}$ /s.

Table 2.2 Values to parameterize the diet selection model including a toxin constraint.

Parameter	Value	Unit	Description
e_d	5.7	mg	$AFDM_{\text{flesh}}$ per ind. <i>Dosinia</i>
e_l	9.7	mg	$AFDM_{\text{flesh}}$ per ind. <i>Loripes</i>
k_d	102.7	mg	DM_{shell} per ind. <i>Dosinia</i>
k_l	69.6	mg	DM_{shell} per ind. <i>Loripes</i>
s_d	0	NA	Toxicity of ind. <i>Dosinia</i>
s_l	1	NA	Toxicity of ind. <i>Loripes</i>
c	2.75	mg s ⁻¹	Max. tolerable DM_{shell} intake rate
q	0.012	s ⁻¹	Max. tolerable toxin intake rate

Note.- *Dosinia* (d) and *Loripes* (l) are assumed to be of medium size (8–9 mm in length), as used in the preference test. The unit of toxin is chosen to be one individual *Loripes*, that is, $s_l = 1$. *Dosinia* is assumed to contain no toxin, that is, $s_d = 0$. Value q is calculated from the data as the maximum ballast dry mass (DM_{shell}) intake rate on *Loripes* (0.82 mg s⁻¹) divided by k_l , the fitted DM_{shell} per individual *Loripes* (69.6 mg); e = ash-free dry flesh mass, $AFDM_{\text{flesh}}$; k = ballast mass of individual prey; s = toxin content; c = digestive constraint; q = toxin constraint; NA = not applicable.

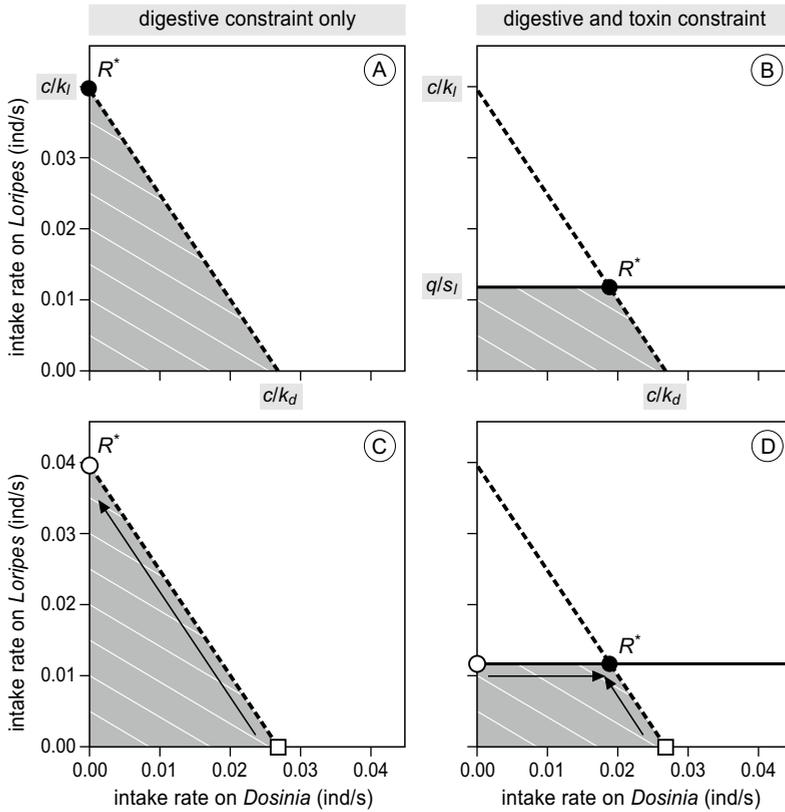


Figure 2.3 Optimal diet predictions for red knots foraging on *Dosinia* and *Loripes* under a digestive constraint (A, C), or under both a digestive constraint and a toxin constraint (B, D). Dashed lines indicate the maximum digestion rate, and solid lines indicate the maximum rate of toxin intake. The gray area represents all possible combinations of intake rates of *Dosinia* and *Loripes* given the constraint(s). Intake rates are expressed as individuals per second, referring to medium-sized prey (8–9 mm, as in experiment 2). White lines are energy indifference lines (c.f. Fig. 2.1). Slope of the lines is given by $-e_d/e_l$ (based on estimates obtained in this study; Table 2.2). The point of highest possible energy intake rate within the gray area is denoted as R^* . The lower panels predict the outcome of experiment 2 under a digestive constraint (C) under both a digestive and a toxin constraint (D). Arrows show how the birds on either a *Dosinia* diet (open squares) or a *Loripes* diet (open circles) should arrive at R^* when both are offered. Slopes and intercepts of the constraint lines are based on the results of experiment 1 (see Table 2.2).

We calculated predictions of the diet selection model for two different situations. In the first, we assumed that intake rate is limited only by a digestive constraint (Fig. 2.3A). In the second, we assumed that the *Dosinia* intake is limited by a digestive constraint, and that the *Loripes* intake is limited by its toxic effect (Fig. 2.3B). In the first case, optimal diet R^* is given by $(r_d^*, r_l^*) = (0, c/k_l) = (0 \text{ individuals s}^{-1}, 0.040 \text{ individuals s}^{-1})$ (Fig. 2.3A), resulting in an energy intake rate of $0.39 \text{ mg AFDM}_{\text{flesh}}/\text{s}$ (eq. 2.3). The model thus predicts that *Dosinia* is always rejected, resulting in a diet of only *Loripes* (Fig. 2.3A). In the second case, where the model includes a toxin constraint, a mixed diet is predicted (Fig.

2.3B), resulting in $R^* = (r_d^*, r_l^*) = (0.019 \text{ individuals s}^{-1}, 0.012 \text{ individuals s}^{-1})$, as calculated by equation (4), which gives an energy intake rate of 0.22 mg AFDM_{flesh}/s. Thus, partially accepting both *Dosinia* and *Loripes*, resulting in a diet of both *Dosinia* (61%) and *Loripes* (39%), should lead to a higher energy intake rate than eating only *Dosinia* (0.15 mg AFDM_{flesh}/s) or only *Loripes* (0.12 mg AFDM_{flesh}/s). Note that in addition to changing the expected preferences, the inclusion of the toxin constraint considerably lowers the maximum predicted energy intake rate.

Diet-dependent preference test

Prey preference strongly differed between birds on a *Loripes* diet and birds on a *Dosinia* diet. When given the choice between the two, the *Dosinia* diet birds strongly preferred *Loripes* and vice versa. However, this effect slowly disappeared over the course of 20 prey choices (Fig. 2.4, model 2.5 in Table 2.1; data deposited in the Dryad Digital Repository: <http://10.5061/dryad.5fp4g> [Oudman *et al.* 2014]). This strong initial difference in preference between the two diet groups and their convergence during the course of the trial toward a slight preference for *Dosinia* is predicted by the multiple constraint model (Fig. 2.3D), but not by a model with only a digestive constraint, which predicts that all birds will always choose *Loripes* irrespective of previous diet (Fig. 2.3C). The inclusion of treatment during the previous day did not yield better fits in any statistical model (not shown in Table 2.1). This suggests that there was no effect of *Loripes* consumption during the previous day on diet choice in the subsequent experiment.

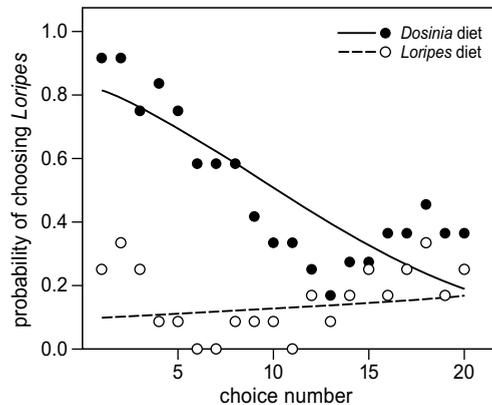


Figure 2.4 Probability of choosing *Loripes* (8–9 mm) over *Dosinia* (8–9 mm) after a 3-h exposure to ad libitum *Dosinia* (filled circles) or *Loripes* (open circles), calculated as the proportion of birds that chose *Loripes*. A total of 20 choices were made in succession by each bird in each trial ($n = 24$, balanced). Lines show estimated values of the best statistical model (model 2.5 in Table 2.1) after a *Dosinia* diet (solid line) and after a *Loripes* diet (dashed line).

DISCUSSION

Experiment 1 confirmed that red knots feeding on *Dosinia* were limited by a digestive constraint, whereas red knots feeding on *Loripes* were limited by a toxin constraint. As *Loripes* have a higher digestive quality than *Dosinia*, red knots should prefer *Loripes* with respect to digestibility and *Dosinia* with respect to toxicity. Consequently, the multiple constraint model predicts that partial acceptance of both *Dosinia* and *Loripes* yields the highest energy intake rate when both are offered *ad libitum*. The outcome of experiment 2 is consistent with these model predictions and demonstrated that red knots take into account their state with respect to both these constraints when selecting their diet (Whelan and Brown 2005). Red knots that were feeding on the limit of their digestive constraint but not their toxin constraint (i.e. when fed *Dosinia*), had increased preference for *Loripes*, whereas red knots that were feeding on the limit of the toxin constraint but not the digestive constraint (i.e. when fed *Loripes*) had increased preference for *Dosinia*. However, we also observed that through eating, the state of the animal changed and thereby so did the nature of the limiting constraint(s). In both treatments, the strong preference for the previously unavailable prey type decreased gradually as that prey type was included in the diet, and preference returned toward a mix of both prey types. Hence, our studies validate that red knots prefer a mix of *Loripes* and *Dosinia* over a diet of either one of them, and we have shown that this behaviour can be explained by the constraints that limit their food intake.

Water consumption and food intake

Birds with access to freshwater (i.e. without the burden of physiological salt removal) drank more water (Fig. 2.2B) and increased food intake independent of diet (Fig. 2.2A). This is a common finding in contexts where freshwater is scarce (Winchester and Morris 1956; Hochman and Kotler 2006; Shrader *et al.* 2008; but see Druce *et al.* 2009). Apparently water slightly alleviates the toxic effect of *Loripes* and ameliorates the digestive constraint. The diarrhetic effect might explain why birds eating *Loripes* drank more water than birds on a *Dosinia* diet. It is plausible that water and toxic *Loripes* are partially complementary resources (sensu Rapport 1971; Tilman 1982). However, increased water intake could not free the experimental birds from the toxin constraint, as their food intake remained far below the digestive constraint. In the field, *Loripes* intake might thus be increased to a limited extent by increasing the excretion capacity of the salt glands (Gutiérrez *et al.* 2011a, 2011b).

Adding water as a variable in the presented diet selection model would cause both c and q to change with increasing water intake. This, in turn, would influence the ratio between r_d^* and r_l^* (eq. 2.4), suggesting that temporal changes or spatial gradients in salinity, or changes in salt excretion capacity will influence the composition of the preferred diet (Hochman and Kotler 2006; Shrader *et al.* 2008). Another factor that we did not take into account is decreased energy assimilation efficiency, which would occur if diarrhea decreases retention time in the gut. Extending the model to take this in account would lead to a lower predicted share of *Loripes* in the diet (see Appendix 7.1 on page 135).

Explaining diet choice in the field

This experimental study shows that energy-maximizing red knots face multiple intake constraints and consequently prefer a mixed diet. In the field, however, red knots may have other objectives than energy intake maximization, and might not encounter *ad libitum* food conditions either. Nonetheless, the feeding limitation by the toxin constraint and its relation to other constraints as outlined in this study should apply in the field. To test the consequences of the toxin constraint for free-living red knots. In the next chapter, we constructed a more complex model that includes search and handling times, digestive and toxin constraints, and yearly mean abundances of both *Dosinia* and *Loripes* (coined the toxin-digestive rate model, TDRM). The TDRM predicted that in 6 out of 8 years in which prey abundances were measured, the toxin constraint limited the intake of *Loripes*. In contrast to a similar model without a toxin constraint, the predictions of the TDRM were in accordance with actual diet choice of free-living red knots as determined by fecal analysis. It was concluded that red knots in Banc d'Arguin are dependent on the presence of both *Dosinia* and *Loripes* for their survival.

Many predators face conflicting constraints when foraging, including the choice between toxic but energy rich versus nontoxic but energy-poor prey. The foraging preferences of red knots in Banc d'Arguin confirm that multiple foraging constraints are a likely cause for mixed diets.

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Toxin constraint explains diet choice,
survival and population dynamics
in a molluscivore shorebird

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ABSTRACT

Recent insights suggest that predators should include (mildly) toxic prey when non-toxic food is scarce. However, the assumption that toxic prey is energetically as profitable as non-toxic prey misses the possibility that non-toxic prey have other ways to avoid being eaten, such as the formation of an indigestible armature. In that case, predators face a trade-off between avoiding toxins and minimizing indigestible ballast intake. Here we report on the trophic interactions between a shorebird (red knot, *Calidris canutus canutus*) and its two main bivalve prey, one being mildly toxic but easily digestible and the other being non-toxic but harder to digest. A novel toxin-based optimal diet model is developed and tested against an existing one that ignores toxin constraints on the basis of data on prey abundance, diet choice, local survival and numbers of red knots at Banc d'Arguin (Mauritania) over 8 years. Observed diet and annual survival rates closely fit the predictions of the toxin-based model, with survival and population size being highest in years when the non-toxic prey is abundant. In the 6 out of 8 years when the non-toxic prey is not abundant enough to satisfy the energy requirements, red knots must rely on the toxic alternative.

INTRODUCTION

Toxic food is better avoided and there is a large literature on how predators learn to avoid toxic prey (Gittleman & Harvey 1980; Alatalo & Mappes 1996; Speed 2000; Endler & Mappes 2004; Greenlees, Phillips & Shine 2010; Halpin & Rowe 2010). Nevertheless, an emerging, alternative view is that predators should not entirely neglect toxic prey as long as this could increase their opportunity to gain energy (Speed 1993; Sherratt 2003; Sherratt, Speed & Ruxton 2004; Barnett, Bateson & Rowe 2007; Skelhorn & Rowe 2007; Skelhorn & Rowe 2010; Barnett *et al.* 2012). Mildly toxic prey species that are not directly lethal upon ingestion could be valuable during times when non-toxic food is in short supply (Lindström *et al.* 2001; Kokko, Mappes & Lindström 2003). There are a number of cases where predators have been reported to consume toxic but not-immediately-lethal prey (Kicklighter, Fisher & Hay 2004; Gray, Kaiser & Green 2010; Beckmann & Shine 2011; Garcia, Sulkin & Lopez 2011; Lincango *et al.* 2011; Williams *et al.* 2011), but the dietary choices (Kicklighter, Fisher & Hay 2004; Gray, Kaiser & Green 2010; Skelhorn & Rowe 2010; Beckmann & Shine 2011; Lincango *et al.* 2011) and subsequent demographic consequences (Garcia, Sulkin & Lopez 2011) remain unexplained in mechanistic and functional terms.

Optimization models may help us to understand how predators should strategically trade off the minimization of toxin ingestion with the maximization of energy gain. Recent state-dependent models predict that the hungrier a predator, the more likely it is to accept toxic prey (Sherratt 2003; Sherratt, Speed & Ruxton 2004), a prediction that was upheld empirically (Barnett, Bateson & Rowe 2007; Barnett *et al.* 2012). Furthermore, through a predator's hunger state, the willingness to include mildly toxic prey should depend on the abundance and availability of non-toxic food, which is a prediction that allows field testing. However, when it comes to field testing, in both the models and the experiments the only difference between prey types was their degree of toxicity, and this may be quite unrealistic.

In nature, prey species differ in many more defense traits than degrees of toxicity. By making it difficult for a predator to detect, capture, ingest or digest prey (Jeschke & Tollrian 2000; Caro 2005), non-toxic and nutritious prey species may escape predation. Predators, therefore, need to deal with multiple constraints and may face much steeper trade-offs between energy gain and toxin avoidance than hitherto assumed. Here we will focus on such a system in which a predator faces the choice between an easy to digest toxic prey and a much harder to digest non-toxic prey. Building upon the existing digestive rate model (DRM) developed by Hirakawa (Hirakawa 1995), which includes a digestive constraint but not a toxin constraint, we have developed a novel toxin-digestive rate model (TDRM) to generate food-density-dependent predictions on optimal diet and maximum energy intake rates for systems where prey differ in toxicity. The predictions of both DRM and TDRM are then put to the test in an 8-year field study on food abundance, diet choice, survival rate and population size in a molluscivore vertebrate predator, the red knot (*Calidris canutus canutus*; hereafter knot), in their nonbreeding area at Banc d'Arguin (Mauritania), characterized by a highly sulfidic environment in which the most abundant mollusc prey is toxic while other prey types are not.

Study system

The intertidal flats at Banc d'Arguin are densely covered by seagrass (mainly *Zostera noltii*) (Wolff & Smit 1990). Detritus is produced at a high rate, which is degraded anaerobically by sulfate-reducing bacteria (Jørgensen 1982), causing a build-up of high concentrations of hydrogen sulfide (H₂S) in sediment pore water (Calleja, Marbà & Duarte 2007; van Gils *et al.* 2012). Sulfide is toxic to many organisms as its lipid solubility enables it to freely penetrate biological membranes, eventually slowing down the functioning of mitochondria and the production of ATP (Bagarinao 1992). A specialized group of organisms that can profit from high sulfide concentrations in seagrass beds are Lucinidae (Taylor *et al.* 2011), heterodont bivalves that live in symbiosis with chemoautotrophic bacteria inside their gill structures (Taylor & Glover 2006). These bacteria oxidize sulfide that is provided by the lucinid host to synthesize sugars which fuel both the growth of the lucinid host and its endosymbiotic bacteria (Johnson, Diouris & Le Pennec 1994). The lucinid *Loripes lucinalis* (hereafter *Loripes*) is the dominant bivalve in Banc d'Arguin, with densities of up to 4,000 individuals per m² (van der Geest *et al.* 2011; van der Heide *et al.* 2012), and hence Banc d'Arguin can be considered as a chemosynthesis-based ecosystem (Dubilier, Bergin & Lott 2008).

Banc d'Arguin is an important nonbreeding area for Arctic-breeding shorebirds, hosting more than 2 million individuals in winter, with knots being the most abundant molluscivore (Altenburg *et al.* 1982). Knots face a trade-off between feeding on the super-abundant but toxic *Loripes* (Chapter 2) and a much less abundant but non-toxic prey, *Dosinia isocardia* (hereafter *Dosinia*; numerically *Loripes* and *Dosinia* together make up 75% of all molluscs that are ingestible by knots (Honkoop *et al.* 2008) and dominate the diet of knots (Onrust *et al.* 2013). Knots face an additional trade-off: *Loripes* has a very thin shell, whereas *Dosinia* has a thicker armature. As knots ingest their prey whole (Piersma, Koolhaas & Dekinga 1993), they often face a digestive processing constraint (van Gils *et al.* 2003a), which can be alleviated by selecting bivalves that have high flesh-to-shell mass ratios (van Gils *et al.* 2005b). The toxicity of *Loripes* for knots has recently been investigated experimentally (Chapter 2). Captive knots that were given a diet of *Loripes* only quickly developed diarrhea, thereby losing significant amounts of water. Their compensatory water consumption could not prevent a decrease in food intake. When given a diet of non-toxic *Dosinia*, birds recovered within an hour. Intake rates on *ad libitum* available *Loripes* were three times lower than expected on the basis of maximal shell mass processing rates, whereas intake rates on *ad libitum* available *Dosinia* matched the prediction of a model that predicted intake as constrained by the processing of shells. When given the choice between *Dosinia* and *Loripes*, the captive birds included both prey types in their diet, which maximized their energy intake rate as predicted by a model developed for *ad libitum* situations.

Toxin-Digestive Rate Model (TDRM)

The TDRM is developed for non-*ad-libitum* circumstances, where foragers need to search for their prey. In its most simple form, it assumes that there are just two prey types $i = 1, 2$, which can each be characterized by energy contents e_i , indigestible ballast mass k_i , toxin

contents s_i , handling time h_i , searching efficiency a_i and density D_i . The problem is finding the acceptance probabilities $\mathbf{P} = (p_1, p_2)$ for both prey types which maximize the forager's long-term energy intake rate Y , the latter is given by the multi-species version of Holling's disc equation (Holling 1959):

$$Y = \frac{p_1 a_1 D_1 e_1 + p_2 a_2 D_2 e_2}{1 + p_1 a_1 D_1 h_1 + p_2 a_2 D_2 h_2} \quad (3.1)$$

In the 'classical prey model' (Stephens & Krebs 1986), which ignores possible digestive and toxin constraints, finding the optimal solution is straightforward. First, rank prey types such that $e_1/h_1 > e_2/h_2$. Always accept type 1 ($p_1 = 1$), and accept type 2 ($p_2 = 1$) whenever $a_1 D_1 e_1 / 1 + a_1 D_1 h_1 \leq e_2 / h_2$, otherwise reject ($p_2 = 0$). This model, coined the 'contingency model' CM (Belovsky 1984), has been upheld in many diet studies on a variety of foragers (Sih & Christensen 2001), but was refuted in the case of knots (van Gils *et al.* 2005b; Quaintenne *et al.* 2010). As knots face a digestive constraint they should and do take a prey's ballast mass into account when selecting their diet (van Gils *et al.* 2005b).

If ballast intake rate X for the optimal solution in the CM exceeds digestive constraint c , then the forager faces a digestive bottleneck, in which case the CM yields a suboptimal solution (Hirakawa 1995). Then the rate-maximizing diet choice can be found using the digestive rate model DRM (Hirakawa 1995). This model can be solved graphically by plotting energy intake rate Y against ballast intake rate X for all possible combinations of \mathbf{P} , including partial preferences for either type (Fig. 3.1A). Then, by drawing digestive constraint c (vertical bar in Fig. 3.1A), one can work out which diet choice \mathbf{P} yields the maximum sustainable energy intake rate Y under constraint c (asterisk in Fig. 3.1A). For details we refer to the original paper by Hirakawa (Hirakawa 1995) and its first applications in knots (van Gils *et al.* 2005b), for which such an 'all-or-nothing constraint' has explained intake rate (van Gils *et al.* 2003a), prey choice (van Gils *et al.* 2005b; Quaintenne *et al.* 2010), patch choice (van Gils *et al.* 2005c), selection of stopover sites (van Gils *et al.* 2005a) and even digestive organ sizes (van Gils *et al.* 2003a; van Gils *et al.* 2006; van Gils *et al.* 2007). As already mentioned by Hirakawa (Hirakawa 1995), the same graphical procedure can be followed when the forager faces a toxin *rather* than a digestive constraint (replacing ballast intake rate X by toxin intake rate Z and ballast contents k_i by toxin contents s_i).

However, a forager's energy intake rate may be bottlenecked by *both* a digestive and toxin constraint. This occurs when, accounting for digestive constraint c in the DRM (i.e. when $X > c$ in the optimal CM solution), toxin intake rate Z in the optimal DRM solution exceeds q . This can only occur when the highest digestive quality prey (i.e. the one with the highest e_i/k_i) is most toxic (i.e. the one with the highest e_i/s_i ; in our *Loripes-Dosinia* case this condition was always upheld; Table A3.1). Graphically, the optimal solution under both constraints can be found by adding a third axis to Hirakawa's state space (Fig. 3.1B; mind we have added the third axis to the existing two-dimensional plane making reading the details easier, we could have also plotted X , Y and Z three-dimensionally). Solving the model analytically is equally straightforward and we will refer to it as toxin-digestive rate model TDRM (note that TDRM equals a DRM when only one of both

constraints operates, which in turn equals a CM when none of the constraints is present). First, maximal sustainable ballast intake rate X is set by digestive constraint c :

$$X = c \quad (3.2a)$$

which can be written as:

$$\frac{p_1 a_1 D_1 k_1 + p_2 a_2 D_2 k_2}{1 + p_1 a_1 D_1 h_1 + p_2 a_2 D_2 h_2} = c \quad (3.2b)$$

Similarly, maximally tolerable toxin intake rate Z is set by toxin constraint q :

$$Z = q \quad (3.3a)$$

which can be written as:

$$\frac{p_1 a_1 D_1 s_1 + p_2 a_2 D_2 s_2}{1 + p_1 a_1 D_1 h_1 + p_2 a_2 D_2 h_2} = q \quad (3.3b)$$

Solving eqs. 3.2b and 3.3b for the two unknown variables p_1 and p_2 yields the optimal acceptance probabilities:

$$p_1 = \frac{s_2 c - k_2 q}{a_1 D_1 (s_2 (k_1 - h_1 c) + s_1 (h_2 c - k_2) + q (h_1 k_2 - h_2 k_1))} \quad (3.4)$$

$$p_2 = \frac{k_1 q - s_1 c}{a_2 D_2 (s_2 (k_1 - h_1 c) + s_1 (h_2 c - k_2) + q (h_1 k_2 - h_2 k_1))} \quad (3.5)$$

MATERIAL AND METHODS

Benthos

Our study period spans from 2003-2010, in which we collected 1,024 benthos samples in 13 consecutive expeditions (Dec. 2003 [n = 84], Dec. 2004 [n = 26], Apr. 2005 [n = 39], Dec. 2005 [n = 8], Nov. 2006 [n = 6], Apr. 2007 [n = 229], Aug. 2007 [n = 8], Oct. 2007 [n = 12], Feb. 2008 [n = 142], Apr. 2008 [n = 78], Nov. 2008 [n = 56], Oct. 2009 [n = 224], and Oct. 2010 [n = 112]). Following procedures described elsewhere (van Gils *et al.* 2005b; van Gils *et al.* 2005c; van Gils *et al.* 2012), a benthos sample represented a sediment core (\varnothing 15 cm) taken to a depth of 20 cm and sieved over a 1-mm sieve. Top (0–4 cm) and bottom (4–16 cm) part of the sample were sieved separately in order to distinguish between prey that are accessible and inaccessible to knots (Zwarts, Blomert & Wanink 1992). In the laboratory, each mollusc was identified to species level and shell length was determined (\pm 0.1 mm). The latter allowed us to distinguish between ingestible and non-ingestible prey (knots can ingest all size classes of *Loripes* and *Dosinia*

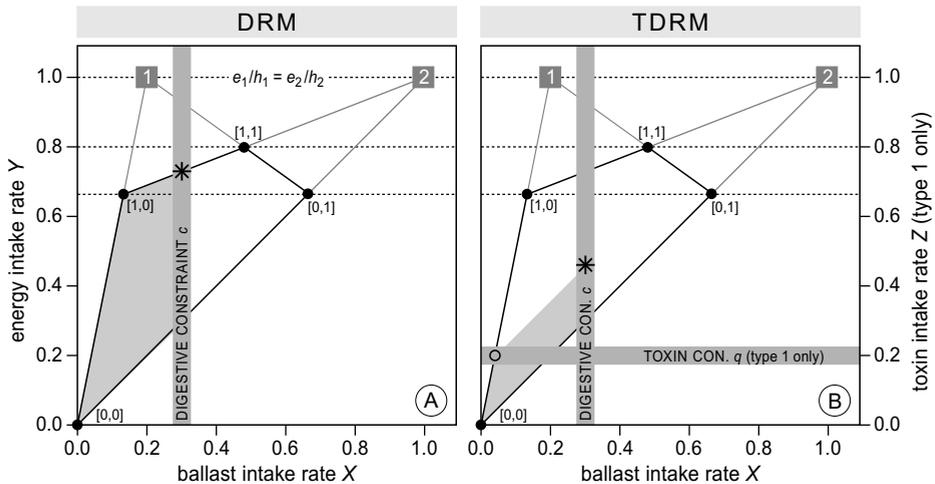


Figure 3.1 Graphical solution to find the optimal choice between two prey types which maximizes energy intake rate under one (A) or two (B) constraints. In both graphs, asterisk denotes the maximum energy intake rate under both constraints, squared symbols give maximum intake rates (e/h) at infinite densities of either type 1 or type 2 when there would be no constraints, kite-shaped surface in between the black solid lines gives feasible intake rates under (given) finite prey densities, grey area within the kite shape gives feasible intake rates under the acknowledgement of (A) a digestive constraint and (B) both a digestive and a toxin constraint. Numbers in squared brackets give diet choice as $[p_1, p_2]$. (A) Accounting only for a digestive constraint, the digestive rate model (DRM) ranks prey types on the basis of digestive quality (e/k) and predicts for this case that the high-quality prey (type 1) should be fully accepted ($p_1 = 1$), while the poor-quality prey (type 2) should only be partially selected ($0 < p_2 < 1$). (B) Accounting for both constraints, the toxin-digestive rate model (TDRM), predicts partial preference on both prey types ($0 < p_1 < 1$ and $0 < p_2 < 1$). Maximum intake rate is found by drawing a line parallel to the lower line of the kite shape (this line is parallel because toxin intake rate Z is kept at q across this line), starting where toxin constraint q crosses the left-most line of the kite shape (open dot) until it hits digestive constraint c (asterisk). Note that the scenario plotted here mimics our study qualitatively (the only toxic prey is the type with the highest e/k ratio), but not quantitatively (parameter values have been chosen arbitrarily).

< 13.2 mm). By drying (3 d at 60°C), weighing (± 0.1 mg), and incinerating (5 h at 550°C) flesh and shell separately we determined individual flesh ash-free dry mass $\text{AFDM}_{\text{flesh}}$ and shell dry mass DM_{shell} from subsamples. The relationships of $\text{AFDM}_{\text{flesh}}$ and DM_{shell} with shell length were used to predict missing values for those prey items that were not weighed. Next, numerical density (D in eqs. 3.1–3.5), $\text{AFDM}_{\text{flesh}}$ (e in eq. 3.1) and DM_{shell} (k in eq. 3.2b) were averaged per year per species (available items only, i.e. those accessible and ingestible) and were used to calculate available biomass densities and as input variables in the two digestive rate models (Table A3.1; toxin contents s was equated to flesh contents e in case of *Loripes* since toxin constraint q is expressed in terms of *Loripes* flesh intake). Further parameter values used were searching efficiency $a = 4 \text{ cm}^2/\text{s}$ (Piersma *et al.* 1995; van Gils *et al.* 2012), handling time $h = 1$ s (van Gils *et al.* 2012), toxin constraint $q = 0.1 \text{ mg AFDM}_{\text{flesh}}/\text{s}$ (Chapter 2; *Loripes* only), and gizzard mass = 10 g (van Gils *et al.* 2005a), resulting in digestive constraint $c = 5 \text{ mg DM}_{\text{shell}}/\text{s}$ (van Gils *et al.* 2003a).

All samples were taken in the vicinity (< 5 km) of Iwik, Banc d'Arguin (19°53'N, 16°18'W). Samples collected in 2003, 2004 and 2006 were taken closer to Iwik (0–3 km) than in other years (1–5 km). Spatial differences at this scale might have had only little influence. Yet, smaller scale spatial parameters such as distance to gullies, affecting the presence of seagrass (Folmer *et al.* 2012), might have had a larger effect. *Loripes* is mostly found in seagrass, whereas *Dosinia* is almost as abundant in bare as in seagrass habitat (Honkoop *et al.* 2008), and differences in prey densities between years may thus in part be due to differences in spatial design (on average, seagrass covers 80% of the intertidal surface at Banc d'Arguin; Wolff & Smit 1990). We tested potential biases for both spatial scales by comparing our 2004 data (0–3 km to Iwik) with those of an independent study also from 2004 by Honkoop *et al.* (2008), who sampled mudflats 1–5 km away from Iwik and took an equal number of samples in bare and in seagrass habitat. 2004 was a notable year in which *Dosinia* was more abundant than *Loripes* (1142.7 vs. 23.9 m⁻² in our study and 216.6 vs. 198.2 m⁻² in the study by Honkoop *et al.*, after correcting their stratified data for the 80% seagrass-coverage of the intertidal flats and for the species-specific availability fractions, 0.73 for *Dosinia* and 0.70 for *Loripes* [van Gils *et al.* 2012]). We repeated all analyses by replacing our 2004 benthos data by those of Honkoop *et al.*, which revealed that neither the outcome of the survival analyses, nor the outcome of the diet comparisons were sensitive to our spatially inconsistent sampling program (see Appendix 3.1).

Diet composition

During 6 out of the 13 expeditions we collected 77 faecal samples (2003 [n = 21], 2004 [n = 6], Apr. 2007 [n = 8], Oct. 2007 [n = 14], Feb. 2008 [n = 11] and 2009 [n = 17]), samples usually containing 40–60 droppings. Samples were sorted using standard methodology (Dekinga & Piersma 1993), which has recently been calibrated for knots feeding on *Dosinia* and *Loripes* (Onrust *et al.* 2013). In short, after drying (3 days at 60°C), shell fragments that retained on a 300-µm sieve were sorted out and weighed per species, yielding species-specific estimates of ingested DM_{shell} (after correcting for 35% of DM_{shell} not being retained on the sieve; Onrust *et al.* 2013). Next, hinges were assorted to species and their heights were determined in order to reconstruct ingested size-distributions. The latter was needed to express a species' relative diet contribution in terms of total AFDM_{flesh} consumed, since AFDM_{flesh}/DM_{shell} ratios are size-dependent (Dekinga & Piersma 1993). Relative diet compositions were logit-transformed before calculating the annual averages (Warton & Hui 2011).

Annual survival rates

Survival estimates were based on capture/resighting data of a total of 1,595 individually marked knots. The birds were captured and resighted during annual three-week expeditions in November/December 2002–2010 (Leyrer *et al.* 2012), yielding annual survival estimates for 7 consecutive years (2003–2009; because survival rate cannot be separated from resighting probability for 2010 when modeled with time-dependence). The birds were aged upon capture (Prater, Merchant & Vuorinen 1977), distinguishing hatch-year

birds (juveniles) from older birds (adults). Apparent (or local) survival (Φ) and recapture probabilities (p) were estimated from live encounter data using Cormack-Jolly-Seber (CJS) models (Lebreton *et al.* 1992). As benthos and diet data were collected throughout the entire study area we pooled the data of the two sites in our study area, Abellgh Eiznaya and Baie d'Aouatif (Leyrer *et al.* 2006; Leyrer *et al.* 2012). Based on knowledge gained from earlier analyses, we made some *a priori* assumptions to reduce the number of parameters in order to increase the precision of the survival estimates: it has been shown that a time-since-marking effect (tsm) explained most of the variation in annual survival (Leyrer *et al.* 2012), and we thus considered tsm-effects to account for transients or handling effects on survival in the first year after capture (Φ^1) vs. subsequent years (Φ^{2+}). It has further been shown that age at capture (adult vs. juveniles) explained a significant part of the variation in survival (Leyrer *et al.* 2012), and we thus included age at capture in our models. Note that knots were treated as adults after their first year (>12 months of age), and consequently no age differences existed within the Φ^{2+} category. As we were interested in which of the two diet models best explained the annual variation in survival rate, we included intake rates predicted by the TDRM and DRM, respectively, as continuous variables in the models. Additionally, to test for survival differences between years we included time as a factor (time), but also tested whether there was a linear trend in survival rate over time (Time) since an earlier analysis indicated a decline in knot survival over time (Leyrer *et al.* 2013). In all models, resighting probability p was modeled as a function of time (again as a factor) and site, as observation effort differed between the two sites and logistic improvements suggested resighting efforts differed between years (Leyrer *et al.* 2012). Both adults and juveniles forage on open mudflats during low tide and assemble at roosts during high tide and we had no reason to expect p to differ between age classes.

The global model was $\Phi_{\text{age*tsm+time}} p_{\text{site+time}}$ and we tested the goodness of fit using the median- \hat{c} (c-hat) test implemented in the MARK software (ver. 6.0; White & Burnham 1999). The level of overdispersion was estimated at $\hat{c} = 1.05 \pm 0.00$. Models were constructed and run in R (ver. 2.15.0) using the RMark package (Laake 2012; ver. 2.1.4) as an interface for program MARK (White & Burnham 1999). We used model averaging to calculate survival and resighting probability and present parameter estimates as $\hat{\theta} \pm 1$ SE. Model selection was based on Akaike's Information Criterion corrected for small sample size and overdispersion (\hat{c}) (QAICc). Based on the assumptions mentioned above, the candidate model set consisted of all biologically and ecologically plausible combinations of parameterizations for Φ and p (Table A3.2).

Estimating and predicting population dynamics

Each year between 2002 and 2010 we carried out a single count of all knots roosting in the Iwik study region. This took place during a daytime spring high tide in November/December. Birds were counted using telescopes by two or three groups of observers, each counting a subsection of our study area.

We modeled the population trend for 2002–2010 using adult and juvenile survival rates estimated by the most parsimonious model (i.e. survival model 1 in Table A3.2). In

this statistical model, TDRM energy intake rates Y served as input, which were predicted on the basis of eq. 3.1 using (1) the observed densities of both *Loripes* and *Dosinia*, and (2) the observed densities of *Loripes* only, and (3) the observed densities of *Dosinia* only. These latter two hypothetical scenarios allow us to hypothesize how much knot population dynamics depend on the presence of either *Loripes* or *Dosinia*. As applied before when modeling knot population dynamics (Baker *et al.* 2004), we used a two-dimensional matrix population model, in which fecundity (f ; equal to 0 for juveniles and 0.14 yr^{-1} for adults [van den Hout *et al.* 2014]), juvenile survival (Φ_{juv}) and adult survival (Φ_{ad}) determine how the number of juveniles (N_{juv}) and adults (N_{ad}) in year t affect the number of juveniles and adults in year $t + 1$:

$$\begin{bmatrix} N_{\text{juv}} \\ N_{\text{ad}} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & f \\ \Phi_{\text{juv}} & \Phi_{\text{ad}} \end{bmatrix}_t \begin{bmatrix} N_{\text{juv}} \\ N_{\text{ad}} \end{bmatrix}_t \quad (3.6)$$

The 2002 count was used as the initial population size in the model.

RESULTS

Annual survival rate

TDRM models were substantially better supported than models including DRM intake rates (accumulated QAICc weight: 0.38 for models including TDRM intake rates, and 0.00 for models including DRM intake rates; Table A3.2; Figs 3.2A-B). Although models including annual variation as explanatory factor (i.e. factor time) scored high in the model selection process (accumulated QAICc weight: 0.48; Table A3.2), they added extra parameters (complexity) to the models and should thus be less favored. There was no evidence for a time trend in survival (i.e. models including Time; accumulated QAICc weight: 0.14; Table A3.2). Furthermore, there was no support for adult survival being different in the first year after marking, compared to subsequent years (model 2 vs. model 3, $\Delta\text{QAICc} = 0.34$). Model averaged survival estimates can be found in Table A3.3.

Diet composition

The observed contribution of *Loripes* to the diet was less than predicted by the DRM (Fig. 3.2C; $t = -3.44$, $df = 4$, $P = 0.03$). For 3 out of 5 years for which we had diet data available, the DRM predicted that knots should fully ignore *Dosinia* (Fig. 3.2C). In those three years (2007, 2008, 2009), the abundance of *Loripes* was so high that, even if knots would feed on *Loripes* only —the prey with the highest flesh-to-shell mass ratio—, their gizzard would not be able to achieve the required shell mass processing rate; i.e. knots would face a digestive constraint. Hence, only a proportion of encountered *Loripes* should have been accepted (Table A3.4; note that this is different from conceptual Fig 3.1A where, for reasons of visual clarity, we assumed that even maximum ballast intake rates on prey type 1 (i.e. k_1/h_1) are below digestive constraint c).

In contrast, diet compositions predicted by TDRM matched the observed diets (Fig. 3.2D; $t = -1.26$, $df = 4$, $P = 0.28$). In 3 out of 5 years the intake rate on *Loripes* would have

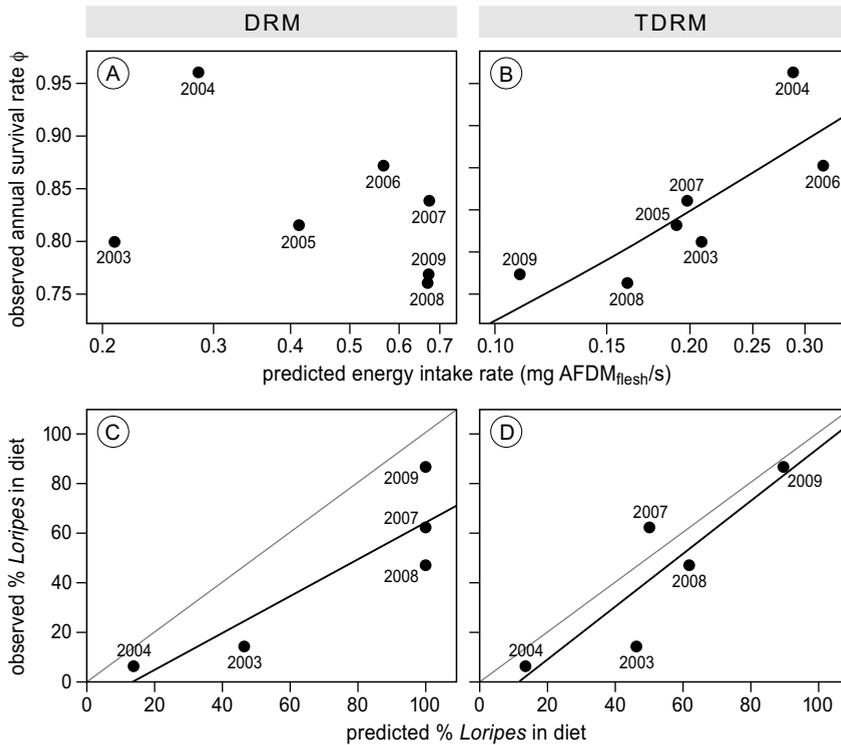


Figure 3.2 Year-specific adult survival rate as a function of DRM and TDRM predicted intake rate (estimated by model 2 in Table A3.2; year runs from Nov/Dec of the previous year to Nov/Dec of the plotted year). Year-specific adult survival rate does not correlate with DRM-predicted intake rate (A), but correlated positively with TDRM predicted intake rate (B). Line gives model fit (model 1 in Table A3.2). (C) Observed amounts of *Loripes* in the diet (relative to *Dosinia*) are lower than predicted by the DRM, (D) but match with TDRM-predictions. Dashed lines represent $y = x$ lines, and solid lines are significant regression lines.

exceeded the toxin constraint if all encountered *Loripes* were accepted. Hence, only a proportion of the encountered *Loripes* should have been accepted for this reason (Table A3.4). In those years, knots following the TDRM could accept all encountered (ingestible) *Dosinia* as the occurrence of the toxic constraint kept required shell mass processing rates low and thereby prevented a digestive constraint. Only in the year that *Loripes* was less abundant than *Dosinia* (2004), the TDRM predicts a digestive rather than a toxin constraint. In 2004 knots should thus have accepted all encountered *Loripes* and only a fraction of the encountered (ingestible) *Dosinia* (Table A3.4).

Predicted and observed population dynamics

Predicted knot population size declined over time, with the decline being steepest if *Dosinia* would have been removed from the system (−79% from 2002 to 2010), followed by the scenario when *Loripes* would have been removed (−74%). However, even with both

prey included in the diet, knot numbers were predicted to decrease over time (-39% ; Fig. 3.3). This last model agreed best with the observed decline in knot numbers from 22,859 in 2002 to 12,465 in 2010 (-45% ; Fig. 3.3).

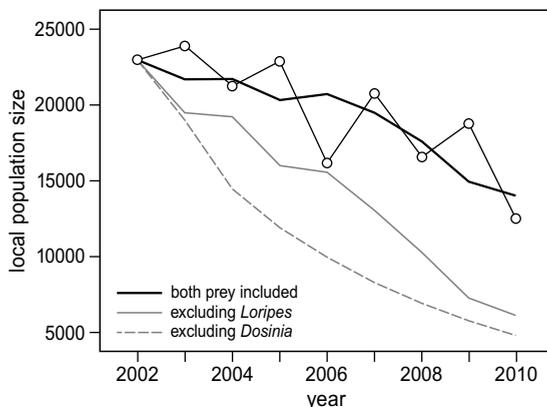


Figure 3.3 Predicted population dynamics of red knots in the presence of both prey (thick solid black line), in the absence of *Loripes* (solid grey line), and in the absence of *Dosinia* (dashed grey line). Observed population size (squares connected by thin line) follows predicted population decline based on both prey.

DISCUSSION

Knot annual survival rates correlated strongly with annual variations in *Dosinia* abundance (Fig. 3.4A; Pearson's $r = 0.91$), but showed no trend with *Loripes* abundance (Fig. 3.4B; Pearson's $r = -0.72$). This strongly suggests that knots need non-toxic *Dosinia* to survive and cannot rely on *Loripes* only, even though *Loripes* is much more abundant and has a much higher flesh-to-shell ratio. The reasoning for this dependency is rather simple: in order to prevent lethal intoxication, knots can ingest *Loripes* up to a rate that is only half of their required intake rate (Chapter 2), and they need prey such as *Dosinia* to meet their energy demands. On the other hand, *Dosinia* was not abundant enough for knots to fully rely on them as an energy source.

The TDRM optimization model, which seems to capture the essence of the knots' dietary problem, assumes the following strategy: accept toxic but energy-rich *Loripes* until the toxin constraint is met, then add bulky *Dosinia* until the digestive constraint is met. According to our calculations, knots faced both constraints only in 2006 when both prey species occurred in high densities (Fig. 3.4C; for details see Appendix 3.2). In most years (6 out of 8; Fig. 3.4C) however, *Dosinia* was not abundant enough for the birds to become digestively constrained, while the presence of *Loripes* was usually high enough to meet the toxic constraint (Fig. 3.4C). This explains the negative correlation between the relative amount of *Loripes* in the diet and the available density of *Dosinia* (Fig. 3.5A): whereas the absolute rate at which *Loripes* was eaten was likely to be constant each year (equal to toxic

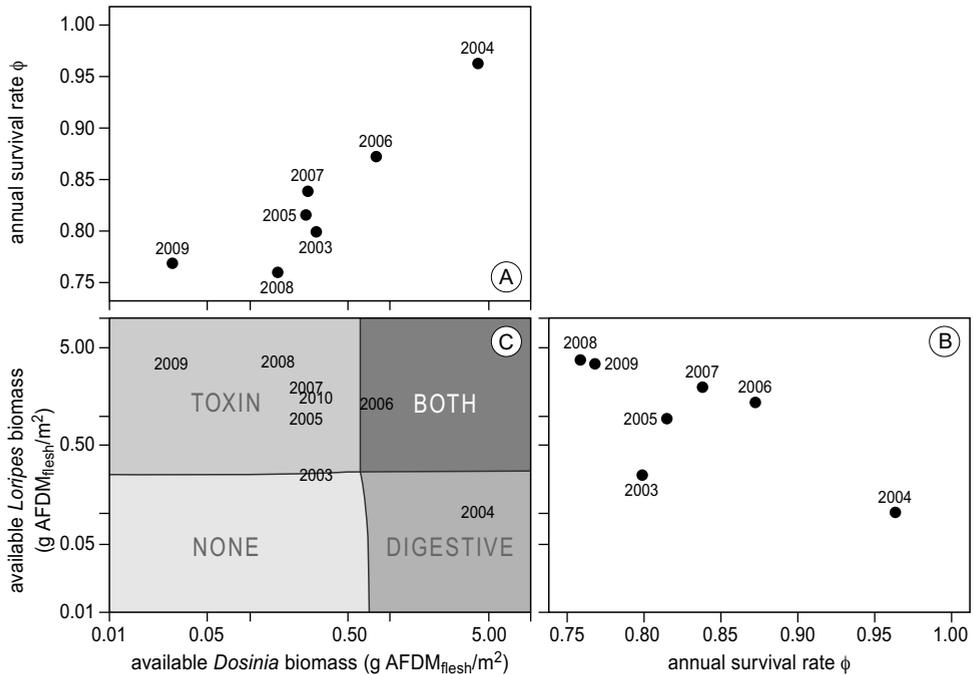


Figure 3.4 Year-specific adult survival rate as a function of prey density (estimated by model 2 in Table A3.2). Adult survival rate does correlate with the available biomass density of *Dosinia* (A), but not with *Loripes* density (B). These prey densities themselves correlate negatively (C). Grey shading in the background indicates whether knots would either face a toxin constraint, a digestive constraint, both constraints, or none of both. For details behind these calculations see Appendix 3.2.

constraint q), the *absolute* rate at which *Dosinia* was eaten increased with the available *Dosinia* density as long as birds were not digestively constrained (this would occur at a *Dosinia* density of 0.6–0.7 g AFDM_{flesh}/m²). A recent study showing year-round changes in *Dosinia* and *Loripes* densities also suggests that the relative contribution of *Loripes* to the diet of knots increased as *Dosinia* stocks became depleted throughout winter (Ahmedou Salem *et al.* 2014).

In Banc d’Arguin, knots need an average energy intake rate of c. 0.2 mg AFDM_{flesh}/s in order to maintain body mass (van Gils *et al.* 2009). In a normal year, knots would only achieve half of this rate if they would fully neglect *Loripes* and only accept *Dosinia* as their prey. By adding *Loripes* to their diet knots would just meet their required energy demand. A plot of the predicted intake rate with (grey band; Fig. 3.5B) and without (dashed line; Fig. 3.5B) *Loripes* on the available *Dosinia* densities, shows that energy intake rate without accepting *Loripes* would be insufficient for subsistence in 6 out of 8 years (also see Table A3.4). Only in 2004 and 2006 knots would have been able to achieve their minimum energetic requirements on *Dosinia* alone (Table A3.4; although we modeled knots as ‘intake rate-maximizers’, they could just as well have featured as ‘sulfide minimizers’ in these two years by fully ignoring *Loripes*; however the diet data available for 2004 suggest they did not – Fig. 3.5B).

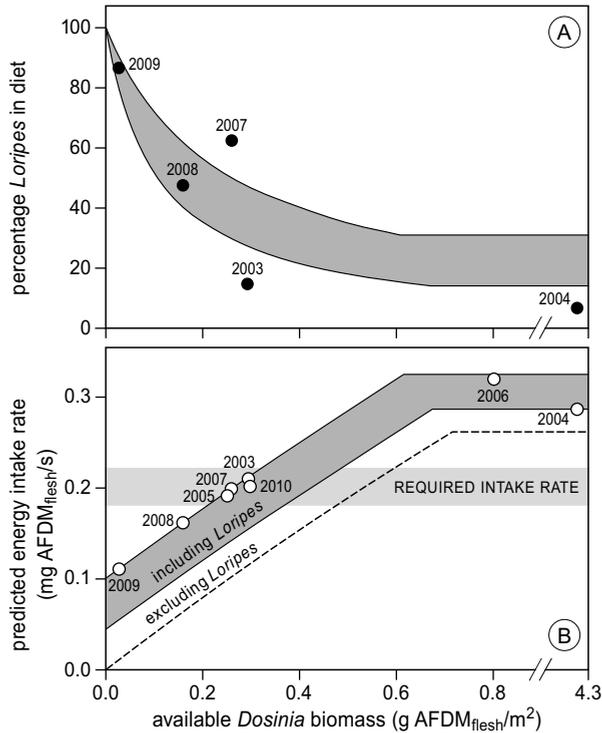


Figure 3.5 Predicted red knot diet as a function of available *Dosinia* biomass. (A) How the amount of *Loripes* in the diet (relative to *Dosinia*) relates to the available density of *Dosinia*, both theoretically (TDRM) and empirically. Theoretical predictions are given by the grey band, with lower line representing a poor *Loripes* density (0.1 g AFDM/m^2) and upper line a higher *Loripes* density ($\geq 0.25 \text{ g AFDM/m}^2$); as knots face a toxin constraint at *Loripes* densities of at least 0.25 g/m^2 , diet composition becomes independent of *Loripes* abundance above such densities). Diet composition becomes independent of *Dosinia* density when the digestive constraint is met, i.e. above *Dosinia* densities of $0.6\text{--}0.7 \text{ g/m}^2$. (B) TDRM functional response to variations in *Dosinia* density. Grey band as in (A) shows that most variation in intake rate is due to density variations in *Dosinia* rather than in *Loripes*. Nevertheless, without *Loripes*, intake rates would be substantially lower (dashed line) and often below the level required for subsistence. Dots denote year-specific predictions based on *Loripes* and *Dosinia* densities.

Note that rate-maximization *whilst* feeding allows for the minimization of *daily* feeding time if a fixed amount of daily energy is required (Schoener 1971). Minimizing daily feeding time can be beneficial if foraging comes at a cost, such as for example enhanced predation risk (McNamara & Houston 1994). This justifies our approach to analyze survival as a continuous function of intake rate rather than as a simple step function of whether metabolic demands are met. Note further that in poor *Dosinia* years, notably in 2009 (Fig. 3.5B, Table A3.4), knots would not even have been able to survive on the combination of *Loripes* and *Dosinia* alone and would have needed to include other prey types in their diet (which knots indeed did, especially in 2009; Onrust *et al.* 2013).

With *Loripes* and *Dosinia* being by far the most abundant available bivalves at Banc d'Arguin (Honkoop *et al.* 2008), there are not many alternative mollusc prey to include in

the diet. This notion, and the fact that the last years of our study period have not shown high densities of *Dosinia* (Fig. 3.4C), may explain why the local knot population has declined during especially the second half of our study period (Fig. 3.3). However, TDRM energy intake rate showed no trend over time ($r = 0.51$; $F_{1,6} = 2.07$; $P = 0.20$). In addition, also in 1980s, when knot numbers were 40–50% times higher than nowadays (Hagemeijer *et al.* 2004), *Dosinia* and other non-toxic alternatives were never very abundant (Wolff *et al.* 1993). Being a migratory species, it may thus very well be that the carrying capacity of the population is set elsewhere outside Banc d'Arguin (van Gils *et al.* 2009), for example in the Wadden Sea southward staging area where commercial fisheries led to impaired (re)fuelling opportunities (Kraan *et al.* 2010).

It is yet unclear what determines the probability of high densities of *Dosinia*, but the negative correlation between annual averages of *Dosinia* and *Loripes* densities is remarkable (Fig. 3.4C; $r = -0.76$, $F_{1,6} = 8.30$, $P = 0.03$). As has been suggested elsewhere (van Gils *et al.* 2012), this indicates some form of competition between the two species. Alternatively, there may be differences in environmental conditions among years that steer the negative correlation. For example, observed dynamics in seagrass abundance may underlie this correlation (Folmer *et al.* 2012; Leyrer *et al.* 2012), with *Loripes* more strongly linked to seagrass habitat than *Dosinia* (Honkoop *et al.* 2008).

It is exciting to hypothesize about how defense strategies in one prey may have been selected for given the defense strategy in another prey. For example, is the bulkiness of *Dosinia* an evolutionary response to the toxicity of *Loripes*? The comparison between the DRM and the TDRM allows us to hypothesize along these lines: it suggests that toxicity of *Loripes* might have increased predation pressure on *Dosinia*, inducing, on an evolutionary time scale, extra armature in *Dosinia*. The reason behind this is that intake rates on *Dosinia* are much higher in TDRM than in DRM, especially in years of high *Loripes* abundance (Table A3.4). Under DRM, that treats *Loripes* as if it was non-toxic, knots can reach their digestive constraint on *Loripes* only, leaving no room to add bulky *Dosinia*. In contrast, under TDRM, many *Dosinia* can be added to the diet since intake rates on *Loripes* are reduced because of the toxicity constraint.

At the same time the evolution of thick-shelled armature in *Dosinia* may have led to increased predation pressure on *Loripes*, which in turn may have increased *Loripes*' toxicity. Namely, if *Dosinia* would have been relatively thinner shelled than *Loripes* (i.e. when $e_D/k_D > e_L/k_L$), knots would be unable to add *Loripes* if they faced their digestive constraint on *Dosinia* only (i.e. which would happen in *Dosinia*-rich years). Note that the mechanism of enhanced predation pressure on one prey type as a consequence of induced anti-predator defense in the other prey type proposed here is a classic example of 'trait-mediated indirect interactions' (TMII), which have received renewed attention in the ecological literature (Bolker *et al.* 2003; Werner & Peacor 2003; Yamauchi & Yamamura 2005).

With the chemoautotrophic-fuelled *Loripes* being the top most abundant bivalve in the system, Banc d'Arguin can be classified as a chemosynthesis-based ecosystem (Dubilier, Bergin & Lott 2008). In contrast to Banc d'Arguin, most chemosynthesis-based ecosystems, such as deep-sea vents and seep systems, are renown for their lack of predators

(Carney 1994; Bergquist *et al.* 2003; Kicklighter, Fisher & Hay 2004). Possibly, such systems lack predators because of the overwhelming densities of toxic prey while non-toxic alternatives are not at hand (Tunncliffe 1991). The presence of a suitable non-toxic prey may explain why predators are able to thrive at Banc d'Arguin. Hydrothermal vents and deep-sea cold seeps are geographically more isolated than seagrass beds, and also more hostile because of the limited availability of dissolved oxygen in the deep sea. Their isolated positions makes it costly for predators to switch between "phototrophic" and "chemotrophic" prey, which could be the reason that such systems are frequented little by predators originating from photosynthetic communities (Carney 1994; MacAvoy *et al.* 2008; Cordes, Becker & Fisher 2010). By contrast, in seagrass beds the difference between the anaerobic sulfidic and the aerobic non-toxic environment is just a matter of meters in a horizontal direction (bare versus seagrass mosaics [Honkoop *et al.* 2008; van der Heide *et al.* 2010]), or even centimeters when considered vertically (sulfide concentrations strongly increase in the first 12 cm of the sediment layer [van Gils *et al.* 2012]). This allows predators to "make the best of both worlds" by adding toxic prey to their non-toxic diet as long as toxin levels do not exceed a given threshold. This mimics the problems recognized long ago for terrestrial herbivores, in which diet selection (Schmidt 2000; Dearing, Foley & McLean 2005), habitat use (Moore & Foley 2005), and fitness and population processes (DeGabriel *et al.* 2009) are governed by the occurrence of toxins in the form of secondary plant metabolites or as products from endosymbiotic relationships (Saikkonen *et al.* 1998; Verstraete *et al.* 2011). Our work seems to be the first to make similar problems apparent in a system with predators and prey rather than herbivores and plants.

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APPENDIX 3.1. Figure 3.4C explained

This section explains the theoretical basics underneath figure 3.4C, with *Loripes* being denoted by prey type 1 and *Dosinia* by prey type 2.

Minimal *Loripes* density (D_q) at and above which toxin constraint q is achieved

Toxin intake rate Z is given by:

$$Z = \frac{a_1 D_1 s_1 + a_2 D_2 s_2}{1 + a_1 D_1 h_1 + a_2 D_2 h_2} \quad (\text{A3.1a})$$

Since type 2 is not poisonous in our case (i.e. $s_2 = 0$) eq. A3.1a simplifies to:

$$Z = \frac{a_1 D_1 s_1}{1 + a_1 D_1 h_1 + a_2 D_2 h_2} \quad (\text{A3.1b})$$

Toxin constraint q is met when:

$$Z = q$$

Solving eqs. A3.1b and A3.2 for D_1 yield type 1's density D_q at and above which q is reached:

$$D_q(\text{type 1}) = \frac{D_2 a_2 h_2 q + q}{a_1 (s_1 - h_1 q)} \quad (\text{A3.3})$$

Note that D_q increases slightly with an increase in D_2 (solid line in Fig. A3.1), which is due to increasing time loss to handling type 2, which goes at the expense of available search time and thus hampers the intake rate on type 1 at a given density D_1 .

Minimal density (D_c) of *Loripes* or *Dosinia* at and above which digestive constraint c is achieved

Ballast intake rate X is given by:

$$X = \frac{a_1 D_1 k_1 + a_2 D_2 k_2}{1 + a_1 D_1 h_1 + a_2 D_2 h_2} \quad (\text{A3.4})$$

Digestive constraint c is met when:

$$X = c$$

Solving eqs. 3.4 and 3.5 for N_1 yields type 1's density N_c at and above which c is reached:

$$D_c(\text{type 1}) = \frac{D_2 a_2 h_2 c - D_2 a_2 k_2 + c}{a_1 (k_1 - h_1 c)} \quad (\text{A3.6})$$

Vice versa, D_c can also be expressed for type 2 by solving eqs. A3.4 and A3.5 for D_2 :

$$D_c(\text{type 2}) = \frac{D_1 a_1 h_1 c - D_1 a_1 k_1 + c}{a_2(k_2 - h_2 c)} \quad (\text{A3.7})$$

Note that D_c decreases with an increase in D_1 (dashed line in Fig. A3.1), which is because the more of type 1 is ingested, the less of type 2 needs to be ingested in order to reach the digestive constraint.

Minimal densities of *Loripes* (D_1^*) and *Dosinia* (D_2^*) at which both constraints q and c are met

These densities are found by equating eq. A3.3 with eq. A3.6 and solving for D_1 and D_2 , yielding:

$$D_1^* = \frac{k_2 q}{(a_1 k_2 - a_1 c h_2) s_1 + (a_1 h_2 k_1 - a_1 h_1 k_2) q} \quad (\text{A3.8})$$

$$D_2^* = \frac{c s_1 - k_1 q}{(a_2 k_2 - a_2 c h_2) s_1 + (a_2 h_2 k_1 - a_2 h_1 k_2) q} \quad (\text{A3.9})$$

Density 'regions' with or without constraint(s)

As visualized in Fig. A3.1, both constraints operate when $D_1 > D_1^*$ and $D_2 > D_2^*$. Only the toxin constraint operates when $D_1 > D_q$ and $D_2 < D_2^*$. Only the digestive constraint acts when $D_1 < D_1^*$ and $D_2 > D_c$. None of the constraints act when $D_1 < D_q$ and $D_2 < D_c$. Note that within these larger regions there are two interesting 'subregions'. First, there is a subregion where D_1 is high enough for the digestive constraint to be met – however the

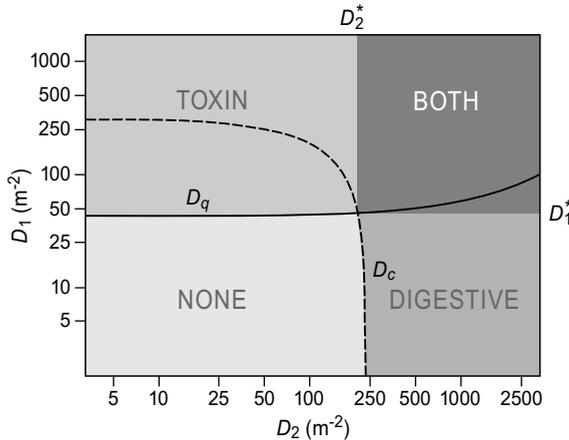


Figure A3.1 The basis underlying Fig. 3.4C in the paper, showing how we derived critical density thresholds above which the toxin and the digestive constraints operate (for the average year, i.e. by taking as inputs the means of e_L , e_D , k_L , and k_D listed in the last row of Table A3.3). Note that axes are log-transformed, making D_q and D_c curved instead of straight lines.

existence of the toxin constraint precludes this. This is where $D_1 > D_c$ and $D_2 < D_2^*$. Second, there is subregion where the existence of the digestive constraint makes the toxin constraint being faced at a lower density than D_q , which happens because the slowing down effect of handling type 2 prey has disappeared due to digestive constraint c setting a limit to the handling frequency. This is where $D_1 < D_q$ and $D_1 > D_1^*$ (where by definition $D_2 > D_2^*$).

APPENDIX 3.2. Sensitivity analysis with respect to benthos sampling

Here we explore whether our conclusion that the TDRM is the best-supported model has been affected by our spatially inconsistent sampling program. We do so by replacing our benthos data collected in 2004 by those from an independent study by Honkoop *et al.* (2008), also carried out in 2004 in our study area. Honkoop *et al.* sampled stratified with respect to habitat, and found lower densities in bare (219.4 and 60.0 m⁻² for *Dosinia* and *Loripes*, respectively) than in seagrass habitat (316.1 and 338.9 m⁻² for *Dosinia* and *Loripes*, respectively). Correcting these densities for species-specific availability fractions (0.73 in *Dosinia* and 0.70 in *Loripes*; van Gils *et al.* 2012) and for the fact that on average at Banc d'Arguin bare-seagrass habitat occurs in a 20–80% ratio (Wolff & Smit 1990), leads to the following available densities of *Dosinia* and *Loripes*: 216.6 and 198.2 m⁻². Assuming the same values for e_1 , e_2 , k_1 and k_2 as we found in our study in 2004 (Table A3.3) predicts that knots would face both their toxin and their digestive constraint in 2004 at an energy intake rate Y of 0.45 (DRM) and 0.33 mg AFDM_{fresh}/s (TDRM; compared to 0.29 mg AFDM_{fresh}/s for both DRM and TDRM when using our own 2004 benthos data; Table A3.4).

The outcome of the survival analyses is hardly affected by this data replacement (Table A3.5). There is an even stronger support for the models including TDRM (accumulated QAICc weight: 0.63), and again no support for the DRM models (accumulated QAICc weight: 0.00). Also the models including time as a categorical factor (accumulated QAICc weight: 0.29) and time as a continuous variable (accumulated QAICc weight: 0.08) found little support.

Also the outcomes of the diet statistics were unaffected. DRM still overestimated the proportion of *Loripes* in the diet ($t = -4.70$, $df = 4$, $P = 0.01$), while TDRM diets still matched the observed diets ($t = -1.61$, $df = 4$, $P = 0.18$).

Table A3.1 List of all candidate models tested for estimating apparent annual survival Φ and resighting probability p . Factors included in models were age (adult/juvenile), time (year as categorical variable), Time (year as continuous variable), tsm (time-since-marking), site (Abelgh Eiznaya/Baie d'Aouatif), TDRM (energy intake rate predicted by TDRM) and DRM (energy intake rate predicted by DRM). Model statistics listed are quasi-likelihood adjusted Akaike's Information Criterion corrected for small sample size, number of parameters (np), QDeviance, ΔQAICc and QAICc weight.

No.	Model	np	QDeviance	ΔQAICc	QAICc weight
1	$\Phi_{\text{age+TDRM}} p_{\text{site+time}}$	12	941.44	0.00	0.23
2	$\Phi_{\text{age+time}} p_{\text{site+time}}$	18	929.33	0.01	0.23
3	$\Phi_{\text{age*tsm+time}} p_{\text{site+time}}$	19	927.65	0.35	0.19
4	$\Phi_{\text{age*tsm+TDRM}} p_{\text{site+time}}$	13	941.05	1.63	0.10
5	$\Phi_{\text{age+Time}} p_{\text{site+time}}$	12	943.72	2.28	0.07
6	$\Phi_{\text{age*tsm+Time}} p_{\text{site+time}}$	13	942.20	2.77	0.06
7	$\Phi_{\text{time}} p_{\text{site+time}}$	17	934.13	2.78	0.06
8	$\Phi_{\text{TDRM}} p_{\text{site+time}}$	11	946.50	3.05	0.05
9	$\Phi_{\text{Time}} p_{\text{site+time}}$	11	949.67	6.21	0.01
10	$\Phi_{\text{age+DRM}} p_{\text{site+time}}$	12	949.69	8.25	0.00
11	$\Phi_{\text{age*tsm+DRM}} p_{\text{site+time}}$	13	948.87	9.45	0.00
12	$\Phi_{\text{DRM}} p_{\text{site+time}}$	11	957.21	13.76	0.00
13	$\Phi_{\text{age}} p_{\text{site+time}}$	11	967.03	23.57	0.00
14	$\Phi_{\text{age*tsm}} p_{\text{site+time}}$	12	967.00	25.56	0.00
15	$\Phi_{\text{constant}} p_{\text{site+time}}$	10	973.76	28.30	0.00

Table A3.2 Parameter estimates obtained by model averaging. Presented are estimate, standard error (SE), and upper and lower 95% confidence interval (CI) for apparent survival Φ (Φ^1 = adult survival in year after capture, Φ^{2+} = adult survival in subsequent years, Φ^{juv} = juvenile survival in the year after capture) and recapture probability p (subscript A for site Abelgh Eiznaya and B for site Baie d'Aouatif).

	year	estimate	SE	lower CI	upper CI
apparent survival					
Φ^{2+}	2004	0.92	0.05	0.77	0.98
Φ^{2+}	2005	0.83	0.03	0.76	0.88
Φ^{2+}	2006	0.88	0.03	0.80	0.93
Φ^{2+}	2007	0.83	0.02	0.78	0.87
Φ^{2+}	2008	0.78	0.03	0.72	0.83
Φ^{2+}	2009	0.76	0.03	0.69	0.81
Φ^1	2003	0.82	0.05	0.72	0.90
Φ^1	2004	0.92	0.05	0.76	0.98
Φ^1	2005	0.82	0.03	0.75	0.87
Φ^1	2006	0.87	0.04	0.78	0.93
Φ^1	2007	0.82	0.03	0.76	0.87
Φ^1	2008	0.77	0.03	0.69	0.83
Φ^1	2009	0.75	0.04	0.67	0.81
Φ^{juv}	2003	0.77	0.06	0.64	0.87
Φ^{juv}	2004	0.89	0.07	0.68	0.97
Φ^{juv}	2005	0.76	0.05	0.67	0.84
Φ^{juv}	2006	0.83	0.05	0.71	0.91
Φ^{juv}	2007	0.77	0.05	0.66	0.85
Φ^{juv}	2008	0.70	0.04	0.61	0.78
Φ^{juv}	2009	0.68	0.05	0.57	0.78
resighting probability					
p_A	2003	0.30	0.04	0.23	0.38
p_A	2004	0.34	0.03	0.29	0.40
p_A	2005	0.47	0.03	0.41	0.52
p_A	2006	0.50	0.03	0.45	0.56
p_A	2007	0.56	0.03	0.50	0.60
p_A	2008	0.52	0.03	0.47	0.57
p_A	2009	0.65	0.03	0.60	0.71
p_B	2003	0.24	0.04	0.18	0.32
p_B	2004	0.28	0.03	0.21	0.35
p_B	2005	0.40	0.04	0.32	0.47
p_B	2006	0.43	0.03	0.37	0.50
p_B	2007	0.48	0.03	0.42	0.55
p_B	2008	0.44	0.03	0.39	0.50
p_B	2009	0.58	0.03	0.52	0.65

Table A3.3 Year-specific input parameters used in the diet models. Listed are available numerical density (D ; m^{-2}), AFDM_{flesh} (e ; mg) and DM_{shell} (k ; mg) of available *Loripes* (subscript L) and *Dosinia* (subscript D). Since the toxin constraint is defined in terms of maximally tolerable flesh mass intake rate, we expressed toxin contents $s_L = e_L$ and $s_D = 0$. Last row gives overall averages of e_L , e_D , k_L and k_D , which have been used to generate theoretical predictions in Figs 3.4C and 3.5.

Year	D_L	D_D	$e_L (= s_L)$	e_D	k_L	k_D
2003	68.0	46.5	3.7	6.3	28.1	119.4
2004	23.9	1142.7	4.4	3.7	32.9	72.5
2005	93.5	223.3	9.8	1.1	74.8	22.9
2006	141.5	235.8	9.6	3.4	73.3	67.4
2007	376.3	98.7	5.2	2.6	39.4	52.9
2008	563.0	59.3	6.7	2.7	50.7	53.1
2009	725.5	8.3	4.6	3.4	35.2	63.4
2010	357.2	375.4	4.5	0.8	34.1	17.0
Average			6.1	3.0	46.1	58.6

Table A3.4 Output from the two diet models for each of the study years. p refers to the probability that a prey item is accepted upon encounter for *Loripes* (subscript L) or *Dosinia* (subscript D), Y giving the predicted energy intake rate (mg AFDM_{flesh}/s), Y_L and Y_D giving the absolute contributions of respectively *Loripes* and *Dosinia* to Y , $X = c$ indicating whether the digestive constraint is met (y) or not (n), and $Z = q$ indicating whether the toxin constraint is met or not.

Year	DRM						TDRM						
	p_L	p_D	Y	Y_L	Y_D	$X = c$	p_L	p_D	Y	Y_L	Y_D	$X = c$	$Z = q$
2003	1.00	1.00	0.21	0.10	0.11	n	1.00	1.00	0.21	0.10	0.11	n	n
2004	1.00	0.16	0.29	0.04	0.25	y	1.00	0.16	0.29	0.04	0.25	y	n
2005	1.00	1.00	0.41	0.33	0.09	n	0.30	1.00	0.19	0.10	0.09	n	y
2006	1.00	0.21	0.57	0.51	0.06	y	0.20	0.74	0.32	0.10	0.22	y	y
2007	0.99	0.00	0.67	0.67	0.00	y	0.14	1.00	0.20	0.10	0.10	n	y
2008	0.50	0.00	0.67	0.67	0.00	y	0.07	1.00	0.16	0.10	0.06	n	y
2009	0.58	0.00	0.67	0.67	0.00	y	0.08	1.00	0.11	0.10	0.01	n	y
2010	1.00	0.53	0.58	0.53	0.05	y	0.18	1.00	0.20	0.10	0.10	n	y

Table A3.5 As Table A3.1, but having our 2004 benthos data replaced by those from Honkoop *et al.* (2008).

Model	np	QDeviance	Δ QAICc	QAICc weight
$\Phi_{\text{age+TDRM}} \rho_{\text{site+time}}$	12	939.39	0.00	0.38
$\Phi_{\text{age*tsm+TDRM}} \rho_{\text{site+time}}$	13	938.89	1.52	0.18
$\Phi_{\text{age+time}} \rho_{\text{site+time}}$	18	929.33	2.06	0.14
$\Phi_{\text{age*tsm+time}} \rho_{\text{site+time}}$	19	927.65	2.40	0.12
$\Phi_{\text{TDRM}} \rho_{\text{site+time}}$	11	944.81	3.41	0.07
$\Phi_{\text{age+Time}} \rho_{\text{site+time}}$	12	943.72	4.33	0.04
$\Phi_{\text{age*tsm+Time}} \rho_{\text{site+time}}$	13	942.20	4.83	0.03
$\Phi_{\text{time}} \rho_{\text{site+time}}$	17	934.13	4.83	0.03
$\Phi_{\text{Time}} \rho_{\text{site+time}}$	11	949.67	8.26	0.01
$\Phi_{\text{age+DRM}} \rho_{\text{site+time}}$	12	952.20	12.81	0.00
$\Phi_{\text{age*tsm+DRM}} \rho_{\text{site+time}}$	13	951.64	14.27	0.00
$\Phi_{\text{DRM}} \rho_{\text{site+time}}$	11	958.99	17.59	0.00
$\Phi_{\text{age}} \rho_{\text{site+time}}$	11	967.03	25.62	0.00
$\Phi_{\text{age*tsm}} \rho_{\text{site+time}}$	12	967.00	27.61	0.00
$\Phi_{\text{constant}} \rho_{\text{site+time}}$	10	973.76	30.35	0.00



Chapter 4

The effect of digestive capacity on the intake rate of toxic and non-toxic prey in an ecological context

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ABSTRACT

Digestive capacity often limits food intake rate in animals. Many species can flexibly adjust digestive organ mass, enabling them to increase intake rate in times of increased energy requirement and/or scarcity of high-quality prey. However, some prey species are defended by secondary compounds, thereby forcing a toxin limitation on the forager's intake rate, a constraint that potentially cannot be alleviated by enlarging digestive capacity. Hence, physiological flexibility may have a differential effect on intake of different prey types, and consequently on dietary preferences. We tested this effect in red knots (*Calidris canutus canutus*), medium-sized migratory shorebirds that feed on hard-shelled, usually mollusc, prey. Because they ingest their prey whole and crush the shell in their gizzard, the intake rate of red knots is generally constrained by digestive capacity. However, one of their main prey, the bivalve *Loripes lucinalis*, imposes a toxin constraint due to its symbiosis with sulphide-oxidizing bacteria. We manipulated gizzard sizes of red knots through prolonged exposure to hard-shelled or soft foods. We then measured maximum intake rates of toxic *Loripes* versus a non-toxic bivalve, *Dosinia isocardia*. We found that intake of *Dosinia* exponentially increased with gizzard mass, confirming earlier results with non-toxic prey, whereas intake of *Loripes* was independent of gizzard mass. Using linear programming, we show that this leads to markedly different expected diet preferences in red knots that try to maximize energy intake rate with a small versus a large gizzard. Intra- and inter-individual variation in digestive capacity is found in many animal species. Hence, the here proposed functional link with individual differences in foraging decisions may be general. We emphasize the potential relevance of individual variation in physiology when studying trophic interactions.

INTRODUCTION

Constraints on food intake rate determine the shape of the functional response, an equation that is fundamental in population dynamical theory as it relates a forager's intake to the density of its prey (Holling 1959; MacArthur & Pianka 1966). The nature of these intake constraints also determines food preferences (i.e. the proportion of a prey type in the diet when not limited by availability of prey) (Westoby 1974; Belovsky 1978). Many animals appear to be constrained by internal processing of the prey (Jeschke, Kopp & Tollrian 2002). In these animals, flexibility in stomach- and/or gut size is often observed, allowing them to adjust their digestive capacity to changes in requirements and/or food availability (Secor & Diamond 1995; Starck 1999; Dekinga *et al.* 2001; Olsson *et al.* 2007; McWilliams & Karasov 2014). However, not all food-processing pathways may be equally dependent on digestive organ size. For example, the maximum intake rate of prey with high ballast-mass may be dependent on stomach size, whereas the intake of toxic prey may be constrained by other processes that are independent of stomach size, such as the removal of toxic compounds from the body. Consequently, changing digestive organ size may not only change maximum food intake rate, but also the relative aversion for prey containing toxic compounds.

The relations between organ size, digestive capacity, prey intake rates and diet preferences have been studied step by step in experiments with red knots (*Calidris canutus*) (Table 4.1). Red knots are medium-sized migratory shorebirds that feed on different species of mollusc prey which they ingest whole and crush in their gizzard (Dekinga & Piersma 1993; Piersma, Koolhaas & Dekinga 1993; Buehler & Piersma 2008). Gizzard size in red knots is highly variable both between and within individuals (van Gils *et al.* 2003a; van Gils *et al.* 2005a), and is related to the digestive quality of the diet, calculated as ash-free flesh mass over dry ballast mass (Piersma, Koolhaas & Dekinga 1993; van Gils *et al.* 2005b). In captivity experiments, gizzard size can increase or decrease by 50% within one week by offering a diet of hard-shelled or soft prey items, respectively (Dekinga *et al.* 2001). The intake rate of bivalve prey is limited by its shell-mass content as shown by van Gils *et al.* (2003a), who found that shell-mass processing rate relates linearly to squared gizzard mass. Since then, only two exceptions have been found to this 'rule'. The first one is in red knots staging in the Yellow Sea, *C. c. rogersi* and *C. c. piersmai* (Battley *et al.*

Table 4.1 Experimental studies on gizzard size and diet in red knots.

Study result	Reference
Gizzard size is related to diet	Piersma, Koolhaas & Dekinga (1993)
Gizzard size responds to changes in diet	Dekinga <i>et al.</i> (2001)
Shell-mass processing rate is a function of gizzard size	van Gils <i>et al.</i> (2003a)
Shell-mass processing rate explains diet preferences	van Gils <i>et al.</i> (2005b)
Shell-mass processing rate is higher on easy-to-crush prey	Yang <i>et al.</i> (2013)
Maximum intake on toxic prey not set by shell-mass processing rate	Chapter 2

2005), which digest the bivalve *Potamocorbula laevis* faster than expected from their gizzard size, probably because the force needed to crush this species is very small (Yang *et al.* 2013). The second exception was found in Banc d'Arguin, Mauritania, the main wintering area of the red knot subspecies *C. c. canutus* (Buehler & Piersma 2008; Leyrer *et al.* 2013). There, the most abundant mollusc prey, *Loripes lucinalis*, is easy to digest due to its thin shell. However, *Loripes* contains high levels of sulphur, which is produced by endosymbiotic bacteria in their gills (Johnson, Diouris & Lepennec 1994). Sulphur content of *Loripes* in Mauritania was estimated at 2–4% of dry flesh mass (van der Heide *et al.* 2012), and in such concentrations may be toxic to any animal species (Hall 2007).

In Chapter 2, we showed experimentally that red knots foraging *ad libitum* on *Loripes* are limited by the presumably toxic concentration of sulphur rather than by shell-mass processing rate. This toxic effect also explained the observed prey preferences, both in the laboratory (Chapter 2) and in the field (Chapter 3). Whereas red knots *C. c. islandica* in the Wadden Sea are solely limited by shell-mass processing rate and always preferred the prey with the highest digestive quality (van Gils *et al.* 2005b), *C. c. canutus* in Mauritania preferred a mixed diet of toxic but easy-to-digest *Loripes* and *Dosinia isocardia*, the latter which is harder to digest but not toxic (Chapters 2 and 3). The preferred proportion of *Loripes* in the diet appeared to depend on the strength of the toxin constraint relative to the digestive constraint. Hence, if gizzard size changes digestive capacity but not detoxification rate, the preference for *Loripes* is expected to be higher in birds with a small gizzard than in birds with a large gizzard.

In this study we tested (1) whether the maximum intake rate of sulphur-containing *Loripes* is indeed independent of gizzard size, and (2) whether maximum intake rate of *Dosinia* matches the earlier observed linear relation with squared gizzard size. This was done by manipulating gizzard sizes of 6 captive red knots in Mauritania through prolonged diets of either soft or hard-shelled prey, and afterwards measuring intake rates on both prey species in separate trials. Subsequently, the procedure was repeated with the soft- and hard-shelled diets reversed. In the discussion section we extend the linear programming model (Westoby 1974; Belovsky 1978; Belovsky & Schmitz 1994) that is described in Chapter 2, to quantify the expected diet preferences as a function of gizzard size.

METHODS

Birds and gizzard manipulation

The experiment was performed at the Iwik research station located on the peninsula of Iwik in the Banc d'Arguin, Mauritania. Six adult red knots were caught using mist nets on the night of 20 January 2012, and ringed with unique combinations of colour-rings for identification. Birds were held in an indoor cage (1.5 × 1 × 0.5 m) in a room with windows, and temperatures varying between 18 and 22°C. Food availability outside experimental trials was adjusted to maintain a low but not unnatural body mass, between 100 and 110 g (Leyrer *et al.* 2012). Together with food deprivation for at least 2 h before each trial, this

ensured that all birds were motivated to feed during the experimental trials. Gizzard masses were non-invasively measured regularly using ultrasonography (Dietz *et al.* 1999; Dekinga *et al.* 2001) (for more details see Appendix 4.1).

Birds were randomly divided into two groups of three birds with each group receiving a different gizzard-manipulating food regime outside the experimental trials. Initial differences in gizzard mass between groups were not significant ($F_{1,4} = 3.9, P = 0.12$). Group 1 received hard-shelled prey to maintain a large gizzard. Prey for this group were collected on the sandy beach near the research station and consisted mainly of *Dosinia isocardia* but also small *Senilia senilis* and *Bittium reticulatum*. Additionally, flesh of large *Senilia senilis* was provided because not enough hard-shelled prey could be collected to satisfy the energy demands of the birds. Group 2 was provided only with flesh of *Senilia senilis*, which is a food type that decreases gizzard mass (Dekinga *et al.* 2001). Outside the experimental trials, birds had constant access to freshwater. Fourteen days after the birds had been caught, a first series of experimental trials was performed, spread over a period of ten days. After this period, the food regimes outside the trials were reversed between the groups, now with group 1 being provided soft food and group 2 a mixture of hard-shelled prey and soft food. Seven days after the reversal, a second series of experimental trials was performed over a period of eight days.

Experimental design

The experiment comprised a total of 60 trials. The first series of trials (thus before the gizzard-manipulation reversal) consisted of 39 trials, measuring intake rate of isolated birds either on *Dosinia isocardia* (3 or 4 trials per bird, 19 in total) or *Loripes lucinalis* (3 or 4 trials per bird, 20 in total). In the second series (thus after the gizzard-manipulation reversal), two *Dosinia* trials and two *Loripes* trials were performed with each bird (24 trials in total). During the second series of trials, one bird in group 2 started showing general signs of illness such as improper preening, ruffled feathers, reduced feeding and docile behaviour. The trials of this bird after the onset of illness (3 trials: 2× *Loripes* diet, 1× *Dosinia* diet) were removed from the intake-rate analysis as well as from the gizzard-mass analysis. *Dosinia* and *Loripes* were gathered daily in a sieve (mesh size 2 mm) from a sandy beach and a seagrass bed, respectively. Bivalves were offered alive, one day after gathering. During each trial, food (either *Dosinia* or *Loripes*) and seawater was provided *ad libitum* for 2 h, during which total intake was measured.

We estimated the number and size distribution of the eaten prey items by counting and measuring shell lengths of a sub-sample of each species to the nearest 1 mm at the start and at the end of each trial. Each sub-sample consisted of 100 prey items, or all prey items if less than 100 prey were left after the trial. Size distribution was estimated in length classes of 1 mm. To determine length-specific dry mass of shell (DM_{shell}) and ash-free dry mass of flesh ($AFDM_{\text{flesh}}$), 100 individuals of each prey species were stored in 4% borax-buffered formalin before analysis at the NIOZ Royal Netherlands Institute for Sea Research. Length of each individual was measured to the nearest 0.1 mm, after which flesh and shell were dried separately at 60°C for 3 days, weighed, incinerated at 560°C for 5 hours (only the flesh) and weighed again. The estimated number of ingested prey items

in each size-class was multiplied by its estimated DM_{shell} to arrive at an estimation of total ingested DM_{shell} . These estimates were compared with measured dry-mass of the faeces produced from the start until 4 h after the end of each trial. Pooling all before-trial shell measurements per species and setting negative estimations of the eaten number of prey in a size class to zero (which occurred only in the rare length classes) improved the correlation with dry faeces mass from 0.81 (Pearson's coefficient, $t = 11.7$, $df = 69$, $P < 0.001$) to 0.84 ($t = 13.0$, $P < 0.001$).

Statistical analysis

Statistics were performed in R version 3.1.0 (R Development Core Team 2013). The effects of group (group 1 or group 2) and diet (soft prey or hard-shelled prey) on gizzard mass during the experimental trials were tested by AICc comparison (function "ipv" in package "ipv") of linear mixed-effects models (function "ipv" in package "ipv"), estimating parameter values by maximizing log-likelihood (Burnham & Anderson 2002). Bird ID was included in each model as a random effect. Trends in the rate of change in gizzard mass from catch until the end of the experiments were analysed by local regression (function "ipv", $\text{span} = 0.5$) on 13–16 measurements for each bird, spread over the whole period. These regressions were used to estimate gizzard mass during each particular experimental trial.

The effects of gizzard size (large or small gizzard) and prey species (either *Dosinia* or *Loripes*) on intake rate in the experiment were tested by AICc comparison of linear mixed-effect models, including Bird ID as a random effect. A variance structure was incorporated to correct for different variances in *Dosinia* and *Loripes* intake rates. *Dosinia* had a larger size range (3–15 mm) than *Loripes* (4–12 mm), and as larger bivalves contained exponentially more shell and flesh, estimations of DM_{shell} eaten from larger size classes gave exponentially larger variances. For *Loripes* as well as for *Dosinia*, the relation between DM_{shell} and shell length was estimated with a local regression function (function "ipv", $\text{span} = 0.6$), as non-linear regression did not give a satisfying fit (Bijleveld *et al.* 2015a) (for details see Appendix 4.2).

Ethics statement

The experiment was performed under full permission by the authorities of the Parc National du Banc d'Arguin (PNBA). No animal experimentation ethics guidelines exist in Mauritania. However, the experiment was carried out in strict accordance with Dutch animal experimentation guidelines. The NIOZ Royal Netherlands Institute for Sea Research has been licensed by the Dutch Ministry of Health to perform animal experiments under license number 80200. This license involves capture and handling of animals, and performing experiments, which nonetheless should be individually approved by the Animal Experimentation Committee (DEC) of the Royal Netherlands Academy of Arts and Sciences (KNAW). The DEC does not provide permits for experiments in foreign countries, but provided approval for equivalent experiments in the Netherlands by the same persons under permit number NIOZ 10.05, involving the capture of red knots, performing non-invasive experiments consisting of prolonged diets of

natural food types (i.e. foods that regularly occur in the diet of wild red knots) and repeated gizzard size measurements, and includes permission to release healthy animals in the wild after the experiment.

All possible efforts were made to minimize physical and mental impact on the experimental animals. Each bird was weighed and visually inspected for general condition daily, and removed from the experiment when not healthy (one bird). The reasons for the experiment to take place in Mauritania were purely scientific and by no means to avoid ethics guidelines. All experimental animals were released in the wild in healthy condition after the experiment.

RESULTS

The diet treatments successfully resulted in gizzard mass changes in the experimental red knots (Fig. 4.1, model comparison in Table 4.2, see Table A4.1 for model estimates). Although all birds initially reduced gizzard mass, a diet of hard-shelled prey resulted in larger gizzards (estimate \pm SE: 8.3 ± 0.3 g) than soft prey (6.1 ± 0.3 g). Group (group 1 or group 2) had no significant effect on gizzard mass. However, the hard-shelled diet led to a larger rate of gizzard mass increase in group 2 than in group 1 (significant interaction between diet and group, see Table 4.2 and model estimates in Table A4.1), presumably because the birds were less eager to increase gizzard mass soon after the catch (see also Fig. 4.1). The diet-induced rates of change in gizzard mass were comparable to those found earlier (Dekinga *et al.* 2001) (for details see Appendix 4.3).

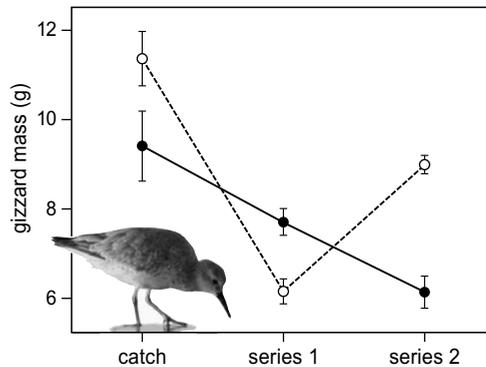


Figure 4.1 Mean gizzard mass of birds directly after catch, during the first and second series of trials. Directly after catch, the 6 red knots were randomly divided into two groups (group 1 and group 2). Both groups received different diets outside the experimental trials (soft or hard-shelled prey) to manipulate gizzard size. Initial differences in gizzard mass between groups were not significant ($F_{1,4} = 3.9$, $P = 0.12$). After catch, all birds decreased gizzard mass, but Group 1 had larger gizzards than group 2 during the first series of trials, and smaller gizzards during the second series (Table 4.2, models 1.1 to 1.5), showing that the manipulation of gizzard size was successful. Each group consisted of three birds. However, data collected on one bird from group 2 after it became sick during series 2 was omitted from the graphs and the analysis. Error bars show standard error.

Gizzard mass manipulations had an effect on intake rate (expressed as DM_{shell}), dependent on prey species (model 2.1 in Table 4.2, see Table A4.1 for model estimates). As expected, DM_{shell} intake of toxic *Loripes* did not change with an increase in gizzard mass (estimated change from 1.25 to 1.31 mg/s, $t = 0.65$, $P = 0.52$), whereas intake of non-toxic *Dosinia* did increase with gizzard mass (estimated change from 2.00 to 3.12 mg/s, $t = 3.73$, $P < 0.001$). DM_{shell} intake on a *Loripes* diet was lower than on a *Dosinia* diet for small gizzard birds (estimated difference 0.75 mg/s, $t = 3.21$, $P = 0.002$) as well as for large gizzard birds (estimated difference 1.81 mg/s, $t = 8.37$, $P < 0.001$). These results are depicted in Figure 4.2, where gizzard masses are also shown on a continuous scale. The results indicate that the shell-mass processing constraint was alleviated with an increase

Table 4.2 Second-order Akaike's information criterion (AICc) comparison of statistical models.

Model	Fixed effects ^a	K ^b	ΔAICc	AICc weight	Cumulative weight	LL ^c
Response variable: Gizzard mass						
1.1	Diet × group	6	–	0.69	0.69	–81.2
1.2	Diet	4	2.90	0.16	0.85	–85.2
1.3	Diet + group	5	3.00	0.15	1	–84.1
1.4	1	3	44.23	0	1	–107.1
1.5	Group	4	44.89	0	1	–106.2
Response variable: DM_{shell} intake rate of either <i>Loripes</i> or <i>Dosinia</i>						
2.1	Gizzard × species	7	–	0.96	0.96	–40.4
2.2	Species	5	7.45	0.02	0.98	–46.7
2.3	Gizzard + species	6	7.76	0.02	1	–45.6
2.4	1	4	35.52	0	1	–61.9
2.5	Gizzard	5	37.09	0	1	–61.5
Response variable: log transformed DM_{shell} intake rate						
3.1	Log(gizzard)	4	–	0.85	0.85	–17.07
3.2	Log(gizzard) + species	6	4.34	0.10	0.95	–16.86
3.3	Log(gizzard) × species	8	5.65	0.05	1	–14.96
3.4	species	5	20.53	0	1	–26.17
3.5	1	3	22.11	0	1	–29.26

Model selection based on AICc, with a penalty of 2 per added parameter (Burnham & Anderson 2002). Models are ordered by adequacy, starting with the minimum adequate model. Model 1.2 is competitive with model 1.1. Model 2.1 and 3.1 do not have competitors. All models are linear mixed models with a Gaussian error structure, and contain bird ID as a random effect. Models 2.1 to 2.5 contain a variance structure based on prey species.

^a In model 1.1 to 1.5, factor “diet” refers to the diet outside the experimental trials, being either soft or hard-shelled. Factor “group” refers to the order of these diet treatments (group 1 or group 2). In models 2.1 to 2.5, factor “gizzard” refers to gizzard size during the trial, which was either small or large; “species” refers to the prey species being offered, which was either *Dosinia* or *Loripes*. In models 3.1 to 3.5 log(gizzard) is a continuous variable that refers to the logarithm of estimated gizzard mass during the trial; species refers to prey species, which was either *Dosinia isocardia*, *Cerastoderma edule* or *Macoma balthica*. The symbol × means that the main terms as well as their interaction are fixed effects in the model. Models 1.4, 2.4 and 3.5 contain only an intercept, no fixed effects.

^b The number of parameters in the model.

^c Log likelihood.

^d Dry ballast mass.

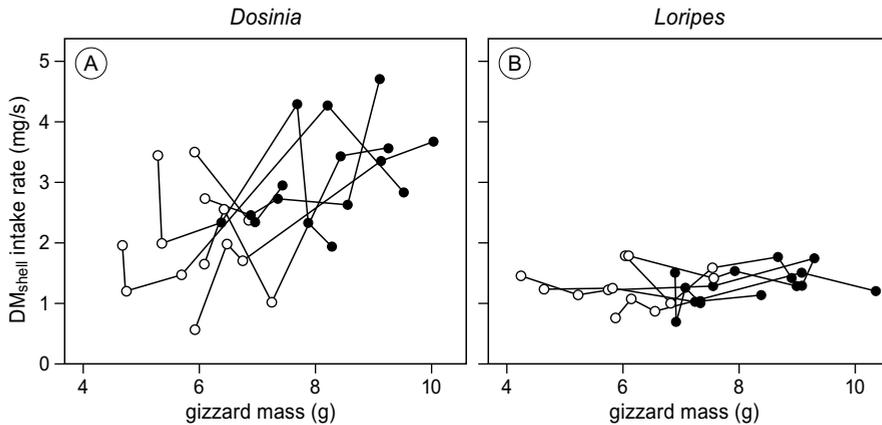


Figure 4.2 Dry shell mass (DM_{shell}) intake rate on a *Dosinia* diet (A) and on a *Loripes* diet (B). Lines connect all trials of the same bird when it was in the small gizzard group and in the large gizzard group. Intake of *Dosinia* was higher for birds with large gizzards, whereas intake of *Loripes* was not affected by gizzard size (model 2.4 in Table A4.1). *Loripes* intake rate was generally lower than *Dosinia* intake rate. These results confirm that intake of *Dosinia* is limited by a digestive constraint, whereas intake of *Loripes* is limited more stringently, presumably by its toxic load, and independent of gizzard mass.

in gizzard mass, as predicted, and that the toxin constraint was independent of gizzard mass. To test if morphological characters of individual birds other than gizzard size influenced intake rate, body mass, bill length, tarsus length and wing length of the individual birds were separately added as explanatory variables to model 2.1. None of these variables improved the statistical fit of the model (results not shown).

DISCUSSION

Maximum intake rate as a function of gizzard mass

To confirm that the relation between gizzard mass and dry shell-mass (DM_{shell}) intake rate on *Dosinia* agreed with the relations earlier observed by van Gils *et al.* (2003a), we compared the two outcomes. Van Gils *et al.* measured maximum DM_{shell} intake rates in 6 captive red knots (*C. c. islandica*) in the Dutch Wadden Sea on two non-toxic bivalve species, *Cerastoderma edule* and *Macoma balthica*. Similar to the present study, they manipulated gizzard masses by placing birds randomly in one of two groups, one with a soft prey diet and the other with a hard-shelled diet. They estimated gizzard mass in each bird as the mean of a series of gizzard measurements in the course of the experimental trials. By comparing linear models, they concluded that DM_{shell} intake was independent of bird individual, prey species and prey size. They found a linear relationship with gizzard mass on log-transformed data ($R^2 = 0.48$, $P < 0.001$, Fig. 4.3).

The effect of gizzard mass on prey intake rate, and a potential difference between the two studies on this relation was tested by combining both datasets, and comparing AICc values of linear mixed-effect models on log-transformed data (models 3 in Table 4.2),

containing bird ID as a random effect. As expected, the model that best explained DM_{shell} intake rate did not include prey species (*Dosinia*, *Cerastoderma* and *Macoma*; model 3.1 in Table 4.2, see Table A4.1 for model estimates), but did contain gizzard mass in the following way:

$$c = 10^{-1.244} G^{1.9} , \quad (4.1)$$

where c is DM_{shell} intake rate (mg/s) and G is gizzard mass (g). This estimated relation does not differ from $c = 10^{-1.293} G^{2.0}$ as found by van Gils *et al.* (2003a), as standard errors completely overlap (Fig. 4.3).

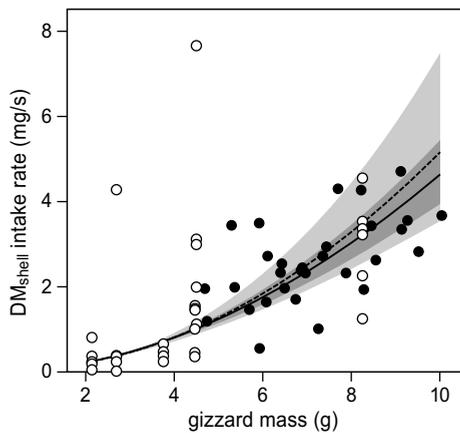


Figure 4.3 Linear regression on log-transformed DM_{shell} intake on non-toxic prey against log-transformed gizzard mass. Data from this study on *Dosinia* was combined with data from van Gils *et al.* (2003) on other non-toxic prey species. Adding the current data to the regression derived by van Gils *et al.* (2003) slightly changes the regression line (though not significantly; from dashed to solid line), but greatly reduces standard error (from light to dark grey area). Parameter estimates are shown in Table A4.1 (model 3.1). Note that van Gils *et al.* (2003a) averaged gizzard mass measurements per bird, whereas we estimated gizzard mass in each trial by interpolating measurements.

Within- and between-year variation in the toxin constraint

Maximum intake rate of *Loripes* in this study did not differ between large- and small-gizzard birds (Fig. 4.2). Because sulphur, presumably the toxic compound in *Loripes*, resides in the flesh and not the shell, we will from here on refer to the toxin constraint in terms of ash-free dry flesh mass ($AFDM_{\text{flesh}}$) instead of DM_{shell} . The best estimate of $AFDM_{\text{flesh}}$ intake rate is given by an intercept mixed-effect model on the *Loripes* data, with bird ID as a random effect, giving an estimate of 0.21 mg/s, with a within-individual variance of 0.002 and a between-individual variance of 0.0005 (Dingemanse & Dochtermann 2013). One year earlier, the intake constraint on *Loripes* was estimated at 0.12 mg/s (Chapter 2), with a within-individual variance of 0.0003 and a between-individual variance of 0.001 (T. Oudman, unpublished data). The large difference between the two years

in the intake constraint, despite small within- and between-individual variances within each year, is remarkable. This difference may be explained by yearly variation in the toxic load of *Loripes*, and/or by a difference in the capability or costs paid by red knots to deal with the toxic load of *Loripes*. The high consistency in *Loripes* intake between birds within years favours the first explanation. Differences in toxic load may relate to the mixotrophic life style of *Loripes* (van der Geest *et al.* 2014) and potentially has effects on the spatial distribution and population dynamics of *Loripes*, by influencing predation risk (van Gils *et al.* 2012; Curley, Rowley & Speed 2015).

(In)flexibility of the toxin constraint

Most of the mollusc biomass available to red knots in Banc d'Arguin consists of *Loripes* (van der Geest *et al.* 2011; van Gils *et al.* 2012; Ahmedou Salem *et al.* 2014; van den Hout *et al.* 2014), but its observed proportion in the diet is low (Chapter 3; van Gils *et al.* 2012; Onrust *et al.* 2013; van den Hout *et al.* 2014). Hence, releasing the toxin constraint would likely enable red knots to increase energy intake rate or decrease required foraging time in the field. The physiological processes that make *Loripes* toxic to red knots have not been studied, but may involve sulphide formation in the intestines during digestion. Most vertebrates can detoxify sulphide to a limited extent by oxidation to sulphate in the mitochondria of liver cells and red blood cells, and excretion by the kidney (Bagarinao 1992; Grieshaber & Völkel 1998). Energy investment in these detoxification pathways may enable red knots to increase their sulphur tolerance, but the consistent low fraction of *Loripes* in the diet and the low individual variation in the toxin constraint (this study; Chapter 2) suggests that sulphur tolerance either cannot be adjusted or is very costly to increase.

Diet preferences as a function of gizzard size

Gizzard masses of red knots caught in Banc d'Arguin are variable between individuals (mean = 9.89 g, SD = 1.30 g; van Gils *et al.* 2005a), ranging from 4 to 15 g (A. Dekinga, unpublished data). These differences in gizzard mass may accompany differences in diet preferences, as gizzard mass influences potential intake on *Dosinia*, but not on *Loripes*. Linear programming models can be used to quantify optimal diet preferences as a function of the constraints on intake rate under the assumption of energy maximization (Westoby 1974; Belovsky 1978; Belovsky & Schmitz 1994). In Chapter 2, we use a linear programming model to calculate expected diet preferences for energy intake maximizing red knots foraging on *ad libitum* *Loripes* and *Dosinia*. This model calculates which combinations of intake rates on *Dosinia* and *Loripes* are possible given both the shell-mass processing constraint and the toxin constraint on *Loripes*, and subsequently determines which of these combinations provides the highest energy intake rate. Based on measured values of the shell-mass processing constraint and the toxin constraint on *Loripes*, but without taking gizzard mass into account, it is deduced that the optimal proportion of *Loripes* in the diet is 39% in terms of dry shell mass, when both prey occur in *ad libitum* abundances. In Chapter 3, we show how this optimal proportion varies with densities of both prey types. Replacing a constant shell-mass processing constraint by the here

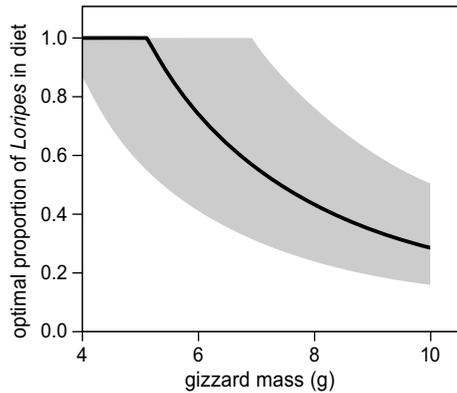


Figure 4.4 The predicted optimal proportion of *Loripes* in terms of dry shell mass in the diet of an energy intake maximizing red knot that has *ad libitum* access to both *Loripes* and *Dosinia*. Red knots with small gizzards are expected to feed exclusively on *Loripes*, whereas red knots with large gizzards are expected to have a large share of *Dosinia* in the diet. Grey area shows 95% prediction interval.

derived gizzard-mass dependent shell-mass processing constraint (eq. [4.1]) and parameterizing the model with the here obtained values (see Appendix 4.4 for a detailed model description) shows that this proportion changes considerably with gizzard mass (Fig. 4.4). The model predicts that energy maximizing birds with a gizzard mass below 5.2 g prefer an exclusive *Loripes* diet. Red knots with greater gizzard masses are expected to have a lower proportion of *Loripes* in the diet, which is less than 40% of total DM_{shell} intake rate in birds with a 10 g gizzard. Hence, model predictions show that, given the observed variation in gizzard sizes of red knots in the wild, considerable inter- and intra-individual variation in diet preferences can be expected. This result may translate to many other species, because flexibility in digestive organ mass is a general phenomenon (Piersma & Lindström 1997), being observed in mammals (Hammond *et al.* 1994), reptiles (Secor & Diamond 1995), fish (Olsson *et al.* 2007) and birds (McWilliams & Karasov 2014). Toxin constraints are observed widely too, especially in herbivores, (e.g. Rosenthal & Berenbaum 1992), but are not a prerequisite to explain a functional link between individual variation in physiology and diet preferences. For example, external handling constraints may also, in combination with digestive capacity, cause a mixed diet that depends on the strength of the digestive constraint (Belovsky & Schmitz 1994).

To experimentally test the here predicted link between digestive capacity and diet preferences comes with complications. If the animals adjust their preferences to gizzard mass in an experiment with gizzard manipulations, it is clear that they base their choice on physiological state. However, if the animals do not adjust their preferences, the here predicted link may still be correct, but the causality reversed; in that case, gizzard mass may be adjusted to individual differences in diet (see Bijleveld *et al.* 2014). Hence, the model cannot be proven incorrect in the experimental setting presented in this paper, but should be accompanied by field observations. This will be the subject of the next chapter.

ACKNOWLEDGEMENTS

We thank Parc National du Banc d'Arguin staff for providing permission and the necessary circumstances for the experiments. Lemhaba Ould Yarba is thanked for logistic support. Amadou Abderahmane Sall, Mohamed Vall Ahmedou Salem, Emma Penning, Eva Kok, Jim de Fouw, Lenze Hofstee, Els van der Zee, Anita Koolhaas, Petra de Goeij and Theunis Piersma are thanked for their help with the experiments. Theunis Piersma, Allert Bijleveld and two anonymous reviewers contributed valuable comments on earlier drafts. Dick Visser polished the graphs. The red knot in Fig. 4.1 was photographed by Jeroen Onrust. All data are available in the online supporting information files.

APPENDIX 4.1. Gizzard mass measurements

Gizzard size of each bird was measured within one day after catch, and every third day during both series of trials. They were measured non-invasively by AD and TO with an ultrasound apparatus (model Aquilla, Pie Medical Benelux, Maastricht, The Netherlands), according to the procedure described in Dekinga *et al.* (2001). The observer did not know to which experimental group each bird belonged. Height (H) and width (W) were always measured twice and both averaged. Average H and W were transformed to gizzard mass (G) by the formula $G = -1.09 + 3.78HW$, derived in a calibration study on 29 dead red knot bodies with variable gizzard masses (A. Dekinga, unpublished data). Gizzard mass estimations did not differ between AD and TO when repeated by both observers ($n = 35$). The slope of the major axis regression (function “ipv” in R package “ipv”) did not differ from 1 (95%CI [0.96,1.66], $r = 0.28$, $P = 0.1$) and the elevation did not differ from zero (95%CI [-4.97,0.48], $t = -1.6$, $P = 0.1$). Gizzard mass on each day was modelled for each bird with a polynomial model, fitted to all measurements (function “ipv” in the basic package in R, span = 0.5).

APPENDIX 4.2. Estimating dry shell mass from shell length

Allometric relations are classically estimated as power functions of the form $Y = aX^b$ (Huxley 1932). When this method is applied to the relation between shell length and shell dry mass (DM_{shell}) in *Loripes* and *Dosinia*, DM_{shell} of individuals between 8 and 10 mm are underestimated (see Fig. A4.1). The exponent of the allometric equation appears to rise after 8 mm of length. This appears to be a general tendency in bivalves (Katsanevakis *et al.* 2007; Hendriks *et al.* 2012; Bijleveld *et al.* 2015a). Therefore, we expect the inflected curve to be a consequence of the ontogeny of bivalves. Fitting a loess function instead of a power function accounts for the changing exponent (Bijleveld *et al.* 2015a).

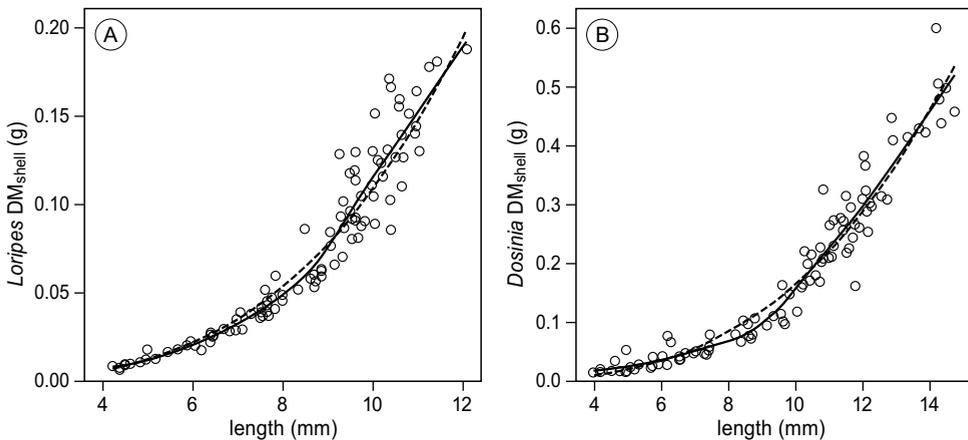


Figure A4.1 Dry shell mass (DM_{shell}) as a function of length for *Loripes* (A) and *Dosinia* (B). Fitting a power curve (dashed line) gives an overestimation of DM_{shell} in medium sized (8–10 mm) individuals, in both prey species. Fitting a loess curve (span = 0.6) solves this issue (solid line). Note the different scalings of the axes.

APPENDIX 4.3. Rates of change in gizzard mass

Initially, all birds decreased gizzard mass after catch (mean \pm between-individual SE: 0.40 ± 0.09 g/day). After reaching a minimum around day 10 after catch, group 1 birds slightly increased gizzard mass again (0.23 ± 0.02 g/day), whereas group 2 on average remained stable (0.04 ± 0.08 g/day). After the diet switch at day 24, group 1 decreased gizzard mass (0.24 ± 0.02 g/day) whereas gizzard masses of group 2 increased (0.30 ± 0.06 g/day). The observed rate of diet-related gizzard mass increase was identical to the rate observed by Dekinga *et al.* (2001) who found a diet-induced rate of increase of 0.30 ± 0.05 g/day. The diet-induced rate of decrease was slightly weaker in this study than in Dekinga *et al.* (-0.38 g/day, SE not given), which however fits well with the here observed initial decrease rate after catch.

Table A4.1 Parameter estimates in fixed part of minimum adequate statistical models.

Parameter	Estimate	SE	DF ^a	t-value	P-value
Model 1.1: Gizzard mass ~ diet × group + (1 Bird)					
Intercept	6.09	0.38	49	16.03	<0.0001
Hard-shelled diet	1.62	0.39	49	4.16	0.0001
Group 2	0.06	0.52	4	0.11	0.91
Hard-shelled diet : group 2	1.23	0.53	49	2.32	0.02
Model 2.1: DM_{shell}^b intake rate ~ gizzard × species + (1 Bird)					
Intercept	1.25	0.10	51	12.66	<0.0001
Large gizzard	0.07	0.10	51	0.65	0.52
Dosinia	0.75	0.23	51	3.21	0.002
Large gizzard : Dosinia	1.06	0.32	51	3.35	0.002
Model 3.1: log(DM_{shell} intake rate) ~ log(gizzard) + (1 Bird)					
Intercept	-1.21	0.17	53	-6.88	<0.0001
Log(gizzard)	1.87	0.24	53	7.83	<0.0001

NB: All models are linear mixed-effects models (function “lme” in package “nlme” in R), with bird-ID as a random effect. Parameters were estimated by maximizing the log-likelihood. In model 1.1, gizzard mass is measured in g, diet refers to either a soft or a hard-shelled diet, and group refers to experimental group (either 1 or 2, differing only in the order of the diet treatments). In model 2.1, DM_{shell} intake rate refers to dry shell-mass intake rate (mg/s), gizzard refers to the experimental treatment (being either small on a soft diet or large on a hard-shelled diet), and species refers to the prey species, being either *Loripes* or *Dosinia*. In model 3.1, log(gizzard) refers to the natural logarithm of gizzard mass (measured in g). A variance structure was incorporated in model 2.1 to correct for different variances in the *Loripes* and *Dosinia* trials.

^a Degrees of freedom

^b Dry shell mass

APPENDIX 4.4. Predicting diet preferences from gizzard mass: a linear programming model

A situation is assumed in which both *Loripes* and *Dosinia* are offered *ad libitum* to red knots that are maximizing energy intake rate. The idea of the linear programming model is to first derive all possible combinations of dry shell mass intake rates on *Dosinia* and *Loripes* (r_d and r_l , measured in mg/s; see Table A4.2 for a list of all used symbols) while respecting both the ballast-mass processing constraint and the toxin constraint (Fig. A4.2 A). Then it is determined which of all possible combinations of r_d and r_l provides the highest energy intake rate, denoted as $R^* = (r_d^*, r_l^*)$. In Chapter 2, we deduced that as long as *Loripes* is limited by a toxin constraint, R^* is found by drawing both constraints in a plane spanned by r_d and r_l . R^* is the point where both constraint lines intersect. It is calculated as:

$$(r_d^*, r_l^*) = (c - q, q), \quad (\text{A4.1})$$

where c is the digestive constraint (maximum dry shell-mass (DM_{shell}) intake in mg/s); q is the toxin constraint (maximum DM_{shell} intake *Loripes* in mg/s). The units differ from Chapter 2, where intake rates were measured in individuals per second. Instead, we measured intake rate in mg DM_{shell} per second to facilitate the implementation of the current experimental results, where prey of variable sizes were used. We can do so because no relation between prey length and the ratio of ash-free dry flesh-mass over dry shell mass ($\text{AFDM}_{\text{flesh}}:\text{DM}_{\text{shell}}$) was found, neither in *Dosinia* ($R^2 = 0.006$, $P = 0.22$) nor in *Loripes* ($R^2 = 0.005$, $P = 0.22$). Energy content of *Dosinia* and *Loripes* (r_d and r_l), measured as $\text{AFDM}_{\text{flesh}}$ per unit of DM_{shell} , was estimated for both *Dosinia* and *Loripes* by averaging all measured individuals without accounting for size, resulting in 0.057 ± 0.001 (mean \pm SE) and 0.163 ± 0.005 mg $\text{AFDM}_{\text{flesh}}$ per mg DM_{shell} , respectively.

The optimization procedure can be performed graphically by drawing both constraints as lines in a plane spanned by r_d and r_l . In each point in this plane, total intake rate of ash-free flesh mass can be calculated by for each prey species multiplying DM_{shell} intake rate with energy content, and adding them up:

$$Y = r_d e_d + r_l e_l. \quad (\text{A4.2})$$

The optimal combination of r_d and r_l (R^*) is found by maximizing Y , given that neither constraint line is crossed. Fig. A4.2 B shows that changing gizzard mass from 6 g to 9 g leads to an increase in the digestive constraint, but not the toxin constraint. Fig. A4.2 B shows the constraint lines both for a 6 and a 9 g gizzard in the plane spanned by r_d and r_l , showing a shift in r_d^* but not in r_l^* . Hence, the absolute amount of *Loripes* in the diet remains constant, but the proportion of *Loripes* in the diet decreases when gizzard mass increases (Fig A4.2 C).

The relation between gizzard mass and R^* can be formalized by inserting equation 4.1 from the main text, denoting c as a function of gizzard mass G (g), into equation A4.1. Contrastingly, q is constant and estimated as 1.29 mg DM_{shell} per second (linear mixed-

effect intercept model on *Loripes* data, containing bird-ID as random effect). Hence, R^* is dependent on gizzard mass in the following way:

$$(r_d^*, r_l^*) = (10^{-1.244} G^{1.9} - 1.29, 1.29). \quad (\text{A4.3})$$

When gizzard mass drops below 5.2 g, then *Loripes* intake rate is no longer limited by the toxin constraint, but becomes limited by the shell-mass processing constraint. In that case r_d^* becomes zero (see for details Chapter 2). The expected diet preferences, which we define as the optimal proportion of *Loripes* in the diet, is calculated by dividing r_l^* by total DM_{shell} intake:

$$\frac{r_l^*}{r_d^* + r_l^*} = \frac{22.6}{G^{1.9}} \quad \text{if } G > 5.2\text{g} \quad (\text{A4.4a})$$

$$\frac{r_l^*}{r_d^* + r_l^*} = 1 \quad \text{otherwise} \quad (\text{A4.4b})$$

This relation is shown in Fig. S4.2 C. In conclusion, red knots with a gizzard below 5.2 g are expected to always prefer *Loripes* over *Dosinia*, and birds with larger gizzard sizes to include a proportion of *Dosinia* in their diet that increases with gizzard size. The uncertainty in the predicted preferred diet that results from the variances in the constraint measurements was relatively large (grey area in Fig. S4.2 C), as they are multiplied in the estimation. The prediction interval was calculated by drawing 100.000 values for each of a sequence of gizzard masses from simulated constraint values, which were assumed to follow the normal distribution.

Table A4.2 Variables and parameters used in the diet selection model.

Symbol	Value	Unit	Description
r_d	variable	mg/s	DM_{shell} Intake rate on <i>Dosinia</i>
r_l	variable	mg/s	DM_{shell} Intake rate on <i>Loripes</i>
R^*	variable		Optimal combination of r_d and r_l
G	variable	g	Gizzard mass
c	variable	mg/s	Digestive constraint, i.e. the max. $DM_{\text{shell}}^{\text{a}}$ intake rate on non-toxic prey
q	1.29	mg/s	Toxic constraint, i.e. the max. DM_{shell} intake rate on <i>Loripes</i>
e_d	0.057	mg/mg	AFDM _{fflesh} ^b per DM_{shell} in <i>Dosinia</i>
e_l	0.163	mg/mg	AFDM _{fflesh} per DM_{shell} in <i>Loripes</i>

^a Dry shell mass

^b Ash-free dry flesh mass

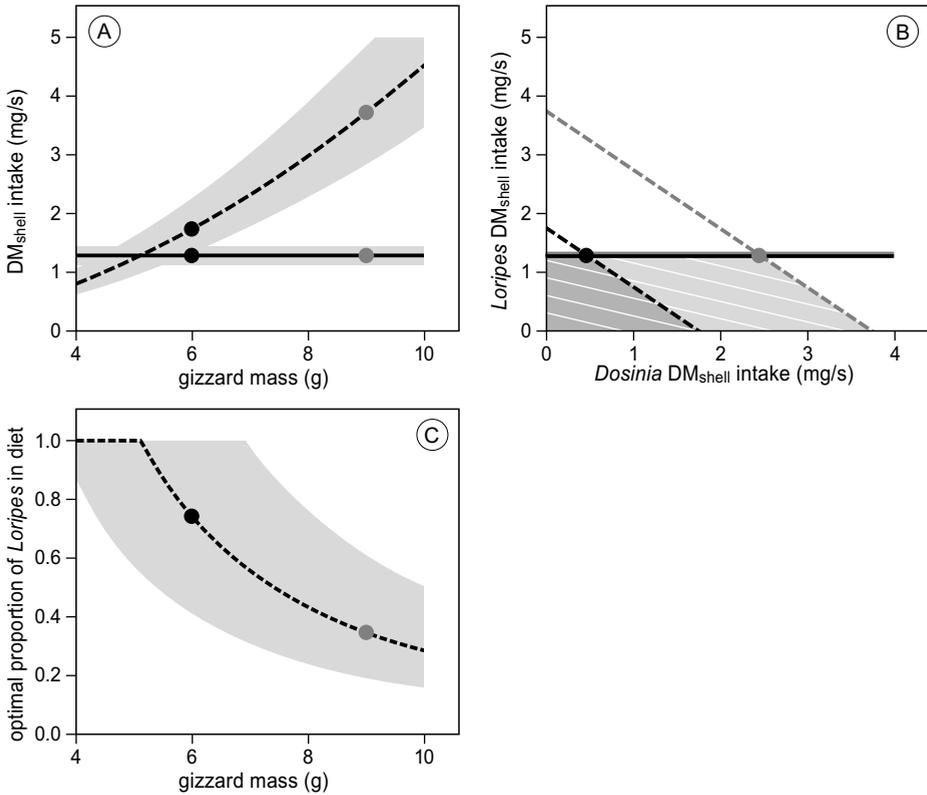


Figure A4.2 Graphical representation of the linear programming model. A) The observed relations between gizzard mass (G) and two intake constraints. Toxin constraint (q), represented by the solid line, only limits the intake of *Loricipes* and is independent of gizzard mass. Digestive constraint (c), shown by the dashed line, limits the intake of both *Loricipes* and *Dosinia* and increases exponentially with gizzard mass. Black dots show q and c at $G = 6$ g (comparable to small gizzard group), and grey dots show q and c at $G = 9$ g (comparable to the large gizzard group). Grey areas are estimated values \pm SD. SDs were calculated as the square root of the sum of the fixed and random effect variances from the linear mixed-effect models (model 2.1 in Table 4.1 for *Dosinia*, intercept model on *Loricipes* data for *Loricipes*). B) Optimal diet choice when both *Dosinia* and *Loricipes* are available *ad libitum* for a gizzard mass of 6 g (black dot and lines) and 9 g (grey dot and lines). Solid lines show q and dashed lines show c at levels corresponding to the dots in panel A. Dark grey area shows all possible combinations under both constraints for a 6 g gizzard, light grey area for a 9 g gizzard. White lines connect points of equal energy intake rate, calculated from e_d and e_l , with increasing energy intake to the right and up. The maximum energy intake is reached where constraint lines intersect (dots). Thus, when G changes from 6 to 9 g, the digestive constraint increases (from black to grey dashed line), whereas the toxin constraint remains unchanged (black and grey solid line), leading to an increased optimal intake on *Dosinia* but not on *Loricipes*. C) Expected relation between gizzard mass and the optimal proportion of *Loricipes* in the diet. Dotted line connects mean predicted proportions as calculated. Grey area encloses the 95% prediction interval. Black dot shows the expected proportion at $G = 6$ g, grey dot shows expected proportion at $G = 9$ g, corresponding to the predictions in panel B.



Chapter 5

Diet preferences as the cause of individual differences rather than the consequence

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ABSTRACT

Behavioural variation within a species is usually explained as the *consequence* of individual variation in physiology. However, new evidence suggests that the arrow of causality may well be in the reverse direction: behaviours such as diet preferences cause differences in physiological and morphological traits.

Recently, diet preferences were proposed to underlie consistent differences in digestive organ mass and movement patterns (patch residence times) in red knots (*Calidris canutus islandica*). Red knots are molluscivorous and migrant shorebirds for which the size of the muscular stomach (gizzard) is critical for the food-processing rate. In this study, red knots (*C. c. canutus*, $n = 46$) were caught at Banc d'Arguin, an intertidal flat ecosystem in Mauritania, and released with radio-tags after the measurement of gizzard mass. Using a novel tracking system (time-of-arrival), patch residence times were measured over a period of three weeks. Whether or not gizzard mass determined patch residence times was tested experimentally by offering 12 of the 46 tagged red knots soft diets prior to release; this reduced an individual's gizzard mass by 20–60%. To validate whether the observed range of patch residence times would be expected from individual diet preferences, we simulated patch residence times as a function of diet preferences via a simple departure rule.

Consistent with previous empirical studies, patch residence times in the field were positively correlated with gizzard mass. The slope of this correlation, as well as the observed range of patch residence times, were in accordance with the simulated values. The 12 birds with reduced gizzard masses did not decrease patch residence times in response to the reduction in gizzard mass. These findings suggest that diet preferences can indeed *cause* the observed among-individual variation in gizzard mass and patch residence times. We discuss how early diet experiences can have cascading effects on the individual expression of both behavioural and physiomorphic traits. This emphasises that to understand the ecological consequences of individual differences, knowledge of the environment during development is required.

INTRODUCTION

Individuals are often constrained in the expression of behavioural traits relative to the overall range of expression in the population (Réale & Dingemanse 2010). Individual-specific behavioural characteristics have been captured with the terms 'behavioural syndromes' and 'animal personality' (Sih, Bell & Johnson 2004; Réale *et al.* 2010). Behaviour has often been regarded as flexible, with behavioural differences being considered to result from individual-specific physiological and morphological characteristics (Krebs & Davies 1997). Many morphological and physiological traits are highly plastic too (Pigliucci 2001), even into the adult stage (Piersma & van Gils 2011). Consequently, the causal direction of a correlation between what we will subsequently call 'physiomorphic' traits and behavioural traits is not self-evident (see also Stamps 2003). The two can be seen as complementary aspects of the phenotype (Dingemanse *et al.* 2010), both of which will be shaped during ontogeny in interaction with each other and the environment (Stamps 2003). Hence, behavioural syndromes may also *cause* consistent variation in others traits, be it behavioural or physiomorphic (e.g. Eklöv & Svanbäck 2006; Bijleveld *et al.* 2014, 2016).

Individual diet preferences are among the best studied behaviours, and consistent differences therein have been shown to result from dietary experiences early in life (Burghardt & Hess 1966; Provenza & Balph 1987; Estes *et al.* 2003; Villalba, Provenza & Han 2004; Darmaillacq, Chichery & Dickel 2006). Hence, the early development of diet preferences may well function as the basis of individual variation in other traits later in life. Variable dietary experiences are more likely when the availability of different food sources is variable. This is the case for red knots (*Calidris canutus*, Linnaeus), a medium-sized migrating shorebird (Piersma 2007; Buehler & Piersma 2008) that primarily feeds on molluscs (Prater 1972; van Gils *et al.* 2005a). The quality and diversity of the food landscape that they live in is variable in space (Compton *et al.* 2013) as well as in time (Kraan *et al.* 2013; Chapter 3). In captive as well as free-living red knots (*C. c. islandica*), diet preferences were put forward as a possible cause of differences in movement behaviour and digestive organ mass (Bijleveld *et al.* 2014; Bijleveld *et al.* 2016). Red knots ingest their mollusc prey whole and crush them in the gizzard (Piersma, Koolhaas & Dekinga 1993), the size of which can be measured non-invasively by ultrasonography (Dietz *et al.* 1999). Gizzard mass was shown to be highly variable between individuals and flexible within individuals and to reflect the digestive quality of the previous diet (where prey quality is measured as ash-free dry flesh mass divided by dry shell mass; Piersma, Koolhaas & Dekinga 1993; Dekinga *et al.* 2001; van Gils *et al.* 2003a; Chapter 4).

In an experiment with captive red knots, gizzard mass was positively correlated with the average duration of patch visits (patch residence time) (Bijleveld *et al.* 2014). The lack of behavioural change after manipulating an individual's gizzard mass suggested that variation in digestive organ mass resulted from the consistent behavioural differences, rather than the other way around. Measurements in the wild also showed that gizzard mass was negatively correlated with the average digestive quality of prey in their selected habitat (van Gils *et al.* 2005b; Bijleveld *et al.* 2016). Together, these findings suggest that

the individual variation in gizzard mass and differences in movement behaviour may be consequences of variation in diet preferences between individuals, and ask for an experimental test under natural conditions.

This study provides: (i) field measurements of the correlation between patch residence times and gizzard masses; (ii) an experimental test of the causal direction of this correlation; and (iii) a conceptual mechanism to explain the observed differences in patch residence times between red knots as a function of diet preferences. Using the novel time-of-arrival tracking system (MacCurdy, Gabrielson & Cortopassi 2012; Piersma *et al.* 2014; Bijleveld *et al.* 2016), patch residence times were measured in 34 free-living red knots (*C. c. canutus*) on the intertidal flats of Banc d'Arguin, Mauritania. Additionally, after having been held captive for two weeks on diets of medium (six birds) and high digestive quality (six birds), 12 tagged red knots were released with reduced gizzard masses. To test whether this manipulation caused a decline in patch residence times after release in the wild, we compared the observed relation between gizzard mass and mean patch residence time for these 12 treated birds (to be referred to as 'treatment birds') with the 34 unmanipulated birds (to be referred to as 'reference birds'). Finally, the observed range of patch residence times and gizzard masses was compared to simulated patch residence times where animals were assumed to have constant patch giving-up times, but differ in the minimum digestive quality of accepted prey.

MATERIALS AND METHODS

Time-of-arrival tracking

Between 9 January and 13 February 2013, 46 red knots were tracked with the time-of-arrival tracking system (MacCurdy, Gabrielson & Cortopassi 2012; Piersma *et al.* 2014; Bijleveld *et al.* 2016) in the Baie d'Aouatif in Parc National du Banc d'Arguin, Mauritania, West Africa (19°53'N, 16°17'W) (Piersma *et al.* 2014). The birds were caught adjacent to the islet Zira, on the southwest entrance of the bay, using mist nets (14 birds, between 8 and 11 January) and a cannon net (32 birds, 12 January). All birds were released with a 6-g (range 5.5 – 6.5 g) tag glued to the skin of their rump with cyanoacrylate (Warnock & Warnock 1993). Gizzard mass was measured by ultrasonography (Dekinga *et al.* 2001; Chapter 4) within 4 h after catch. The 34 reference birds were released within 1 day after catch between 9 and 12 January (Fig. 5.1), except for one bird that showed signs of illness after being caught on 12 January. It was released in a healthy condition and with a tag on 20 January and was omitted from the analyses. The 12 treatment birds were released on 23 January after 11 days of captivity.

Each tag emitted a tag-specific radio signal each second, which could be received by up to nine radio receiver stations placed in the area (Piersma *et al.* 2014, Fig. A5.1). These stations then registered the time-of-arrival of the tag-specific signal. The differences in signal arrival times between the stations were used to calculate the tag's position (MacCurdy, Gabrielson & Cortopassi 2012). Position error estimates were produced when the signal was received by at least four stations (MacCurdy, Gabrielson & Cortopassi



Figure 5.1 Christine Lagarde, director of the International Monetary Fund, visits Parc National du Banc d'Arguin, Mauritania, on 10 January 2013. Here she has just personally released one of the radio-tagged red knots at the shore of the fishing village Iwik. Banc d'Arguin is the most important wintering site for Palearctic shorebirds, and comprises the majority of Mauritania's coast line. It is declared by UNESCO as a site of outstanding universal value. Nonetheless, this pristine state is threatened by international offshore fisheries, urban development, and an increase of unregulated fisheries inside the national park. Photo credit: Marieke Feis.

2012). Signals that were received by less than four stations were not considered for the analyses, and only position estimates with an error above 125 m (the radius of residence patches). For comparing the treatment group with the reference group, only data from 23 January onwards were used for the analyses, which is the date when the treatment birds were released.

Summarizing the tracking data into patch residence times

To calculate the mean patch residence times of each bird during each low tide, the position estimates were combined into residence patches (Bijleveld *et al.* 2016) according to the method of Barraquand & Benhamou (2008). We will describe the basics only and refer to both papers for detailed methodology. First, the data was median-filtered with a 5-points sliding window to reduce the error. For each position estimate (Fig 5.2A), the duration of the stay within 125 m of that position, without any excursions outside the radius

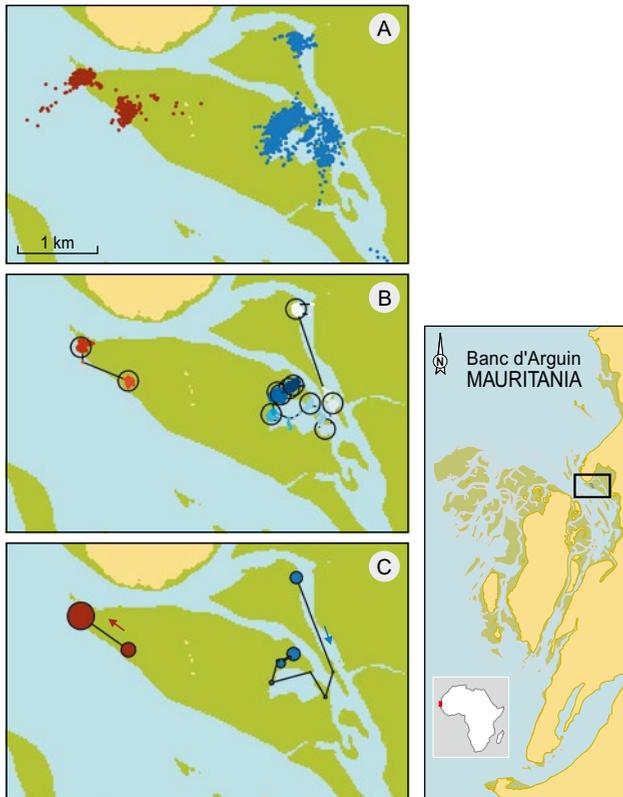


Figure 5.2 Example of time-of-arrival tracking data. (A) The dots show the estimated positions of two randomly chosen red knots during one low tide in the Baie d'Aouatif. The underlying map shows the mudflats that are exposed during low tide. (B) The position estimates are combined into residence time patches, shown by open circles. The median-filtered data underlying patches are shown in different shades. Subsequent positions are connected by lines. (C) Circles show the sequence of patch visits in the direction of the arrows. The size of circles show the relative duration of patch visits, that is patch residence times.

for more than 30 s, was calculated. Subsequently, the sequence of residence times was segmented into so-called residence patches, using the penalized contrasts method described by Lavielle (2005). Then, adjacent residence patches of which the median position was within 125 m of each other were combined (Fig. 5.2B). Finally, patch residence times were calculated as the interval between the first and last position estimate within a patch (Fig. 5.2C).

Because we were interested in low-tide (foraging) distributions, patch visits that started or ended within 2 h before and after astronomical low tide (4.5 h after Dakar, retrieved from tides.mobilegeographics.com) were selected. Patch visits that extended into the high tide (2 h before to 2 h after astronomical high tide) were removed from the analysis (80 of 3141 patches), as it was likely that birds were roosting. Patches visited shorter than 10 min were not considered ($n = 167$), as they might indicate bouts during which birds were travelling (Bijleveld *et al.* 2016). Finally, when not receiving signals from a tag for more than 1 h, this bird during that low tide was excluded from the analysis (98 of 1019 cases). Patch residence times were log-transformed and then averaged per bird per tide. This resulted in a total of 921 mean patch residence times from 35 birds (26.3 per bird, SD = 11.5), of which 337 were from the 12 treatment birds (28.1 per bird, SD = 11.2).

Experimental treatment

Twelve red knots, caught by cannon net on 12 January, were kept for eleven days in two in-house aviaries (1.5 × 1 × 0.5 m) at the scientific station adjacent to the Baie d'Aouatif. The birds were divided at random into two treatment groups of six birds each. To reduce gizzard mass of individuals, one group received only the flesh of the bivalve *Senilia senilis* (see also Chapter 4). In an attempt to maintain original gizzard masses, the other group was additionally offered 1200 hard-shelled *Dosinia isocardia* per day. These prey were collected every day in the Baie d'Aouatif. All birds had ad libitum access to fresh water. Gizzard masses were measured within four hours after catch and on the evening before the release. Gizzard mass of the birds on the soft diet decreased from 8.7 ± 0.5 g at the day of catch to 5.0 ± 0.5 g on the day before release (mean \pm SE, $t = -5.6$, $P = 0.0002$). Gizzard mass of the birds on the partly hard-shelled diet decreased from $9.2 \text{ g} \pm 0.7$ at catch to $6.6 \text{ g} \pm 0.7$ before release ($t = -2.8$, $P = 0.02$); the decrease in gizzard mass did not differ significantly between treatment groups ($t = 1.4$, $P = 0.20$), and the gizzard masses were not significantly different at release either ($t = 1.9$, $P = 0.07$).

Prey density, prey quality and giving-up times

The study area was systematically searched for tagged red knots. On 44 occasions, tagged birds were filmed from a distance of ~200 m. Excluding cases in which birds were obviously disturbed by the observers, 12 giving-up times were measured, where giving-up time is defined as the time between last prey encounter and take-off. At each of the 44 locations, next to where the bird left traces (footprints, droppings or probing holes), eight sites were marked with small pegs and sampled for prey availability within the following week. Each sample was taken with a PVC-core (diameter 15 cm) to a depth of 20 cm in the sediment.

The top 4 cm (coinciding with the maximum probing depth of red knots) was separated and sieved over a 1-mm mesh. All molluscs were sorted in the field station and brought to NIOZ (the Netherlands) in a 4% formaldehyde solution, where they were identified to genus level and measured to the nearest 0.1 mm. Mollusc density was calculated by dividing the summed number of observed molluscs by the summed sampled surface per location (0.14 m^2 , $n = 8$). Only prey of ingestible sizes were considered (Zwarts & Blomert 1992).

To determine dry flesh mass and dry shell mass (DM_{shell}), flesh and shell were separated for a subset of all bivalves and the gastropod *Bulla* sp., dried at 60°C for 3 days and weighed (mg). Flesh was then incinerated for 5 h at 560°C and weighed again to determine ash-free dry flesh mass ($AFDM_{\text{flesh}}$). Flesh and shell could not be separated in gastropods other than *Bulla*. These gastropods were incinerated whole, assuming that 12.5% of organic matter resides in the shell (Dekker 1979). By linear regression on log-transformed values, $AFDM_{\text{flesh}}$ and DM_{shell} were estimated as a function of shell length for each species separately. Based on these regressions, digestive quality was estimated for each individual prey by dividing $AFDM_{\text{flesh}}$ by DM_{shell} (van Gils *et al.* 2005b). To arrive at the estimated prey quality distribution to be used in the simulations, the observed variation in digestive quality was taken into account by adding to the estimates a value drawn randomly from the normal distribution (Gaussian noise), with the standard deviation as measured for the concerning prey species.

Statistics

First, the slope of the correlation between gizzard mass and patch residence times was tested in the reference birds. Secondly, we determined whether the treatment birds adjusted their patch residence times as a consequence of the change in gizzard mass. We did this by testing whether the treatment birds obeyed the observed relationship given their gizzard mass at release and whether there was a difference in the response of the two treatment groups. Thirdly, we tested whether the treatment birds obeyed the observed correlation given their gizzard mass at catch, which would alternatively suggest that the treatment birds did not adjust patch residence times to their manipulated gizzard mass.

The correlation between patch residence time and gizzard mass in the reference birds was tested by comparing linear mixed effects models (function 'lmer' in R package 'lme4'; Bates *et al.* 2015; R Core Team 2015), including low-tide ID and bird ID as random effects. Patch residence times and gizzard mass were log-transformed before the analysis. In addition to gizzard mass, time-of-day and low-tide water level were included as explanatory variables. When astronomical low tide was within 2 h before sunrise and 2 h after sunset, the low tide period was classified as 'day', and otherwise as 'night'. All possible combinations of variables were compared, including all interactions between two variables, but not more than two, resulting in 14 different candidate models. Model selection was performed by calculating AICc-weights of all the candidate models (Burnham & Anderson 2002). Models were regarded as competitive to the best model (the model with lowest AICc-score) if the cumulative AICc-weight was below 0.95 and did not contain uninformative parameters (parameters that did not decrease AICc-score when added to the model; Arnold 2010).

Because the duration of each low tide is fixed, mean patch residence time per tide was negatively collinear with the number of patches visited per tide and did not follow a normal distribution, nor any other parametric distribution. However, a histogram of the model residuals and a plot of the residual values against the fitted values did not show strong violation of normality assumptions. An alternative analysis was performed on the number of patches visited per tide instead of mean patch residence time. Although this alternative procedure gave the same results and conclusions (not shown), this method was not preferred because 234 out of 584 data points had to be removed, since the number of patch visits could not be accurately assessed when birds were out of range of the receiver stations during parts of the low tide period.

Because patch residence times could not be measured in the treatment birds before they underwent the treatment, we assumed that the relation between patch residence times and gizzard mass before treatment was the same as in the reference birds. Hence, if the treatment had no effect, patch residence times after the treatment should have the same relation with gizzard mass *at catch* as found for the reference birds. On the other hand, if the treatment birds adjusted patch residence times to their gizzard mass after the treatment, the relation between gizzard mass *at release* and patch residence times should be the same as observed in the reference birds. This was tested by comparing the explanatory power of linear mixed-effects models with and without including a treatment parameter, fitted on the data of both the reference birds and the treatment birds, using either gizzard mass *at catch* or gizzard mass *at release*. The coefficients for the model intercept and log-transformed gizzard mass were constrained to the values that were estimated for the reference birds alone (by specifying an 'offset' in the function 'lmer'). Additional models were added to test for an effect of diet on patch residence times within the treatment birds, even though no effect of diet group on gizzard mass was found. To reveal a potential treatment effect that wore off after a few days in the field, which may be masked in the analysis of the full 3 weeks after release of the treatment birds, an additional analysis was performed with only the data of the first 2 days after the day of release.

A simulation to explain differences in patch residence times from diet preferences

Foragers may individually differ in the minimum prey quality that they accept. Given that the decision of a foraging animal to leave a patch should be related to the encounter rate of acceptable prey at that patch, this is likely to affect average patch residence time (Charnov 1976). Red knots foraging on mollusc prey were shown to increase acceptance probability for prey of higher quality (van Gils *et al.* 2005b). Diet quality was expressed in terms of digestibility, measured as the amount of ash-free flesh mass per unit of dry shell mass. In red knots, gizzard masses were shown to reflect the digestive quality of the previous diet (Dekinga *et al.* 2001). Hence, if birds maintain the minimum gizzard mass that is needed to fulfil energy demands on prey of minimum acceptable digestive quality (at an ash-free dry flesh intake rate of 0.2 mg/s; van Gils *et al.* 2009), gizzard mass and patch residence time are expected to correlate. This expectation was formalized in a simulation.

We assumed a patchy distribution of food that varies in quality, and foragers that depart from a patch when prey of acceptable quality is not encountered within a fixed period of time (giving-up time; Krebs, Ryan & Charnov 1974). More sophisticated and perhaps more realistic behavioural rules exist (McNair 1982; Olsson & Holmgren 1998; van Gils *et al.* 2003b), but the predictions with the simple fixed giving-up time rule come reasonably close (with an approximately 10% lower encounter rate than when using more complex rules; Green 1984). Assuming that individuals do not differ in giving-up times, the predicted patch residence time is dependent on the total prey density and the prey quality distribution. Expected patch residence times were simulated for a sequence of minimum acceptable prey qualities by repeatedly drawing expected search times from an exponential distribution (Rita & Ranta 1998), where the average encounter rate ($1/\text{search time}$) was defined as the average searching efficiency (de Fouw *et al.* 2016) times the density of acceptable prey. Patch residence time was then defined as the cumulative search time until search time exceeded the giving-up time, plus the cumulative handling time on all accepted prey. This procedure was repeated 100 times for each of the 44 locations where prey density and prey digestive quality were measured. A detailed description is given in Appendix A5.1.

RESULTS

Patch residence times of reference birds

As expected, patch residence times of the reference birds showed a positive loglinear correlation with gizzard mass (Fig. 5.3, model 1.1 in Table 5.1). Patch residence times were longer in the night than during the day, but their correlation with gizzard mass did

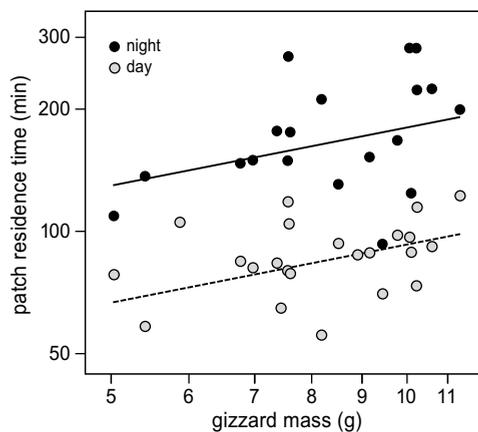


Figure 5.3 Patch residence times of reference birds increase with gizzard mass. Dots show the duration of patch visits per bird, averaged per low tide and then over all low tides. Regression lines show predicted values (model 1.1 in Table 5.1), which include the differences between low tides in the night (solid line) and during the day (dashed line). Note that the axes are log-scaled.

not differ between day and night (i.e. no interaction was observed between time-of-day and gizzard mass, Fig. 5.3, model 1.3 in Table 5.1). The low-water level did not explain any variation in patch residence times (model 1.2 in Table 5.1). Patch residence time estimations of the best model ranged from 67 min (95% CI: 54–82 min) for birds with a 5-g gizzard to 97 min (95% CI: 83–114 min) for birds with a 11-g gizzard during the day, and from 130 (95% CI: 96–174 min) to 189 min (95% CI: 146–244 min) during the night (Fig. 5.3, see table A5.1 for model 1.1 parameter estimates). The model without gizzard mass and only time-of-day showed very little support (model 1.7, AICc-weight = 0.05).

Table 5.1 AICc comparison of statistical models.

Model	Fixed effects ^a	K ^b	ΔAICc	AICc weight	Cum. weight	LL ^c
1.1	Gizzard + daytime	6	–	0.43	0.43	–76.1
1.2	Gizzard + daytime + height	7	2.01	0.16	0.59	–76.1
1.3	Gizzard × daytime	7	2.04	0.15	0.74	–76.1
1.4	Gizzard × height + daytime	8	3.49	0.07	0.81	–75.8
1.5	Gizzard × daytime + height	8	4.06	0.06	0.87	–76.1
1.6	Daytime × height + gizzard	8	4.06	0.06	0.93	–76.1
1.7	Daytime	5	4.34	0.05	0.98	–79.3
1.8	Daytime + height	6	6.37	0.02	0.99	–79.3
1.9	Daytime × height	7	8.42	0.01	1	–79.3
1.10	Gizzard + height	6	17.85	0	1	–85.0
1.11	Gizzard	5	18.34	0	1	–86.3
1.12	Gizzard × height	7	19.15	0	1	–84.7
1.13	Height	5	22.60	0	1	–88.4
1.14	1	4	22.89	0	1	–89.6
2.1	Offset(model 1.1, giz at catch) + treatment	4	–	0.69	0.69	–121.6
2.2	Offset(model 1.1, giz at catch) + treatment + diet	5	2.01	0.25	0.94	–121.6
2.3	Offset(model 1.1, giz at catch)	3	4.76	0.06	1	–125.0
3.1	Offset(model 1.1, giz at release) + treatment	4	–	0.72	0.72	–122.4
3.2	Offset(model 1.1, giz at release) + treatment + diet	5	1.93	0.28	1	–122.4
3.3	Offset(model 1.1, giz at release)	3	20.02	0	1	–133.4

NB. Linear mixed-effects models (function ‘lmer’ in R package ‘lme4’; Bates *et al.* 2015; R Core Team 2015) with tide ID and bird ID as random intercepts. Best models and competitive models are in boldface (Burnham & Anderson 2002).

Parameters were estimated by maximizing the log likelihood. Log-transformed patch residence time is the response variable in all models, which is averaged per bird per low tide after transformation.

^a In models 1, ‘Gizzard’ refers to gizzard mass at catch. ‘Daytime’ is a factor with two levels: day and night. ‘Height’ refers to the astronomical water level at the specific low tide. To test whether the treatment birds deviate from the predictions derived from the reference bird data, the estimated coefficients of the fixed effects of model 1.1 are used as an offset in models 2 and 3. Models 2 contain gizzard masses as measured when the birds were caught; models 3 contain gizzard masses before release. Factor ‘Treatment’ refers to whether the bird was in the treatment group or the reference group. ‘Diet’ refers to the diet group within the treatment group (either a soft diet or a partially hard-shelled diet).

^b The number of parameters in the model.

^c Log-likelihood.

Patch residence times of treatment birds

The treatment birds had longer residence times than predicted on the basis of their gizzard mass at release (on average 58 min, Fig. 5.4A and C, model 3.1 in Table 5.1), and no effect of treatment group was observed. This suggests that the birds did not adjust patch residence time to their new gizzard mass. Patch residence times was also longer than expected from gizzard mass at catch (on average 31 min, see Fig. 5.4B and D, model 2.1 in Table 5.1). With an AICc-weight of 0.06, the model without a treatment effect had little support (model 2.3 in Table 5.1). No difference was found between the diet groups within the treatment birds (models 2.2 and 3.3 in Table 5.1). Statistical summaries of the best models are given in Table A5.1.

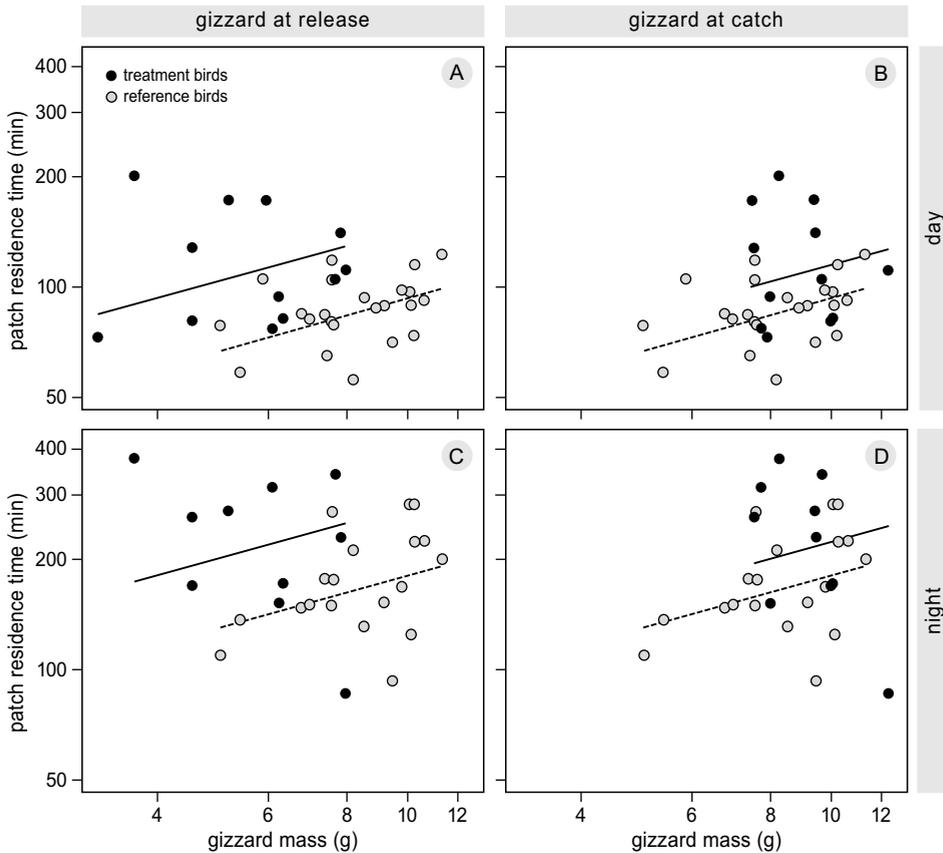


Figure 5.4 Patch residence time of treatment birds compared to the reference birds. Panels A and C show patch residence time as a function of gizzard mass *at release*, and panels B and D show them as a function of gizzard mass *at catch*. Each dot is the mean value of one bird. Dotted lines show model predictions for the reference birds (model 1.1 in Table 5.1, see lines in Fig. 5.3). Solid lines show the treatment birds, where the slope is set equal to the dotted line (models 2.1 and 3.1 in Table 5.1, in which model 1.1 is used as offset). As shown by the vertical distance between the regression lines, the observed patch residence times match better with their gizzard mass *at catch* (panel B and D, models 2 in Table 5.1) than with their gizzard mass *at release* (panel A and C, models 3 in Table 5.1). Note that the axes are log-scaled.

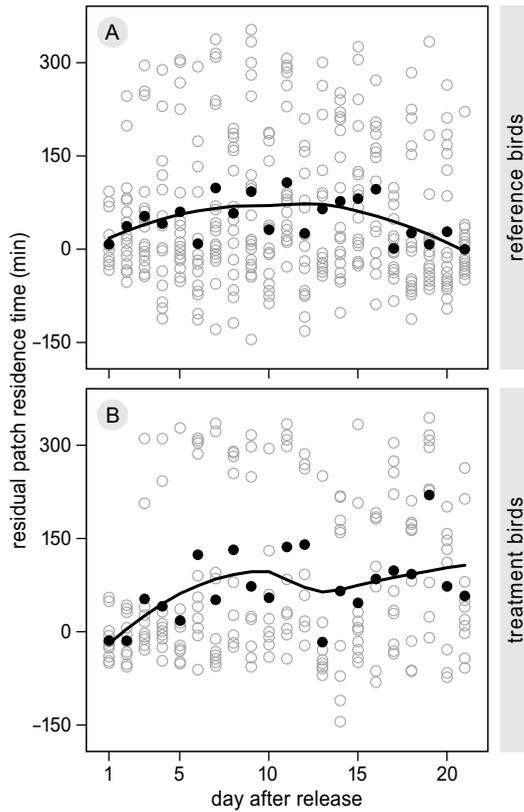


Figure 5.5 The effect of day since release on patch residence times. Shown are the residual values of model 1.1 (Table 5.1) against the day since release of the reference birds (A) and the treatment birds (B). The predicted log-transformed patch residence times are back-transformed before subtraction from the observed values. Open grey dots show the mean values per low tide averaged per bird. Black dots show the mean of those values per day since release. Black lines show LOESS regressions (span = 0.7) on the model residuals.

Temporal trend in patch residence times of treatment birds

There was a tendency for increasing patch residence times in the treatment birds in the first week after release (Fig. 5.5). However, restricting the data to only the first two days after release, when mean patch residence times by the treatment birds appeared to be lower, did not change the qualitative outcome of the analysis. Even then, patch residence times remained longer than predicted from gizzard mass at release (on average 18 min, model A2.1 in Table A5.3, Fig. A5.2), and were as expected from gizzard mass at catch (on average 1 min longer, model A1.1 in Table A5.3, Fig. A5.2). Hence, although patch residence times were lower in the first days after release than thereafter, the treatment birds did not show lower patch residence times than expected from their original gizzard mass.

Explaining patch residence times from diet preferences

At the 44 identified feeding locations, average available and ingestible prey densities were 1104 molluscs m^{-2} , ranging from 0 to 9394 m^{-2} (SD = 1644). The frequency distribution of their digestive quality is given in Fig. 5.6A. The average giving-up time of free-living radio-tagged birds in the wild was 33 s, ranging between 3 s and 245 s. Based on the densities and prey quality distribution at the individual locations, simulations predicted that patch residence time should decrease when the minimum acceptable prey quality is increased (Fig. 5.6B). Repeating the simulations with giving-up times of 20, 30 and 40 s showed that expected patch residence time increases with giving-up time. Independent of the used giving-up time, the expected patch residence time decreased considerably with an increase in the minimum acceptable prey quality (Fig. 5.6B). The range of expected patch

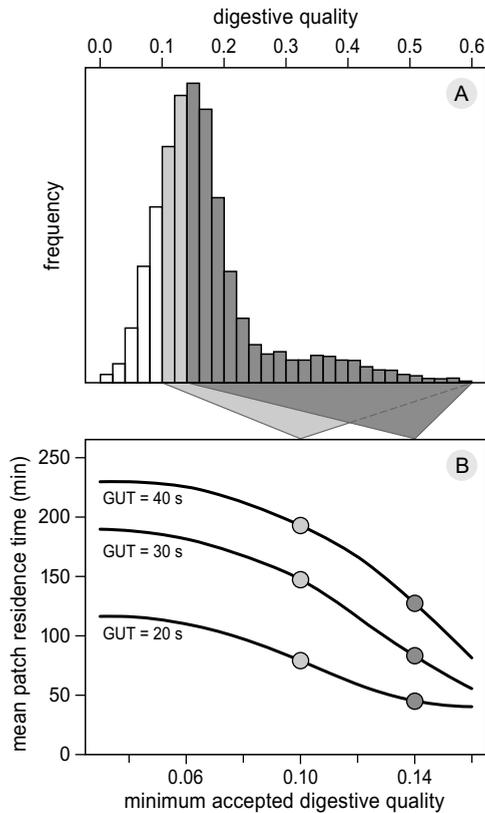


Figure 5.6 Proof of principle: simulating the effect of prey preferences on patch residence times using measured prey abundances. (A) Given the observed densities and frequency distribution of prey qualities, a forager that accepts all prey above a quality of, for example, 0.14 (dark grey bars) perceives a lower prey abundance than an animal that accepts all prey above a lower quality of, for example, 0.10 (light and dark grey bars combined). (B) When assuming that all animals have a fixed searching efficiency and giving-up time (GUT), the animal that accepts all prey above a quality of 0.10 is expected to depart later (light grey symbols vs. dark grey symbols). Simulations for three different giving-up time values are shown. Average measured giving-up time was 33 s.

residence times from the statistical models and the simulations are of the same order of magnitude, as are the estimated effect sizes of gizzard mass (Fig. 5.7).

DISCUSSION

The results of this study validate the proposed positive correlation between gizzard mass and patch residence time in free-roaming red knots (Bijleveld *et al.* 2016, Fig. 5.3), and show that individual diet preferences can indeed explain the observed among-individual variation in gizzard mass and patch residence time (Fig. 5.7). In agreement with an earlier test in captive red knots, a reduction in gizzard mass did not cause an adjustment in patch residence times of free-roaming red knots (Fig. 5.4A and C). These results are consistent with the suggestion that gizzard mass variation is the consequence rather than the cause of behavioural differences in red knots (Bijleveld *et al.* 2014).

Individual differences in giving-up time

Consistent differences in parameters such as searching efficiency and giving-up time may explain part of the large residual variation in a mean patch residence times (Fig 5.3, Table A5.1). Fig. 5.7 shows that differences in giving-up time are expected to have a large effect on patch residence time. Indeed, variation in the observed giving-up times was high, and hence, these field measurements should be regarded as an indication of the order-of-magnitude rather than a precise estimate. In reality, giving-up time is expected to differ

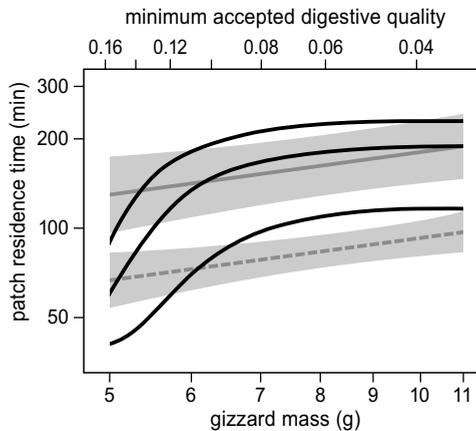


Figure 5.7 Predictions of the giving-up time model, compared to observed patch residence times. The black lines show simulated patch residence times as a function of gizzard mass for three giving-up time values (20, 30 and 40 s, from lower to upper line), assuming that birds maintain the gizzard capacity that is needed to fulfil energy demands on prey of the minimum accepted quality (upper x-axis). The thick grey lines show the loglinear regressions of the observed patch residence time against gizzard mass in the reference birds during the night (solid) and in daytime (dotted) (see Fig. 5.3). The 95% confidence intervals of the regressions are shown by the grey areas (only the uncertainty in the fixed effects of the regression model is considered). Note that the lower x-axis and the y-axis are log-scaled.

between individuals that differ in diet preferences and hence perceive a different food distribution, since giving-up time should depend on the expected prey encounter rate in the patch relative to the expected encounter rate in other patches (McNair 1982; Green 1984; van Gils *et al.* 2003b). This also may explain why the simulated values actually extended beyond the 95% confidence-interval of the mean observed patch residence times as a function of gizzard mass and time-of-day (Fig. 5.7). Birds with very small gizzards may in reality have higher giving-up times because their expected encounter rate may be lower in general.

Treatment effect

Although patch residence times were lower in the first days after the release than thereafter (Fig. 5.5), the treatment birds did not show lower patch residence times than expected from their original gizzard mass (Fig. A5.2). Contrarily, after a few days in the field, the treatment birds started showing a tendency for even longer patch residence times than expected from their original gizzard mass (Fig. 5.4B and D). This may have resulted from other potential effects of the treatment, including e.g. stress or feather damage. Furthermore, the temporary absence from the field in itself may have had short-term effects on mean patch residence times, for example, by influencing up-to-date information on the environment and social status among conspecifics.

Differences between night and daytime

Interestingly, patch residence times at night were longer than in daytime (Fig. 5.3). Because mollusc prey are sessile and are found by touch rather than by sight (Piersma *et al.* 1995), this is unlikely caused by day-night differences in searching efficiencies. Instead, we propose that the longer patch visits during the night were a consequence of predation avoidance behaviour. Predation risk is a factor known to influence habitat selection in general (Lima & Dill 1990), and is known to influence the spatial distribution of red knots at Banc d'Arguin (van den Hout, Spaans & Piersma 2008; van den Hout *et al.* 2014). Falcons and harriers are mainly active during the day, whereas owls are active mainly during the night (Bijlsma 1990; van den Hout *et al.* 2014). Differences in the effectiveness of escape behaviours may lead to longer patch residence times at night (Sitters *et al.* 2001; Gillings *et al.* 2005). Sitting still as a defence may be common in the night (Mouritsen 1992), whereas evasion by way of flocking flights (see van den Hout *et al.* 2009) may be more common during the day (Gillings *et al.* 2005; Conklin & Colwell 2007). Although the relative contribution of these effects remains to be studied, antipredation behaviour is likely to have had considerable influence on the observed foraging movements (Bijleveld *et al.* 2014).

The ontogenetic development of individual variation

Since many behavioural traits are known to be influenced by experience, and diet preferences in particular (e.g. Gillingham & Bunnell 1989; Whiteside, Sage & Madden 2015), the results of this study highlight the potential cascading effect of experiences on individual trait expression in general, behavioural as well as physiomorphic. Because individual

differences in trait expression are essential to take into account when estimating ecological dynamics on the population level (Araújo, Bolnick & Layman 2011; Bolnick *et al.* 2011), it is of importance to know the extent to which experience drives the expression of different traits, behavioural and physiomorphic alike. To this end, research on the ontogenetic development of traits and their consistency over the animal's lifetime is highly relevant (Stamps & Grootuis 2010a). For example, the influence of the environment on expression may decrease with age in some traits, but not in others (Senner, Conklin & Piersma 2015). Comparing these developmental effects between different populations may provide knowledge on the conditions that determine them. These may include, for example, the amount of spatial or temporal heterogeneity in prey density, prey quality and predation risk (as proposed by e.g. Gabriel *et al.* 2005; Mathot *et al.* 2012).

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DATA ACCESSIBILITY

Data is available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.2s8rr> (Oudman *et al.* 2016)

APPENDIX 5.1. Simulating patch residence times

Under the assumption that birds differ in the minimum digestive quality of prey that they ingest (Bijleveld *et al.* 2016), we constructed a quantitative simulation model to predict patch residence times of individuals with different digestive capacities (as expressed by gizzard mass). We also assume that the decision to leave a patch is a function of the expected encounter rate of acceptable prey, independently of previous encounters (e.g. van Gils *et al.* 2003b). For the sake of simplicity, we define that a bird will leave a patch when it does not encounter any acceptable prey within a critical period of time (giving-up time; Krebs, Ryan & Charnov 1974). When we further assume that red knots search for their prey randomly (van Gils *et al.* 2003b), the search times between prey encounters should be exponentially distributed. Residence times were estimated by drawing a sequence of search times from the exponential distribution with an average encounter rate of ax , where x is the density of acceptable prey (Olsson & Holmgren 1998; van Gils *et al.* 2003b) and a is searching efficiency ($4 \times 10^{-4} \text{ m}^2/\text{s}$; Piersma *et al.* 1995; de Fouw *et al.* 2016). The sequence ended when a search time was drawn that surpassed the giving-up time. Residence time was calculated by adding all search times and handling times (1 s per prey; de Fouw *et al.* 2016), with a maximum of 6 hours (the length of one low tide period).

Prey densities and prey qualities were estimated at 44 locations where foraging tagged red knots were visually observed, as described in the main text. The density of acceptable prey (individuals/ m^2) was estimated by dividing the total number of prey items with a predicted digestive quality above the minimum acceptable quality by the sampled surface area. The simulation was repeated 100 times for each observed prey density and the corresponding distribution of prey qualities, making a total of 4400 simulations. The model predictions in figures 5 and 6 were compiled by repeating these simulations for 27 different values of minimum accepted prey quality, ranging from 0.03 to 0.16.

Giving-up time was estimated by video-recording the observed tagged red knots. In 12 cases we registered a prey ingestion and a subsequent departure event. Time between the last prey capture and patch departure was on average 33 s, with a large standard error (SE = 18 s). Therefore, the procedure was repeated with different giving-up times (Fig. 5.5 in the main text; 20, 30 and 40 s). This shows that the absolute expected patch residence times were largely dependent on the giving-up time estimate. Nonetheless, the predicted change with diet preferences was similar (see Fig. 5.5 in the main text).

The relationship between diet preferences and gizzard mass was estimated by assuming that birds maintained the gizzard mass necessary to meet the required energy intake (appr. 0.2 mg ash-free dry flesh per second in Mauritania, van Gils *et al.* 2009) on prey of the least acceptable quality. Shell mass processing capacity has been shown to be a quadratic function of gizzard mass, $IR = 10^{-1.293}G^2$, where IR is the intake rate of dry shell mass (mg/s) and G is the gizzard mass (g) (van Gils *et al.* 2003a; Chapter 4).

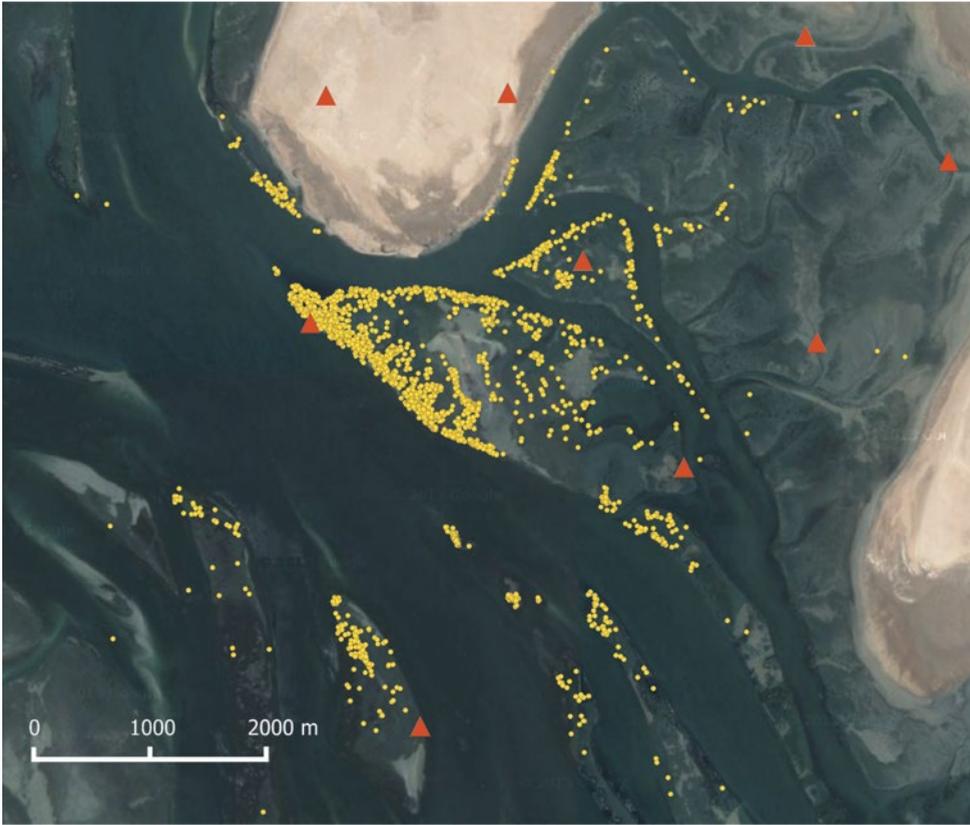


Figure A5.1 Map of all residence patches. Shown is an image of the research area, and the positions of all residence patches that were used in the analysis, marked as yellow dots. The islet of Zira is in the middle. Positions of the nine radio receiver stations are marked by orange triangles.

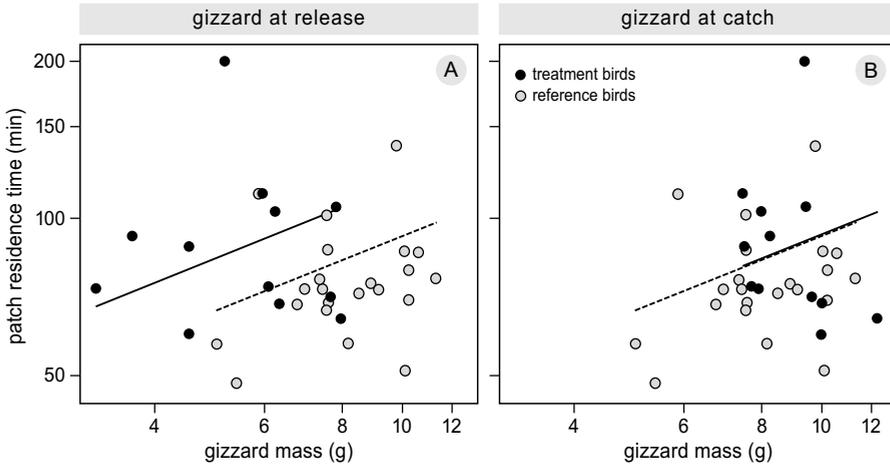


Figure A5.2 Patch residence times of the treatment birds during daytime on the first two days after release. Panels A and B are equivalent to Figure 5.3A and B respectively, except for that the data is restricted to the first two days after release of the treatment birds. During these two days, there was no tide during the night. Panel a shows patch residence time as a function of gizzard mass at release, panel b shows them as a function of gizzard mass at catch. Each dot is the mean value of one bird. Dashed lines show the statistical model predictions for the reference birds (model 1.1 in Table 5.1). Solid lines show the estimated intercept of the treatment birds, where the slope is set equal to the dashed line (models A1.2 and A2.1 in Table A5.2, in which model 1.1 is used as offset). Note that the axes are log-scaled.

Table A5.1 Parameter estimates of the best statistical models.

	Effects	Offset	Estimate	SE	t-value
Model 1.1	Intercept		1.49	0.16	9.36
	Gizzard	0.48	0.17	2.79	
	Night		0.29	0.06	5.13
	(1 Bird)		0.05		
	(1 Tide)		0.12		
	Residual		0.26		
Model 2.1		$1.49 + 0.48 * \text{Giz}^{\text{catch}} + 0.29 * \text{Night}$			
	Treatment		0.09	0.03	2.7
	(1 Bird)		0.09		
	(1 Tide)		0.14		
	Residual		0.26		
Model 3.1		$1.49 + 0.48 * \text{Giz}^{\text{release}} + 0.29 * \text{Night}$			
	Treatment		0.19	0.04	5.4
	(1 Bird)		0.10		
	(1 Tide)		0.14		
	Residual		0.26		

NB: All models are linear mixed-effects models (function 'lmer' in package 'lme4'), with $\log_{10}(\text{patch residence time})$ as response variable, measured in minutes. Parameters were estimated by maximizing the log-likelihood. Gizzard masses were measured in g and \log_{10} -transformed. $\text{Giz}^{\text{catch}}$ in the offset of model 2.1 refers to gizzard mass at catch, $\text{Giz}^{\text{release}}$ in the offset of model 3.1 refers to gizzard mass at release. (1|Bird) and (1|Tide) refer to the random variables Bird-ID and Tide-ID. Estimates of the random variables and the residuals refer to standard deviations from the fixed estimates.

Table A5.2 AICc comparison of statistical models, using only data from the first two days after release of the treatment birds.

Model	Fixed effects ^a	K ^b	ΔAICc	AICc weight	Cum. weight	LL ^c
A1.1	Offset(model 1.1, giz at catch)	3	–	0.68	0.68	–3.8
A1.2	Offset(model 1.1, giz at catch) + Treatment	4	2.13	0.24	0.92	–3.8
A1.3	Offset(model 1.1, giz at catch) + Treatment + Diet	5	4.24	0.08	1	–3.8
A2.1	Offset(model 1.1, giz at release) + Treatment	4	–	0.56	0.56	–122.4
A2.2	Offset(model 1.1, giz at release) + Treatment + Diet	5	1.39	0.28	0.84	–122.4
A2.3	Offset(model 1.1, giz at release)	3	2.47	0.16	1	–133.4

NB. Models are linear mixed-effects models (function 'lmer' in package 'lme4' in R), with tide-ID and bird-ID as random intercepts. Best models are in bold (Burnham & Anderson 2002). Parameters were estimated by maximizing the log likelihood. Log-transformed patch residence time is the response variable in all models, which is averaged per bird per low tide after transformation.

^a Models A1 contain gizzard masses as measured when the birds were caught, models A2 contain gizzard masses before release. Factor 'Treatment' refers to whether the bird was in the treatment group or the reference group. Diet refers to the diet group within the treatment group (either a soft diet or a partially hard-shelled diet).

To test whether the treatment birds deviate from the predictions derived from the reference bird data, the estimated coefficients of the fixed effects of model 1.1 are used as an offset in the models.

^b The number of parameters in the model.

^c Log likelihood.



Movement as an orchestration by the
environment: from grouping nomads to
solitary residents in one species

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ABSTRACT

Developmental and behavioural plasticity allow fine-tuning of movements to the environment. They can enhance individual variation in space use, but also underlie space-use patterns at the population level. Consequently, patterns of aggregation and site fidelity, usually considered species-specific, may reflect environmental context more directly than often assumed. We studied space use of red knots (*Calidris canutus*, a migratory shorebird) in two similar intertidal areas but with contrasting resource distributions, the Wadden Sea in The Netherlands and the Banc d'Arguin in Mauritania. Resource patches were much larger in the Wadden Sea, and red knots there showed strong aggregation and weak site fidelity, the opposite of red knots in Banc d'Arguin. We suggest that population space-use patterns reflect individual responses to the resource environment, implying direct consequences of environmental change on population space-use. This calls for studies on the individual development of movement that include the relevant environmental details.

INTRODUCTION

Animal space use is in continuous interaction with the environment, ultimately because all species characteristics that enable and limit movement evolve through natural selection in interaction with that environment (Nathan *et al.* 2008). More directly, individuals adjust to the environment via developmental plasticity in these characters (West-Eberhard 2003; Piersma & van Gils 2011). Even more directly, individuals adjust to their surroundings via individual decisions, which are informed by cues on environmental resources (e.g., Stephens & Krebs 1986). The latter two mechanisms may explain part of the individual variation *within* populations (Stamps & Groothuis 2010; Bolnick *et al.* 2011; Dall *et al.* 2012), also in space use (e.g., Spiegel *et al.* 2017). What has received less attention in movement ecology, is that the same mechanisms also cause differences *between* populations of the same species in different environments. Even if a trait shows little or no individual variation within a population, its expression may still be largely a consequence of plastic development and/or individual decisions, and hence a direct consequence of the environment (Piersma & van Gils 2011).

An ability to adjust space use to local circumstances would be a particularly helpful characteristic of migratory species, which in the course of an annual cycle encounter sequences of habitats (Greenberg & Marra 2005). Indeed, considerable variation in space-use patterns has been described within single migratory bird species, in terms of *aggregation* (e.g., Myers 1980; Ens 1983; Colwell 2000) as well as in terms of *site fidelity* (e.g., Tim Tinker *et al.* 2012; Patrick *et al.* 2014). Here, we define *aggregation* as spatial patterns in the locations of multiple individuals at one point in time (e.g., inter-individual distances, group size, sociality), and *site fidelity* as spatial patterns in the locations of single individuals over time (e.g., home range, return rate, exploration). Both are relevant when asking how movement patterns of foragers depend on the characteristics of the environment, and specifically the distribution and availability of resources. Matched observations with enough detail on both resources landscapes and population space-use, between individuals as well as over time, have only been too rare.

Aggregation and site fidelity: a concert, orchestrated by the resource landscape

Both the optimal degree of aggregation and site fidelity can be constrained by local resource density and depletion (Fretwell & Lucas 1970; Switzer 1993). Through competition, higher degrees of aggregation and site fidelity become increasingly incompatible as the local resource abundance decreases. To clarify this interaction, consider a landscape with a number of patches, each containing a number of resource units (Fig. 6.1). Ideal and free foragers move between resource-containing patches and consume one resource unit at each time step. Now consider different levels of aggregation and site fidelity by the foragers. In this context, we define aggregation as the number of individuals that simultaneously visit the same patch, and site fidelity as the number of time steps spent by an individual in the same patch. With the lowest degrees of aggregation and site fidelity (Fig. 6.1C, we could call these foragers “solitary nomads”), each visited patch needs to contain only one resource unit. In contrast, with full aggregation and full site fidelity (so-called

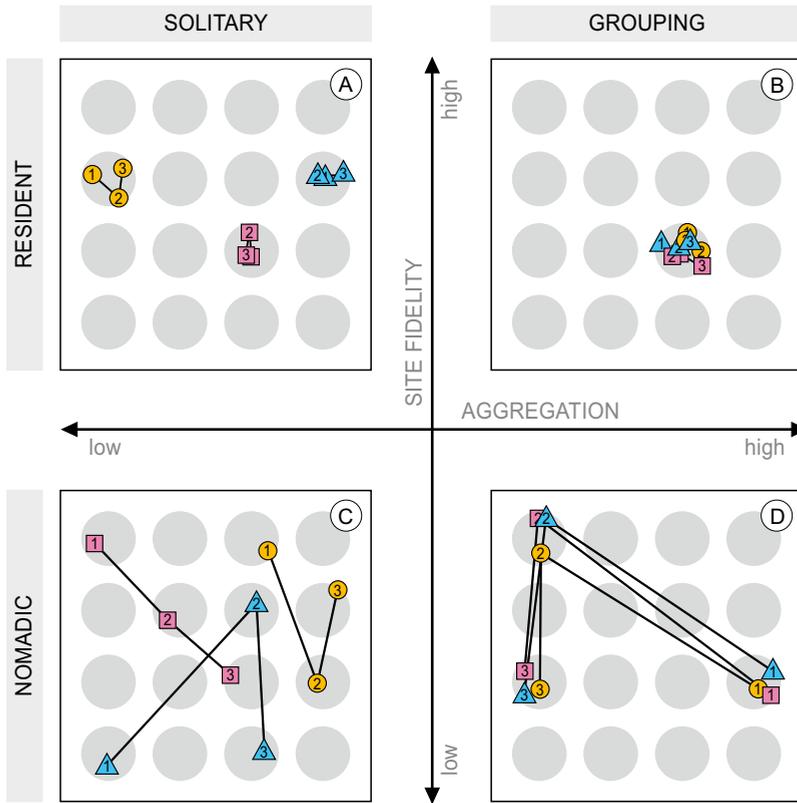


Figure 6.1 The two fundamental patterns in population space use, with degree of aggregation on the x-axis and degree of site fidelity on the y-axis. Simulations of the four extreme strategies are plotted in the panels, which we named “solitary residents” (A), “grouping residents” (B), “solitary nomads” (C) and “grouping nomads” (D). Of course, intermediate strategies also exist. Grey circles represent resource patches. Coloured symbols denote three different individuals, and the thin lines connect subsequent positions of the same individual in three time steps, which are denoted by the numbers in the symbols. Individual positions within patches are arbitrary.

“grouping residents” Fig. 6.1B), the patch needs to contain enough resources for each individual during all time steps. At intermediate resource abundances, either full aggregation (“grouping nomads”, Fig. 6.1A) or full site fidelity (“solitary residents”, Fig. 6.1D) are possible, but not both at the same time. Because the consequences of aggregation and site fidelity act in concert, understanding either one of them may require an understanding of both. Here, we make a start in studying them simultaneously.

Space use by one species in two contrasting environments

We exploited an opportunity to determine whether levels of site fidelity and aggregation were adjusted to local resource landscapes in a molluscivore specialist and migratory shorebird, the red knot (*Calidris canutus*) in superficially similar intertidal habitats that

contrasted in the distribution of food resources. The forager's morphological traits were similar in the two areas (Piersma 2007), which allowed to study the specific effect of the distribution of resources on forager movement behaviour. Using a novel automated tracking system with a high resolution both in space and time (MacCurdy *et al.* 2012; Piersma *et al.* 2014), detailed tracks of individual red knots were collected in the two main wintering areas of red knots along the East-Atlantic Flyway: the Wadden Sea in The Netherlands (53°15'N, 5°15'E), and the Banc d'Arguin in Mauritania (19°53'N, 16°17'W) (Piersma 2007).

Individual foraging itineraries were described as a sequence of patch visits during a single low tide period (Bijleveld *et al.* 2016). In both study areas, using exactly the same technology, we described (1) the degree of aggregation, i.e. whether red knots were distributed across the whole used area in each tide, or aggregated in part of it, and (2) the degree of site fidelity, i.e. whether individual tagged red knots visited the whole area used by the population, or showed individual site fidelity. To explain the differences observed, we compared differences in the resource landscape. These were based on standardized, spatially explicit resource sampling efforts (Bijleveld *et al.* 2012b), interpreted in the light of an experimentally tested diet-choice model (van Gils *et al.* 2005b; Chapters 2 to 4). This allowed the spatial mapping of potential intake rates, much more explicit and precise than indirect indices of food such as via satellite-based chlorophyll indices (e.g., Sims *et al.* 2008; Avgar *et al.* 2013; Hopcraft *et al.* 2014). We determined local food densities and the spatial scale of heterogeneity in the distribution of potential food intake rates in the two non-breeding areas. Comparing these to the scale of movement by red knots, we discuss whether these parameters explain the observed differences in the degree of aggregation and site fidelity of red knots between the two areas.

METHODS

Setting the scale

During low tide, red knots move over intertidal mudflats in search of buried mollusc prey, which they find by repeated probing of the sediment with their ca. 3.5 cm long bill (Piersma *et al.* 1995; van Gils *et al.* 2016). As the tide retreats, red knots fly to foraging locations, roughly 100 m to 10,000 m away from the roost, and visit one or several different locations before returning to the roost when the water returns (Bijleveld *et al.* 2016; Chapter 5). After landing, red knots search for prey on foot, and may walk 100 m or more between flights. Hence, red knots search for resources on two spatial scales. They move between foraging locations by flight, and move on foot within these locations.

Tracking red knots

In the Wadden Sea 47 red knots were tracked between 12 and 26 August 2011. At Banc d'Arguin, 46 red knots were tracked between 9 January and 13 February 2013. In the Wadden Sea we tracked the subspecies *C. c. islandica*, who spends the winter in intertidal systems in north-western Europe, including the Wadden Sea. At Banc d'Arguin, tracked

red knots were of the subspecies *C. c. canutus*, who winter in West-Africa, with a majority at Banc d'Arguin, and with some staging in the Dutch Wadden Sea in late summer when returning from the breeding grounds in Taimyr, north-central Siberia (Piersma & Davidson 1992; Nebel *et al.* 2000). The two subspecies are genetically barely distinct (Buehler & Baker 2005; Buehler *et al.* 2006), and occur in mixed flocks in the Wadden Sea (Nebel *et al.* 2000) where they cannot be distinguished visually (Nebel *et al.* 2000; van Gils *et al.* 2006). In the Wadden Sea in August, daily temperatures were roughly the same as at the Banc d'Arguin in January, and given the similarity in the tidal movements, so would be daily energy expenditures (Wiersma & Piersma 1994).

The 6.5 g radio tags (ranging from 5.5 to 7.5 g; <5% of body mass) were glued on the rump with Superglue (Warnock & Warnock 1993). Every sec the tags emitted an individual-specific radio signal, to be received by an array of receiver stations in the study area. When received by at least three receiver stations, the tag's location was calculated from arrival times at the different stations (Piersma *et al.* 2014).

The raw position data was summarized into a series of residence patch visits during each low tide period (2h before to 2h after low tide). This was done in four steps. First, the raw position data was median-filtered using a 5-point sliding window. Then, using a the method described by Barraquand & Benhamou (2008), the duration of stay within 125 m of each position was calculated, allowing excursions outside the radius for less than 30 sec. The resulting sequence of "residence times" was segmented by the penalized contrasts method (Lavielle 2005) into locations with an arrival and departure time. Finally, adjacent residence patches closer than 125 m were combined into one residence patch. Patch visits shorter than 10 min were not used in the analysis, because birds were then probably travelling rather than foraging (Bijleveld *et al.* 2016). The subsequent patch visits of a single bird during a single low tide period were defined as one foraging itinerary. This resulted in 144 foraging itineraries of 13 different birds in the Wadden Sea, and 1323 itineraries of 38 birds in the Banc d'Arguin. For further details we refer to Bijleveld *et al.* (2016) for the Wadden Sea study and Chapter 5 for the Banc d'Arguin study.

Measuring aggregation and site fidelity

The degree of aggregation can be calculated from location data by comparing the average distance between the locations of different individuals regardless of time, with the average distances between the locations of different individuals at the same point in time. Similarly, the degree of site fidelity can be calculated by comparing the average distances between all locations regardless of individual with the average distances between all locations of a single individual (an inverse measure of site fidelity, see Fig 6.1; Guilford *et al.* 2011; van Bemmelen *et al.* 2017). Figure 6.2 shows the result of these measures for simulated data of the four contrasting strategies (depicted in Fig. 6.1).

To compute an absolute measure of the mean distance between two red knot itineraries, the distance between them was calculated each 5 min from 2 h before to 2 h after low tide, as the shortest distance between the patch location in the first itinerary to the nearest patch location in the second itinerary within one hour (time relative to the low

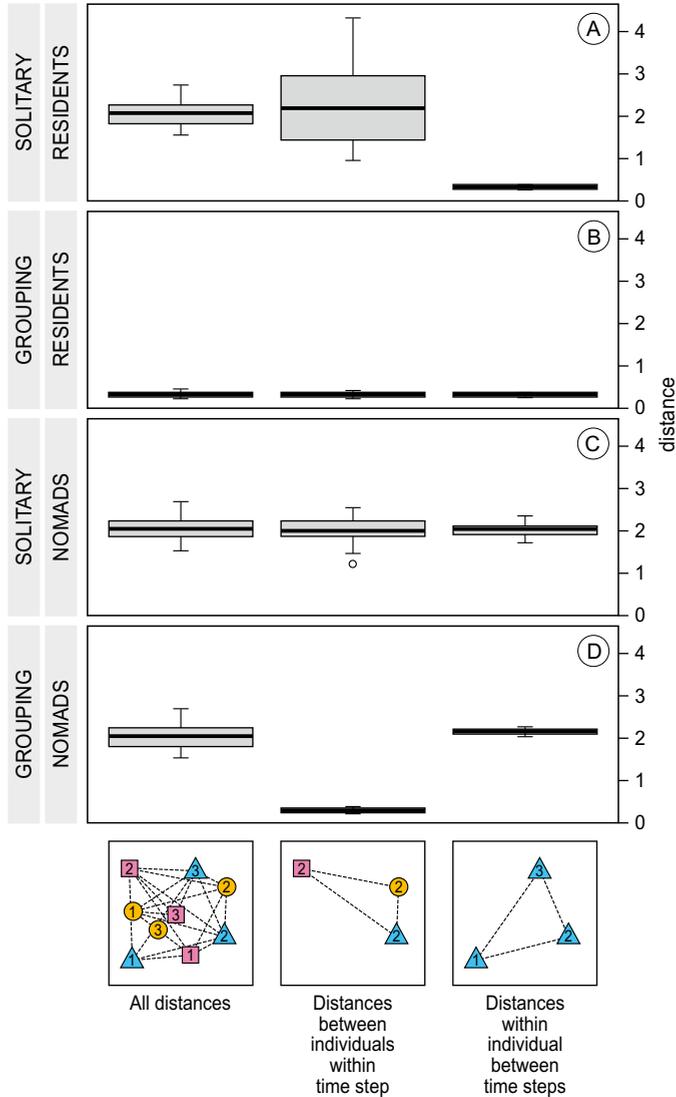


Figure 6.2 Mean distances between individuals in simulations of four different space use strategies. For each of the four extreme strategies shown in Fig. 6.1, data was simulated for 16 individuals during 16 time steps. Fig. 6.1 shows the first 3 time steps of 3 simulated individuals. The distance between neighbouring patches is taken as the unit of distance. Left boxes show the distances between all combinations of locations, averaged per individual. Middle boxes show the distances between all locations and the other locations in the same time step, averaged per individual. Right boxes show the distances between all locations and the other locations of the same individual, averaged per individual.

tide). These nearest-neighbour distances were averaged to obtain a single mean distance between the two itineraries, i.e. the mean nearest-neighbour distance. Because of a difference in behaviour between day and night (Chapter 5; Bulla *et al.* in review), daytime locations were only compared with other daytime locations, and night time locations were only compared with other locations at night. Locations recorded in the hour before sunrise and after sunset were not used at all. Mean distances between itineraries within birds in different low tide periods were calculated by averaging, for each itinerary, the distances to all other itineraries by the same bird. Likewise, mean distances between itineraries of different birds in the same low tide period were calculated by averaging for each itinerary the distances to all itineraries by other birds in the same tide.

Due to the complex structure of the data, significance of the observed differences between nearest-neighbour distances of all itineraries and nearest-neighbour distances between individuals within tides (to show aggregation), as well as the differences between nearest-neighbour distances of all itineraries and nearest-neighbour distances within individuals between tides (to show site fidelity) was tested by a repeated (10,000 times) randomization procedure. For each randomization, all tag-IDs and tide-IDs from the original itineraries were randomly re-assigned, the distances between all pairwise combinations of itineraries calculated and then averaged per itinerary, to arrive at a randomized estimate for the average distance between itineraries. To calculate a randomized estimate for its difference with between-individual distances within tides, tide-IDs were randomized per individual, all pairwise distances between itineraries within the same tide calculated, and then averaged per itinerary. To arrive at a randomized estimate for mean distances within individuals between tides, tag-IDs were randomized per tide, all pairwise distances between itineraries within the same tag calculated, and then averaged per itinerary. Significance was assessed by calculating the proportion of simulations that resulted in a more extreme difference than the actual observed difference (two-tailed p-value). To assess significance of differences between the Wadden Sea and Banc d'Arguin, mean-nearest neighbour distances were averaged per tag to arrive at independent observations, and tested by linear regression.

Resource sampling

The mollusc food of red knots was sampled at 880 locations in the Wadden Sea between 15 and 19 July 2011, and at 265 locations at Banc d'Arguin between 4 and 17 January 2013. Both sampling schemes consisted of a 250 m grid with a spatial accuracy of approximately 10 m, with an additional 20% locations placed randomly on the grid lines (Bijleveld *et al.* 2012b; Bijleveld *et al.* 2016). Samples were taken by pushing a core into the sediment to at least 20 cm depth, and sieving the top 4 cm over a 1 mm mesh (either one core with a surface of $1/56 \text{ m}^2$ or two cores of $1/112 \text{ m}^2$). All molluscs were collected and stored in 4% formaldehyde, except for bivalves longer than 8 mm in the Wadden Sea, which were frozen.

All individual molluscs were identified to the species level, and length was measured to the nearest 0.1 mm. Dry mass of the shell (DM_{shell}) and ash-free dry mass of the flesh ($AFDM_{\text{flesh}}$) was measured in a subset of the samples as described in Piersma *et al.*

(1993). Individuals below 8 mm (Wadden Sea) and 5 mm (Banc d'Arguin) in length were pooled before weighing when in the same sample. In *Limecola balthica* (until recently *Macoma balthica*), *Ensis directus* and *Mya arenaria*, flesh and shell were weighed together, and the ash-free dry mass of the shell was estimated with calibration lines from Zwarts (1991). The gastropod *Peringia ulvae* was also weighed as a whole, assuming that 12.5% of organic matter resided in the shell (Dekker 1979). For bivalve species weighed whole, DM_{shell} and $AFDM_{\text{flesh}}$ of the unweighted individuals were estimated by non-linear local regression of the log-transformed masses and lengths of the weighed individuals (Bijleveld *et al.* 2015a).

To determine which potential prey species contributed to the diet of red knots, we analyzed the composition of the droppings and calculated the relative contribution of different prey species to the diet (Dekinga & Piersma 1993; Onrust *et al.* 2013). Droppings were collected in the field at locations where radio-tagged red knots were observed foraging (2 – 10 droppings at 32 locations in the Wadden Sea and 45 locations in Banc d'Arguin). The droppings were aggregated per location and sieved over a 300 μm mesh. All bivalve hinges and last coils of gastropods were identified to the species level and measured. Each measurement was converted to an estimated $AFDM_{\text{flesh}}$ mass, using species-specific calibration measurements of whole individuals (Dekinga & Piersma 1993; Onrust *et al.* 2013).

Calculating potential resource intake rates

Potential intake rates (mg $AFDM_{\text{flesh}}$ per second) of the relevant mollusc species were estimated at each sampling station as a function of the observed densities by using an experimentally tested optimal diet choice model for red knots that takes into account search time, size-dependent handling time, size- and species-dependent digestive quality, and the toxicity of the main available prey species at Banc d'Arguin, *Loripes lucinalis* (Chapters 2 and 3). Digestive capacity varies among individual red knots, with diet and with season (van Gils *et al.* 2005a) and scales to the square of gizzard mass (van Gils *et al.* 2003a; van Gils *et al.* 2005b). Gizzard masses were measured by ultrasonography (Dietz *et al.* 1999; Dekinga *et al.* 2001) immediately after the catch, and were lower in the Wadden Sea (mean \pm SD, 7.0 ± 2.0 g) than at Banc d'Arguin (8.5 ± 1.8 g). This resulted in predicted maximum processing rates of $2.5 \text{ mg } DM_{\text{shell}} \text{ s}^{-1}$ in the Wadden Sea and $3.7 \text{ mg } DM_{\text{shell}} \text{ s}^{-1}$ at Banc d'Arguin (note that only those mollusc species were taken into account that were estimated to comprise at least 1% of the red knots diet, in terms of $AFDM_{\text{flesh}}$). Search efficiency was estimated at $6.4 \text{ cm}^2/\text{s}$ in the Wadden Sea (Piersma *et al.* 1995) and, due to obstruction by seagrass roots, at $2.0 \text{ cm}^2/\text{s}$ at Banc d'Arguin (de Fouw *et al.* 2016). Handling times (s) were assumed to be a function of shell size, previously estimated for *Cerastoderma edule* as $3.3 \times \text{length} [\text{cm}]^2$ (Piersma *et al.* 1995). The relevant molluscs at Banc d'Arguin (*Loripes lucinalis*, *Dosinia isocardia*, *Diplodonta circularis* and *Abra tenuis*) were assumed to have handling times similar to *Limecola balthica* ($2.1 \times \text{length}^2$ when buried at an average depth of 2 cm) (Piersma *et al.* 1995), as they are all relatively flat and round burying bivalves with a smooth surface. The toxin constraint on the intake of *Loripes lucinalis* was set at $0.1 \text{ mg } AFDM_{\text{flesh}} \text{ s}^{-1}$ (Chapter 2).

The distribution of resources

To determine range of autocorrelation in the resource landscape, spatial autocorrelation in the predicted AFDM_{flesh} intake rates was calculated at discrete distances of 50 with the function “correlog” in R-package “ncf” (R Core Team 2015), using *Moran’s I* index as the measure of autocorrelation (Kraan *et al.* 2009a; Kraan *et al.* 2009b; Bijleveld *et al.* 2016). The autocorrelation range was estimated by the distance at which the spatial autocorrelation went below 0.1, which can be interpreted as a measure of resource patch size (Kraan *et al.* 2009a).

RESULTS

Aggregation and site fidelity of tagged red knots

In the Wadden Sea, during each low tide red knots aggregated in some part of the total foraging range; mean distances between itineraries *in the same tide* were significantly smaller than the mean distances between *all* combinations of itineraries (on average 1900 m and 2500 m, $p < 0.001$, Fig. 6.3A). Red knots did not show site fidelity in the Wadden Sea, as mean distances between itineraries *of the same bird* were not significantly smaller than the mean distances between *all* combinations of itineraries (both 2500 m on average, $p = 0.09$, Fig. 6.3A). These differences agree with the differences in the simulated data of “grouping nomads” (Fig. 6.2D).

In contrast, red knots at Banc d’Arguin showed strong site fidelity, as mean distances between all combinations of itineraries *of the same bird* were much smaller than mean distances between *all* combinations of itineraries (on average 600 m and 1600 m, $p < 0.01$, Fig. 6.3B). Red knots at Banc d’Arguin also did aggregate, but the area used per tide was only slightly smaller than the area used by the study population. Distances between itineraries of birds in the same tide were on average 100 m smaller than distances between *all* combinations of itineraries (1500 m and 1600 m, $p = 0.01$, Fig. 6.3B). These differences agree best with the simulated data of “solitary residents” (Fig. 6.2A).

Note that all absolute distances averaged per bird in the Wadden Sea were larger than at the Banc d’Arguin (2500 and 1600 m, $F_{1,49} = 27.3$, $p < 0.001$), suggesting that overall the tagged red knots used a larger area within the range covered by the receiver stations in the Wadden Sea than at Banc d’Arguin. Average distances between tagged birds within the same tide were also larger in the Wadden Sea than at the Banc d’Arguin (1800 and 1500 m, $F_{1,49} = 4.5$, $p = 0.04$).

Resource densities and resource patch sizes

Maximum resource densities, in terms of available ash-free dry flesh mass per square meter, were much larger in the Wadden Sea (26.2 g AFDM/m²) than in Mauritania (7.7 g AFDM/m²). Nevertheless, due to the various constraints that red knots face on intake rate, particularly their digestive and toxin constraints (van Gils *et al.* 2005b; Chapter 2), the mean potential resource intake rates (mean \pm SD, 0.07 ± 0.10 mg AFDM/s in the Wadden Sea and 0.09 ± 0.08 mg AFDM/s in the Banc d’Arguin, $p > 0.1$), as well as the maximum

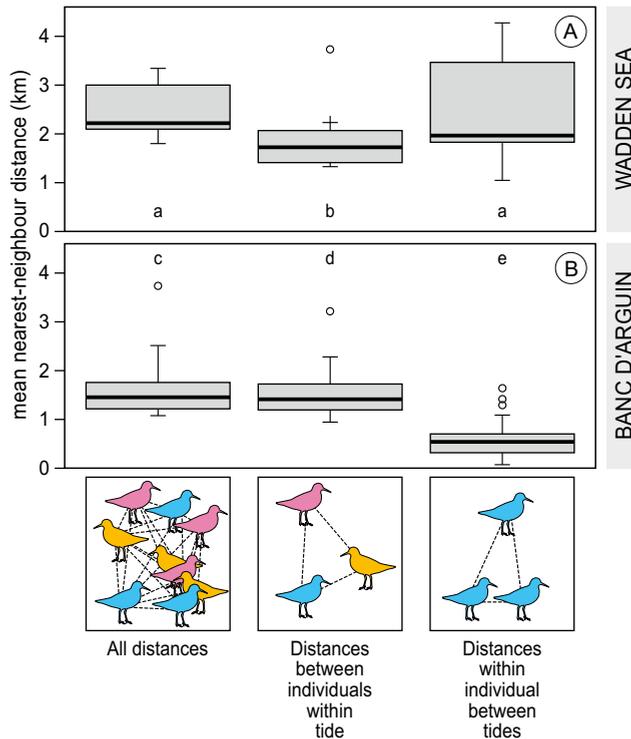


Figure 6.3 Aggregation and site fidelity of red knots in the Wadden Sea and at Banc d'Arguin. Shown are the mean distances between all itineraries (left), the mean distances between itineraries of the same bird in different low tide periods (middle, a measure of site fidelity), and mean nearest-neighbour distances between itineraries of different birds during the same low tide (right, a measure of aggregation). Data is averaged per bird. Boxes a, b, c, d and e differ significantly from each other.

potential resource intake rates (0.28 mg AFDM/s in the Wadden Sea, and 0.40 mg AFDM/s in Banc d'Arguin) were similar in the two areas (Fig. 6.4). However, the intercept as well as the range of spatial autocorrelation intercept in the potential resource intake rate was strikingly different between the Wadden Sea (intercept = 0.97, range = 1700 m) and Banc d'Arguin (intercept = 0.18, range < 50 m, Fig. 6.5, Table 6.1). Hence, the size of resource patches strongly differed. In the Dutch Wadden Sea, estimated patch size was on average larger (1700 m) than the Banc d'Arguin (50 m, the minimum resolution allowed by the measurements, Figs 6.4 and 6.5, Table 6.1).

Dropping analyses showed that during the studied red knots in the Wadden Sea had a virtually monospecific diet, which for more than 99% of the estimated consumed ash-free dry flesh mass consisted of *Cerastoderma edule* (Table 6.1). In Banc d'Arguin, four different species each contributed more than 10% to the diet (Table 6.1). In addition, on average 15% of the dropping dry mass in Banc d'Arguin consisted of plant material (ranging between 0 and 85%), presumably rhizomes of seagrass *Zostera noltii* (van Gils *et al.* 2016).

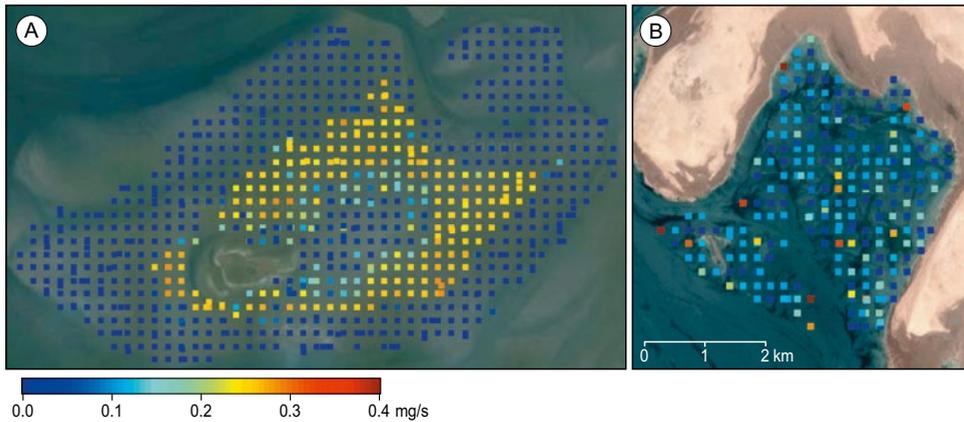


Figure 6.4 Intake rate by red knots in the Wadden Sea (A) and at Banc d'Arguin (B) predicted on the basis of estimates of food abundance using grid-sampling. The two maps are to scale, and each square represents one sampling location. The potential intake rate of ash-free dry flesh mass (AFDM_{flesh}) was calculated by an experimentally tested diet choice model. Calculations were based on mollusc species making up at least 1% of the red knot's diet (Table 6.1). Differences in mean digestive capacity between the tagged Wadden Sea and Banc d'Arguin red knots were taken into account.

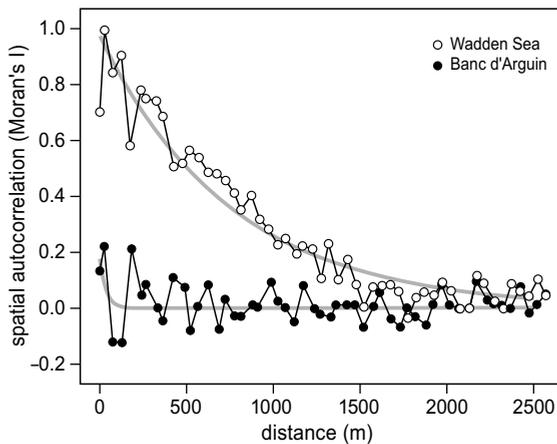


Figure 6.5 Correlogram of estimated maximum AFDM_{flesh} intake rates in the Wadden Sea and at Banc d'Arguin. Spatial autocorrelation was estimated by calculating Moran's *I* values, based on the estimated potential AFDM_{flesh} intake rates at the sampling stations shown in Fig. 6.4. Grey lines show exponential regression of the Moran's *I* values.

DISCUSSION

In the Wadden Sea red knots showed aggregation, but no site fidelity, whereas at Banc d'Arguin red knots showed strong site fidelity, but barely any aggregation. We will discuss how these differences can be explained as a consequence of differences in the benefits and costs of aggregation and site fidelity. Because predicted individual energy intake rates and expenditure levels were similar, we will focus on the spatial grain of the resource distributions. We also discuss the potential influences of individual diet specializations and predation risk in explaining the observed differences between the areas.

Aggregation and site fidelity: in need of a joint theory

Until now, aggregation and site fidelity have structurally been studied with different methods. The commonly used framework that relates the resource landscape to forager aggregation is the ideal-free model and its descendants (Fretwell & Lucas 1970; Sutherland 1983; Tregenza 1995). This simplistic model has been successful as a null

Table 6.1 Diet proportion, availability and spatial autocorrelation of molluscs in the Wadden Sea and at Banc d'Arguin.

Species ^a	Proportion in diet ^b	Numerical density (1/m ²)	AFDM _{flesh} (mg/m ²)	Autocor. intercept	Autocor. range ^c (m)
Wadden Sea					
<i>Cerastoderma edule</i>	0.99	762	760	0.51	900
<i>Limecola balthica</i> ^d	<0.01	31	268	0.04	0
<i>Peringia ulvae</i>	<0.01	427	134	0.52	1600
<i>Ensis directus</i>	<0.01	35	70	0.26	600
<i>Mya arenaria</i>	<0.01	40	38	0.44	1100
<i>Abra tenuis</i>	<0.01	36	34	0.52	700
AFDM _{flesh} intake rate (mg/s) ^e				0.97	1700
Banc d'Arguin					
<i>Loripes lucinalis</i>	0.51	251	1337	0.63	400
<i>Diplodonta circularis</i>	0.19	8	101	0.03	0
<i>Dosinia isocardia</i>	0.16	25	77	0.00	0
<i>Abra tenuis</i>	0.14	32	31	0.65	0
<i>Senilia senilia</i>	<0.01	6	29	0.15	200
AFDM _{flesh} intake rate (mg/s) ^e				0.18	50

^a Only mollusc species with more than 10 mg AFDM_{flesh} per m² that are in the upper 4 cm of the sediment and ingestible by red knots.

^b AFDM_{flesh} proportion of all listed mollusc prey in the diet, based on dropping data (hinge measurements).

^c Range is defined as the distance at which the spatial autocorrelation drops below 0.1. The autocorrelation function is estimated by exponential regression of the Moran's *I* index at discrete distances. Species specific autocorrelation functions are based on the summed AFDM_{flesh} density at each location.

^d Until recently *Macoma balthica*

^e Autocorrelation function of the predicted intake rate (see Fig. 6.5), taking in account only those prey species that had an estimated average proportion of more than 0.01 in the diet.

hypothesis to deduce which mechanisms underlie patterns of aggregation (Fretwell 1972; Sutherland & Parker 1985; Switzer 1993; van Gils *et al.* 2006). However, this approach has been less useful in explaining site fidelity patterns, because it does not predict individual movement, but only the resulting population distribution at a given moment in time. The study of the relation between the resource distributions and site fidelity has been approached mainly by modelling individual movements (Switzer 1993; Börger *et al.* 2008; Bartumeus *et al.* 2016; Spiegel *et al.* 2017; Bastille-Rousseau *et al.* 2017) and the empirical analysis of individual tracks (Weimerskirch 2007; Barraquand & Benhamou 2008; Fryxell *et al.* 2008; van Moorter *et al.* 2016; Bastille-Rousseau *et al.* 2017). However, models of individual movement generally do not consider the interactions between conspecifics that form the basis of the ideal-free model approach, and as a consequence they do not predict the degree of aggregation. The consequence is that their interplay basically goes unaccounted in theoretical predictions of space use.

Benefits and costs of aggregation

Aggregation allows shared vigilance for predators and decreases per capita predation risk (Lima & Dill 1990), as well as the communication of social information (Giraldeau & Caraco 2000). Red knots use social information to assess foraging opportunities; they observe and respond to the foraging success of others (Bijleveld *et al.* 2015b). However, foraging success of conspecifics provides information on foraging opportunities only within the spatial autocorrelation range of resources, i.e. within a resource patch. Hence, the benefits of aggregation increase with increasing spatial heterogeneity in the resource distribution.

The main cost of forager aggregation is competition for resources (Pulliam & Caraco 1984). When resource abundance is below the level at which the functional response rate reaches a plateau (e.g., Duijns *et al.* 2015), then aggregation will decrease the *per capita* resource intake rate (Vahl *et al.* 2005; Bijleveld *et al.* 2012a). As resource density increases, the cost of aggregation lowers. In some particular cases, e.g., when culling enhances prey growth rates, aggregation may even increase resource availability (Fryxell 1995; Giraldeau & Caraco 2000). Hence, the optimal degree of aggregation depends both on absolute resource density and on the scale of spatial heterogeneity. When both local resource abundance and autocorrelation range become higher, aggregation is expected to increase. Indeed, this can explain why red knots aggregated more strongly in the Wadden Sea, where maximum resource abundance was much higher and resource patch size much larger than at Banc d'Arguin.

Benefits and costs of site fidelity

As site fidelity allows animals to return to good patches and stay away from bad patches, high fidelity is beneficial for individual foragers especially when the difference in quality between different foraging locations is high, i.e. when spatial heterogeneity is high (Switzer 1993; van Moorter *et al.* 2016). Qualitative differences between patches in heterogeneous landscapes may be enhanced from the viewpoint of the forager if local experience increases the energy intake only there, e.g., because of spatial differences in

prey species composition (Estes *et al.* 2003; Araújo *et al.* 2011), or through phenotypic effects of previous experiences (Piersma & van Gils 2011; Bijleveld *et al.* 2016). High site fidelity has costs when foraging has consequences for resource availability through depletion (Sutherland & Anderson 1993) or predator avoidance behaviour by the prey (Lima & Dill 1990).

In the Wadden Sea, the average distance between used foraging locations ranged from 2 to 3 km (left box in Fig. 6.3A). The spatial range of resource intake autocorrelation was 1700 m (similar to previous years; Kraan *et al.* 2009a), but Fig. 6.4A shows that the resource landscape in the year of study actually consisted of one large resource patch stretching over more than 4 km. Hence, even though the terrain as a whole shows large heterogeneity, the used area was relatively homogeneous. At Banc d'Arguin, the average distance between used foraging locations ranged from 1 to 2 km (left box in Fig. 6.3B). This is a much larger distance than the measured autocorrelation range of resources there, estimated at 50 m or less (Figs 6.4B and 6.5). This means that there is a large potential difference in maximum resource intake rate between locations. This provides an explanation for the high site fidelity, and it may also help to explain the low degree of aggregation. Resource density is low at Banc d'Arguin, and because foraging patches are small and site fidelity is high, there may simply not be enough resources to have high site fidelity and maintain a high degree of aggregation (Fig. 6.1).

Because resource patches were smaller than the inter-sample distance, the resource sampling scheme at Banc d'Arguin is likely to have missed many foraging patches (Figs 6.4B and 6.5). Indeed, red knots found locations where potential resource intake rate was high, in between our sampling locations where it was not (Appendix 6.1, Fig. A6.1).

Predation risk

Predation risk is a main determinant of habitat quality for red knots in Banc d'Arguin (van den Hout *et al.* 2014; Chapter 5) as well as the Wadden Sea (Piersma *et al.* 1993). However, the large differences in space use between the Banc d'Arguin and the Wadden Sea are unlikely to be explained by differences in predation risk (Piersma 2012). Being depredated mainly by falcons, which attack by surprise from behind concealing habitat structures such as ridges of dunes, predation pressure will be relatively low when foraging on the offshore intertidal mudflats (van den Hout *et al.* 2016). Indeed, predation is thought to mainly take place in the two hours before high tide (Bijlsma 1990), a period that was not included in the analyses. Moreover, even when spaced out, shorebirds maintain the potential to coalesce into tight flocks when necessary (Myers 1980; van den Hout *et al.* 2009).

Conclusions and future directions

This study shows that in superficially very similar habitats and at similar energy expenditure levels, contrasts in the spatial grain of food resource distributions can lead a single species (and probably single individuals in different seasons, see below) to show highly diverse patterns of aggregation and site fidelity, behavioural adjustments which seem to be adaptive. We encourage theoreticians working on individual movement decisions to

emphasize the interaction between aggregation and site fidelity, thereby bridging the current gap between the advanced mathematical models of individual movement and the classic ideal-free model literature that has provided so many ecological predictions.

Secondly, although our results stress the overriding importance of the environment in explaining differences in space use, the results do not show to what extent individual foragers can adjust their space use to the environment. This begs for research on how individual animals develop and adjust their behavioural strategies to resource landscapes. Did the different observed strategies evolve to be individually innate, or are they the result of plastic development or behavioural flexibility in response to the environment (West-Eberhard 1989; Danchin *et al.* 2004; Piersma & van Gils 2011)? The high phenotypic similarity between the two populations under study (Piersma & Davidson 1992; Piersma *et al.* 1993), and especially the observation that *canutus* red knots seem to blend in with *islandica* red knots when visiting the Wadden Sea during migration (Piersma *et al.* 1993; Nebel *et al.* 2000), imply that these birds continuously adjust their space use behaviour to their environment. Such observations call for a more inclusive theory of animal space use, and emphasize the need for measurements, with enough relevant detail, of the resource landscapes experienced by tracked individuals. Right now, it is not the tracking technology that limits progress (Kays *et al.* 2015), but the grain size at which we can measure relevant aspects of the environment.

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APPENDIX 6.1. Additional sampling at foraging locations at Banc d'Arguin

The estimated range of resource patches in the Banc d'Arguin, 50 m, was smaller than the inter-sampling distance of 250 m. Given the low autocorrelation intercept (*Moran's I* = 0.18), resource patches may have been smaller than the sampling accuracy, approximately 10 m. Therefore, it is expected that many resource patches were actually missed by the sampling grid. To verify this, we additionally performed an alternative sampling scheme, based on the idea that red knots are the champions when it comes to finding resource patches. Sampling locations were determined in the field. Two observers with telescopes searched for tagged red knots in the field, careful not to disturb foraging flocks of red knots. When a tagged red knot was observed, usually from a distance of 150–250 m, the knot and its precise location was carefully observed. After flying away, one of the observers was guided to the exact foraging location by the other observer. The location was stored in a GPS, and eight wooden picks were placed at foraging traces (holes left by a red knot bill, droppings, or footprints). A sample was taken at each of the picks within the following week, according to the same protocol as described in the main text, but on foot during low tide rather than by boat during high tide.

Given that red knots need an average energy intake of $0.2 \text{ mg AFDM}_{\text{flesh}} \text{ s}^{-1}$ to maintain a stable body mass in Banc d'Arguin (van Gils *et al.* 2009), only 7% of the locations in the sampling grid in the Banc d'Arguin harboured enough mollusc biomass (Fig. 6.4B). Contrarily, at 70% (34 out of 44) of the locations where tagged birds were observed foraging, at least one sample surpassed this threshold (Fig. A6.1). This way of sampling uncovered many more resource patches than the grid (compare Fig. A6.1 to Fig. 6.4B)

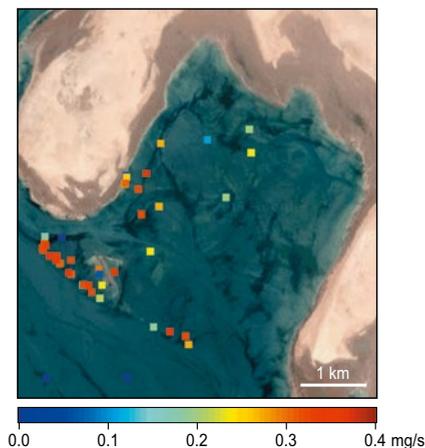


Figure A6.1 Potential intake rates by red knots at additional sampling locations at Banc d'Arguin. See Appendix 6.1 for explanation of this additional sampling scheme. Each square refers to one location, and the colour refers to the potential intake rate ($\text{mg AFDM}_{\text{flesh}} \text{ s}^{-1}$) at those locations. Samples with higher intake rates are plotted on top of samples with lower intake rates. Spatial scale and colour scale are equivalent to Fig. 6.4.

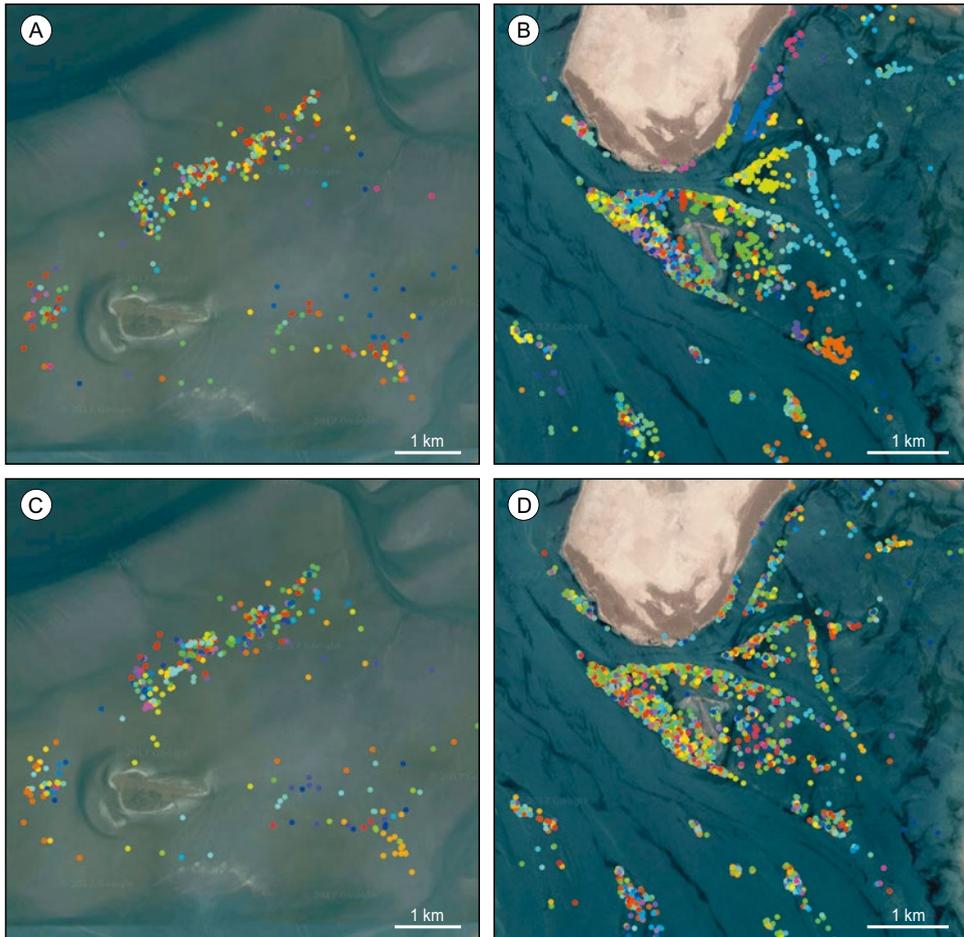


Figure A6.2 Map of residence patches of tracked red knots in the Dutch Wadden Sea (A and C) and at Banc d'Arguin (B and D). Each dot denotes one residence patch. In panels A and B, each colour denotes a different individual. Panels B and D show the same residence patches, but now each color refers to a single low tide period. Note that the spatial scale differs between the panels.



Chapter 7

General Discussion



Thomas Oudman

“With habitat and food selection - behavioural phenomena - playing a major role in the shift into new adaptive zones, the importance of behaviour in initiating new evolutionary events is self-evident.”

Ernst Mayr (in *Animal Species and Evolution*, 1963, p. 604)

This thesis examines the details of the foraging ecology of a single species at a few selected sites. In the previous chapters, the relevance of the findings for ecology in general is only briefly, and usually quite implicitly, addressed. In an attempt to place the results presented in wider contexts, in this last chapter I will allow myself more speculative reasoning. Firstly, I will discuss how and when the active diet selection observed in red knots and presented in Chapters 2 and 3 may contribute to ecosystem stability. Secondly, I will discuss the implications of the observed relationships of diet choice with gizzard mass (Chapters 4 and 5) and with habitat selection (Chapters 5 and 6) for the ontogeny of individual foraging specializations and the development of individual phenotypic variations more generally. Finally, in an attempt to contribute ideas for future research, I will discuss the potential contribution of the interaction between behavioural decisions and development to the processes that generate heritable variation (Piersma 2007). To what extent do behavioural decisions contribute to the phenotypic divergence between populations?

PREY CHOICE AND ECOSYSTEM STABILITY

We (humans) have had enormous impacts on the way that our world looks today. Ecological investigations make us aware that our activities change the Earth's biodiversity. The observation that so many species now face the danger of extinction does not come as a surprise to most ecologists, although it is often difficult to explain which of the many potential causes is most important. Rather, we have been wondering at least since Aristotle why so many species do *not* go extinct, and instead persist in coexistence (Hutchinson 1959).

This question has been difficult to answer. Ecosystems are complex: they consist of many (and often non-linear) intra- and interspecific interactions in ever changing environments. Therefore, one of the more appealing answers to this question is that the complexity itself stabilizes ecosystems. The idea that "complexity begets stability" was formalized by Robert MacArthur (1955), who suggested that the opportunities for stable coexistence between species increases as the number of interactions between species increases. Eighteen years later, this argument was convincingly destroyed by Robert May (1973) who showed that the stable parameter space of a given population actually decreases when more species are added to a model system of linear differential equations. One of the mechanisms that might explain the apparent contradiction between this prediction and the observed natural world, is that foragers adjust their behaviour to changing conditions, and particularly to changing prey populations.

Behavioural responses of foraging red knots

In this thesis, we have investigated the behavioural responses of foraging red knots to the complex environment offered by the seagrass-covered intertidal mud- and sandflats of the Banc d'Arguin. Firstly, we described how the main mollusc prey types cause red knots at Banc d'Arguin to choose a mixed diet, instead of taking the single most preferred prey (Chapters 2 to 4). These so-called partial preferences comprise a reaction to the different

constraints that different prey types pose to their consumers. These different constraints are expected to lead to individual differences in food preferences as a consequence of physiological differences among individuals (Chapter 4). An analysis of the arrows of causality underlying the correlation between behaviour and physiology, suggested that individual food preferences actually determine individual differences in gizzard mass and movement decisions rather than the other way around (Chapter 5). We proposed that individual red knots at Banc d'Arguin learn specialized foraging strategies to individually optimize prey consumption rates locally.

Diet choice and population dynamics

Theoretical studies have investigated the long-term consequences of consumers foraging on multiple prey species (focussing on indirect interactions between prey species known as apparent competition; Holt 1977). They find that such systems are generally unstable (Holt 1977; Holt 1984; Bonsall & Hassell 1997), leading to the extinction of one or several (prey) species. As the authors acknowledge, this is not what we see in nature, as there are many examples where coexisting prey species share a single species that consumes them. Many additions have been suggested by which such interactions could be part of a stable food web. These include the presence of spatial and temporal heterogeneity of the environment (Tilman 1994) and niche differentiation among prey and consumer species (Hutchinson 1959). I wondered whether individual diet choice could also be one of them. After all, our findings sketch a picture of behavioural adjustments in foraging red knots that allow for more complex individual diets in reaction to a more complex resource landscape. When habitat complexity increases, so may the variety of potential prey and also the variety of constraints on prey intake. The diet of individual consumers may not just include more species, but also the number of considerations that influence dietary decisions may increase. Could this have qualitative consequences on the population dynamics of prey species?

The history of prey choice in population models

The emergence of studies on habitat- and diet selection was sparked by the idea that they should provide a deeper understanding of population dynamics and species interactions (MacArthur & Levins 1964; MacArthur & Pianka 1966). Murdoch (1969) was the first to formalize population dynamic consequences of diet choice. He proposed 'switching' as a potential explanation for stable coexistence of species. This involves a consumer that prefers the most common of two prey types so that as their availabilities change, the consumer may switch its focus from one prey type to the other (assuming that searching for one prey type precludes finding the other). Since then, a rich body of work on adaptive diet choice has been built over several scientific generations (for reviews see eg. Stephens & Krebs 1986; Houston & McNamara 1999). This work has primarily focused on foraging behaviour itself, sometimes on the short-term consequences of the feedback between prey density and adaptive foraging behaviour, but rarely on long-term ecological consequences. Only the most basic ideas of optimal diet choice have been implemented in population models. These models typically assume a single axis of prey quality, usually

profitability (energy over handling time), and model the optimal acceptance probabilities after encounter (p_i) of both the 'main' and an alternative prey type that is less profitable, as a function of their densities (Fryxell & Lundberg 1994; Křivan 1996). A 'partial preference' may occur ($0 < p_i < 1$), but never for more than a single prey type. These modelling studies conclude that adaptive foragers can in some cases stabilize multi-prey systems that would be unstable with a *rigid* forager, but only under specific conditions in a small parameter range. Fryxell and Lundberg (1994) therefore conclude that adaptive diet selection is unlikely to be a ubiquitous stabilizing factor in trophic interactions.

Some studies underline that animals may not have necessary information to make perfect choices (Kotler & Mitchell 1995). This justifies the use of slightly sub-optimal feeding strategies, which introduces the possibility of partial preferences for more than one prey species (Fryxell & Lundberg 1994; van Baalen *et al.* 2001; Abrams & Matsuda 2003). It turns out that dynamics are especially sensitive to these model changes. As the prey densities at which partial preferences occur for two prey species increases, the parameter range of stable coexistence of the two prey species also increases (Fryxell & Lundberg 1994; Abrams & Matsuda 2003).

There may be other, larger, and more fundamental mechanisms that cause partial preferences for multiple prey types. The described studies all modelled prey choice as the result of a fixed preference hierarchy (prey type A is preferred over prey B is preferred over C). Not only humans, but also red knots and several insects (Mayntz *et al.* 2005; Jensen *et al.* 2012) are shown to make more complex diet choices than to have a fixed hierarchy of prey preferences. In previous chapters (Chapters 2, 3 and 4) we have shown elaborately that partial preferences for two prey species are actually the optimal strategy for energy-maximizing red knots in Banc d'Arguin, and in other cases where multiple constraints act on a forager's food intake simultaneously. Hence, modelling of partial preferences by red knots as exhibited in Banc d'Arguin may change the predicted population dynamic interaction between red knots and their bivalve prey.

A population model of red knots and their main prey

In our study system, at least in the years investigated, mortality of adult red knots takes place mainly in winter (Leyrer *et al.* 2013). This implies that their survival may be largely determined by the abundances and condition of their bivalve prey in Banc d'Arguin. In Chapter 3 we show that annual survival is indeed correlated with the availability of food there, but not with the abundance of their most abundant prey species (not even when assuming a type-II functional response taking into account search, handling and digestion time). Only when adding prey choice to the equation as a function of prey toxicity and digestive quality, a correlation between food availability and yearly survival emerges. This implies that prey choice is an essential asset in the response of red knot population size to the density of their bivalve prey. However, to show the significance of prey choice not only to red knots themselves, but also to their prey (and via their prey to the rest of the food web), a change in the long-term population dynamic interaction between red knots and their bivalve prey should be demonstrated. A simple comparison between annual total prey intake by red knots and yearly secondary production of bivalves does not suffice,

because they tend to be highly interdependent (van der Meer, Piersma & Beukema 2001). To arrive at a more relevant expectation, this interdependency should be made explicit; it demands a population dynamical model.

An important aspect when modelling this system is the occurrence of discrete events in the annual cycle of both red knots and their bivalve prey, causing at least partial decoupling between their population dynamics. Red knots breed in the High Arctic. This has two important consequences. Firstly, their reproductive success should be - at least partly - independent of food conditions in the Banc d'Arguin, and determined by the situation in the Arctic (van Gils *et al.* 2016). Secondly, the temporary absence of red knots during the summer months means a strong decrease in predation pressure for bivalves. Bivalve reproduction at Banc d'Arguin is also a discrete event, in the case of *Loripes lucinalis* happening twice a year (in January/February and in July/August; van der Geest *et al.* 2014), with the second one being more significant for the two main prey species of red knots, *L. lucinalis* and *Dosinia isocardia* (Ahmedou Salem *et al.* 2014). Hence, the large majority of juvenile bivalves become available to red knots within a short time period, just before or after their return from the breeding grounds.

However, the annual number of juvenile bivalves that survives to the size at which they become available to red knots (at approximately at 2 mm length) is only to a certain extent determined by the abundance of reproductively active adults. Food limitation, availability of suitable sediment and predation of larvae influence their survival (Ólafsson, Peterson & Ambrose 1995) and diffuse the relation between the extent of predation of bivalves by red knots over the winter and their recruitment in the following autumn (van der Meer, Beukema & Dekker 2001; van der Meer, Piersma & Beukema 2001). Obviously, the nature of this stock-recruitment relation is key in determining the effect of prey choice by red knots on the long-term interaction between red knots and their bivalve prey.

In a preliminary modelling exercise, I circumvented the lack of data on the stock-recruitment relation by modelling two extreme scenarios. In the first scenario *Loripes* and *Dosinia* recruit to a fixed population size in one discrete event annually at 1 October. The system is modelled with a series of discrete difference equations in which the total per capita prey intake by red knots is calculated each day. Daily red knot survival decreases below a standard survival probability when the per capita energy intake rate falls below the minimum requirements. A mortality term is then added that increases linearly towards a maximum when no food is consumed. All adult red knots (older than 1 year), and half of the juveniles, are assumed to leave the system each year on 1 June and return on 1 October. A new juvenile cohort then also arrives, that is 30% of the adult population size.

Obviously, a long-term effect on bivalve populations is absent in this scenario. What this model does allow though, is a consideration of the effect of diet selection on the equilibrium density of a dynamic red knot population. When red knots optimize the acceptance probabilities of *Dosinia* or a *Loripes* according to the predictions of the diet choice model (see Appendix 7.1), the predicted equilibrium density of red knots is expected to be roughly 1.5 times larger than when red knots do not distinguish between them and maximize prey intake rate indifferent of the prey type (T. Oudman and V. Hin, unpublished

data). In this scenario, equilibrium densities of red knots strongly depend on the timing of red knot arrival in autumn relative to the recruitment date of the bivalve populations, which were here both assumed to be on 1 October.

In the second scenario, I determined whether the bivalve populations either benefit or suffer from optimal diet choice by a constant red knot density. The populations of *Loripes* and *Dosinia* are now assumed to exhibit continuous logistic population growth. Now the red knot population is assumed to be constant, and hence independent of the bivalve populations. The system is modelled by a set of two continuous differential equations, describing the population dynamics of *Loripes* and *Dosinia*. Per capita growth rates r_l and r_d (individuals/s), fitted to result in a realistic equilibrium densities at an intermediate density of red knots, and K_l and K_d are set at maximum observed densities of *Loripes* and *Dosinia*, roughly 2000 and 400 individuals/m² (J.A. van Gils, unpublished data). The per capita intake rates of *Loripes* and *Dosinia* by red knots are the same as in the previous scenario (see Appendix 7.1). Equilibrium densities of *Loripes* and *Dosinia* as a function of red knot density were determined by numerical continuation of bifurcations, using the Matcont package in Matlab (Dhooge, Govaerts & Yu 2003). In this scenario, the range of red knot densities resulting in stable non-zero populations of *Loripes* and *Dosinia* is roughly 1.3 times larger when assuming optimal prey choice instead of an indifferent forager (T. Oudman and V. Hin, unpublished data). At red knots densities where both optimal and indifferent diet choice lead to stable bivalve populations, adaptive diet choice generally leads to higher equilibrium densities of *Loripes*, but lower densities of *Dosinia* than in case of no diet choice.

The preliminary analyses suggest that optimal prey choice by red knots is expected to have a positive influence on prey persistence when red knot density is constant, and on red knot population persistence when annual initial prey densities are constant. This implies that prey choice in this system may indeed have a positive effect on the coexistence of red knots and their bivalve prey in Banc d'Arguin. However, whether these positive effects of adaptive prey choice on population sizes will be maintained when they are allowed to interact in a fully dynamic model remains to be tested. It should be clear that the density-dependent rates of reproduction and growth in *Loripes* and *Dosinia*, as well as alternative prey types, need to be carefully described to arrive anywhere near an accurate prediction of the population dynamics.

INDIVIDUAL VARIATION: A DEVELOPMENTAL PERSPECTIVE

One of the most eye-catching features of the red knot body can actually not be seen with the bare eye for as long as the bird is alive. It is its muscular stomach, the gizzard. Gizzard masses can vary between healthy red knots from 4 to 15 g on a total body mass of ca. 120 g, even in a single mist net catch (e.g. Chapter 5). Red knots are not alone in showing plasticity in gizzard mass (Piersma, Koolhaas & Dekinga 1993), but the variation that is observed between individuals within one population at the same time is remarkable. This makes red knots particularly suited to study individual variation. Since variation in

gizzard size was first considered, the question has been whether diet choice is either a cause or a consequence of gizzard size (Piersma, Koolhaas & Dekinga 1993; Piersma 1994; van Gils 2004; Bijleveld 2015). This thesis is largely an extension of these studies, showing how diet preferences are expected to change with gizzard mass (Chapter 4), and considering individual diet preferences as a cause of variation in gizzard size (Chapter 5). Foraging experiments and optimal foraging theory have proven their value as tools to gain insight in the relation between gizzard size and diet, and the interactions between the environment and red knot behaviour. But can these tools be used to infer the causes of individual variation?

The limitations of optimal foraging theory

In attempts to lift ideas from “story telling” to explicit, quantitative hypotheses that allow an examination of the logical implications and a testing of the congruence between theory and observation, optimal foraging models are used to formalize expectations (Stephens & Krebs 1986). In the diet choice models (Chapter 2 to 4) as well as in the movement models (Chapters 5 and 6) we have assumed that foraging red knots optimize their diet choice with the objective to maximize their energy intake rate, and have been explicit on the different constraints that they face (limited time for searching and handling prey, a digestion limitation, and a toxin limitation on the intake of *Loripes lucinalis*). These comprise specifications of the general assumption of optimal foraging theory, which states that the animal under study has evolved to choose the “optimal diet”, that is the diet that is expected to maximize the currency that determines fitness, given the constraints that the animal faces (Stephens & Krebs 1986).

Stephens & Krebs (1986) see this approach as a respectable attempt to move beyond the classic ‘adaptationist approach’, which acts on the false idea that each trait is separately adapted by evolution (Gould & Lewontin 1979). I agree, although optimal foraging theory cannot be entirely excused either, because it fundamentally assumes a strict distinction between traits that are constraints and traits that are to be optimized. It may be true on the short time scale on which a single decision is made (to accept or to reject a prey, to stay or to move elsewhere), but on a slightly longer time scale, the forager may actually not just adjust its diet to fit its constraints, but also adjust these constraints to better fit its diet.

I will provide two examples for red knots. The first is that in the optimal diet models that we used, search efficiency and handling time are assumed to be fixed parameters. In reality, they will at least partly be the result of the diet, because individual experience in foraging on a specific diet increases the foraging efficiency on that diet (Davis & Stamps 2004; Villalba, Provenza & Han 2004). Hence, the optimal diet is not simply a consequence of handling time and search efficiency, the diet feeds back to increase search efficiency and decrease handling time on that specific diet. This would increase the ‘optimality’ of that diet. Similarly, and this is the second example, as discussed in Chapters 4 and 5, gizzard mass is not a fixed constraint either. To large degree, even the first studies on gizzard size in red knots have suggested it to be adjusted to the previous diet (Piersma, Koolhaas & Dekinga 1993; Dekinga *et al.* 2001). The diet is not just limited by digestive

capacity, but there is a feedback by the diet to adjust the limit set by digestive capacity towards its requirements for that diet (see also Bijleveld 2015). Consequently, the assumption that underlies the optimal diet tests in red knots, namely that red knots maximize their energy intake rate given the digestive capacity of their gizzard, is somewhat self-evident if gizzard size is on the long term adjusted to the realized intake rate. If that is the case, red knots will appear to be maximizing their energy intake rate with respect to their gizzard mass even when their actual strategy is to reduce intake rate to the minimum required energy intake (the so-called ‘satisficer’ strategy).

These two examples show that the difference between optimized traits and constraining traits is in fact arbitrary on a longer timescale. Many (if not all) traits to some extent interact with other traits, and should ideally be incorporated in the trade-offs that determine the theoretical optimal phenotype. Although the response rate may be slower as we move from behavioural traits such as prey preferences, via physiological traits such as digestive capacity, to structural traits such as bill size (page 197 in Bijleveld 2015), this does not imply any order in how different traits are to be prioritized when optimizing the phenotype to the environment. It also does not imply the extents to which plasticity is involved in the expression of these traits (Piersma & van Gils 2011; Stamps 2015). Before an optimization model can predict individual variation in the phenotype, it must include the limitations in the plasticity of each trait, and the costs that are involved in its adjustment. To determine these limitations, it must be acknowledged that traits adjust at different paces (Bijleveld 2015) and may be plastic during certain ages but not at others (Bateson 1979; Desai & Hales 1997).

Studying the limits of plasticity is necessary when wanting to infer the role of behaviour in the origin of individual variation in a wild population. This begs for experimental studies over longer timescales, at all ages (Stamps 2003), and in the context of the natural environment (Gilbert 2001; Senner, Conklin & Piersma 2015).

Development of diet preferences and gizzard size

The observation that adult red knots do not adjust their preferences after a change in gizzard mass (Chapter 5), shows that diet choice is not directly influenced by gizzard size. This does not reveal how individual diet preferences were formed in the first place, and whether digestive capacity played a role in it (Chapter 5; Mathot, Dekinga & Piersma 2017). Dietary preferences are influenced by individual experience early in life (Distel & Provenza 1991; Provenza & Cincotta 1993; Estes *et al.* 2003). In mammals, they are influenced by experiences even before birth through food particles that pass the placenta and during weaning by the mother milk (Nolte & Provenza 1991; Nolte *et al.* 1992), in that way being “softly” inherited. In red knots, conception and breeding takes place on the tundra where both parents and hatchlings feed on insects. Mother leaves the hatchling after the eggs have hatched, and father leaves after taking care for another 2–3 weeks. Juveniles migrate without their parents, so when they land on a mudflat for the first time, they do so without their parents. Although we cannot rule out the possibility that hatchlings entirely inherit their parents’ dietary preferences, it is likely that preferences are influenced by dietary experiences during their first attempts to forage on mudflats, along

the flyway or after arrival on the wintering grounds. If so, then temporal and spatial variation, both considerable on the mudflats of Banc d'Arguin and on mudflats in general, help to explain individual variation in diet preferences.

This individual variation in dietary experiences may be amplified by inherited individual variation in gizzard size, or differences in its plasticity, which limits the range of potential dietary experiences. Similarly, pre-existing variation in exploratory behaviour, as proposed by Bijleveld *et al.* (2014), will help to further divert individual differences. Because the resulting preferences in turn affect gizzard mass, and may also influence the development of personality (Dall *et al.* 2012), we cannot make a distinction between traits that cause, and traits that follow the development of the individual phenotype.

Developmental canalization

To clarify the developmental approach to the role of behaviour as a source of individual variation in red knots, I now turn to a widely used graphical metaphor introduced by Conrad H. Waddington (Waddington 1942; Waddington 1953). To clarify his ideas on the interaction between genes and the environment during development, he drew a sloping surface, the epigenetic landscape (Fig. 7.1A), that is shaped by the complex interactions between the genes (Fig. 7.1B). In that landscape a ball, representing the development of the individual, starts at the top and rolls down the slope. The rolling ball, and the continuum of locations where it may end up at the end of the slope, denote the continuum of different phenotypes. It is then proposed that selection has acted on the surface of the epigenetic landscape, such that canals have been formed that stabilize development; a single genetic mutation usually has only little or no impact on the surface. As a consequence, the ball does not roll down the slope at random. Development of the phenotype is *canalized*. The environment is brought into this metaphor as an external stimulus that may push the ball sideways, and alter the canal into which the ball rolls.

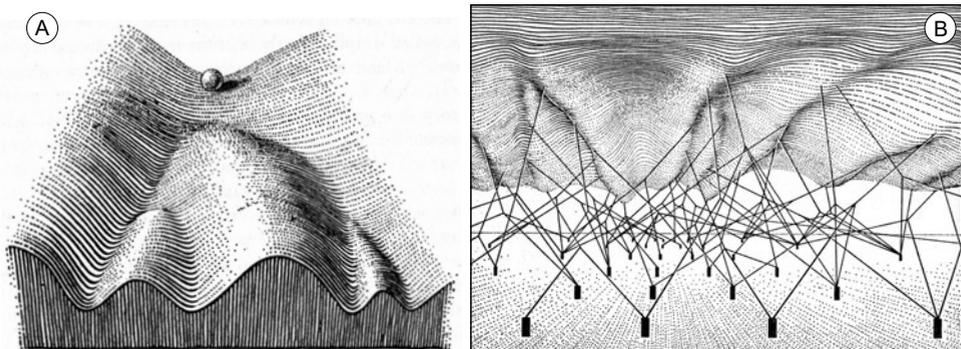


Figure 7.1 The original drawing of the epigenetic landscape as envisaged by Waddington viewed from above (A), showing a ball that is canalized (representing the phenotype) while rolling down a slope (representing development), and viewed from below (B) to show the complex interactions (the ropes) between genes (the pegs) that shape the landscape (Waddington 1957).

Behaviour as the sum of genes and environment

We can think about behaviour from a developmental perspective by asking how behaviour should be represented in the epigenetic landscape. One could argue that behavioural traits should be included in Waddington's landscape just like any other phenotypic trait: the expression of a behavioural trait is determined by the complex interaction between genes, including plasticity in the response to environmental circumstances. The relation between gizzard mass and diet preferences can then be reduced to a genetic coupling between the two. The genetic basis of behaviour is being studied with the help of another classic metaphor, the 'reaction norm' (Dingemans *et al.* 2010). In this metaphor, both the environment and some specific behavioural trait are represented by a one-dimensional gradient. The relation between the two, for a single genotype, is drawn by a curve in the plane spanned by the environment and the potential expressions of the behavioural trait. This curve can be drawn for any genotype, because it assumes that the expression of a behavioural trait is the result of a genetically coded plastic response to the environment. This implies that although behaviour may interact with other traits during development, individual variation in behaviour or any other trait can be decomposed into a genetic and an environmental part.

Behaviour as a force in itself

An alternative view is that the causes of individual variation cannot be reduced to its environmental and genetic components (Lewontin 2001; Bateson 2005; Jablonka & Lamb 2005; Laland *et al.* 2015). A main argument is that "the environment" is not a simple gradient, but the result of complex interactions between many environmental factors, very much like the genetic interactions that underlie the epigenetic landscape (Noble 2015). In addition, the environment will not be constant during development (Stamps 2003). During development, coincidental combinations of different environmental factors can lead to many, potentially novel, expressions of behavioural traits (Baldwin 1896; West-Eberhard 2003), which can be selectively incorporated by the organism (e.g. through learning) and have a major influence on development. As a consequence, behavioural responses to the environment often cannot be traced back to the genes, but should instead be considered as a primary source of variation (Jablonka & Lamb 2005). Another, and related, argument is that the environment cannot be defined without the animal that inhabits this environment (Lewontin 2001). Behaviour allows organisms to influence their own environment, either by habitat selection or by physically altering it (Darwin 1881; Waddington 1959; Lewontin 1983). Individuals can also influence each other's behaviour via social information (Avital & Jablonka 2000; Hoppitt & Laland 2013).

In this view, behaviour influences development in two ways. It is a force that (1) exploits coincidence and conspecific behaviour to create directional phenotypic variation, and (2) changes the environment in which development takes place. As such, behavioural differences may be a powerful source of individual variation in many traits (Stamps 2003; Piersma & van Gils 2011). Such behavioural forces, forces that may influence the path of development, are not explicit in Waddington's epigenetic landscape (Fig 7.1). It is hard to imagine how the path of the ball would influence external forces. To accommodate this

notion in the metaphor, we may turn it upside down (very carefully though, to respect the functionality of the original position for other purposes). Instead of the genetic interactions, we could imagine all factors shaping the environment as pegs; their complex interactions shape the environmental landscape, and shape the separate developmental canals in which the ball may roll. Behaviour can then be viewed as a force that influences the ball's sideways movement, perhaps from inside the ball. Genes and other sources of developmental constraint can be thought of as external forces, that limit the ball's sideways movement. Individual decisions may bring the ball in a direction that comforts the individual, although they must be allowed by the external forces, the developmental constraints. But the individual cannot see the future; it cannot look down the slope to see in which canal it will end up. Hence, sideways movements by the ball may be intentional, but this implies no knowledge of the canal in which it rolls. Rather, the decisions to move sideways may be guided by an evolved biased quality space (Dennett 2001); the organism can use its senses to provide it with a feeling about good or bad. For example, stomach ache may help an animal to judge a novel prey type, and gather "nutritional wisdom" (Richter 1943; Stephens & Krebs 1986). It may decide not to forage on foods that cause stomach pain, alter its searching behaviour and thereby change its environment; it may change the developmental canal in which it rolls. Similarly, the looks and behaviour of a stranger may help an animal to decide whether it should flee or not, or even copy its behaviour, and have "social wisdom". Of course the feeling will not necessarily be right, but it certainly makes novel behavioural variation in reaction to a new environment non-random (Jablonka & Lamb 2007).

Learning as a pathway of inheritance

If learning influences the development of behaviour, and that learned behaviour can be transmitted socially, it follows that learning is a non-genetic pathway of inheritance (Jablonka & Lamb 2005). Similarly, if individuals construct their environment, and with that influence the environment of the next generation, this can also be regarded as a pathway of inheritance (Lewontin 1983; Jablonka & Lamb 2005; Piersma & van Gils 2011). Just as in the evolution of human psychology, this complicates the question of which proportion of individual variation is of environmental origin and which of genetic origin, to the extent that the question itself becomes questionable (Bateson 2005). To explain the developmental origin of individual variation, is not enough to assess the statistical relationship between a behavioural trait and the level of genetic relatedness. Also the other pathways must be considered. How do individuals learn about food selection? How does the animal learn which habitat to select? How do these choices influence the environment to which the animal adjusts its phenotype?

That the ability to learn appears to be widespread especially among mammals, may be a consequence of our mammalian perception of the world (Laland & Hoppitt 2003). Researchers have questioned why songbirds and parrots, with their wonderful ability to imitate sound, did not evolve any sophisticated traditions in natural populations (e.g. page 174 in Jablonka & Lamb 2005). These researchers were thinking of symbolic language as we use it, but the cognitive abilities that these birds display may well be used in other

complex behaviours (e.g. Templeton, Laland & Boogert 2014). When certain habits are passed from generation to generation via social learning, we could call them traditions (Avital & Jablonka 2000). Examples of traditions across animal taxa are increasing exponentially, in vertebrates as well as invertebrates (Avital & Jablonka 2000; Hoppitt & Laland 2013). Also the effect of social learning on behavioural variation in wild populations is increasingly recognized (Healy & Rowe 2014). Studying traditions in the wild rather than in the laboratory may be a particularly fruitful exercise, because the expression and the function of complex behaviours may become apparent only when studied in the environmental setting in which the behaviour has actually evolved (Healy & Rowe 2014).

The next step is to show how socially induced behavioural variation interacts with physiological and structural traits in the course of development. What is the importance of the social inheritance pathway in producing the individual variation – not only in behaviour but in the phenotype in general – that we observe in wild populations? Is the red knot a suitable study species to answer this question?

RED KNOT TRADITIONS

Traditions are habits, passed from generation to generation by social learning (Avital & Jablonka 2000). The ecosystems in which red knots are studied, covering wintering and staging areas across the globe, provide a uniquely rich toolbox to study the causes and consequences of behavioural habits, and their relation with physiological and morphological traits. This is exemplified by the number of dissertations on the subject (Piersma 1994; van Gils 2004; van den Hout 2010; Leyrer 2011; Folmer 2012; Bijleveld 2015; de Fouw 2016). With the availability of this toolbox, the red knot may be an ideal model species to study how social learning affects development (Piersma 2011). May differences in red knot habits in between areas involve behavioural traditions? And might these traditions be involved in shaping other parts of the phenotype? Could behavioural traditions even influence the evolutionary divergence of these populations?

Traditions in habitat selection

Knowledge on the ontogeny of red knot behaviour and the role of social learning in the development of individual red knots is largely lacking. Nonetheless, the scientific literature on red knots does provide several clues to suggest that red knots use social information to decide where to forage. Firstly and most importantly, red knots are a classic example of a social foraging species (Goss-Custard 1970). Beyond doubt, habitat selection by red knots largely depends on habitat selection by conspecifics. More specifically, patch choice by captive red knots depended on the success of conspecifics in those patches, and the time to locate a food patch decreased with increasing group size (Bijleveld *et al.* 2015). Bijleveld *et al.* (2010) suggested that communal roosting enables red knots to gather public information on where to forage. Furthermore, (van den Hout *et al.* 2016) showed that juvenile red knots in Banc d'Arguin forage in more dangerous places than adults. The

authors suggest that this is due to a social hierarchy that prevents juveniles to forage where the adults do. This implies that habitat selection by red knots in the Banc d'Arguin involves a great deal of social interactions. In addition, red knots there show highly consistent foraging routines and are highly site faithful (Chapter 6), even over multiple years (Leyrer *et al.* 2006; T. Oudman, unpublished data).

The observed importance of social interactions for habitat selection opens up the possibility for the emergence of traditions. If juvenile red knots arrive in Banc d'Arguin after their first migration from the Arctic, the adults in general already have arrived and have come to a spatial distribution. The juveniles must then decide on where to forage, and it is likely that this decision is influenced by the distribution of the adult population. If juveniles are indeed 'forced' to feed at certain places by the adult population, and later as adults do the same to new juveniles, this means that social structures determine early-life experiences and the development of foraging routines. A tradition is passed from generation to generation.

Dietary traditions

Considering that mudflats are highly heterogeneous habitats (e.g. Chapters 5 and 6), habitat selection has far-reaching consequences on the diet. If the habitat selection of juveniles is influenced by adult habitat selection, so is the resource availability that juveniles encounter after their arrival in the wintering area. Hence, resource availability, perhaps the most important aspect of the environment (Piersma 2012), is not a given to which they must adapt; it is partly constructed by their conspecifics. Consequent diet choice will depend on this availability and is potentially influenced by genetic variation, but may also be influenced by the foraging habits of conspecifics. Although purely speculative, it is easy to imagine that dietary habits such as the consumption of toxic *Loripes lucinalis* in Mauritania, or the 'slurping' of *Hydrobia ulvae* in the Wadden Sea is transferred socially.

An observation to provide some credibility to this speculation is that red knots do not instantaneously start consuming artificial food items in captivity (Piersma, Koolhaas & Dekinga 1993). Captive red knots encounter trout pellets, *trouvit*, for the first time in their lives after it is presented to them in captivity, where it is often used as staple food. Virtually all red knots initially ignore this food and may continue to do so for several days before they sample it. Some will even starve without touching *trouvit*, but most red knots will try, and after some initial hesitation prefer pellets even over a bivalve diet (Piersma, Koolhaas & Dekinga 1993). Interestingly, captured red knots are more likely to start eating pellets when a conspecific is placed in their cage that is familiar with pellets (T. Piersma and A. Dekinga, unpublished data). Presumably, this is because their motivation to consume this new food type increases by watching another red knot do it. This implies that red knots may at least partly build up food preferences by learning through social information.

Another interesting case is the currently popular dietary habit by red knots in Mauritania to consume seagrass rhizomes. Isotope data from 2002 to 2015 (van Gils *et al.* 2016, van Gils *et al.* in prep) shows that this behaviour has increased in recent years (Figs

2A and C). Could it be that seagrass consumption is a recent discovery by red knots that is learned by social interactions? If so, the spread of seagrass foraging among the red knots of Banc d'Arguin is the mudflat equivalent of the famous example in blue tits and great tits near Southampton, England, that invented the behaviour to remove the caps from milk bottles, which was socially transmitted across the UK within a few years (Fisher & Hinde 1949; Aplin, Sheldon & Morand-Ferron 2013).

The proportion of seagrass in the diet has been proposed to be an adaptive dietary response to the combined changes in the density of bivalves and a change in the population distribution of a morphological trait (van Gils *et al.* 2016). The average bill size of juveniles has been reducing in recent years, a proposed consequence of an increasing mismatch between hatching date and the insect peak in the Arctic (van Gils *et al.* 2016). This may lead to a lower availability of bivalves in the diet, as a larger proportion is buried too deep to be reached. As predicted from this hypothesis, the proportion of seagrass in the diet is higher in years where the maximum intake rate of bivalves is low, due to their limited availability (Figs 2B and D, van Gils *et al.* in prep). Unfortunately, the annual predicted intake of bivalves is collinear with time (Pearson's coefficient -0.73). Therefore, their explanatory powers cannot be separated statistically.

A sudden increase in the expression of this behaviour without a change in densities of any prey type would have been a strong case for the birth of a new tradition. This does not mean that seagrass foraging cannot be explained as a tradition. The consumption of seagrass may be a behaviour that is expressed by all red knots when the availability of other prey is low, but that does not imply how the behaviour is inherited.

Traditions and developmental canalization in red knots

The possibility of foraging traditions in red knots is particularly exciting because we have so many clues already on the intricate relation between diet, physiology and morphology. Once it would be shown that traditions play a role in the diet of red knots, there is a rich literature to substantiate its potential influence on the development of the entire phenotype. Recalling my own version of Waddington's landscape, traditions in red knot diet choice can be represented as a path in the environmental landscape that was formed by earlier balls (other individuals), and a certain preference by the ball to follow that path. A tradition has the potential to lead the ball into directions that otherwise would not have occurred, even though in principle it would have been able to do so. The individual just wouldn't have thought of it, or it wouldn't have thought it to be a good idea. Red knot traditions may induce the development of phenotypes that otherwise would not occur.

Let me take the consumption of seagrass as a hypothetical example of a tradition. A behaviourally induced increase in this behaviour changes the requirements of the digestive tract, and is likely to have consequences for gizzard mass and gut morphology. Seagrass foraging may also influence the microbial content of the gut and particularly the caeca, which influence the digestibility of plant material. Red knots have well-developed caeca (P. Battley, unpublished data), which in many herbivore and omnivore birds contain high concentrations of gut bacteria, helping the digestion of plant material (McNab 1973). In humans, microbial communities in the gut make up an important phenotypic trait that

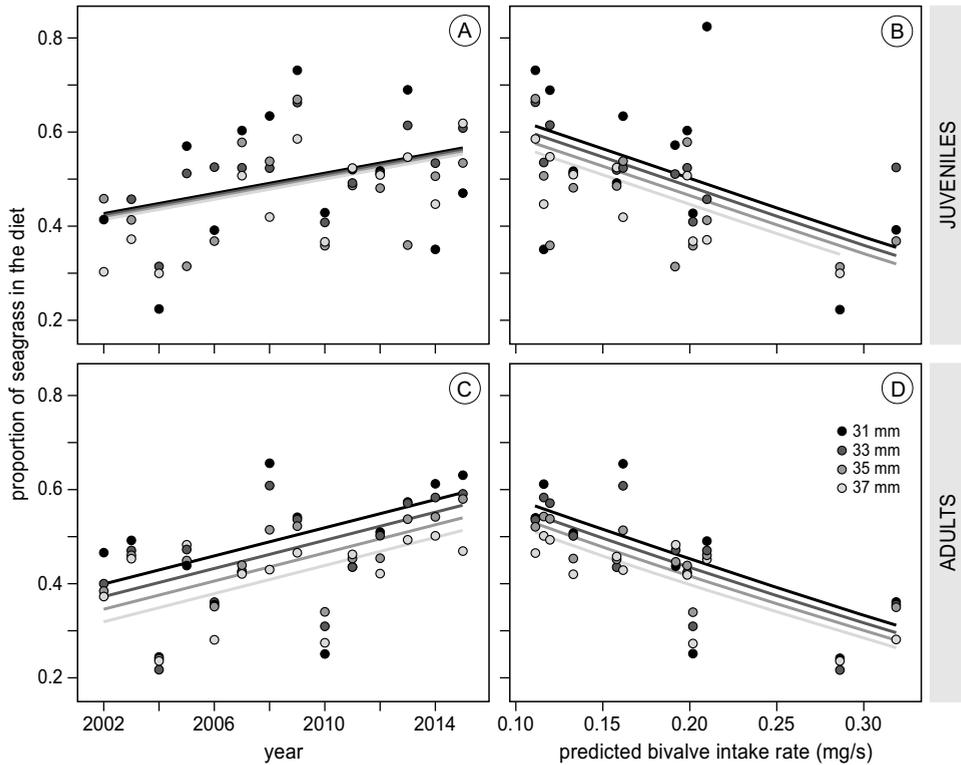


Figure 7.2 Mean proportion of seagrass in the red knot diet. The proportions of seagrass in the diet were estimated from N and C isotope levels of blood samples from 2,649 red knots, collected between 2002 and 2015 (van Gils *et al.* 2016). In panels A and C, each point shows the mean per year for juveniles and adults, separated in four classes of bill length. In panels B and D, the same isotope data is plotted as a function of the yearly average maximum predicted bivalve intake rate ($\text{mg ash-free dry flesh mass s}^{-1}$). This was calculated using a diet-choice model, based on the yearly average observed densities of *Loripes* and *Dosinia* (Chapter 3). Regression lines show the results of the best statistical model. AICc-values were compared of linear models with all combinations of explanatory variables ('Year', 'Age' and 'Bill length' for panels A and C, and 'Bivalve intake rate', 'Age' and 'Bill length' for panels B and D) and second order interactions. *Zostera* proportions were logit-transformed before analysis. The effect of 'Year' and 'Bivalve intake rate' could not be separated because they showed strong collinearity (Pearson's coefficient -0.73).

inherits non-genetically, with important and non-reversible consequences on behavioural and physiological development (Cox *et al.* 2014). Also in red knots, early experiences with toxic food, plant material and other specific food characteristics may permanently shape development. They may influence the development of the gut microbiome, the ability to detoxify, and the rate at which the gizzard muscle responds to training. They may also influence the development of the relation between physiological workloads and behavioural responses (e.g. the amount of ingested toxins before the animal refrains from eating more *Loripes*, or the level of gut fullness at which the animal considers it full).

It is possible that the gut bacteria involved in digesting plant material in red knots are also associated with the toxic effect of *Loripes* consumption. Sulphur consumption is

particularly dangerous for ruminants, due to the presence of specialized bacteria in the rumen that help digesting plant material and have the ability to convert dietary sulphur and sulphate to toxic sulphide (Kandylis 1984; Hall 2007). As a consequence, the evolved habit of seagrass foraging in *canutus* red knots may come at a cost of the ability to consume *Loripes*. If indeed the gut microbiome is formed partly by parental effects in juvenile knots and has lasting effects on physiology, then this may explain life-long and heritable differences in dietary preferences of non-genetic origin. Continued foraging traditions may, through behavioural and gut-microbial inheritance, lead to a change in the selective pressures on diet and physiology, and contribute to the evolutionary divergence of red knot subspecies.

Testing foraging traditions

The existence of foraging traditions in red knots is speculative. It is not easy to test these speculations. Unfortunately, the isolated breeding areas and dispersed breeding greatly hinder the study of inheritance in red knots. We cannot test whether diet preferences are influenced by genetic variation or other parental effects, because we have no information on (genetic) relatedness. However, the possibility to test diet preferences in juvenile and adult red knots from different subspecies on different prey types offers many possibilities for an inquiry into the existence of traditions. This may offer some logistic problems, but previous attempts at the Radboud University in Nijmegen to grow *Zostera noltii* from Banc d'Arguin in aquaria were successful (L.L. Govers, personal communication). Growing seagrass in the laboratory provides the potential to test at NIOZ whether there are differences in the propensity to consume seagrass rhizomes between juvenile and adult *canutus* red knots, caught in autumn in Poland. These juveniles have never been in the Banc d'Arguin and cannot have learned this behaviour socially (although both *islandica* and *canutus* juvenile red knots have been observed eating plant material, on the tundra and on the Poland shore, J.A. van Gils and J. Wilson, personal communication). Another experiment could test whether juveniles are more likely to pick up the habit of seagrass consumption when in the presence of experienced adults. Repeating the same experiment with *islandica* red knots would be interesting as well, as it might provide clues on whether evolution has led to differences between the subspecies in seagrass preference, handling time and propensity to learn this behaviour socially.

Until the 1930s, large beds of *Zostera noltii* existed also in the Dutch Wadden Sea. Seagrass beds spanned approximately 150 km², including subtidal seagrass (van der Heide *et al.* 2007). We can only speculate whether *islandica* red knots consumed rhizomes in these beds, and how this history has affected their current behavioural reaction if encountered with seagrass. Another prey type that is present in Banc d'Arguin but not in the Wadden Sea, and has not been common in the Wadden Sea since red knots have started to use it after the last ice age (Buehler, Baker & Piersma 2006), is *Loripes lucinalis*. The capacity to process toxic *Loripes* (Chapters 2 and 4) is likely to have been an important evolutionary pressure for red knots in Banc d'Arguin, as *Loripes* is their most common food source. It is therefore expected that the physiological pathways for detoxification are better developed in *canutus* red knots than in *islandica* red knots. Social and individual

learning may be involved in the behavioural response to the availability of *Loripes* as a food source. Do juvenile and adult *islandica* and *canutus* react differently? How do juvenile *canutus* red knots learn to adjust their diet choice to optimize their intake? Can *islandica* red knots learn it? How does the presence of experienced adult *canutus* red knots influence this process?

To investigate the extent to which juvenile experience and traditions determine adult routines in the wild, an experiment could be carried out where juvenile *islandica* or *canutus* red knots are offered different prolonged diet treatments, before being released in the wild with satellite tags. Currently, juvenile as well as adult *canutus* and *islandica* red knots are present in captivity at the NIOZ, and plans are indeed being made to use the latest satellite technology to record their locations after release in the wild (K. Mathot and E. Kok, personal communication). Together with additional observations of their behavior in the field (by telescope, camera and benthos sampling, such as described in Chapters 5 and 6), this exercise has the potential to offer insights in the extent to which foraging behavior by red knots, diet choice as well as the degree of site fidelity and aggregation, is influenced by social interactions and different pathways of inheritance. An exciting, but logistically even more challenging, potential experiment would be to transport juvenile and adult *islandica* and *canutus* red knots from the Wadden Sea to the Banc d'Arguin, and follow them after release with the TOA system or modern satellite tags.

Finally, the potential significance of an interaction between gut microbiota and diet can be tested by physiological investigation of casualties, including their gut bacteria, and isotopic analysis of the blood. The potential parental inheritance of the gut bacterial community can be tested by faeces and cloacal samples of parent and young at the Arctic breeding sites. Laboratory experiments with foraging red knots can further test the relation between the microbiota and relative preferences and maximum intake rates of *Loripes* and seagrass rhizomes, and could include an antibiotics treatment.

CONCLUSIONS

In this thesis, we have investigated which environmental factors influence the foraging decisions of red knots wintering in the Banc d'Arguin. I hope that the results are of interest in themselves, but they become especially interesting when comparing them to the factors that we know to influence red knots wintering in the Wadden Sea, or in other parts of the world (Piersma 2007). The different decisions that they make can be used as behavioral indicators, and hint on the different selection pressures that act on the subspecies of red knots in the different areas; the forces that underlie their evolution. To interpret these hints, it is essential to take individual development into account. We must acknowledge that red knots are not 'optimal machines', but that each individual is constructed under the confluence of information from genes and the environment in the broadest sense, and that each decision is a consequence of all previous ones. Despite the logistic difficulties to determine genetic relatedness between red knots and to study parents and their offspring, the knowledge that we now have on foraging decisions, and

the sophisticated study methods that are developed, may enable unprecedented detail in the study of the role of behaviour in the development of individual variation and evolution in a wild animal species.

I have also highlighted the potential of complex foraging decisions to affect population dynamics of red knots and their bivalve prey, and increase the potential for stable coexistence. This was done from an optimality approach. The subsequent discussion on the importance of development, and the potential existence of red knot foraging traditions, implies that also social interactions may affect the functional response on different prey types, and thereby population dynamics. This adds another layer of complexity to the functional response. Of course it is in no one's interest to make the functional response as complex as possible, and of course it must be made as simple as possible to answer the question that is asked. But not simpler. I think that the implications of complex behaviour, including social behavioural traditions, on population dynamics and ecosystem functioning deserves further thought.

The prime reason why red knot studies have been so successful in showing the intricate relationships between animals and their natural environment, is that these relationships still exist to be studied. When compared to most terrestrial ecosystems, intertidal areas all over the world are relatively untouched by humans. But all are currently under threat of destruction, some more than others (Ma *et al.* 2014; Piersma *et al.* 2016). A simple advice is to reduce human impact in any possible way. This thesis does not offer more concrete directions on how to preserve these areas and what it is exactly that must be protected within these areas. What this thesis does show, is that everything matters. Red knots are not static; the behavioural decisions that they make, and even the way that they look, are directly affected by their environment. The Banc d'Arguin may still harbour the greatest number and highest densities of wintering shorebirds of all intertidal areas in the world (van de Kam *et al.* 2004). The beautiful diversity and complexity in their behaviour, of which this thesis shows only a glimpse, exists only because the rest of the Banc d'Arguin ecosystem is so diverse and complex as well. We can be just as creative and diverse as our surroundings allow us to be. And therefore we must protect it.

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APPENDIX 7.1. The functional response of diarrheic red knots

In previous chapters, we have modelled both the digestive constraint and the toxin constraint as fixed maximum rates that cannot be surpassed. Indeed, red knots in the experiments of Chapters 2 and 4 do seemed to maximize their intake of *Loripes* until reaching this threshold value, which justified the use of a fixed value for functional purposes. However, when specifically modeling energy intake rate as a function of *Loripes* intake rate, it may be necessary to consider the diarrheic effect that *Loripes* consumption has on red knots, which appears to seriously impair energy assimilation efficiency (V. Hin and T. Oudman unpublished data).

With increasing consumption of *Loripes*, energy intake rate increases. On the other hand, energy assimilation efficiency decreases. As a consequence, the maximum energy assimilation rates may be at intermediate intake rates of *Loripes*. Thus, the apparent constraint by red knots on *Loripes* intake may actually not be a fixed threshold, but the result of optimizing the intake rate of *Loripes* to maximize the assimilated energy intake. If we assume that this is the case, and further assume that assimilation efficiency decreases linearly with the ash-free dry flesh (AFDM_{flesh}) intake rate of *Loripes*, then we can calculate the function that describes this decrease. Resource intake rate (Y , mg AFDM_{flesh} s⁻¹) can then be described as a function of the densities of *Loripes* D_l and *Dosinia* D_d (nr/m²), and acceptance probabilities p_l and p_d :

$$Y = a \frac{p_l D_l e_l + p_d D_d e_d}{1 + ah(p_l D_l + p_d D_d)} \text{Eff} \quad (\text{A7.1})$$

$$\text{where } \text{Eff} = \text{eff}_0 - q \frac{p_l a D_l e_l}{1 + p_l a D_l h} \quad (\text{A7.2})$$

$$\text{and } a \frac{D_l k_l + D_d k_d}{1 + ah(D_l + D_d)} \leq c \quad (\text{A7.3})$$

where a is the searching efficiency (m²/s), h is the handling time per prey item (s) and e_l and e_d are the energy contents of a single prey item (mg AFDM_{flesh}). Energy assimilation efficiency (Eff) is described by a linearly decreasing function, starting at eff_0 and decreasing at a rate proportional to the AFDM_{flesh} intake rate of *Loripes*. Shell mass intake rate was assumed to be limited by a digestive constraint c (mg/s), given the individual dry shell masses of *Loripes* and *Dosinia* (k_l and k_d in mg). The optimal acceptance probabilities of *Loripes* and *Dosinia* (p_l and p_d) can be analytically derived from the above equations. The solutions however are not straightforward, and to solve them we used the mathematical software Maple (Maple 9.0 Math & Engineering software).



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Summary
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SUMMARY

The environment affects all aspects of the animal's body and mind, ultimately because their evolution is steered by the environment. On a much shorter timescale animals interact with the environment by behavioural decisions that they make throughout the day. Therefore, studies of animal behaviour can improve our understanding of the ecological consequences of the interactions between the environment and the animal phenotype (the combination of all its morphological, physiological and behavioural traits). They can tell us about the effects of human activities on ecosystems.

This thesis is aimed at an understanding of the environmental determinants of foraging decisions in a migrant shorebird population that is in decline: the red knot (*Calidris canutus canutus*), wintering at Banc d'Arguin in Mauritania. To enable comparison, the behaviour of other red knots (*C. c. islandica*) in another environment, the Dutch Wadden Sea, is taken as a reference. To formulate hypotheses that explain the decisions that red knots make, I assumed that red knots respond to information from their natural environment in a way that maximizes their fitness. This simplifying approach is the basis of 'optimal foraging theory'. I used all available tools to quantify and test these hypotheses: mathematical modelling, experiments with red knots in captivity and radio-tagged red knots in the wild, and field observations using telescopes and benthos sampling equipment.

A varied diet to prevent diarrhea

In Mauritania, the main diet of red knots consists of two bivalve species, *Loripes lucinalis* and *Dosinia isocardia*, which the birds swallow whole and crush in their muscular stomach, the gizzard. The first study in this thesis (Chapter 2) shows that red knots at Banc d'Arguin actively balance the intake of *Loripes* and *Dosinia*. We explain this as a compromise between two constraints on intake rate that act simultaneously. On the one hand, red knots must limit the intake of diarrhea-causing sulfur compounds, which are naturally present in *Loripes*. This is a reason for the knots to prefer *Dosinia* (which does not contain such compounds) over *Loripes*. On the other hand, they must also minimize the intake of ballast mass, which takes time to digest: a reason to prefer the thin-shelled *Loripes* over the thicker-shelled *Dosinia*. The result is that red knots at Banc d'Arguin prefer a mixed diet of both. In this they differ from the Wadden Sea red knots, who simply prefer the prey type with the highest digestive quality when given the choice.

Using many years of observations on red knot survival and food abundance, we show that a mixed diet indeed increases survival chances: survival decreases when *Dosinia* abundance is low, even when *Loripes* densities are high (Chapter 3). This explains why in recent years, with steadily lowering densities of *Dosinia*, red knot survival has decreased. It also explains why red knots supplemented their diet with increasing amounts of seagrass rhizomes, a low quality food.

Individual differences in food preferences

In the Wadden Sea, all red knots prefer prey of higher digestive quality when given the

choice. In Mauritania, prey preferences are expected to change with the size of the gizzard, because a larger gizzard should allow for faster shell-mass processing, but not for faster sulfide detoxification.

In an experiment with captive red knots, we show that this is indeed the case (Chapter 4). Birds with larger gizzards show higher intake rates of non-toxic *Dosinia*, but not of toxic *Loripes*. Gizzard sizes vary greatly between individuals, and by deploying red knots with radio tags, we show that this variation correlates with behavioural choices in the field (Chapter 5). Hence, behaviour may be adjusted to individual differences in gizzard size, or gizzard size may be adjusted to behavioural differences. Our results suggest the latter. Radio-tagged red knots, fed on soft diets for two weeks leading to decreased gizzard sizes, did not adjust their habitat choice to those changes after their release in the wild (Chapter 5). We propose that the observed behavioural differences between individuals may have developed during ontogeny. Early environmental experiences influence physiological development and learning processes, which influence individual habits, which in turn determine subsequent experiences, and so forth. This feedback loop may enlarge initially small or absent individual differences, and canalize phenotypic development in different ways.

Habits are orchestrated by the environment

Finally, by quantifying and comparing the resource environments as well as the space use of tagged red knots between the Wadden Sea and Banc d'Arguin, we examined whether red knots adjust the criteria underlying movement decisions to the environment in which they live (Chapter 6). Whereas food patches in the Wadden Sea ranged over more than 1.5 km, the food patches at Banc d'Arguin measured less than 50 m. In addition, the richest samples in the Wadden Sea contained three times more food than those at Banc d'Arguin. Red knots in the Wadden Sea based their foraging movements primarily on the movements of conspecifics, roaming in groups across these large patches as they deplete resources locally. In great contrast and in adjustment to the environmental differences, red knots at Banc d'Arguin based their foraging movements primarily upon prior individual experiences, going to the same foraging locations each tide, and being more individualistic.

These findings emphasize that environmental change may affect population characteristics quite directly via changes in the decisions that individual animals make (Chapter 7). To quantify the rate of population adjustment to the environment, further research must show which environmental cues are used to inform individual decisions, how these are learned in the course of ontogeny, and to what extent animals remain flexible in the expression of learned behaviours throughout their lives.

The importance of the Banc d'Arguin

The results and ideas presented in this thesis imply that the survival of red knots necessitates a rich and diverse environment, because (i) a varied diet is necessary for survival, and (ii) a diverse environment may allow red knots to adjust their habits in response to changing conditions. The ultimate reasons for the current decline of red knots at Banc

d'Arguin may be found in the changing environments of the Wadden Sea and the Arctic. Nonetheless, the dynamic habits that allow red knots to persist may increasingly rely on the riches of the Banc d'Arguin – a good quality wintering ground could mitigate negative effects of rapid changes occurring higher up north. That is just one reason to protect the astonishing ecosystem that the Banc d'Arguin still is.

SAMENVATTING

De omgeving beïnvloedt alle aspecten van het lichaam en gedrag. Dat gebeurt op evolutionaire tijdschaal via natuurlijke selectie, maar ook op een veel kortere tijdschaal interacteren dieren met het milieu door middel van gedragsmatige beslissingen die ze de hele dag door nemen. Daarom kunnen studies aan diergedrag bijdragen aan ons begrip van de interacties tussen het milieu en het fenotype (de combinatie van alle eigenschappen van een organisme: morfologisch, fysiologisch en gedragsmatig). Ze vertellen ons over de gevolgen van veranderingen in de omgeving, en ook over de effecten van menselijke activiteit op ecosystemen.

Dit proefschrift richt zich op een begrip van de omgevingsfactoren die het foerageergedrag bepalen van een migrerende steltloper, wiens aantallen hard achteruit lopen: de kanoet (*Calidris canutus canutus*), die overwintert op de Banc d'Arguin in Mauritanië. Om dat mogelijk te maken nemen we het bekende gedrag van een andere kanoetenpopulatie (*C.c. islandica*) in een andere omgeving, de Nederlandse Waddenzee, als uitgangspunt. Om hypothesen te kunnen opstellen die de beslissingen van foeragerende kanoeten verklaren, heb ik aangenomen dat kanoeten op hun natuurlijke omgeving reageren op een manier die hun fitness maximaliseert. Deze simplistische maar handige aanname is de basis van 'optimale foerageer theorie'. Om deze hypothesen te kwantificeren en te meten, heb ik alle methodes gebruikt die voor handen zijn: wiskundige modellen, experimenten met kanoeten in gevangenschap en kanoeten in het wild met een radiozendertje, en observaties aan kanoeten en hun voedsel op het wad met behulp van telescoop en steekbuis.

Een gevarieerd dieet voorkomt diarree

Het dieet van kanoeten op de Banc d'Arguin bestaat vooral uit schelpdieren, met name *Loripes lucinalis* en *Dosinia isocardia*. Ze slikken deze tweekleppigen heel in, en kraken ze in hun spiermaag. De eerste studie in dit proefschrift (Hoofdstuk 2) laat zien dat kanoeten de inname van *Loripes* en *Dosinia* actief balanceren. We verklaren dit als een compromis tussen twee kwaden. Aan de ene kant moet een kanoet de inname beperken van zwavelcomponenten die diarree veroorzaken en van nature in *Loripes* aanwezig zijn. Dit is een reden om *Dosinia* (die die gifstoffen niet bevat) te verkiezen boven *Loripes*. Aan de andere kant moeten kanoeten ook de inname van teveel onverteerbaar materiaal voorkomen, omdat die de vertering van het schelpenvlees vertraagd. Dat pleit er juist voor om de dunschelpige *Loripes* boven *Dosinia* te verkiezen, die een veel dikkere schelp heeft. Het resultaat is dat kanoeten op de Banc d'Arguin een mix verkiezen van verschillende prooitypes. Daarin verschillen ze van kanoeten in de Waddenzee, die simpelweg kiezen voor de prooi met de hoogste verteringskwaliteit, als ze de keus krijgen.

Aan de hand van vele jaren observaties aan de overleving van kanoeten en voedselbeschikbaarheid, is duidelijk geworden dat kanoeten inderdaad naast *Loripes* ook *Dosinia* nodig hebben: de kans om de winter te overleven was lager in jaren dat de *Dosinia* dichtheid laag was, ook al was *Loripes* ruim voorhanden (Hoofdstuk 3). Dat verklaart waarom juist in de laatste jaren, met steeds lagere *Dosinia* dichtheden, veel mortaliteit onder kanoeten heeft plaatsgevonden. Het verklaart ook waarom kanoeten recent steeds meer

wortelstokken van zeegras aan hun dieet toevoegen, een voedseltype dat voor kanoeten moeilijker te verteren is dan schelpdieren.

Individuele verschillen in dieetvoorkeuren

Kanoeten in de Waddenzee verkiezen in het algemeen voedsel van de hoogste verteringskwaliteit, als ze de keus krijgen. In Mauritanië echter, verwachtten we dat voedselvoorkeur afhankelijk is van maag grootte, omdat een grotere maag leidt tot een hogere verteringssnelheid, maar niet tot een snellere sulfide ontgiftig.

In een experiment tonen we aan dat dit inderdaad het geval is (Hoofdstuk 4). Kanoeten met een grotere maag aten wel meer *Dosinia* per tijdseenheid, maar hun maximale *Loripes* inname bleef gelijk. In het wild verschillen maag groottes behoorlijk tussen individuen. Door kanoeten met bekende maag grootte (gemeten met een echoscoop) los te laten met een radio zendertje, bleek dat vogels met een grotere maag langer op dezelfde plek blijven foerageren (Hoofdstuk 5). Maar is dat een gevolg van hun grote maag, of juist de oorzaak? Onze resultaten suggereren het laatste. Gezenderde kanoeten die eerst twee weken gevoerd waren met een zacht dieet, die daardoor een kleine maag kregen, pasten na loslaten in het veld hun gedrag niet aan hun nieuwe maag grootte (Hoofdstuk 5). We vermoeden dat deze gedragsverschillen tussen individuen ontstaan in de loop van hun ontwikkeling. Ervaringen vroeg in het leven beïnvloeden leerprocessen en fysiologische ontwikkelingen zoals maag grootte, wat zijn weerslag heeft op mogelijke foeragegewoontes, dat op zijn beurt weer invloed heeft op nieuwe ervaringen, enzovoorts. Deze spiraal kan verschillen vergroten die aanvankelijk klein of zelfs afwezig zijn, en zo de ontwikkeling van het fenotype kanaliseren.

Gewoontes: georkestreerd door het milieu

In de laatste studie in dit proefschrift hebben we het voedsellandschap in de Waddenzee en op de Banc d'Arguin gekwantificeerd en met elkaar vergeleken, en onderzocht of kanoeten de criteria waarop zij hun plaatskeuze baseren, aanpassen aan de omgeving waarin ze leven (Hoofdstuk 6). Schelpenbanken in de Waddenzee hadden een lengte van meer dan 1.5 km, terwijl ze op de Banc d'Arguin kleiner waren dan de kleinst gemeten afstand, 50 m. Ook bevatten de rijkste monsters in de Waddenzee drie keer zoveel voedsel als die op de Banc d'Arguin. Kanoeten in de Waddenzee bleken hun plaatskeuze tijdens het foerageren vooral te baseren op de bewegingen van soortgenoten: ze zwierven in grote groepen over het wad, waar ze lokaal een hoge predatiedruk uitoefenden. Tegengesteld hieraan, en passend bij de verschillen in voedselverspreiding, baseerden de kanoeten op de Banc d'Arguin hun beslissingen vooral op eigen ervaringen: ze keerden veelal naar eerder bezochte plekken terug, en waren veel individualistischer.

Deze bevindingen laten zien dat omgevingsveranderingen de karakteristieke eigenschappen van soorten heel direct kunnen veranderen, via de beslissingen die individuele dieren maken (Hoofdstuk 7). Om de snelheid van deze veranderingen te bepalen is meer onderzoek nodig naar welke omgevingsfactoren dieren gebruiken om hun beslissingen op te baseren, hoe ze deze aanleren in de loop van hun ontwikkeling, en in hoeverre de aangeleerde gewoontes van dieren zich nog kunnen aanpassen in de loop van hun leven.

Het belang van de Banc d'Arguin

De resultaten en ideeën die ik heb beschreven impliceren dat een rijke en diverse omgeving van belang is voor de overleving van kanoeten, omdat (i) kanoeten behoefte hebben aan een gevarieerd dieet, en (ii) een rijke omgeving kanoeten de kans geeft om zich aan te passen aan veranderende condities. De uiteindelijke oorzaken van de achteruitgang van de aantallen kanoeten op de Banc d'Arguin moeten misschien gezocht worden in het Arctisch gebied en de Waddenzee. Niettemin zouden de dynamische gewoontes van de kanoet wel eens meer en meer afhankelijk kunnen worden van de rijkdommen van de Banc d'Arguin. Een goed wintergebied zou de negatieve gevolgen van de snelle veranderingen in het noorden kunnen afremmen. Dat is één van de vele redenen om het rijke ecosysteem dat de Banc d'Arguin nu nog is, te beschermen.

RÉSUMÉ

L'environnement affecte tous les aspects du corps et de l'esprit de l'animal, en fin de compte parce que leur évolution est dirigée par l'environnement. Sur une échelle de temps plus courte, les animaux interagissent avec l'environnement au cours de la journée grâce aux décisions de comportements que les animaux prennent. Par conséquent, les études du comportement animal peuvent améliorer notre compréhension des conséquences écologiques des interactions entre l'environnement et le phénotype de l'animal (qui comprends tous ses traits morphologiques, physiologiques et comportementaux). Les études de comportement animal peuvent nous faire apprendre au sujet des effets des activités humaines sur les écosystèmes.

Cette thèse vise à améliorer notre compréhension des déterminants environnementaux des décisions liées à la recherche de nourriture dans une population de limicoles migrateurs dont la population est en déclin: le bécasseau maubèche (*Calidris canutus canutus*), qui hiverne au Banc d'Arguin en Mauritanie. Pour permettre la comparaison, le comportement d'une autre sous-espèce de bécasseau maubèche est pris comme référence (*C. c. islandica*). Le bécasseau *islandica* hiverne dans le Mer des Wadden Néerlandais. Pour me permettre de développer des hypothèses concernant la manière dont les bécasseaux maubèches prennent des décisions, je commence par la supposition qu'ils utilisent de l'information provenant de leur environnement d'un façon qui maximise leur aptitude phénotypique. Cette approche réducteur est la base de la théorie de l'alimentation optimale. J'ai utilisé tous les outils disponibles pour quantifier et tester ces hypothèses: la modélisation mathématique, des expériences avec des bécasseaux maubèche en captivité ainsi que les bécasseaux maubèche en nature portant des émetteurs radio, les observations sur le terrain à l'aide de télescopes et l'échantillonnage de la faune benthique.

Prévenir la diarrhée avec une alimentation variée

Deux espèces de bivalves comprennent les proies principales des bécasseaux maubèche en Mauritanie : *Loripes lucinalis* et *Dosinia isocardia*. Ces deux proies sont avaler au complet (incluant le coquille), et doivent être écrasé dans l'estomac musculaire du bécasseau, le gésier. Dans la première étude de cette thèse (Chapitre 2), nous démontrons que les bécasseaux sur le Banc d'Arguin équilibrent activement l'apport de *Loripes* et de *Dosinia*. Nous supposant que cela est le résultat d'un compromis entre deux contraintes sur le taux d'ingestion qui agissent en même temps. D'une part, les bécasseaux doivent limiter la consommation de composés de soufre, qui causent la diarrhée, et qui sont naturellement présents dans *Loripes*. Ceci est une raison pour lequel les bécasseaux pourraient préférer *Dosinia* contre *Loripes* car *Dosinia* ne contient pas des composés de soufre. D'une autre part, les bécasseaux doivent aussi minimiser leur taux d'ingestion de la masse de ballast, parce que cela occupe beaucoup d'espace dans le gésier et prends beaucoup de temps pour passer à travers le système digestif. Ceci est un raison pour lequel les bécasseaux pourraient préférer *Loripes* contre *Dosinia*, parce que le coquille de *Loripes* est moins épaisse comparer au coquille de *Dosinia*. Le résultat de ces deux contraintes est que les bécasseaux sur le Banc d'Arguin préfèrent une diète mixte. Cela est en contraste avec

les bécasseaux dans le Mer des Wadden, qui préfèrent simplement les proies dont la qualité de digestion est la meilleure.

Grâce à plusieurs années d'observations sur le taux de survie chez le bécasseau et la densité de *Loripes* et de *Dosinia*, nous avons pu démontrer qu'une diète mixte porte des avantages pour le taux de survie. Le taux de survie décline quand l'abondance de *Dosinia* est faible, même si l'abondance de *Loripes* est élevée (Chapitre 3). Cela explique l'observation que dans les années récentes, lorsque l'abondance de *Dosinia* a été constamment en déclin, que le taux de survie chez les bécasseaux est aussi en déclin. En plus, cela pourra expliquer pourquoi les bécasseaux ont commencé à compléter leur diète avec les rhizomes de l'herbe de mer, une alimentation de qualité faible.

Les préférences alimentaires diffèrent entre les individus

Lorsqu'ils ont le choix, les bécasseaux dans le Mer des Wadden préfèrent les proies avec une meilleure qualité digestive. Par contre, en Mauritanie, on suppose que les préférences alimentaires pourraient changer avec la masse du gésier, parce qu'un gésier plus grand peut traiter les composantes indigestibles (par exemple, les coquilles) des proies plus rapidement, mais un gésier plus grand ne sera pas plus rapide à désintoxiquer des composés de soufre.

Nous avons démontré que ceci est bien le cas (Chapitre 4). Dans une expérience avec des bécasseaux en captivité, nous avons observé que les oiseaux avec les gésiers les plus grands ont un taux d'ingestion de *Dosinia* plus élevé. En même temps, nous avons observé aucune relation entre la masse du gésier et le taux d'alimentation de *Loripes*. La taille du gésier diffère entre les individus. Nous avons démontré que cette variation interindividuelle est en corrélation avec le comportement en nature grâce à nos données sur le choix d'habitat et temps de résidences dans les parcelles requis sur les individus portant des émetteurs radio (Chapitre 5). Cela indique que le comportement pourrait être ajusté à la taille du gésier, ou que la taille du gésier pourrait être ajustée au comportement. Nous proposons que c'est le gésier qui s'ajuste aux différences comportementales, parce que les bécasseaux qui ont reçu une diète de très haute qualité pendant deux semaines, et donc qui ont beaucoup réduit la masse de leurs gésiers, n'ont pas ajusté leur comportement lorsqu'ils ont été libérés dans la nature (Chapitre 5).

Nous proposons que les différences de comportement observées entre les individus ont été mises au point au cours du développement de l'organisme (l'ontogénie). Le développement de la physiologie et les processus d'apprentissage sont influencés par l'environnement et les expériences vécues par l'organisme au cours de sa vie, ce qui, par la suite, influence les expériences suivantes et le développement suivantes, ainsi de suite. Ce genre de boucle de retour pourrait faciliter la canalisation des différences interindividuelles.

L'environnement orchestre les habitudes

Enfin, nous avons étudié si les bécasseaux ajustent les critères qui dirigent leurs décisions de mouvement selon l'environnement dont ils se trouvent (Chapitre 6). Pour réaliser cet objectif, nous avons quantifié et comparé la distribution de ressources et le mouvement des bécasseaux portant des émetteurs radio sur le Mer des Wadden et le Banc d'Arguin.

Les parcelles d'alimentation sur le Mer des Wadden varié sur plus de 1,5 km, celles du Banc d'Arguin varié sur moins de 50 m. En plus, les parcelles les plus riches sur le Mer des Wadden comprenaient trois fois plus de nourriture comparées aux parcelles les plus riches sur le Banc d'Arguin. Les bécasseaux sur le Mer des Wadden semblaient basés leurs décision de mouvement surtout sur le mouvement de leurs congénères, et restaient pour la plus part en groupes à travers ces grandes parcelles lorsqu'ils épuisaient les ressources sur une échelle locale. Contrairement, les bécasseaux sur le Banc d'Arguin paraissaient basé leurs décision de mouvement surtout sur leurs expériences individuel précédent; les mêmes individus utilisant les mêmes parcelles au cours de plusieurs marées.

Ces résultats démontrent que les changements environnementaux peuvent affecter les caractéristiques des populations tout à fait directement par des changements dans les décisions que les individus prennent (Chapitre 7). Pour bien comprendre comment les populations peuvent ajuster aux changement environnementaux, il nous faut plus de recherche sur les indices environnementaux qui dirigent la prise de décision chez les animaux, la manière dont ceci est appris au cours de l'ontogénie, et a quelle point les animaux restent flexibles dans l'expressions des comportements qui ont été appris au cours de leurs vies.

L'importance du Banc d'Arguin

Les résultats et les idées présentées dans cette thèse impliquent que la survie des bécasseaux maubèche nécessite un environnement riche et diverse parce que (i) une alimentation variée est nécessaire pour la survie, et (ii) un environnement diverse peut permettre aux bécasseaux maubèche d'ajuster leurs habitudes en face de conditions changeantes. Les raisons ultimes pour le déclin de la population de bécasseau maubèche sur le Banc d'Arguin pourraient se trouver dans les environnements changeants de la Mer des Wadden et de l'Arctique. Néanmoins, le comportement dynamique des bécasseaux maubèche qui leur permet de persister, pourrait aussi leur faire reliés de plus en plus sur les richesses du Banc d'Arguin – un habitat d'hivernage de bon qualité pourrait atténuer les effets négatifs des changements environnementaux rapides qui se produisent dans le nord. Cela n'est qu'une des raisons pour protéger l'écosystème du Banc d'Arguin, qui est encore formidable.

الملخص العلمي

يؤثر الوسط البيئي على جسم وعقل الحيوان في جميع النواحي ، لأنه هو الموجه الأساسي لتطورهما. فعلى المدى القصير، تتفاعل الحيوانات مع الوسط من خلال القرارات السلوكية التي تتخذ على مدار اليوم. ولذلك فإن دراسات السلوك الحيواني يمكن أن تحسن فهمنا للتأثيرات البيئية للتفاعلات بين الوسط والنمط الظاهري الحيوان (مزيج من الصفات المورفولوجية، والصفات الفسيولوجية والسلوكية). كما يمكن أن يساعدنا على فهم آثار الأنشطة البشرية على النظم البيئية.

تهدف هذه الأطروحة إلى فهم المحددات البيئية لقرارات البحث عن الغذاء لدى تجمع سكان الطيور المنفعية المهاجرة من نوع عقدة حمراء (*Calidris canutus canutus*)، والتي تمضي الفترة الشتوية في حوض ارغين في موريتانيا. وكمراجع للمقارنة، يتم أخذ سلوك عقدة حمراء أخرى (*C. c. islandica*) في بيئة أخرى، بحر وادين الهولندي. لإعداد الفرضيات التي تفسر القرارات التي تتخذها العقدة الحمراء، فقد افترضت أن العقدة الحمراء تستجيب للمعلومات من بيئتها الطبيعية بطريقة تزيد من لياقتهم البدنية. هذا النهج التبسيطي هو أساس "نظرية البحث الأمثل عن الغذاء". لقد استخدمت جميع الأدوات المتاحة لتأهيل واختبار هذه الفرضيات: النمذجة الرياضية، والتجارب على طيور العقدة الحمراء في أقفاص والعقدة الحمراء الطليقة الموسومة بهوانيات إشعاعية ، وكذلك الملاحظات الميدانية باستخدام التلسكوبات ومعدات أخرى لأخذ العينات الغذائية.

نظام غذائي متنوع للوقاية من الإسهال

يتكون النظام الغذائي الرئيسي للعقدة الحمراء في موريتانيا من نوعين من ثنائيات الصدفة *Loripes lucinalis* و *Dosinia isocardia* ، والتي يبتلعها الطائر كاملة ويسحقها في معادته العضلية. وتظهرت الدراسة الأولى في هذه الرسالة (الفصل 2) أن العقد الحمراء في حوض ارغين توازن بين تناول النوعين. ويعتبر هذا كحل توفيق بين شكلين من القيود يؤثران في وقت واحد على معدل الاستهلاك. فيجب على العقدة الحمراء من ناحية الحد من تناول مركبات الكبريت المسببة للإسهال، والتي هي موجودة بشكل طبيعي في *Loripes*. لذلك فإن الطيور تفضل *Dosinia* (التي لا تحتوي على مثل هذه المركبات) على *Loripes*. من ناحية أخرى، فيجب أيضا تقليل استهلاك الصدفة ، التي يستغرق هضمها وقتا طويلا: فهذا سبب اخر لتفضيل *Loripes* رقيقة الصدفة على *Dosinia* ذات الصدفة السمكية. والنتيجة هي أن العقدة الحمراء في حوض ارغين تفضل اتباع نظام غذائي مختلط. ولهذا يختلف هذا التجمع عن العقدة الحمراء في بحر وادين ، التي تفضل ببساطة نوع الفريسة حسب جودتها الغذائية.

باستخدام سنوات عديدة من مراقبة معدل النجاة لدى العقدة الحمراء ووفرة غذاءها، تبين لنا أن اتباع نظام غذائي مختلط في الواقع يزيد من فرص البقاء على قيد الحياة: ينخفض معدل النجاة عندما تنخفض وفرة *Dosinia* ، حتى عندما تكون *Loripes* متوفرة جدا (الفصل 3). وهذا ما يفسر انخفاض معدل نجاة هذه الطيور في السنوات الأخيرة، مع انخفاض مطرد لكثافة *Dosinia*. كما يفسر لماذا العقدة الحمراء تكمل نظامها الغذائي مع كميات متزايدة من جذور الأعشاب البحرية، رغم انخفاض جودتها الغذائية.

الفروق الفردية في تفضيلات الأغذية

في بحر وادن، كل الطيور ذات العقدة الحمراء تفضل فريستها حسب جودتها الغذائية عند الاختيار. في موريتانيا، اختيار الفريسة يتغير مع حجم العضلة المعدية، لأن العضلة المعدية تسمح بمعالجة أسرع للصدفة، ولكنها لا تساعد في إزالة السموم الكبريتية.

و بينت التجربة على طيور العقدة الحمراء في الاقفاص، أن هذا هو الحال في الواقع (الفصل 4). فالطيور ذات العضلة المعدية الكبيرة تظهر معدلات تناول أعلى من النوع الغير السام *Dosinia* ، ولكن ليس من *Loripes* السامة.

تختلف أحجام الجيب المعدية اختلافا كبيرا بين الأفراد، ومن خلال نشر مجموعة من طيور العقدة الحمراء مجهزة بهوانيات إشعاعية، تبين لنا أن هذا الاختلاف يرتبط مع الخيارات السلوكية في الوسط البيئي (الفصل 5). وبالتالي فإن السلوكيات يتم تكيفها مع الفروق الفردية في حجم الجيب، أو أن حجم الجيب يمكن تكيفه مع الفروق في السلوكيات. وتشير النتائج إلى أن الحالة الأخيرة هي الواقع.

طيور العقدة الحمراء المجهزة بهوائيات إشعاعية و التي تغذت على الوجبات الغذائية الناعمة لمدة أسبوعين مما أدى إلى انخفاض في أحجام الجيب، لم تكيف وسطها المختار مع تلك التغييرات بعد الإفراج عنها في البرية (الفصل 5). نقترح أن الاختلافات السلوكية الملاحظة بين الأفراد قد تطورت خلال مرحلة النمو الفردي. التجارب الوسطية المبكرة تؤثر على التطور الفسيولوجي وعمليات التعلم، والتي تؤثر على العادات الفردية، والتي بدورها تحدد التجارب اللاحقة، وهكذا دواليك. هذه الحلقة من ردود الأفعال قد تكبر في البداية الفروق الفردية الصغيرة أو الغائبة، و تقنن النمو المظهري بطرق مختلفة.

الوسط البيئية ينظم العادات

وأخيرا، من خلال قياس ومقارنة أوساط الموارد وكذلك استخدام الفضاء للعقدة الحمراء المجهزة بهوائيات إشعاعية بين بحر وادن وحوض ارغين، تمت دراسة ما إذا كانت العقد الحمراء تضبط المعايير التي تستند إليها قرارات الحركة حسب الوسط البيئية الذي تعيش فيه (الفصل 6). في حين تراوحت بقع البحث عن الطعام في بحر وادن أكثر من 1.5 كم، فبقع البحث عن الطعام في حوض ارغين أقل من 50 مترا. وبالإضافة إلى ذلك، فإن أغني العينات في بحر وادن تحتوي على ثلاثة أضعاف الغذاء من تلك الموجودة في حوض ارغين. طيور العقدة الحمراء في بحر وادن تستند حركاتهم البحثية في المقام الأول على تحركات المناوعين (الأفراد من نفس النوع)، متجولة في مجموعات عبر هذه البقع الكبيرة حتى تستنفذ الموارد محليا. و على النقيض و من أجل التكيف مع الاختلافات الوسطية، تستند العقدة الحمراء في حوض ارغين حركاتها البحثية في المقام الأول على التجارب الفردية السابقة، الذهاب إلى نفس المواقع البحثية كل مد وجزر، فهي أكثر فردية.

وتؤكد هذه النتائج على أن التغيير الوسطي الذي يؤثر على خصائص السكان قد يعدل بشكل مباشر في القرارات الفردية التي تتخذها الحيوانات (الفصل 7). ولتحديد معدل التكيف السكاني على الوسط، يجب دراسة الأساليب البيئية التي تستخدم لتشكيل القرارات الفردية، وكيف يتم تعلمها في سياق النمو الفردي، وإلى أي مدى تظل الحيوانات مرنة في التعبير عن السلوكيات المكتسبة من خلال حياتها.

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Twelve red knots fly off to the mudflats at sunrise after eleven long days of captivity, in the morning of 23 January, 2013. But their freedom is not complete: on their backs they are carrying a 5g radio tag that will betray their whereabouts every single second for the next five weeks.

