Foraging decisions in a digestively constrained long-distance migrant, the red knot (Calidris canutus)
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“To do science is to search for repeated patterns, not simply to accumulate facts. Doing science is not such a barrier to feeling or such a dehumanizing influence as is often made out. It does not take the beauty from nature. The only rules of scientific method are honest observations and accurate logic. No one should feel that honesty and accuracy guided by imagination have any power to take away nature's beauty.”

Foraging plays a central role in the life of individual organisms and it is therefore not surprising that the study of foraging plays a central role in ecology. The ability to predict the outcome of foraging decisions, such as where to feed, on what to feed, and for how long to feed, is a fundamental component in understanding life histories and population growth rates and eventually throws light on community functioning. With this aim in mind, Robert MacArthur and others developed in the mid-1960s a theory that would allow us to predict where animals went, what they would feed on and for how long (MacArthur & Pianka 1966; Emlen 1966; see also MacArthur 1972). The theory is generally known as optimal foraging theory (Stephens & Krebs 1986) and is based on optimisation principles that were borrowed from economics. Extensive experimentation and analysis has refined the theory over the last decades (reviewed by Stephens et al. 2005), but the aim of understanding the rules underlying community functioning has remained elusive (Schmitz 1997).

This thesis was prepared in a research group that chose MacArthur's original working hypothesis as the basis of its programme: to understand life histories and population structuring in marine molluscs, we needed to understand the foraging decisions of the predators that eat them. Inspired by long-term observational and experimental studies on rocky shores (Paine 1994), we aimed to reveal the organising principles that mould soft-sediment communities.

As a model predator the red knot (Calidris canutus) was chosen, an amenable species to study. Outside its short breeding season in the Arctic, the red knot is uniquely found in soft-sediment intertidal habitats, where it mainly feeds on mollusc prey for 9-10 months each year. Its habit of ingesting its hard-shelled prey whole and excreting indigestible shell fragments by defecation, allows a precise methodology that enables the quantitative reconstruction of diet composition through faecal analysis (Dekinga & Piersma 1993; see box I). The relative ease with which individual knots can be kept in captivity enables experiments in fully controlled environments (e.g. Piersma et al. 1995). Its long-distance migrations span intertidal habitats worldwide (Figure 1.1A), allowing large-scale comparisons of the effects of shorebird predation on benthic community functioning (Piersma et al. 1993b). Understanding this particular study system could add significantly to the development of bird migration theory (Alerstam & Hedenström 1998), by revealing how migratory flyways of predators solve the coupled constraint of the predator and its prey. And finally, basic parameters from eco-physiology were already known in the knot (metabolic rates, nutrient store dynamics, and metabolic adjustments of organ sizes, see Piersma 1994).
Figure 1.1. (A). Distribution of red knots worldwide. Six subspecies have been recognised, all breeding in the high-arctic tundra (June-July; shaded areas). After their long-distance migrations (arrows), knots spend the non-breeding season (August-May) in intertidal soft-sediment habitats (dots, which are scaled according to population size). (B). Map of our study area, the western Dutch Wadden Sea. Dots give stations that have yearly been sampled for prey densities. This particular example gives the distribution of a favourite bivalve prey, Macoma balthica, in late summer 2000 (at open dots no Macoma was found, while Macoma was present at filled, density-scaled dots; maximum density observed was 2,655 m\(^{-2}\)).
In this study we focus on prey and patch choices. The main study site was the western Wadden Sea (Figure 1.1B), the ‘backyard’ of our institute on Texel (Royal NIOZ). Yearly since 1996, large-scale sampling of densities and qualities of benthic prey animals took place throughout a study area that measured 35 by 15 km (equalling the estimated range of red knots in the western Wadden Sea; Piersma et al. 1993a). Every late summer, about 2,500 stations were sampled and about 80,000 prey items were counted, enabling us to map out the knot’s food environment in fine detail (see Figure 1.1B for an example). On top of this, we mapped feeding itineraries of individual red knots annually by intensive use of radio-telemetry (both automatically from fixed towers and manually from ships and field stations). In order to estimate the amount of energy gained during such feeding trips, we used empirical functional response models (box II) as a tool to translate prey densities into energy intake rates. We did so after distinguishing between available and unavailable prey (based on species, size, and burial depth; Zwarts et al. 1992). Indeed, the functional response forms the backbone of this thesis.

Before the onset of this project, the so-called ‘short-term’ functional responses of knots to variable prey densities were already measured (Piersma et al. 1995, summarised in Box-figure II.1). ‘Short-term’ here indicates that energy intake was measured over active feeding time only (searching and handling times; terminology cf. Fortin et al. 2002 and comparable to the ‘differential’ functional response defined by Mitchell & Brown 1990). By contrast, the knot’s ‘long-term’ functional responses, where intake rate is calculated over total time (including non-feeding periods), were not yet determined. Focussing on intake over total time seems most relevant as foraging theory assumes the maximisation of the long-term average intake rate and not of the intake during selected behavioural activities only (Stephens & Krebs 1986). Thus, one of the major aims here was to quantify intake over total time (as a function of prey density and quality) and to investigate what determines the length of non-feeding bouts.

In many organisms, such non-feeding bouts may be interpreted as digestive breaks in which the predator awaits clearance of its filled gut before feeding can proceed (Jeschke et al. 2002). This could well be relevant for red knots, since they ingest their bivalve prey whole and may need some time to get rid of indigestible and voluminous shell fragments. As the prey are small and usually occur in dense clumps, rates of food encounter and collection are generally high, such that rates of digestion often may not be able to keep up with rates of (potential) prey ingestion (Karasov & McWilliams 2004). In this case, we could characterize the knot as digestively bottlenecked, i.e. forced to take regular digestive breaks.
In the light of optimal design considerations, it would be surprising that, on the one hand knots have evolved highly specialised tools to find and handle food quickly (Piersma et al. 1995, 1998), but on the other hand would possess digestive organs that are often unable to keep pace with the high rates of prey ingestion. The concept of symmorphosis states that a system works most economically when its separate components have processing capacities that are adjusted to each other (Taylor & Weibel 1981; Weibel 2000). Why would digestive organs be too small in relation to the prey-collection capacities, or, the other way around, why would organs involved in finding and handling food usually be oversized?

Answers to these intertwined questions may come from the realisation that digestive organs can be flexibly adjusted to ecological demands, a point of view that has gained momentum over the last couple of years (Piersma & Lindström 1997; Piersma & Drent 2003; see box III). In other words, under some ecological circumstances (place or time of year) digestive organs may be small and unable to keep up with rates of prey encounter and collection actually experienced, whereas in other circumstances organs may be large and provide buffer capacity. Reflecting now on the long-term functional response implies that this will be a flexible response, which varies with reversible changes in the digestive machinery of the bird (in contrast to the ‘static’ short-term functional response).
Unlike measuring searching and handling, which are clearly visible ‘external’ activities, it seems harder to quantify the ‘internal’ component of long-term functional responses, digestive processing capacity. However, a methodological breakthrough occurred just at the onset of this project. The application of ultrasonography enabled us to quite accurately estimate the size of the gizzard in live knots (Dietz et al. 1999; see box IV). The gizzard or muscular stomach plays a pivotal role in the digestive physiology of the knot, as this is the organ with which the hard-shelled prey items are crushed after ingestion (Piersma et al. 1993c). Not surprisingly then, the gizzard plays a central role in this thesis.

There may be time and energy costs associated with crushing and digesting food. Those energetic costs have been quantified in chapter 2 (using doubly labelled water), while the time costs have been quantified in chapter 3. The latter chapter also yielded the relation between digestive processing capacity and gizzard mass in the intact bird (using ultrasonography). This empirical relationship has been used in chapter 4 to predict and present gizzard masses at several stopover sites and wintering sites all around the globe. In chapter 5 we test two optimal diet models, one that does take digestive capacity into account, and one that does not. In chapter 6 we bring the former, so-called ‘digestive rate model’ into the field in order to understand the relation between patch use and gizzard mass (established through the combinational use of ultrasonography and radio-telemetry). Differential patch use throughout single low tide periods is modelled and studied in chapter 7 (again using radio-telemetry). Knots are social foragers and the time-costs of feeding together are quantified in chapter 8. Feeding incurs depletion, and how knots cope with that in an uncertain environment is experimentally studied in chapter 9. Depletion may set the carrying capacity of a system and a fitness-based approach is used to calculate carrying capacities (chapter 10). When carrying capacity is reached, some individuals need to go elsewhere while others can stay. How such large-scale movements may relate to digestive processing capacity (i.e. gizzard mass) is discussed in chapter 11.
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Box I. From droppings to diets

Dekinga & Piersma (1993) developed and calibrated a methodology that enables reconstruction of the knot’s diet on the basis of its faeces. Droppings of knots are easily collectable and recognisable (1.5-2.0 cm long by 0.7 cm wide and usually containing crushed shell fragments; Box-figure I.1). After drying the droppings at 55-60°C for a few days, they are washed over a 0.3-mm sieve in order to separate crushed shell fragments from attached sediment particles (see Box-figure I.2 for an example of shell fragments retained on the sieve). Subsequently, shell fragments and retained ‘hard’ parts of soft-bodied crustaceans (such as legs or pieces of the carapace) can be used for two purposes. Firstly, shell fragments can be identified down to species-level and thus, after sorting and weighing according to species, the species-composition of the diet can be described. Preferably, this is expressed as the relative contribution of each prey species to the ingested fleshmass, which can be calculated by multiplying the observed shellmass-proportions by the species-specific flesh-to-shellmass ratios. Secondly, the size distribution of each ingested prey species can be reconstructed by identifying and estimating the height of unbroken hinges (Box-figure I.3; or the width of partially broken shells in case of Hydrobia), which provides a good

predictor of shell length. Since flesh-to-shellmass ratios are usually size-dependent, taking account of the size distributions fed upon, generally improves the estimated fleshmass equivalent of a dropping. The outlined methodology has been successfully applied throughout this thesis (chapters 3-6, 11) and in other field studies on knots (Piersma 1991; Piersma et al. 1993a; Moreira 1994; Piersma et al. 1994; Tulp & De Goeij 1994; González et al. 1996).

**Box-figure 1.2.** Shell fragments that remain after washing dried droppings over a 0.3-mm sieve. Pieces of mudsnail (Hydrobia ulvae) and cockle (Cerastoderma edule) are clearly visible. Photo: Jan Drent.

**Box-figure 1.3.** Amongst the crushed shell fragments, hinges can be used to reconstruct the ingested size distribution (of Mya arenaria in this case). Photo: Jan Drent.
The functional response describes a forager’s intake rate in relation to the density of its prey (Solomon 1949). If intake rate is calculated over active foraging events only (searching and handling) we deal with the so-called ‘short-term functional response’ (cf. Fortin et al. 2002). Piersma et al. (1995) experimentally quantified the knot’s short-term functional response to densities of respectively Macoma balthica and Cerastoderma edule. They tested whether the two basic assumptions of a well-known functional response model, Holling’s disc equation (Holling 1959), were met. Holling assumed that (1) instantaneous area of discovery and (2) handling time should not vary with prey density. Given such conditions, the functional response is an increasing but decelerating function of prey density (curved line in Box-figure II.1). Although the experimental results were in conflict with an existing prey-detection model based on direct touch (Zwarts & Blomert 1992) and suggested the existence of a more sophisticated prey-detection system (Piersma et al. 1998), they agreed well with Holling’s assumptions (dots in Box-figure II.1). This particular short-term functional response model and its experimental verification in knots became the conceptual underpinning for this thesis.

Box-figure II.1. Experimentally determined short-term functional response of captive red knots to densities of Macoma balthica and Cerastoderma edule (Piersma et al. 1995; both prey species are pooled here since response parameters were indistinguishable). Dots are means, bars are standard errors. The solid curve gives the common fit (Holling’s disc equation), based on the average area of discovery (5.7 cm²/s) and the average handling time (3.8 s).
It is increasingly acknowledged that individual animals flexibly adjust the size of their organs to ecological demands (Piersma & Lindström 1997). This so-called ‘phenotypic flexibility’ typically covers reversible changes and should be distinguished from better known irreversible forms of plasticity (i.e. developmental plasticity, e.g. as embodied in reaction norms; Piersma & Drent 2003). Outstanding examples of rapid and reversible organ size changes come from birds boosting the size of their gonads just before the onset of the reproductive season and subsequently shrinking them afterwards (Hau 2001). Or, snakes doubling the size of their gut, liver, and kidneys in the first few days after prey-ingestion (Secor & Diamond 1995). Mollusc-eating shorebirds, such as red knots, or bar-tailed godwits (Limosa lapponica) to a lesser extent, show dramatic changes in digestive organ sizes in relation to their long-distance migrations. For example, the muscular gizzard, needed to crush the hard-shelled prey, is generally atrophied during the intercontinental long-distance flights and is hypertrophied during fuelling at the stopover or wintering grounds (Box-figure III.1; Piersma & Gill 1998; Piersma et al. 1999). In addition, the hardness of the diet seems to fine-tune the degree of hypertrophy, as shown in captive red knots that were alternately fed soft and hard-shelled food (Dekinga et al. 2001).

Phenotypic flexibility is functionally interpreted as an energy-savings mechanism. On the one hand, larger organs perform better than small ones, but, on the other hand, they are also heavier and metabolically more active and thus require higher transport and maintenance costs. Individuals that are able to turn down the size of temporarily unused organs (such as gonads during non-reproductive periods or digestive organs during fasting) should experience lower metabolic costs. Possible drawbacks are the time-costs involved when changing organ size. For example, already 2-3 weeks before their long-distance flights, knots and godwits are reducing the size of their gizzard (Box-figure III.1; the same time period is required for building-up gizzard mass after the flight; Piersma et al. 1999). In the context of optimal foraging theory, feeding with small digestive organs could be interpreted as a so-called ‘missed opportunity cost’ (Stephens & Krebs 1986; Brown 1988), i.e. the missed additional energy gain rate that could have been obtained if the animal fed with large digestive organs. Several chapters in this thesis (chapters
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2-6, 11) focus on energy gain rates as a function of digestive organ size (notably gizzard size), and thus provide insight in these missed opportunity costs in knots.

Box-figure III.1. Relative gizzard mass in relation to the timing of departure to the arctic breeding grounds in two long-distance migrant shorebird species. Dots refer to canutus-knots preparing for their flight from West-Africa to Europe; triangles refer to islandica-knots flying from Europe to Greenland/NE Canada; squares refer to bar-tailed godwits stopping over in Europe on their way to central Siberia. The most left data-points were collected long before departure (red knots) or right after arrival at the European stopover (bar-tailed godwit). Note that gizzard mass is scaled to the overall average mass c. 1 week before departure. Figure adapted from Piersma & Lindström (1997).

Box IV. Estimating gizzard size using ultrasonography

Changes in the size of the digestive machinery are likely to change the outcome of foraging decisions (Whelan et al. 2000). Until recently, it was impossible to keep track of such reversible shifts in organ sizes within individuals. Organs could only be weighed once, after dissecting the body, and thus the study of the relationship between feeding choices and organ sizes was bound to be a comparison between individuals. Apart from the ethical problem of having to kill birds, this bears the dis-advantage that
part of the variability in feeding choices is due to differences between individuals other than differences in organ sizes (e.g. personality differences, differences in bill morphology, etc.). However, recent advances in a simple non-invasive technique, ultrasono-graphic imaging, opened up the possibility to track changes in organ sizes within individual birds (Dietz et al. 1999; see Dekinga et al. 2001 for an application).

Dietz et al. (1999) successfully developed a technique to ultrasono-graphically measure gizzard size in live knots. In short, the bird is held in the hand, turned on its back, and after adding gel onto the ultrasound probe, the probe is placed transversally on the belly of the bird. In this way, the gizzard is clearly recognisable and its diameter can be measured accurately (both horizontally and vertically; to nearest 1 mm; Box-figure IV.1). In order to ensure an empty stomach, we would always with-hold food from the birds during the two hours preceding the measure-ments. In the field, measured birds always had empty stomachs as they were

**Box-figure IV.1.** Ultrasonographic image from a transversal point of view of the muscular gizzard. The gizzard is distinguishable as the round, slightly ellipse-shaped image in the upper half of the photo. Both the vertical and the horizontal diameter can be measured. Photo: Maurine Dietz.
caught at the end of their resting period during high tide (with the equipment being relatively small and portable, we could do the measurements in situ right after catching; Box-figure IV.2). Calibration of ultrasound estimates with real gizzard masses from carcasses revealed a strong predictive power of the methodology ($R = 0.8-0.9$; absolute discrepancy = 2-3 g; using observer-specific calibration lines).

Box-figure IV.2. Anne Dekinga ultrasonographically measuring gizzard sizes on board of RV Navicula. Photo: Theunis Piersma.

References


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Feeding knots. The energetic cost of making rapid probing movements is about 3-4 times as high as that of walking. Photo: Jan van de Kam.