Foraging decisions in a digestively constrained long-distance migrant, the red knot (Calidris canutus)
van Gils, Johannes
General discussion: scaling up from physiological and behavioural ecology towards population-level processes

Jan A. van Gils
Summary

In this final chapter, we will scale up from physiology and individual decision-making to processes at the level of populations (notably emigration and survival). At the lowest scale of the individual lies the functional response, which describes the relation between energy intake rate on the one hand and prey and competitor density on the other hand. Quantified relationships such as this one are needed if we are to understand the decision-making process of foragers, such as what to feed on (ch. 4-5), when to feed (ch. 7), where to feed (ch. 4, 6-9), for how long to feed (ch. 6-7), and with how many others to feed at the same time and place (ch. 8). In this thesis, it is shown that in red knots functional responses (ch. 2-3, 8) and foraging decisions (ch. 3-9) are shaped by digestive constraints. Scaling up to the population, total rate of prey consumption ultimately sets the number of foragers that can be sustained by the (yearly renewed) prey stocks in an area (i.e. carrying capacity; ch. 10). In case the population of foragers exceeds an area's carrying capacity, only a proportion of birds will be able to stay; all others are forced to make their living elsewhere. Inter-individual differences in foraging ability (digestive capacity) determine who is able to stay and who should abandon the area. In this respect, we distinguish two vulnerable phases in the annual cycle of the knot: (1) during spring stopover, and (2) upon arrival at wintering grounds/autumn stopover sites. In both periods, knots face a trade-off between flying with atrophied gizzards and fuelling with hypertrophied gizzards.
Functional response: searching for prey

The best-known functional response model, Holling’s disc equation (Holling 1959), captures the essence of two crucial foraging states: (1) searching for prey and (2) handling captured prey. In this first section we focus on the searching component, which generally delimits intake rate in the lower prey densities (Figure 11.1). The way a “Holling-forager” finds it food assumes that prey are distributed randomly in space. However, in reality, prey are generally distributed patchily at various spatial scales (Fauchald et al. 2000), which is also the case in the bivalve prey of the knot (Legendre et al. 1997). It is therefore relevant to understand how knots find and exploit such concentrations of food.

Figure 11.1. A comparison among three types of functional response models for a single-prey type environment (all have the following parameters: searching efficiency \( a = 0.05 \) m\(^2\)/s; handling time \( h = 2.5 \) s/prey; upper rate of digestion \( c = 0.25 \) prey/s). Holling’s (1959) type II curve (upper solid line) initially increases with prey density at a rate equivalent to the encounter rate; at higher prey densities it levels off to 1/h due to handling time \( h \). In the digestive rate model (thick grey line), digestion proceeds in the background of other activities. It therefore follows Holling’s type II curve until the rate of prey collection exceeds the upper rate of digestion \( c \); from that prey density onwards intake rate equals upper digestion rate and the forager occasionally needs to take digestive breaks in order to free some space in its digestive tract. Jeschke et al.’s (2002) satiation-based functional response (lower solid line) also assumes digestion to proceed in the background of other activities. However, due to the motivation to search being inversely related to gut fullness, intake rates are depressed relative to the digestive rate model due to ‘moments of feeling satiated’ (during which the gut is never fully stuffed, in contrast to periods of digestive breaks in the digestive rate model). Therefore, intake rate approaches but never reaches rate of digestion \( c \) at infinite prey densities.
At each spatial scale red knots have evolved highly proficient ways of locating such patchily distributed food items. Knots feed on spatfall of marine bivalves that may settle en masse in late summer, yielding local shellfish bonanzas. Even though such large-scale concentrations of prey are hidden in the sediment and their exact locations vary unpredictably between years (Armonies & Reise 2003), knots are able to find them. Individually searching knots are attracted from afar to a big flock of knots feeding on the wide-open mudflats (pers. obs.). Such a flock has likely just hit the jackpot and in this way public information on good feeding sites is transferred smoothly. This mechanism of finding food is technically called conspecific attraction, area copying or local enhancement (Drent & Swierstra 1977; Giraldeau 1997). In addition to this mechanism operating during low tide, knots possibly exchange information about good feeding localities during high tide at communal roosts, which are suggested to act as ‘information centres’ (Ward & Zahavi 1973; see e.g. Wright et al. 2003 for recent empirical verification).

At a finer scale within a prey-rich hotspot, birds get to the hottest ‘sub-spots’ by again making good use of public information. In the outdoor, experimental aviaries on Texel (NIOZ), where we mimic the intertidal, we found that knots keep track of the feeding success of the flock mates that surround them (see box V for more details). We observed that, by making use of public information, an individual feeding in a flock of four birds is able to find food patches four times faster than when ignoring such valuable information. Although such small flocks are rarely seen in the field, we imagine that birds keeping track of the feeding success of their neighbours are able to better anticipate the fine-scaled variations in prey density.

Once at a good patch, prey consumption depletes the local food supply and at some point the knot should decide to move on. The so-called “marginal value theorem” finds the rate-maximising solution for this problem: leave the patch when the estimated intake rate in the patch falls below the long-term average intake rate. Although initially developed for situations where energy is taken up in a continuous flow (such as hummingbirds feeding on nectar; Charnov 1976b), the theory also applies to more “knot-like” situations where encounters with discrete prey items are stochastic events (Oaten 1977; McNamara 1982; Green 1988; Olsson & Holmgren 1998; Olsson & Brown 2004). An experiment on patch use was set up and the results were in full agreement with the stochastic version of the model (Van Gils et al. 2003a: chapter 9). In the experiment we dealt with solitary-feeding knots that could only collect personal information on prey capture rates. However, just as observed for the above-described movement between patches, socially-feeding knots are likely able to collect and weigh public information on local capture
rates when deciding on the length of stay in the current patch (Valone 1989; Sernland et al. 2003).

Note that the aforementioned foraging-experiments (box V; chapter 9) took place in rather simple, artificial environments, in which prey lived in discrete patches with distinct borders. In box VI we describe foraging behaviour in natural, continuous environments in which easily recognisable patches do not exist.

At the smallest spatial scale, the scale of individual prey items, a sophisticated prey detection system has evolved in the bill tip of red knots. There, so-called Herbst corpuscles are able to feel pressure gradients in sediment. This enables knots to detect hard-shelled prey even before the bill actually touches the prey (Piersma et al. 1998). Prey living at a depth just within reach of the 3.5-cm bill would be found ten times slower if knots would lack this sixth sense (Piersma et al. 1995). The physical mechanism behind this novel prey sensory system seems to be the build-up of pressure in pore water when a bill repeatedly probes near a hard object in wet soft-sediment. This idea was tested by experimentally manipulating sediment pore water content. It revealed that food-finding rates in wet sediment were 40% higher than those in dry sediment (box VII).

**Functional response: handling prey**

Due to their habitat of ingesting minute shelled prey items intact, knots have relatively short handling times (1-2 s; Zwarts & Wanink 1993; Piersma et al. 1995). Unlike oystercatchers (Haematopus ostralegus), they do not spend time opening their bivalve prey before swallowing; instead they have ‘chosen’ to literally crack the problem in their digestive tract. In terms of time cost, handling therefore plays a minor role in the foraging ecology of knots (handling usually makes up only 5-10% of the active foraging time, even at high prey densities where searching times are relatively short; Piersma et al. 1995). For example, handling time is not important in explaining the knot’s prey choice (Van Gils et al. 2004a,b; ch. 5-6). Classical models on optimal diet choice that rank prey types according to energy content per unit handling time (Pulliam 1974; Charnov 1976a) therefore do not fit the knot’s case. As another example, interference models that differ in how handling foragers compete with one another (Beddington 1975; Crowley & Martin 1989; Ruxton et al. 1992) normally make contrasting predictions on aggregative responses (Van der Meer & Ens 1997). However, when applied to the knot, the predicted aggregative responses are indistinguishable over their natural
range of prey densities (Van Gils & Piersma 2004: ch. 8). Not surprisingly, such diet and interference models have been successfully applied in studies on oystercatchers (Wanink & Zwarts 2001; Stillman et al. 2002). Oystercatchers need handling times of several minutes to open their bivalve prey in situ and to swallow the flesh afterwards. Especially when feeding on the hard-to-open shellfish, handling takes 25-40% of the active foraging time of oystercatchers (Zwarts et al. 1996).

According to Holling (1959), the maximum intake rate of foragers attained at high prey densities is set by handling time, i.e. a bird can never eat faster than it can handle its prey. Even though this prediction may hold when considering active foraging time only (see for instance box II in the Introduction), intake rates over total time are in any case much lower than handling rates (Van Gils et al. 2003b: chapter 3). Often, digestion is the slowest link in the chain and sets the upper limit to intake rate (Jeschke et al. 2002).

**Functional response: incorporating the digestive process**

The price paid by the knot for its sensitive bill tip, that enables food finding at a high rate but makes the bill unsuitable for opening the two valves that make up a bivalve, lies in the gastrointestinal tract. Knots are only able to digest their food after crushing the shell with their strong muscular gizzard, which is twice the size predicted by allometric equations for shorebirds (Battley & Piersma 2004). Subsequently, in the gut the fleshy parts are separated from the shell. Finally, the bulky ballast is removed from the digestive system by the production of faecal pellets consisting almost entirely of crushed shell fragments. As the gut of feeding knots mostly contains indigestible shells with only little flesh (90% of shell vs. 10% of meat on average), digestion needs to proceed fast in order to make ‘room’ for new prey.

It may be because searching and handling are clearly visible activities, and that digestion is not, that students of foraging have largely ignored digestion and have only considered the former two factors as constraints on energy intake rate (but see Kenward & Sibly 1977; Sibly 1981; Kersten & Visser 1996; Whelan et al. 2000; Jeschke et al. 2002; Karasov & McWilliams 2004; Whelan & Brown 2004). Interestingly, it was Buzz Holling himself who carried his basic type II model further and mechanistically included digestion in his next and more realistic model, the so-called ‘hungry mantid’ model (Holling 1966). In this model, a predator is not always motivated to forage; instead the motivation to search for a new prey depends on gut fullness, i.e. the fuller its gut, the more
satiated it feels and the less eager it is to search for new food. In contrast to his 1959-model, this model has rarely been picked up. Presumably this is because it contains 22 parameters that enter complex equations. Metz and Van Batenburg (1984) have tried to simplify it by solving the model analytically instead of by simulation (see also Sabelis 1986). By removing the stochasticity and thereby simplifying the mathematics even further (at the expense of generality; Metz & Van Batenburg 1984), Jeschke et al. (2002) recently came up with a relatively simple satiation-based functional response that provides a viable and testable alternative to Holling’s disc equation (Figure 11.1).

In spite of their greater realism, these satiation-based models are likely to be applicable only to animals that are energetically satisfied for a while once having a full stomach. This may hold when feeding on highly digestible food, in which case almost all of the stomach-content is metabolisable. By contrast, animals that ingest bulky food items need to fill up their stomach several times before they get the slightest sense of satiation; therefore their feeding motivation should virtually be independent of stomach/gut fullness. Only in case their gut (or stomach) is totally stuffed with food should they stop feeding for a while, not because of lesser motivation but simply because they cannot fit more food into their guts. In red knots feeding on refractory molluscs intake is often limited by passage time (Zwarts & Blomert 1992; chapter 3) and therefore knots furnish an appropriate example here (see box VIII on food passage times; but see box IX for observations on state-dependent feeding motivation in knots). For such animals, it is more appropriate and simple to model digestion as a capacity-problem, which has been done in quite some studies on large herbivores (Fryxell 1991; Schmitz 1995; Hirakawa 1997a; Farnsworth & Illius 1998; Owen-Smith 2002). In such so-called ‘digestive rate models’ (after Verlinden & Wiley 1989), rate of food collection as expected by Holling’s disc equation is compared to the maximum rate at which food can digestively be processed. It is the slower of these two processes that sets energy intake rate, as food cannot be ingested faster than processed and vice versa (Figure 11.1). This way of incorporating digestion into foraging is the approach taken in this thesis.

In this respect, chapter 3 represents the key to this thesis. It describes the digestive capacity or the maximum rate of digestion in red knots. The paper benefited from a methodological breakthrough that enabled us to measure gizzard mass in live knots using ultrasonography (Dietz et al. 1999). Captive knots, that were fasted for at least 6-h and were therefore highly motivated to eat, were offered a range of prey items of variable size and shell mass. Because these prey items were offered ad libitum, the birds did not have to search but only to collect and ingest their food. We show that actual rates of
prey intake were an order of magnitude lower than the rates at which the food could be handled, indicating that it is not handling time but another process that ultimately constrains energy uptake. Two lines of evidence showed that it was digestive capacity setting the limits. Firstly, when expressed as shell mass ingested per unit time, intake rates were similar across all prey types that varied almost two orders of magnitude in size. So, in other words, a prey item containing 300 mg of shell mass requires ten times the processing time of a prey item of 30 mg of shell mass (Figure 3.3). This suggests upper limits in the digestive system upon the rate at which the indigestible shell mass can be processed. Secondly, it was observed that the rate at which shell mass could be processed increased quadratically with an increase in gizzard mass (i.e. the regression-coefficient did not differ from 2). So, enlarging the digestive system, particularly the muscular gizzard, enlarges the digestive-processing capacity. The simplicity of these experimental results can neatly be formalised as \[ I = c \frac{G^2}{DM_{shell}} \], implying that prey intake rate \( I \) is inversely related to prey shell mass \( (DM_{shell}) \) and quadratically to a knot’s gizzard mass \( G \), where \( c \) is constant at \( 5 \cdot 10^{-5} g_{DM_{shell}} s^{-1} g^{-2}_{gizzard} \) (indicating the increase in processing capacity with an increase in squared gizzard mass). Taking it one step further, energy intake rate \( E \) can be written as \( E = mcG^2 \), where \( m \) is the mass-specific energy content of a prey, i.e. the amount of metabolizable energy per g shell mass, also called ‘prey quality’ throughout this thesis.

\[ E = mcG^2 \]

Almost all other results in this thesis are derivations of this empirical-based equation \( E = mcG^2 \). For example, rewriting the equation to \( G = \sqrt{\frac{E}{mc}} \) allowed us to predict gizzard masses \( G \) if prey quality \( m \) and energy intake rate \( E \) are known. Prey qualities were measured by reconstructing the diet from faecal analyses (following Dekinga & Piersma 1993). Energy intake rates were assumed to cover energy expenditure rates for knots that aim to balance their energy budget (so-called ‘satisficing’), while for knots that aim to maximise net daily energy intake they were assumed to match the physiological maximum (as estimated by Kvist & Lindström 2003; but see also Kirkwood 1983). This enterprise yielded good agreement with the data and added new insights into the ecology of migration and stopovers. Year-round in the Wadden Sea, knots adjust their gizzard size to satisficing demands, except in spring, which is when they build rate-maximising gizzards (chapter 3). On a
global scale this pattern is repeated. At the wintering sites knots have ‘satisficing gizzards’ and at spring stopovers they have ‘rate-maximising gizzards’ (Van Gils et al. MSb: chapter 4). Remarkably, rate-maximising gizzards at stopovers were not larger than the satisficing gizzards during winter; in fact they appeared to be even smaller! The reason is that knots capitalise on those stopover sites that (seasonally) harbour prey of super-high quality, which requires relatively small gizzards, even when fuelling at full speed. By doing so, they maximise their overall speed of migration and gain about a week of extra time compared with knots that would ignore prey quality differences between potential stopover sites. We suggest that such ‘hotspots’ play a critical role in the sustained use of all flyways occupied by knots (for an example, see box X).

Knowing the upper digestive limit to energy intake rate $E$, we manipulated prey density in an experimental, single-prey type environment (chapter 9). As we knew prey densities and obtained estimates on handling time and searching efficiency, we were able to predict energy intake rates from Holling’s disc equation assuming no digestive constraint. It turned out that these “Holling intake rates” were about five times higher than the constrained gizzards could process. Knots could solve this discrepancy in several possible ways, with two extreme options (Figure 9.6). On the one hand, they could slow down foraging by a factor five and thereby obtain instantaneous intake rates that matched the maximum digestive processing capacity (i.e. where the thick-curved option line in Figure 9.6C intersects the digestive-constraint line). On the other hand, they could ‘obey Holling’ at full speed but take digestive breaks for about 80% (4/5) of their time, such that the overall energy intake rate (i.e. over total time) could be kept up by their crushing gizzards (i.e. option $O_{net}$ in Figure 9.6C). Both options maximise gross energy gain rate (i.e. the maximum digestive-processing rate), though at quite a price. The first option is costly because the bird would always be feeding (be it at a slower and thus cheaper rate); the second option is costly because feeding takes place at full speed (even though the bird often takes digestive breaks, which are energetically cheap). It turned out that the knots selected a mixed option; they did not feed at full speed nor did they slow down by a factor five. Instead, they alternated between cheap digestive breaks and feeding as efficiently as possible by maximising the amount of gross energy gained per unit of energy lost to foraging (i.e. they maximised the so-called ‘foraging gain ratio’ at option $O_{min}$ in Figure 9.6C; Houston 1995; Hedenström & Alerstam 1995; McNamara & Houston 1997). In this way they maintained a maximum gross energy intake in the cheapest possible way, i.e. they maximised their overall net energy intake rate (vertical axis in Figure 9.6C).
Multiple-prey types

In single-prey type environments such as those discussed above, $E = mcG^2$ can be used to understand and predict energy intake rates $E$ once prey quality $m$ and gizzard mass $G$ are known. In more natural multiple-prey type environments, where knots can choose between different prey types that vary in quality $m$, it is not immediately obvious how energy intake rates are calculated. In a world without digestive constraints, prey selection under rate-maximisation is relatively simple. There, only a prey type's profitability (defined as its energy content per unit handling time) determines whether it should be included in the diet; i.e. prey quality plays no role. Prey types whose profitability exceeds long-term energy intake rate should be eaten while all other types should be ignored (Pulliam 1974; Charnov 1976a; Stephens & Krebs 1986). In a world including digestive constraints, prey quality should play a role, but how should it be traded off against prey profitability? This challenging question is addressed in chapters 5 and 6, where we build upon the optimal solution for a digestively constrained forager as found by Hirofumi Hirakawa (1995, 1997a,b). He predicted that only the highest quality prey should be included in the diet unless profitability falls below a critical threshold (Figure 5.1). We tested both diet models in controlled experiments and in the field. For example, in a particular field situation (mudflats east of Griend, late summer 1996), according to Hirakawa rate-maximising knots should ignore poor-quality cockles (Cerastoderma edule) and only accept the thin-shelled and thus high-quality sandgaper (Mya arenaria). By contrast, the classical diet models would predict a 'balanced' diet, composed of both species. It appeared that the knots followed Hirakawa's model perfectly and thereby maximised their energy intake rate (Figure 5.9). This was true during this particular field case, when the profitable but poor-quality cockles were rejected, but also in two independent lab experiments (chapter 5).

With Hirakawa's model in hand, it was then possible to generate predictions on diet composition as a function of digestive-processing capacity. The larger the digestive-processing capacity, the higher the energy intake rate, and the more the rate-maximising diet tends to mimic a profitability-based diet (Figure 5.1). As gizzard mass sets processing capacity in red knots, an increase in gizzard mass should thus lead to an increase in (gross) energy intake and to an increase in the proportion of poor-quality but highly profitable prey in the diet (such as cockles). Intense tracking throughout the western Wadden Sea of radio-marked red knots with known gizzard masses (determined at catch using ultrasonography) allowed us to test these diet
predictions (chapter 6). By reconstructing the diet from faecal analysis (Dekinga & Piersma 1993), we showed that knots with small gizzards indeed only ate prey of the highest quality, i.e. soft-bodied crustaceans, while birds with large gizzards fed almost entirely upon lower-quality, hard-shelled prey items (Figure 6.3C). Assuming that the daily time spent foraging declines with intake rate, we indirectly showed that intake rate increased with gizzard mass as birds with the largest gizzards stayed longest at the high-tide roosts (Figure 6.3D). In fact, birds with the smallest gizzards (4-g) fed for the maximal duration that mudflats are exposed in the western Wadden Sea, which is 16-17 hours/day. According to our calculations even with such long working days they barely balanced their energy budgets. The knots were able to make such long days by taking advantage of timing differences in the exposure times of intertidal flats in different parts of their home range. Low tide occurs 2 hours later in the eastern part than in the western part of their home range, adding, on a daily basis, a maximum of 4-h of feeding to the 12-h that is normally available in a tidal system (Figure 6.6).

For two reasons red knots with small gizzards are likely to have newly arrived from their breeding grounds. Firstly, nutritional organs, such as the gizzard, tend to atrophy before and during long-distance migrations (Piersma & Lindström 1997; Piersma et al. 1999). Secondly, knots on their high-arctic breeding grounds feed on soft-bodied insects and therefore do not require a big gizzard (Battley & Piersma 2004). Having a small gizzard makes them rely totally upon relatively scarce soft-bodied prey items, which forces them to feed for as long as possible, which makes the post-arrival period in the Wadden Sea a vulnerable phase in the annual cycle of knots. On the one hand, this critical period need not last long as gizzards are flexible organs that can double in size within about a week (but note that this high rate of increase was only found experimentally in captive birds; Dekinga et al. 2001). On the other hand, it should not last long as crustacean numbers rapidly decline during late summer due to depletion and dispersal to the gullies (Figure 6.4A). This also reveals the tight schedule of breeding and southward migration: late arrivals in the Wadden Sea might have a very hard time finding easily digestible food. Indeed, periods of cold or an incidental scarcity in soft-bodied prey could push freshly arrived knots towards starvation thresholds. With respect to incidental scarcity of soft food, we showed that the abundance of Siberian canutus-knots is tightly correlated to the yearly abundance of crustaceans (Figure 6.5). Presumably, they skip the Wadden Sea in poor crustacean-years. A paucity of invertebrate food of adequate quality would especially affect the males that arrive later from the breeding grounds than the females. This is in agreement with the enigmatic occurrence
of canutus-knots in the Wadden Sea, with males almost completely absent (Nebel et al. 2000; the most relevant evidence is presented in box XI). In fact, this skipping-idea tallies neatly to the hotspot-hypothesis postulated in chapter 4: in order to save time, knots should skip stopover sites harbouring only poor quality prey (cf. Gudmundsson et al. 1991).

Is crustacean-abundance in the Wadden Sea the key to fall exploitation by canutus?

Carrying capacity of the Wadden Sea for migrating canutus-knots may thus be set by the abundance of soft-bodied crustaceans in late summer. The rapid decline in crustacean densities (by approximately one prey item per m² per day; Figure 6.4A) seems to indicate that exploitative competition sets the limits to the number of canutus-knots that stop over. Indeed, this rate of crustacean decline equals the expected overall depletion rate exerted by the 5,000 knots that were present in that specific year (1998; Figure 6.5). This expected overall depletion rate takes into account the observed crustacean consumption rates of individual knots (one prey per 3-4 minutes; unpubl. data collected near Richel in Sept. 1997), their daily foraging times (10-12 hours per day based on Figure 6.3D and taking into account the inability to visually find crustaceans during the night; Van Gils et al. 2000), and a crustacean-patch size of about 1-km² (patch B in Figure 6.2A). However, exploitation competition alone cannot explain the positive relation between canutus-abundance and crustacean-abundance. Imagine that poor crustacean-years are simply characterised by fewer crustacean-patches (but crustacean-densities within such patches are comparable to good years). Then, in the scenario of exploitative competition only, we would see the same number of canutus-knots stopping over in the Wadden Sea, but only for a shorter period of time (since the smaller-sized patches would get depleted faster). The fact that we see fewer canutus-individuals in poor crustacean-years (that do not necessarily stay for a shorter period of time) must imply that instantaneous intake rates are depressed if the smaller-scaled food patches become occupied by the same total number of knots (i.e. leading to higher density of knots). In response to such reduced intake rates, some individuals decide to move on and as a consequence intake rates in the crustacean-patches increase again (the problem of which individuals may decide to move on is discussed in the following section). In the light of this interference competition (Goss-Custard 1980), the skipping of stopover sites could be thought of as the establishment of an ideal free distribution on a global scale (Fretwell & Lucas 1970;
although this would be a very unstable distribution as eventually all canutus-
individuals will depart to West Africa).

In apparent contrast to this idea of interference competition amongst
crustacean-eating canutus-individuals, we argued that knots in winter tend to
evade the cost of interference competition (ch. 8). We reasoned that this is the
case when they are digestively bottlenecked, which occurs when they are
feeding on abundant and bulky hard-shelled food. When the time lost to
random interactions overlaps with the time lost to digestion then there is no
time-cost to interference. By contrast, when feeding on soft-bodied food,
intake rate is much less hampered by digestive processing rate, for two simple
reasons. Firstly, digesting soft food proceeds fast (which lifts the value of the
digestive constraint $c$ in Figure 11.1). Secondly, encounter and handling rates
on hiding and manoeuvrable crustaceans are usually rather low (which
reduces the short-term functional response in Figure 11.1 below the $c$-line
across a large range of prey densities). For these reasons, interference and not
a digestive bottleneck is likely to constrain intake rates in knots feeding on
soft-bodied crustaceans. (Note that in Figure 8.5 we do assume crustacean-
feeding knots to hit their digestive constraint. The reason for this is that most
of the knot-flocks in this figure were observed in the late 1980s/early 1990s,
during which the western Wadden Sea contained higher crustacean densities
(unpubl. data) and therefore short-term intake rate on soft-food in Figure
11.1 would exceed the $c$-level).

Summarising, both forms of intraspecific-competition seem to come into
play when considering density-dependent regulation of the canutus-
population. Exploitative competition for soft-food seems to affect late-arriving
birds that cannot join in the crustacean-feast simply because it has been
harvested by early-arriving birds. The larger the canutus-population, the
sooner soft-food would run out, the larger the proportion of birds that would
arrive too late, the larger the proportion of birds that should skip the Wadden
Sea. At the same time, interference competition seems to affect the number of
canutus-knots that can participate in exploiting the crustacean-stocks at a
given moment in time. The larger the canutus-population, the larger the proportion of birds that would competitively be unable to occupy the available
soft-food patches, the larger the proportion of birds that should skip the
Wadden Sea. Assuming a mortality-cost of this migratory skipping (e.g.
through lower levels of body stores upon arrival in West Africa), annual
survival should for these two reasons be density-dependent. This logic
reconciles two schools of thought that express carrying capacity either as a
depletion-problem (e.g. Sutherland & Anderson 1993; Gill et al. 2001; Goss-
Custard et al. 2003; Van Gils et al. 2004c: chapter 10) or as an interference-
problem (e.g. Ruxton et al. 1992; Goss-Custard et al. 1995; Johansson & Sumpter 2003). Admittedly, we still need to demonstrate that skipping the Wadden Sea during southward migration incurs a mortality cost.

Shellfish quality and winter philopatry in islandica

In trying to understand limitations upon the number of islandica-knots overwintering in the western Dutch Wadden Sea, we need to realise that these numbers vary greatly between years (15,000-120,000; SOVON unpublished data; see also Bijlsma et al. 2001). Rather than mirroring temporal changes in population size, this is a consequence of the yearly redistribution of individuals throughout their NW-European wintering grounds. For example, estuaries in Great Britain fill up with knots in years when the numbers are low in The Netherlands and vice versa (Atkinson et al. 2003; G. Austin, S. Delany & T. Piersma, pers. comm.). Presumably, these islandica-knots abandon the Wadden Sea when food conditions are poor, comparable to the canutus-knots that seem to skip the Wadden Sea when soft-bodied prey are scarce in late summer.

To explore this idea further, we analysed the yearly variation in prey quality m. In contrast to prey density, prey quality affects energy gain rates across all prey densities, while prey density only plays a role when not digestively constrained (see Figure 11.1). Although knots might be able to flexibly adjust gizzard mass G to variations in prey quality m by ‘obeying’ E = mcG² (e.g. chapters 3 and 4), leaving for an alternative wintering site with possibly better-quality prey may be a better policy. The time and energy costs associated with building, maintaining and transporting a large gizzard are rather high (Dekinga et al. 2001; chapters 2-3) and might outweigh the costs of moving elsewhere. As before (chapters 3 and 4), prey qualities were estimated by reconstructing diet composition from faeces, collected in the autumns of 1999-2002 (following Dekinga & Piersma 1993). Rewriting E = mcG² to G = \sqrt{\frac{E}{mc}} , we predicted gizzard mass G required for a balanced energy budget by assuming daily foraging times of 16-hours (which is feasible in the western Dutch Wadden Sea – see chapter 6). In July-August, islandica-knots were caught with mist-nets and their gizzard sizes were measured using ultrasonography (sample sizes for respectively 1999, 2000, 2001, and 2002 are 151, 97, 148, and 87 birds). Most birds were caught in August which is when the later arriving islandica (from Greenland and NE Canada) generally outnumber the Siberian canutus-subspecies.
Indeed, knots seem to adjust their gizzard sizes to the yearly variations in prey quality such that their energy budget would be balanced, with gizzards of 5.5-g in good-quality years and gizzards of more than 7-g in poor-quality years (Figure 11.2A; see box XII for a recent decline in Macoma-quality; and see box XIII for the effects of mechanical shellfisheries on year-to-year variation in prey quality). While this close agreement between prediction and observation is gratifying, one should keep in mind the variation around these perfectly matched averages. Apparently in each year, some birds had gizzards that were too small to prevent starvation while some birds had gizzards that were 'unnecessarily' big! Each bird captured was given a unique colour-band combination (see Brochard et al. 2002), which enabled us, to some extent, to follow their fates. It turned out that birds that were never seen again in the

Figure 11.2. (A). Observed gizzard mass (mean ± SE) during late summer declines as a function of prey quality. Lines give expected gizzard mass for knots that balance energy income with energy expenditure that either feed for 12-h or for 16-h per day. (B). The same graph as depicted in (A), but now data are split into birds that were seen and birds that were not seen again in the year of capture.
same year had gizzards that were ‘too small’, while birds that were seen again had gizzards that were higher than required for a balanced budget ($P = 0.01; R^2 = 0.02; N = 483$; Figure 11.2B). Apparently, birds with undersized gizzards left the study area for alternative overwintering sites (or died).

The observation that knots choose to move away from the western Wadden Sea instead of adjusting their gizzards to local circumstances conflicts with the idea of fully flexible organ sizes, which has now settled in the minds of some physiological ecologists (Piersma & Lindström 1997; Piersma & Drent 2003). Were the knots that left the Wadden Sea with undersized gizzards unable to adjust gizzard mass to the required level? Or, alternatively, was their decision to leave the outcome of a trade-off between the net benefits of moving to alternative sites while maintaining a small gizzard and the net benefits of staying at the current site while increasing gizzard size? As knots with undersized gizzards are in a negative energy balance, the degree to which gizzard mass can be increased depends on the amount of fat stored. We calculated that knots which have just arrived in the Wadden Sea, having about 10-g of fat remaining (based on Davidson & Wilson 1992 and Piersma 1994), have sufficient fuel left to enable them to increase gizzard mass by only 1-g. By deriving a distribution of gizzard masses upon arrival from our captures in July, we can predict the proportion of birds able to stay in the Wadden Sea (Figure 11.3; $N = 218$; note that this distribution contains an unknown number of canutus-individuals; selecting only islandica-individuals ($N = 83$; on the basis of wing moult) does not alter the distribution; $\chi^2 = 6.31$, df = 9, $P > 0.7$). Given that years with good prey quality require smaller gizzards than years with poor prey quality, we qualitatively predicted that the proportion of birds that is able to stay increases with prey quality. Indeed, the proportion of birds surviving the first year after catch, increased as a function of prey quality (Figure 11.4). This so called “local survival” is defined as the actual survival minus the (unknown) fraction of birds that emigrate permanently from our study area and was calculated by using the Cormack-Jolly-Seber model of the MARK software package. The quantitative prediction is that the actual proportion of birds that is able to stay equals the proportion of birds that has a sufficiently sized gizzard upon arrival, i.e. a gizzard that is at most 1-g smaller than metabolically required. Indeed, “local survival” matches well with the expected proportion (Figure 11.5).

This exercise refines the definition of prey quality hotspots along the migratory flyway (see above and chapter 4). Whether a site will be good enough to stop by (to be used during the rest of the winter as in this case), now not only depends on the absolute quality of the available prey, but also on gizzard and fat mass upon arrival. Thus, the use of a site is not a matter of
Figure 11.3. In all graphs, bars give observed frequency distribution of gizzard masses upon arrival (N = 218). (A). In a year with high quality prey, required gizzard mass is rather low (vertical line). Therefore, only a minority of the birds has an undersized gizzard upon arrival (light grey bars). The rest has a sufficiently large gizzard to cope (dark grey bars). (B). In a year with low quality prey, required gizzard mass is rather high (vertical line), and the majority of the birds has an undersized gizzard upon arrival (light grey bars). (C). Generally upon arrival, knots with undersized gizzards have sufficient reserves to flexibly increase gizzard mass by 1 gram. Therefore, in this poor-quality example (the same quality as depicted in (B)), an extra of 25% of all birds is able to cope due to gizzard growth (the dark grey bar in between the dotted and the solid line).
**Figure 11.4.** As expected, the proportion of birds surviving the first year after catch (coined “local survival” here), increases as a function of prey quality (or decreases as a function of minimally required gizzard mass as calculated by the \( E = mc^2 \)-equation). Bars give standard errors of the estimates. Local survival is defined as the actual survival minus the (unknown) fraction of birds that emigrate permanently from the study area and was calculated by using the Cormack-Jolly-Seber model in the MARK software package.

**Figure 11.5.** Local survival matches well with the proportion of birds that have large enough gizzards, taking into account the possibility of a 1-grams gizzard growth (filled dots). Ignoring this flexibility aspect underestimates the proportion of birds that is able to stay (open dots). Bars give standard errors of the estimates.
stopping or skipping by the population as a whole. Instead, a site will only be skipped by those birds whose fat store is insufficient to allow regrowth of the gizzard to required size. This underpins the notion that processes at the level of a population can only be understood by zooming in on individuals making up the population (Lomnicki 1999).

At this point it is tempting to speculate whether such large-scale, gizzard-size-based emigrations of islandica-knots are density-dependent. In other words, is the proportion of birds with undersized gizzards an increasing function of population size? If it is, and if such large-scale emigrations bear a mortality-cost, then they have the potential to regulate the islandica-population. Just as for the canutus-population, we envision two possible ways of competition that might lead to such density-dependence.

Firstly, overall rate of exploitation will increase with increasing population density. At first glance, this may be no problem if there is more than enough food and food stocks never run out of supply (they get renewed yearly anyway). However, optimal diet theory (notably Hirakawa’s digestive rate model) predicts the removal of the highest quality prey first, followed by the exploitation of the second highest quality prey, etc. (Figure 5.1). Thus average prey quality $m$ will decline in the course of exploitation, implying that the required gizzard mass $G$ will increase over time (since $G = \sqrt{\frac{E}{mc}}$). As long as flexible gizzards can keep up with this gradually increasing size requirement then there is no problem and everybody who is able to stay initially will be able to stay in a later stage. However, if gizzards are unable to grow as fast as $m$ declines then an increasing proportion of birds will be unable to stay. In addition, if there is variation in dates of arrival in the Wadden Sea (just as in canutus) then the demands on gizzard size become stronger the later the arrival. Now, with an increase in population size, sequential exploitation from high to low prey qualities will proceed faster, thus the decline in $m$ will be faster, consequently the increase in required $G$ will be steeper (both for the new arrivals and for the birds that are already there), and thus the proportion of birds with undersized gizzards (at a given moment in time) will increase. Provided that there is a mortality-cost to having an undersized gizzard (possibly through the need to emigrate), the extra mortality will set the population size back towards an equilibrium-level (i.e. regulation).

Secondly, along the same lines of reasoning, gizzard-size-related interference competition amongst islandica-knots could have population-regulatory potential. Let us now, for reasons of speculation, relax the assumption that digestively constrained knots face no time-cost to interference (chapter 8). Then, the penalty of interference competition may be strongest in birds with small gizzards (even if they do not have undersized gizzards and do not differ
in competitive ability from birds with large gizzards). The reasoning goes as follows. Imagine a population of knots consisting of two phenotypes that occur in equal proportions (50%), one with a large gizzard and one with a small gizzard. There are two sites, and, without interference, both phenotypes obtain their highest intake rates in site 1. Both types face a digestive constraint in site 1, but not in site 2. Therefore, in site 1 intake rate increases with gizzard size, while in site 2 it is independent of gizzard size. We assume that intake rate declines with population density (interference) and that the proportional decline is similar for both phenotypes. At low population sizes, both phenotypes will occupy site 1 since this yields the highest intake rate for both of them, in spite of reductions due to interference. With increasing population size the time lost to interference will increase and therefore the small-gizzard-type will at some point be the first whose intake rate in site 1 has dropped to the level in (competitor-free) site 2. From this moment onwards, small-gizzard individuals will also occupy site 2. Thus the gizzard-size-related proportion of birds moving elsewhere is density-dependent. Provided again such large-scale movements bear extra mortality-costs, the islandica-population could possibly be regulated in this manner. Note that such a differential distribution of different phenotypes due to interference competition is generally called a truncated phenotype distribution (TPD; Parker & Sutherland 1986; Korona 1989; Holmgren 1995; Humphries et al. 2001). In contrast to existing models on TPDs, our example shows that differences in competitive ability are not necessarily a prerequisite for TPDs to arise. Our gizzard-phenotypes do not differ in competitive ability but only in the upper rate of digestive processing.

Epilogue

Summarising the scaling-up to population processes, we can infer that throughout the annual cycle, red knots face two critical switch points. Firstly, during southward migration, both canutus and islandica face “stomach-problems” upon arrival in the Wadden Sea. Secondly, during northward migration, there seems to be strong selection pressures on utilising only those stopovers that harbour the highest quality prey (hotspots) as this guarantees the fastest migration (chapter 4; box X). For both the spring and the autumn case, the problem boils down to trading off the benefits of travelling with atrophied digestive organs (notably the gizzard) against the benefits of feeding with hypertrophied digestive organs. We have argued that during these vulnerable phases in life density-dependent population regulation might
be going on. The strong numerical response of red knots to the abundance (Figure 6.5) and quality (Figure 11.4) of their food provides a nice base to further discern the pattern of density dependence. Obviously, we need to monitor the food supply and bird numbers over a much longer time period, especially since the internal state of the birds is not a constant but a response to prey density and quality (Figure 11.2).

All in all, we currently seem to be able to make at least some linkage between individual behaviour/physiology and population processes. However, populations rise and fall with both birth and death rates, and so far we have only focussed on death rates. This ignorance is not borne out of narrow-mindedness; rather it is inherent to the chosen study system. Red knots breed in desolate high-arctic tundra around the North Pole, their nests and chicks are perfectly camouflaged, and their family bonds fall apart right after fledging (or even after hatching in case of the female!). Thus, it is impossible to keep track of a knot’s reproductive success. Having said that (switching now from ‘we’ to ‘I’), I hope this thesis has shown that the practical disadvantages do not outweigh the species’ advantages (easy to keep in captivity, readily quantifiable prey stocks, and measurable gizzards in live birds).

Just as Darwinian monsters do not exist, there is no species that is perfectly suitable to answer all population-related questions that we have in mind. We simply need to work on the species that is most suited to answer narrowly specified questions. This thesis, and possibly the work on red knots, for now stops at scaling up to processes at the level of the population because of the difficulty of using variations between individuals in the field. Rather, we need differences between years to reveal interesting patterns. Species better suited to link individual (feeding or migratory) behaviour to population dynamics are conspicuous, have strong family bonds, and are easily identifiable at the individual level (using encoded legbands or neckcollars). Large waterfowl, such as Bewick’s swans (Cygnus columbianus bewickii), which attract dense networks of amateur ring-readers, come close to the perfect study system in this respect (Pettifor et al. 2000; Béty et al. 2003). Using resighting databases collected over many years, overwintering site use can be coupled to lifetime reproductive success at the individual level. The same databases can be used to study shifts in habitat selection in relation to long-term changes in climate and/or agricultural land use. Keeping track of individual abdominal profiles and family size in the subsequent winter, allows the linking-up of fat stores with reproductive output (Ebbing & Spaans 1995; Madsen & Klaassen 2004). Subsequently, this could be coupled to individual feeding performance, even though in waterfowl intake rates are not as easily...
quantifiable as in shorebirds (although estimating dropping rates yields satisfying results; Prop & Black 1998). By attaching satellite transmitters or GPS-loggers onto their large bodies, it should be feasible to accurately measure speed of migration (but note that the attachment of such transmitters using harnesses often gives biases; Ward & Flint 1995; Phillips et al. 2003). Dietary switches from highly digestible tubers and sugarbeets to rather indigestible grass occur each winter and presumably incur flexible increases in nutritional organs. With the aid of ultrasonography, changes in gizzard size could perhaps be tracked in individual (captive) birds that undergo such dietary switches. In the field, the repercussions of diet switches can be studied in relation to reproductive success. Fibre-rich grass might be hard to digest; its high protein levels might be needed to enlarge flight muscles and (reproductive) organs.

As I am currently in the fortunate position to contrast and compare the ecology of the latter study system of Bewick’s swans with the ecology of red knots, I hope to continue making progress in unravelling individual decision-making processes that underlie population processes. Such fundamental insights are not only required for the sake of science, they should also help us preserving biodiversity in a rapidly changing world (provided that governments take science-based decisions; Sutherland et al. 2004).
Box V. The use of public information while foraging

When food is patchily distributed, knots find their food faster when living in a flock than when feeding alone. In fact, the bigger the flock, the faster the food is found (Box-figure V.1A). This was shown experimentally by offering a flock of knots an environment with 48 patches of which only one contained buried prey (approx. 240 items) and all other patches were empty (Van Gils & Bruin, unpubl. data). These patches, buckets (0.3-m

Box-figure V.1. (A). Rate of finding food increases with flock size ($P = 0.01; R^2 = 0.07; N = 96$), where rate is calculated as the inverse of an individual's cumulative amount of search time before it found the food patch. On a log-log scale, the slope of the regression line does not differ from 1 ($P > 0.55$), implying that the food finding rate is proportional to flock size. (B). The total number of patches visited as a function of the total number of visits (each dot gives total number per bird per trial). It shows that patches were visited in a random manner (curved line; $P > 0.5$, no effect of flock size), deviating significantly from systematic search (straight line; $P < 0.02$).
In the patch-use experiments presented in this thesis (chapter 9 and box V), knots were offered a set of discrete, clearly bordered, food patches, i.e. small buckets that contained buried prey. The space in between patches was devoid of prey and the knots had to travel (fly) to move between patches (in fact, the experimental patches were standing in water, leading to very obvious patch-borders). This spatial arrangement conforms to most of the patch-use models that have been developed since the conception of optimal foraging theory back in 1966 (MacArthur & Pianka 1966; Emlen 1966). However, although prey in nature are generally patchily distributed (Pielou 1977), this is usually on a continuous basis without concrete patch-borders (Arditi & Dacorogna 1988). The space in between high prey concentrations still contains some prey items and predators should decide whether to travel or to search in such poorer areas in between “patches”. Moreover, if they decide to travel, they should decide on the scale over which to move. These two basic problems are especially met by mudflat-dwelling knots, which search through the seemingly endlessly stretching sediment without any obvious patch-borders.

### Box VI. Area-restricted search in a continuous environment

In the patch-use experiments presented in this thesis (chapter 9 and box V), knots were offered a set of discrete, clearly bordered, food patches, i.e. small buckets that contained buried prey. The space in between patches was devoid of prey and the knots had to travel (fly) to move between patches (in fact, the experimental patches were standing in water, leading to very obvious patch-borders). This spatial arrangement conforms to most of the patch-use models that have been developed since the conception of optimal foraging theory back in 1966 (MacArthur & Pianka 1966; Emlen 1966). However, although prey in nature are generally patchily distributed (Pielou 1977), this is usually on a continuous basis without concrete patch-borders (Arditi & Dacorogna 1988). The space in between high prey concentrations still contains some prey items and predators should decide whether to travel or to search in such poorer areas in between “patches”. Moreover, if they decide to travel, they should decide on the scale over which to move. These two basic problems are especially met by mudflat-dwelling knots, which search through the seemingly endlessly stretching sediment without any obvious patch-borders.
Albeit in the shade of the well-known patch-use models (Charnov 1976b; Parker & Stuart 1976; Brown 1988), models on feeding in such continuous environments have been developed (Benhamou 1992; Walsh 1996; Klaassen et al. in prep.) and tested (Tinbergen et al. 1967; Smith 1974; Hill et al. 2000; Klaassen et al. 2004). For so-called clumped environments, where a prey encounter is a fair indication for more encounters to come, these models predict that animals should search most intensively in the vicinity of where prey have been found before. The further away from such spots, the less likely to encounter more prey, the less intense should the searching be.

We tested these predictions on free-ranging knots, both in the western Dutch Wadden Sea (observing red knots) and in Roebuck Bay, NW Australia (observing the closely related great knots Calidris tenuirostris rather than red knots). From a distance of 40-100 m, feeding individuals were videotaped for as long as possible (ranging between 0.3-8.8 minutes). Back home, we analysed the tapes in slow motion (1/5 times the recording speed; using The Observer; Noldus Information Technology 1997), and scored searching times (defined as probing), handling times, and other activities (mostly looking-up). In addition, we kept track of each

Box-figure VI.1. Search time (s) invested per step made declines with the distance (steps) to the latest successful prey capture, both in red knots in the Wadden Sea (open dots) and in great knots in Roebuck Bay (filled dots). Lines are regression lines (dashed for red knots, solid for great knots).
step taken, which allowed us to calculate the variable of interest: time spent searching per step. In total, we analysed tracks of 33 red knots and 24 great knots. Before the analysis, data were log-transformed (following Berry 1987).

Both species of knots showed area-restricted search. The further away from the latest successful prey capture (measured in steps), the shorter the searching time invested per step (Box-figure VI.1; \( P < 0.0005 \); HLM with 57 level-2 obs. (i.e. individuals) and 7612 level-1 obs. (i.e. steps)). For example, about 10 steps away from the latest prey capture a knot would only search half as long as in the nearest vicinity of the latest prey capture (1 step). Interestingly, the degree of area-restricted search was significantly stronger for great knots in Roebuck Bay than for red knots in the Wadden Sea, i.e. the slope in Box-figure VI.1 was steepest in great knots (\( P < 0.10 \)). Perhaps, this is a reflection of more patchily distributed prey in Roebuck Bay compared to the Wadden Sea (Honkoop in prep.). Alternatively, it could be due to intrinsic differences between great and red knots (possibly through differences in diet breadth). The completely unbalanced design of the measurements (using red knots in the Wadden Sea and great knots in Roebuck Bay) does not allow tearing apart both ideas.

Box VII. Remotely sensing hard-shelled prey

Red knots are able to detect their buried prey even beyond reach of their bills (Piersma et al. 1998). It is hypothesised that this prey-detection mechanism is based on principles of so-called ‘seabed dynamics’, which involves the build-up of pressure in pore water by repeated probes of the bill. In the sediment, hard objects such as shelled prey would block such pore water pressures, which would be sensed by large and specifically structured arrays of Herbst corpuscles in the knot’s bill tip. The idea that pore water is a prerequisite for knots to find hard-shelled prey generates the prediction that searching efficiencies are higher in wet than in dry sediment.

We tested this prediction using captive knots (Van Gils & Brans, unpubl. data). The birds were allowed to feed in a small tray (0.25 m²) in the middle of the seawater-filled basin in one of the outdoor, intertidal aviaries at NIOZ. Before each trial, the tray was filled with sediment and
A great knot finds and swallows a *Tellina piratica*. Photos: Jan van de Kam.
50 prey items were inserted at a depth of 2-cm (see Piersma et al. 1995 and chapters 5, 8-9 for similar methodology). As prey items we used blue mussels *Mytilus edulis* of 12-15 mm long. Dry sediment was changed into wet sediment by adding a fixed volume of seawater. We took small core samples (1/629 m²) down to a depth of 4-cm (i.e. the maximum depth that can be reached by a knot’s bill) as a check on the success of the water-treatment. These samples were weighed before and after drying them to constant mass at 85°C. In the experiment, four different birds were used, always one per trial. Each treatment was repeated three times per bird, leading to 24 trials in total. Each trial was videotaped and tapes were later on analysed at slow motion (1/5 times the recording speed) using The Observer software package (Noldus Information Technology 1997). We scored searching, handling and other activities (mainly looking up). We analysed searching times for the first 10 prey encounters, excluding the firstly encountered item (cf. Piersma et al. 1995). As knots search through such trays in a random fashion (chapter 8), we calculated the searching efficiency a for each prey encounter as (cf. chapters 8-9):

$$a = \frac{1}{T_s X}$$

where $T_s$ is searching time in between two prey encounters, and $X$ is current prey density (i.e. initial prey density minus the number of prey found so far). Searching efficiencies were analysed in a hierarchical linear model (with random slopes, fixed effects of BIRD IDENTITY and SEDIMENT WETNESS, and TRIAL as identifier).

The experimental results were in full agreement with the ‘seabed-hypothesis’: wetness of the sediment affected searching efficiency, with the highest efficiencies found in wet sediment (HLM; P < 0.05; Box-figure VII.1). Wet sediment contained nearly twice the amount of water of dry sediment (29.5 vs. 17.4%; obtained after arc-sinus square root transformation; HLM; N = 20; P < 0.0001).

Extrapolating these laboratory results to the field situation, we speculated that in the course of outgoing tide, natural sediments might dry out and searching efficiencies at a given site might decline over the low tide period. This could be an explanation as to why knots often follow the waterline when feeding. In order to test this idea, we brought the four captive knots into the field and measured their searching
efficiencies at different phases of the low tide period (two hours before low tide, at low tide, and two hours after low tide). This was repeated at four different sites (at Grienderwaard) during 24 low tide periods (6 Aug – 2 Sep 1999). Before each trial, we measured pore water content in a similar way as in the lab-experiment. Searching efficiencies were measured (video-camera; The Observer) and calculated (random search) as explained above; estimates of prey density were obtained by analysing top layers (0-4 cm) of 20 core samples (1/56 m² per core) collected at each site for each tidal phase.

In the field, searching efficiencies did not vary throughout the tidal cycle and were rather constant at 14 cm²/s throughout ($P > 0.4$). This matched with the pore water content that remained rather stable during low tide at about 20.1% (only early in the tide did the sediment contain slightly more pore water; 21.4%; $P < 0.05$).

Summarising, we conclude that pore water content affects searching efficiency in knots, which is a support for the ‘seabed-hypothesis’ postulated by Piersma et al. (1998). However, on natural intertidal flats, fluctuations within tidal cycles in the amount of pore water are too small to affect searching efficiencies of free-ranging knots. Thus, observed shifts in patch use throughout the tidal cycle cannot be due to declining searching efficiencies. More likely, they are a reflection of better sites (in terms of prey density and/or quality) becoming available when the tide recedes (see Van Gils et al. MSa: chapter 7).

**Box-figure VII.1.** Searching efficiency as a function of experimentally manipulated sediment wetness. Dots are least square means, bars are standard errors. Grey line gives searching efficiency observed in the field experiment.
The tip of the knot’s bill is sensitive and full of sensory organs. This enables remotely sensing hard-shelled prey items through the detection of pressure gradients.

Photo: Jan van de Kam.
Box VIII. Food retention times in knots

Knots ingest their bulky bivalve prey whole. During feeding, their gut is filled with indigestible, calcareous shell material, which needs to be excreted as soon as possible to free space for new food. However, rate of food passage trades off with assimilation efficiency (Prop & Vulink 1992), and thus food retention times should not be too short. In order to know more on the ins and outs of knots, we measured food retention times in a captive knot (Van Gils & Piersma, unpubl. data).

During trials that lasted about three hours, this bird was alternately offered dark-coloured Hydrobia ulvae or light-coloured Spisula subtruncata in bouts of respectively 30 or 15 minutes. Consequently, after producing a series of dark-coloured faeces, the bird would produce a series of light-coloured faeces, etc. Per dropping produced, we analysed the species-specific amount of shell mass, which enabled us to budget total shell mass throughput. By using prey species as a marker, we were able to quantify transit times (i.e. the time until the first appearance of the marker in the faeces; Box-figure VIII.1) and median retention times.

Box-figure VIII.1. Example of a feeding bout within a trial (trial #2 in this case). Right from the start of the trial, the bird was offered Spisula for a period of 15 minutes (where after it was given a Hydrobia-bout; not plotted here). The cumulative amount of Spisula ingested is given by the light grey surface. After 36 minutes, the first droppings containing white Spisula-fragments appear (i.e. transit time). The cumulative amount of Spisula-fragments (on the basis of mass) excreted is given by the dark grey surface, showing that 50% of all fragments are excreted 49 minutes after 50% of all Spisula-items are ingested (i.e. median retention time).
(i.e. the time until half of the ingested markers are excreted; Box-figure VIII.1). We performed four trials in total (with 3-9 bouts per trial).

Average (± SE) median retention time was 56.2 ± 5.7 minutes (HLM with 10 level-1 observations; Box-figure VIII.2), average (± SE) transit time was 24.8 ± 3.5 minutes (HLM with 10 level-1 observations; Box-figure VIII.2). These observations match well with the allometric expectation for birds provided by Robbins (1993 p. 331; 50.2 minutes for mean retention time).

Box-figure VIII.2. Frequency distribution of the observed transit and retention times.

Box IX. Trading off safety against energy gain

Foragers face a trade off between avoiding predation and gaining energy. For example, hiding in a burrow might be safe, but it yields no energy (Mougeot & Bretagnolle 2000). Or, being vigilant reduces risk of predation but distracts from finding food (Fernández-Juricic et al. 2004). Here we ask the question what the optimal time allocation between vigilance and foraging should be.

As risk of being killed and rate of energy gain are measured along different scales, finding the optimal solution herein it is not a straight-forward exercise. For example, is a doubling of risk of predation compensated by a doubling of energy gain rate? Modelling this problem should be done under the umbrella of a common currency, namely
reproductive value (abbreviated here as \( V \)). Gaining energy (by \( \delta x \) units) typically increases reproductive value (by \( \delta V \) units) and being killed by a predator leads to a total loss of reproductive value \( V \) associated with its current state. Therefore, the expected rate of change in reproductive value due to foraging (\( \dot{V}_{\text{forage}} \)) is given by:

\[
\dot{V}_{\text{forage}} = \gamma \frac{\delta V}{\delta x} - M V
\]

where \( \gamma \) is rate of energy gain and \( M \) is rate of predation (Houston & McNamara 1999). \( V_{\text{forage}} \) is maximised by the optimal forager. In the state space of \( M \) against \( \gamma \), lines with a slope of \( \frac{1}{V} \frac{\delta V}{\delta x} \) represent lines of equal \( V_{\text{forage}} \) and the best feeding option is thus found in the lower right of the space (high energy intake rates at low risks of predation; Box-figure IX.1). For our vigilance problem, the options available in this space are given by a convex function as in Box-figure IX.1. (cf. Houston et al.)

**Box-figure IX.1.** State space of rate (risk) of predation against rate of energy gain. Thick convex-curved line gives continuum of options available when varying the proportion of time being vigilant (upper horizontal axis): spending more time being vigilant is safer but yields lower energy gain rates. The optimal proportion of time being vigilant \( u^* \) is found by drawing straight lines at which reproductive value changes at the same rate (proportional change is indicated by the number at the lines). Then, the highest feasible rate of change in reproductive value is found in the lower right corner (high energy gain rates at low rates of predation), where the slope of the convex equals the slope of the straight lines.
For two reasons the curve is convex-shaped. Firstly, rate of energy gain declines in a linear fashion with the proportion of time being vigilant (since all the time not being vigilant is spent feeding). Secondly, reducing predation risk by increasing vigilance is most effective when vigilance levels are low. Intuitively, this can be understood by thinking of an animal that alternates between feeding and short vigilance bouts to scan for potential predators. If a predator is around, it will usually be detected at the first instance of a vigilance bout; increasing bout length will only marginally increase the probability of detection.

As a consequence, the optimal vigilance level maximising $\dot{V}_{\text{forage}}$ is where the slope of the convex-curve equals $\frac{1}{V} \frac{\delta V}{\delta x}$ (Box-figure IX.1). Given this, optimal vigilance levels vary with reproductive value $V$ and with the so-called ‘marginal value of energy’ ($\delta V/\delta x$). High values of $V$ and/or low values of $\delta V/\delta x$ lead to shallow slopes and thus lead to high vigilance levels (Box-figure IX.2). Marginal values of energy typically decline with energy reserves (Houston & McNamara 1999; Olsson et al. 2002; chapter 7), i.e. the increase in reproductive value due to energy

In this experiment on state-dependent foraging, captive knots were studied in their natural environment at Grienderwaard. Photo: Jan van Gils.
gain declines with each Joule consumed. In other words, recently fed animals should be more vigilant than recently fasted animals. This prediction was tested in red knots.

For this purpose, we used captive knots, whose marginal value of energy was experimentally manipulated by either feeding or fasting them during the night (Van Gils & Escudero, unpubl. data). In order to create a setting in which predator attacks were a realistic threat to the birds, we ran the experiment outdoors in their natural, wide-open, intertidal environment, where hunting peregrine falcons (*Falco peregrinus*) are of regular occurrence. At a mudflat in the bay of Griens, we removed all prey items from an area measuring 2 m². In this ‘cleaned’ sediment, we subsequently inserted 200 cockles (8-11 mm) at a depth of about 0.5-cm. After fencing the patch we started the experiment. The birds were given two possible treatments. In the night preceding a trial, they were either given no food at all (low-energy state, leading to high marginal values of energy), or they were given ad libitum access to food (trout pellets) for a period of 12 h (high-energy state, leading to low marginal values of energy). In the latter case, food was removed one hour before a trial

**Box-figure IX.2.** When in high-energy state, reproductive value varies stronger with risk of predation than with rate of energy gain (i.e. low marginal value of energy) and vice versa for the low-energy state. Therefore, lines of equal rates of change in reproductive values are shallow in the high-energy state and steep in the low-energy state. Therefore, the optimal proportion of time being vigilant is higher for the high-energy state ($u_H^*$) than for the low-energy state ($u_L^*$).
started in order to prevent a filled-up gut (in which case effects found would be due to satiation). In each trial, a focal bird was allowed to find 10 prey items. After each trial, we added 10 cockles to the patch in order to keep initial prey density constant at 100 m\(^{-2}\) for all trials. As we were running another experiment at the same time (experiment 1 in chapter 3), we could only work with two focal birds, which yielded 48 trials (12 repeats of 2 treatments per focal bird). By videotaping each trial, we afterwards scored time allocation per prey encounter (analysed at slow motion using The Observer; Noldus Information Technology 1997). We categorised behaviour into searching, being vigilant (i.e. looking-up), and other activities. Besides the proportion of time being vigilant (ignoring time devoted to other activities), we analysed searching efficiency, which was calculated over searching time only as in box VII, thus assuming random search (as verified for such artificial patches in chapters 8-9). From both measures, we additionally calculated the overall rate of prey encounter over total time (i.e. searching time and vigilance time) as a proxy for energy intake rate (energy values were rather constant between prey items and handling times in knots are relatively short and thus prey intake rates approach prey encounter rates).

The observations matched the predictions. On days following overnight feeding, knots were twice as vigilant as on days that they were fasted overnight (Box-figure IX.3A). Thus, the perceived need to obtain energy (i.e. the marginal value of energy) was less when fed the night before and therefore the birds scanned longer for potential predators. In addition, searching efficiency was lower for birds in the high-energy state (Box-figure IX.3B). Apparently, the effectiveness of finding food while actually searching is reduced at lower marginal values of energy. This latter observation is a support for the so-called ‘limited attention’ hypothesis, which states that due to cognitive constraints, the brain allocates its limited computation resources to the most relevant information, filtering out less important information (Dukas & Kamil 2000; Dukas 2002; Clark & Dukas 2003). Or stated simpler, it is hard to do more than one thing at a time. To phrase it anthropomorphically, while feeding in the low-energy state, finding food is all that knots have on their minds and therefore they are able to find food at a high rate. On the contrary, knots in the high-energy state keep predator avoidance in the back of their minds while searching for food and therefore foraging is less effective.
This effect on searching efficiency has consequences for the relationship between the proportion of time being vigilant and energy intake rate. Just as assumed above, it is still linear, but now the slope is state-dependent (with the steepest slopes for the lowest energy states). So far, this has not been recognised in the published vigilance models (Houston et al. 1993; McNamara & Houston 1994; Brown 1999). To conclude, rates of energy intake (expressed as rates of prey encounter in Box-figure IX.3C) in well-fed knots are reduced not only because they spend more time being vigilant, but also due to reduced effectiveness in finding food.
Box X. Migrating knots build time-minimizing gizzards, except in the hot tropics

In chapter 4 we saw that red knots select their stopover sites on the basis of prey quality. By doing so, they maximise their overall speed of migration (Figure 4.5). Here, we apply the migration model presented in chapter 4 to the piersmai-subspecies. During its northbound migration from its tropical wintering grounds in NW-Australia towards its breeding grounds at the New Siberian Islands, this population presumably stops over at intertidal flats in the Yellow Sea (Box-figure X.1). Among the four subspecies wintering in the Southern Hemisphere this is the one wintering closest to its breeding grounds (10,400 km; Piersma et al. 2004). Provided that red knots aim to maximise their overall speed of migration, we here predict (1) the optimal (i.e. shortest) time span required to fuel at the NW-Australian wintering grounds and, subsequently, (2) the optimal (i.e. shortest) time span required to fuel at the Yellow Sea stopover site. Fuelling in NW-Australia is known to happen on prey of moderate quality (2.22 kJ/g \( \text{DM}_{\text{shell}} \); Table 4.1). Fuelling in the Yellow Sea is modelled for a range of prey qualities since nothing is

A red knot feeding amongst mudskippers in Roebuck Bay, NW-Australia. Photo: Jan van de Kam.
known about the benthic food supply at this Asiatic stopover. At both sites we predict the gizzard size(s) that minimise the period of fuelling. As in chapter 4, we assume that gizzards can be adjusted flexibly to the local prey quality but that they are kept at this mass during the subsequent migratory flight (with piersmai being the smallest subspecies of knots, we assume a weight of 80-g for a lean body without gizzard and intestine, which is somewhat lower than assumed in chapter 4; cf. chapter 4 we assuming tail wind assistance during flight as observed by Piersma & Jukema 1990).

The results of this simple exercise and the comparison with real-world data are revealing (Box-figure X.2). Fuelling in NW-Australia on prey of moderate quality would only take 24 days at the time-minimising gizzard

Box-figure X.1. Northbound flyway of Calidris canutus piersmai from wintering grounds in NW Australia to breeding grounds at the New Siberian Islands via the Yellow Sea.
mass of 10.6 g (Box-figure X.2A). However, observed fuelling episodes in Australia are known to last much longer (57 days; Piersma et al. 2004). Calculating what gizzard mass is associated with such a leisurely pace of fattening, we arrive at an estimate of approximately 8-g (Box-figure X.2A). Observed gizzards masses of fuelling piersmai-knots in NW-Australia (mean ± SE = 7.4 ± 0.9 g; N = 6) are in agreement with this ‘sub-optimal’ 8-g gizzard mass (P > 0.5) and differ from the time-minimising 10.6-g (P < 0.02; to ensure fuelling birds we selected individuals weighing at least 115 g). Apparently, for some reason, piersmai-knots do not build large, time-minimising gizzards when fuelling at their wintering grounds. This contrasts to their islandica-counterparts in the Wadden Sea, which do build time-minimising gizzards (9-11 g) when fuelling in spring (Figure 3.6C). Possibly, tropically wintering piersmai-knots prevent the build-up of large, time-minimising gizzards in order to reduce heat production, as a way to prevent heat load problems (Battley et al. 2003). Since basal metabolic rate and presumably metabolic heat production increase with an increase in (digestive) organ size (Piersma et al. 1996; Piersma et al. 2003: chapter 2), piersmai-knots appear to face a trade-off between rapid fuelling and the avoidance of overheating.

Box-figure X.2. (A). Time required to fuel for the 6,300-km long flight from NW-Australia to Yellow Sea as a function of gizzard mass (at the observed prey quality of 2.22 kJ/g DMshell). Initially, larger gizzards take shorter to fuel (due to the simple fact that larger gizzards are able to process shell material faster). However, above a certain, time-minimising gizzard mass (10.6 g in this case) gross daily energy intake is at its maximum (Kvist and Lindström 2003) and therefore fuelling time increases (slowly) with gizzard mass (due to the fact that more fuel is needed to carry the larger gizzard during flight). The long fuelling episode of red knots observed by Piersma et al. (2004; 57 days) suggests that knots do not build large, time-minimising gizzards but tend to fuel slower with gizzards of around 8-g. (B). Time required to fuel for the 4,100-km long flight from Yellow Sea to the breeding grounds as a function of gizzard mass at various prey qualities (given by numbers in isoclines in units of kJ/g DMshell). Required fuelling time declines with prey quality as more flesh can be assimilated at the same amount of shell material processed. Observations on departures from NW-Australia suggest that knots in Yellow Sea need only 20-30 days to fuel (Battley et al. in prep; grey box on the right). Provided that the knots kept gizzard size constant since they left Australia (which seems likely given the short time window available), this suggests high prey qualities at the Yellow Sea site (3-4 kJ/g DMshell at which fuelling proceeds fastest with an 8-g gizzard; lower asterisk). For example, if prey quality in Yellow Sea was as low as in NW-Australia (2.22 kJ/g DMshell) then fuelling would take more than 50 days (upper asterisk).
If this heat-loading is truly a problem in fuelling piersmai-knots, the question arises why the birds choose to fuel with gizzards of 8-g; why don’t they fuel at an even slower rate with gizzards of for instance 6-g? Possibly, they anticipate prey conditions at the Yellow Sea site. Given the time it takes to change gizzard size (Piersma et al. 1999; Dekinga et al. 2001), gizzards at the end of winter may already have been adjusted to the expected quality at the subsequent stopover site (especially when the breeding season is approaching). The relatively short stopover at the Yellow Sea site (20-30 days; deduced by Battley et al. (in prep) from NW-Australian departure dates) does not allow big shifts in gizzard size.
If the 8-g gizzard is an anticipation to the Yellow Sea food conditions, then what would these food conditions be? We calculated that the required fuelling rate during this short stopover can only be achieved with time-minimising gizzards (Box-figure X.2B). We therefore expect Yellow Sea prey quality to range between 3 and 4 kJ/g DM\textsubscript{shell} as this is the quality at which 8-g gizzards fuel fastest (lower asterisk in Box-figure X.2B). Such high prey qualities are generally found at other spring stopover sites (2.4-3.7 kJ/g DM\textsubscript{shell}; Table 4.1) and contrast to much lower qualities at the wintering grounds (0.8-2.2 kJ/g DM\textsubscript{shell}; Table 4.1). Such prey-quality hotspots allow for fast migrations along all northbound flyways of red knots worldwide and are probably a prerequisite to get up to the breeding areas on time (chapter 4). For example in this particular case, if Yellow Sea prey were of similar (moderate) quality as those at the Australian wintering grounds (2.22 kJ/g DM\textsubscript{shell}) then fuelling in Yellow Sea with an 8-g gizzard would last approximately 40 days longer (upper asterisk in Box-figure X.2B).

Given the higher prey quality at Yellow Sea compared to NW-Australia, one may wonder why piersmai-knots stay long at their wintering grounds and compress their time at the Yellow Sea site. Their may be two good reasons for this migratory policy. Firstly, thermostatic costs are much lower (even absent) in tropical Australia than in the more

Photo: Jan van de Kam.
northerly located Yellow Sea. Only in late spring thermoregulatory costs are marginal in the temperate zone (Wiersma & Piersma 1994). Secondly, at the Yellow Sea stopover site, there may only be a narrow time window during which prey quality (and availability) peaks. As shown or suggested for other prey-quality hotspots, this usually occurs during (late) spring when the invertebrate prey reproduce en masse (chapters 3-4; Piersma et al. 1994).

Concluding, the ‘enigma of NW-Australia’ can only be solved by expeditionary work in the Yellow Sea. There we need to measure whether prey qualities are indeed that high and whether gizzards live up to our 8-g expectation. If so, this would be a support for the challenging idea that slowly fuelling knots can only escape the hot tropics if the next station harbours super-quality food.

Box XI. Do male canutus-knots skip the Dutch Wadden Sea?

Differential use of the Dutch Wadden Sea by islandica- and canutus-knots was described by Nebel et al. (2000), based on the analysis of occurrence and departure of 95 adult knots that were radio-marked in the western Dutch Wadden Sea in July/August 1995-98. Figure XI.1 summarises their findings. The main message is that females captured in wing moult (filled dots) stayed significantly longer than non-moulting females (open dots). Given that wing moult commences soon after arrival on the wintering grounds (Boere 1976; Davidson & Wilson 1992; Piersma et al. 1992), moultng birds belonged to the islandica-subspecies, while non-moulting birds either belonged to the islandica- or to the canutus-subspecies. The timing of disappearance of non-moulting females from the Wadden Sea corresponds with published dates on canutus-migration. An extra indication that early departing non-moulting females are canutus-individuals is their significantly longer bill in comparison with the rest. In males, there was no relation between moult status and length of stay, nor did non-moulters have longer bills. Nebel et al. therefore concluded that most males captured belonged to the islandica-subspecies and that canutus-males may actually skip the Dutch Wadden Sea during their southward migration to West Africa.
Box-figure XI.1. Daily records for each radio-marked individual (dots), where individuals are sorted according to sex, moult status, and date of last observation. Dots are filled for birds showing wing moult at capture and are open for birds that did not. Triangles give range between date of capture (left triangle) and estimated date of transmitter-battery die-out (right triangle). Shaded area gives estimated length of stay in the Wadden Sea since capture (over the 60-day period of battery life). Average canutus-departure dates for male and female are given by vertical dashed lines (based on Gromadzka 1992; Meissner 1992).
Box XII. Prey populations in danger: burying depth as a behavioural indicator of fitness prospects in Macoma balthica

In the past, studies of predator-prey interactions either considered optimal foraging predators on behaviourally inert prey (Stephens & Krebs 1986), or treated predators as unresponsive ‘black boxes’ that fed on behaviourally flexible prey that exhibit sophisticated antipredator policies (Lima 1998). Currently, however, both attitudes seem to converge (Brown et al. 1999; Lima 2002). The coming together of the behavioural ecology of both the predator and the prey into population and community processes has been referred to as the ecology of fear (Brown et al. 1999). It states that much of the dynamics in populations is driven by indirect, non-lethal effects of the predator on its prey (through costly predator-avoidance behaviour of the prey), rather than by direct kills of the predator (the latter is assumed by more classical predator-prey models such as Rosenzweig & MacArthur 1963; Murdoch & Oaten 1975). For example, with more predators around, prey get more wary at the expense of their time allocated to feeding, and consequently incur higher probabilities of starvation (Houston & McNamara 1999). In order to better understand foraging decisions and consequent population processes in red knots, we need to acquire a good understanding of antipredator strategies of its bivalve prey.

For a burying bivalve like the Baltic clam Macoma balthica, predation risk typically decreases with burying depth; the chance of being detected by probing shorebirds or digging crabs simply declines with depth, but also profitability and thus the predator’s willingness to accept a prey item declines with depth (e.g. Wanink & Zwarts 1985; Zaklan & Ydenberg 1997; see also Santamaria & Rodríguez-Gironés 2002 for a similar effect of swans on sediment-buried pondweed tubers). Also, energy gain rate decreases with burying depth since the sediment surface area that Macoma can cover with its fully stretched siphon decreases with depth (De Goeij & Luttikhuizen 1998). Obviously, Macoma faces a trade-off (Edelaar 2000): should it safely bury deep at the expense of energy gain, or should it risk predation but gain energy at a high rate by burying shallow?

Under the umbrella of the common currency of reproductive value, an elegant theory has been developed how prey animals should weigh risk of predation against rate of energy gain (Brown 1988; Houston &
McNamara 1999; see also box IX). In order to scale predation risk to energy gain rates (expressed in Watts) the term predation cost has been introduced, which expresses the expected instantaneous loss in reproductive value due to predation in Watts (Brown 1988). Formally, \[ P = \frac{MV}{\delta V/\delta x}, \]
where \( P \) = predation cost, \( M \) = predation risk, \( V \) = reproductive value, and \( \delta V/\delta x \) = marginal value of energy, i.e. the change in reproductive value (\( \delta V \)) due to a change in energy state (\( \delta x \)). Typically, marginal values of energy decline with an increase in energy stores (Houston & McNamara 1999). Thus, the (energetic) cost of predation increases linearly with predation risk and with reproductive value and decreases inversely with the marginal value of energy.

When energy gain trades off with risk of predation such as in Macoma balthica, the theory predicts that animals with high reproductive values should generally avoid risky situations at the expense of energy gain (the asset-protection principle; Clark 1994), while animals with low reproductive values should accept larger risks when feeding (they have got less to lose; Edelaar 2002). It also predicts that animals with low amounts of energy stores (i.e. having high marginal values of energy; Houston & McNamara 1999) should be willing to accept greater risks of predation while those with high amounts of energy stores should be more protective about their lives. Translating these expectations to the Macoma-situation, we predict that (1) Macoma should bury shallower when its fitness prospects decline, and (2) Macoma should bury shallower when its body mass declines (i.e. here we assume body mass to be a good measure of energy store, which in turn reflects the marginal value of energy).

In Macoma balthica, the second prediction has been verified experimentally: indeed burying depth increases with body mass (De Goeij & Honkoop 2002; Edelaar 2002). By contrast, the first prediction, the positive effect of reproductive value on burying depth, by and large has remained untested (although Edelaar 2002 considered that body mass was good enough a measure of reproductive value for his study to count as a test). Interestingly, testing this prediction should provide us with valuable information on how Macoma itself perceives its own health status and the quality of its environment (i.e. its own fitness prospects \( V \))! This way of using behavioural ecology as a tool to study animal perception was recognised long ago (Wilson 1976), but has only recently
been put to the test (Olsson et al. 2002). Specifying this for Macoma balthica, it means that burying depth corrected for body mass ($\delta V/\delta x$) is indicative of Macoma’s own fitness prospects ($V$; provided that their perception of predation risk $M$ remains constant). Thus, for a given body mass, deeply buried individuals expect larger fitness payoffs in the near future than shallowly buried individuals. The ability to measure burying depth, body mass, and survival and reproductive success on the level of the whole population, allowed us to test whether interannual variations in perceived fitness prospects match with truly realised fitness in Macoma balthica.

Yearly during Jul-Sep 1996-2002, we sampled Macoma balthica at $\pm$ 2,500 stations in a regular grid laid out throughout the western Wadden Sea (see chapter 7 or Piersma et al. 2001 for more details on sampling). For each station, we counted the number of Macoma per size class (to the nearest mm). As a measure of burying depth we distinguished between individuals living in the top layer of the sediment (0-4 cm depth; i.e. accessible to red knots) and individuals living in the bottom layer of the sediment (4-15 cm; i.e. inaccessible to red knots). In the lab, we measured per individual the ash-free dry mass of the flesh (i.e. body mass) and the dry mass of the shell. The ratio between body mass and shell mass proves to be a relevant measure of prey quality (see chapters 3-6). In order to broaden the scope of the analyses, we included monthly depth and body mass measurements collected by De Goeij (2001) during 1993-2000 at Balgzand (the most western part of the Dutch Wadden Sea).

Between 1996 and 2002 Macoma-densities in the western Wadden Sea have declined in an almost linear fashion (on average, densities reduced yearly by 28 m$^{-2}$; Box-figure XII.1A). A closer look showed that this decline occurred both in the higher (above N.A.P.) and in the lower (below N.A.P.) parts of the intertidal mudflats (thin lines in Box-figure XII.1A). At the same time, prey quality (i.e. body mass per g shell mass) has declined steeply by almost 50% (filled dots in Box-figure XII.1B). A similar drop in body mass was observed at Balgzand (open dots in Box-figure XII.1B).

The observation of a population in decline composed of individuals of increasingly poor body condition lead to the expectation that during the 1996-2002 time span Macoma has decreased burying depth. The observed drop in population growth rate (reflecting $V$) and in body mass
(reflecting \( \delta V/\delta x \)) should have lead to a dramatic reduction in predation cost (P) in Macoma balthica. Assuming that depth-dependent predation risk M has not declined over time (which seems appropriate as then, all else being equal, a decrease in burying depth should be accompanied by an increase in body mass; Houston & McNamara 1999), this should have lead to the acceptance of higher predation risks (M) in order to increase

![Graphs A, B, C showing changes in density, quality, body mass, and proportion accessible over time.](image-url)
energy gain rates. Indeed, the proportion of individuals living in the upper 4-cm of the sediment has almost linearly increased from ± 20% (1996) to ± 90% (2002; filled dots in Box-figure XII.1C). Similarly, average burying depth at Balgzand declined from ± 5-cm (1996) to ± 2-cm (2000; open dots in Box-figure XII.1C).

In order to disentangle effects of body mass and (perceived) fitness prospects on burying depth, we graphed burying depth as a function of body mass (Box-figure XII.2A; now considering the full time span (1993-2000) of the Balgzand dataset of De Goeij & Drent, pers. comm.). Then, 72% of the interannual variation in burying depth can be explained by variation in body mass (GLM; $N = 8; P < 0.01$). The remaining residual variation should reflect *Macoma*’s perception of its own health and reproductive status and its environment. In order to see how these perceived fitness prospects match with the actual realised fitness benefits, we calculated the number of *Macoma*-recruits (< 10 mm) observed in the next year ($t + 1$) per adult ($\geq 10$ mm) in the current year ($t$; using the grid-database). This realised fitness-measure not only takes account of the number of offspring that survive the first half year of their lives (note that the production of free-swimming larvae takes place in spring $t + 1$ while sampling of the settled recruits took place in autumn $t + 1$), but also takes account of the adult survival chances between sampling in autumn $t$ and the reproductive season in the subsequent spring $t + 1$.

Indeed, perceived fitness prospects (residual burying depth) match with realised fitness benefits. In years ($t$) preceding a successful reproductive season in spring ($t + 1$), *Macoma* buried about 1-cm deeper than in years preceding a less successful spring (Box-figure XII.2B; GLM; $R^2 = 0.077; P < 0.001; N = 6,473$ individuals; 10-16 mm; filled dots give mean and associated bars give 95%-confidence intervals). A similar trend was observed in average body mass at Balgzand (open dots give mean and associated bars give SE). (C). The proportion of *Macoma* living in the top sediment layer (upper 4-cm) has increased over time (logistic regression; $P < 0.001; N = 6,403$ individuals; 10-16 mm). A similar trend was observed in average burying depth at Balgzand (open dots give mean and associated bars give SE).

**Box-figure XII.1.** (A). Overall *Macoma*-density has declined over seven consecutive years (GLM; $R^2 = 0.022; P < 0.001; N = 17,117$ stations; all size classes included; dots give mean; bars give 95%-confidence intervals). These trends were similar for densities low in the intertidal (below N.A.P.; lower thin line) and for densities high in the intertidal (above N.A.P.; upper thin line; note that the 1996-density lies at 546 m$^{-2}$). (B). Over the same time span, *Macoma* quality (metabolisable energy per g shell mass) declined by almost 50% (GLM; $R^2 = 0.077; P < 0.001; N = 6,473$ individuals; 10-16 mm; filled dots give mean and associated bars give 95%-confidence intervals). A similar trend was observed in average body mass at Balgzand (open dots give mean and associated bars give SE). (C). The proportion of *Macoma* living in the top sediment layer (upper 4-cm) has increased over time (logistic regression; $P < 0.001; N = 6,403$ individuals; 10-16 mm). A similar trend was observed in average burying depth at Balgzand (open dots give mean and associated bars give SE).
N = 8; P < 0.02). Apparently, Macoma’s predictions on its future reproductive and survival chances are not far off the actual, realised, fitness benefits.

At present, it is still unknown what has caused the recent population decline in Macoma balthica (Drent 2004). However, it is now clear that year-to-year changes were anticipated by Macoma balthica itself (or at least at the level of individual reproductive success). Apart from responding directly to a loss in body mass by burying shallower, deteriorations in other fitness-determining factors have made Macoma come closer to surface. Possibly, declines in net energy gain rate (at a given burying depth) have driven both the reductions in overall body mass and have worsened other factors that contribute to fitness (e.g. quality or size of reproductive organs). Since net energy intake equals gross energy intake minus metabolic costs, gross energy intake has gone down and/or metabolic costs have gone up under such a scenario. If the former has taken place, it might be related to a change in sediment

Box-figure XII.2. (A). Burying depth increases with body mass (GLM; $R^2 = 0.72$; $N = 8$; $P < 0.01$; annual averages across all months from Balgzand-dataset of De Goeij & Drent). In addition, in years preceding a successful reproductive spring (producing more than 1 surviving recruit at $t + 1$ per adult at $t$; filled dots representing 1993, 1995, and 1997), Macoma buries deeper than in other years (with less than 1 recruit per adult; open dots representing 1994, 1996, 1998, 1999, and 2000). (B). The residuals of figure A plotted against the realised reproductive success in the subsequent spring (GLM; $R^2 = 0.67$; $N = 8$; $P < 0.02$; grid-dataset of Dekinga & Piersma).
characteristics that occur after the widespread mechanical cockle-dredging that has affected almost all intertidal areas with Macoma over the last decade (Piersma et al. 2001). Drent et al. (2004) showed profound effects of sediment characteristics (especially silt content) on feeding performance of Macoma balthica. Metabolic costs might have gone up as a consequence of a steady increase in seawater temperature positively affecting metabolic rates in the poikilothermic Macoma (Drent 2004; even though during 1993-2000 winter temperatures (following Honkoop et al. 1998) preceding successful springs were not lower than those preceding less successful spring (GLM; N = 8; P > 0.35); cold winters lead to higher fecundities than mild winters; Honkoop & Van der Meer 1997, 1998).

In the future, the current approach of using burying depth as behavioural indicator of perceived fitness prospects could be extended to include spatial variability. In other words, do we see spatial differences in residual burying depth and do they correspond with spatial differences in survival and reproductive success? For example, is the difference in fecundity between the lower and higher parts of intertidal flats (Honkoop et al. 1998) reflected in differences in residual burying depth? In this way, residual burying depth can be used as an indicator of habitat suitability (Olsson et al. 2002), which eventually could serve conservation purposes if managers see a need to distinguish good habitat from poor habitat. Moreover, it would be interesting to see how much additional variance in Macoma recruitment success could be explained by including residual burying depth in statistical models that already take winter temperature and adult body mass into account. Up to now, such models have had only moderate success in predicting Macoma recruitment variability (Honkoop et al. 1998). This could be further step in elucidating population dynamics in intertidal bivalve populations (Van der Meer et al. 2001), which in turn could contribute to understanding population process in specialized probing predators such red knots (Baker et al. 2004).
Given the huge impact of prey quality on digestive processing rates in knots, we were interested in the (a)biotic factors affecting the spatiotemporal variability in prey quality. As a focal prey species we selected the edible cockle (*Cerastoderma edule*), since this species was the predominant prey for red knots in the western Dutch Wadden Sea over the last 15-years (Van Gils, Dekinga, Koolhaas & Piersma, unpubl. data). Through effects on bivalve feeding performance (Drent *et al.* 2004), grain size of the local sediment is likely an important parameter affecting prey flesh mass and thus prey quality (defined as grams flesh mass per gram shell mass). Given the recent evidence that mechanical cockle-dredging increases local grain size (Piersma *et al.* 2001; RIZA 2004), we suspected effects of mechanical cockle-dredging on cockle quality and accordingly carried out an analysis.

For the years 1998-2002, we determined the quality of cockles that were available to red knots (i.e. those with shell lengths ≤ 16 mm). These cockles were sampled yearly (Jul-Sep) at stations that were spaced apart in a grid at 250-m intervals (see Piersma *et al.* 2001 and chapter 7 for more details on sampling procedures). In the lab, cockle quality was determined by measuring both flesh mass (ash-free dry mass) and shell mass (dry mass) separately. In the analyses we pooled sample stations at the spatial scale of 1-km² (i.e. at most 16 stations were pooled; see Box-figure XIII.1).

It turned out that over the years, cockle quality remained constant at sites that were never fished commercially (Box-figure XIII.2). By contrast, cockle quality declined at sites that were fished, with the steepest declines at those sites that had been fished most (HLM, using 1-km² blocks as identifiers with 57 level-2 obs. and 137 level-1 obs.; *P* < 0.004; Box-figure XIII.2).

Since cockles predominated in the diet of knots (mean ± SE = 57.9 ± 2.8% for 1998-2002; *N* = 174 dropping samples) and since knots preferably fed in sites subsequently exploited by the fishery (Van Gils *et al.*, unpubl. data on radio-marked knots), the negative effects of cockle-dredging on cockle quality were likely to affect diet-quality in knots. Indeed, by reconstructing the diet of knots from faeces collected in 1998-2002, we showed that the quality of ingested prey items declined over
Box-figure XIII.1. The western Dutch Wadden Sea. Dots give stations sampled in 1998-2002 and squares give spatial resolution at which analyses took place (at the 1-km²-level). Dots are filled at stations that have been cockle-dredged at least once in 1998-2002; dots are open otherwise.

Box-figure XIII.2. Change in cockle quality (both on a percentage- and logarithmic-scale) as a function of the number of years that a site was fished (within 1998-2002). Bars give standard errors and line gives (hierarchical) linear regression.
time (Box-figure XIII.3A). Since knots are able to anticipate a decline in prey quality by an increase in gizzard mass ($E = mc^2$), the decline in diet quality was likely accompanied by an increase in gizzard mass. Analysing the estimates of gizzard mass collected ultrasonographically during Jul-Aug 1998-2002 ($N = 644$), we showed that this was indeed the case (Box-figure XIII.3B). However, analysing resighting probabilities showed that this increase is mostly due to birds leaving our study area that have undersized gizzards rather than to gizzard growth within individuals birds. This issue is further elaborated on in the main text of the current chapter.

**Box-figure XIII.3.** (A). Diet quality declined over time. Line gives linear regression (GLM with log-transformed qualities; $N = 174$ dropping samples; $R^2 = 0.05; P < 0.005$). (B). Correspondingly, gizzard mass increased over time. Line gives linear regression (GLM; $N = 644$ birds; $R^2 = 0.02; P < 0.0001$).
References


Klaassen, R. H. G., Nolet, B. A. & De Fouw, J. (2004). Intake rate at different scaled heterogeneous food distributions explained by the ability of tactile-foraging mallard to concentrate foraging effort within profitable areas. Submitted.


Wilson, D. S. (1976). Deducing the energy available in the environment: an application of optimal foraging theory. Biotropica, 8, 96-103.


Photo: Jan van de Kam.