Foraging decisions in a digestively constrained long-distance migrant, the red knot (Calidris canutus)
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Strategic itineraries of patch use by red knots in a tidally structured environment

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Summary

Besides the ‘normal’ challenge in obtaining adequate intake rates in a patchy and dangerous world, shorebirds foraging in intertidal habitats face additional foraging complications. The dictated tidal regime reduces daily available foraging times (12 h/day in our area) and forces birds to roost away from their feeding grounds. In addition, intertidal food patches are not all available at the same time, which forces shorebirds to decide when to feed and to map out an itinerary along patches that are best given the ‘tidal time’. Realising that within single low tides shorebirds do not just make a single decision on where to feed, but take a sequence of multiple coupled decisions, modelling optimal foraging itineraries is performed most effectively by working backwards in time. We therefore constructed a spatially explicit, stochastic dynamic programming model with two state variables (location and energy store). The model was parameterised for red knots (Calidris canutus) living in the western Dutch Wadden Sea in late summer (July-Aug) using data on available prey densities and locally varying tidal-heights. The optimisation model generates three core predictions about where and when red knots should feed as a function of the location of the roost and the amount of energy stored. Firstly, red knots should generally feed in the vicinity of their roost. This is especially so when roosting at Griend which is closer to good feeding grounds than the alternative roost at Richel. By doing so, energetic travel costs are reduced. Secondly, red knots should feed most intense in the midst of the low tide period (5.0-7.5 h after high tide) and should mainly rest around high tide. This is a consequence of a concentration of feeding time and effort at the patches that yield the highest energy intake rates, which are patches that are only available when the tide is lowest. Thirdly, foraging intensity should decline with energy store due to the trade off between risk of starvation and risk of predation. Observed foraging intensity and patch use by radio-marked knots closely matched each of the three predictions, although the furthest but best feeding site, Ballastplaat, was visited somewhat less than predicted. We conclude that red knots in the western Dutch Wadden Sea make state-dependent foraging decisions, by taking both current location and current energy store into account when trading off travel cost against gross daily energy gain. We discuss the central role of roosts as begin- and endpoints in foraging itineraries and which factors determine roost-choice.
Introduction

Resources are often patchily distributed in space (Pielou 1977), posing a major challenge for foragers to exploit them effectively. Foragers that are uncertain about patch quality risk the penalty of spending too much time in poor-quality patches or they may leave good patches too early (Oaten 1977; McNamara 1982; Green 1990; Olsson & Holmgren 1998; Van Gils et al. 2003b). If foragers are omniscient with respect to patch quality, they still bear the cost of travelling and thus face a choice between distant, but good-quality patches, and close, but poor-quality patches (Bernstein et al. 1991; De Leeuw 1997). Usually, the best food patches attract the most foragers, and the most foragers attract the most predators, leading to trade-offs between energy gain and the avoidance of respectively competition and predation (Fretwell & Lucas 1970; Lima & Dill 1990). In addition, the best solution today might not be the best solution tomorrow as optimal solutions are usually state-dependent and therefore vary with, for example, the amount of energy stored (Houston & McNamara 1999; Olsson et al. 2002).

On top of these ‘normal’ problems, shorebirds living in intertidal habitats face additional foraging challenges. Their feeding grounds are only available during low tide, which occurs twice per day for about 12 h/day in most parts of the world. Furthermore, time and energy costs need to be paid to travel, twice per day, back and forth between the high-tide roost and the low-tide feeding grounds. Due to spatial heterogeneity in elevation and in the timing of the tide (Van Gils et al. 2004a), not all food patches will be available at the same time, which forces intertidal foragers to decide when to feed and to map out optimal itineraries along patches which are best, depending on ‘tidal time’ (Connors et al. 1981; Van Gils et al. 2004c).

Among shorebirds, the red knot (Calidris canutus) forms a suitable species to study such ‘intertidal foraging problems’. Knots mainly feed on molluscs (Zwarts & Blomert 1992; Piersma et al. 1993a; Van Gils et al. 2003a), whose abundance and availability are quantified relatively easy because of their immobility (Piersma et al. 1993a; Zwarts & Wanink 1993; Ens et al. 1994; Goss-Custard et al. 2001; Wanink & Zwarts 2001). Through the relative ease with which red knots can be kept in captivity, functional responses (Piersma et al. 1995), prey detection (Piersma et al. 1998), information use (Van Gils et al. 2003b), digestive processing capacity (Van Gils et al. 2003a), the energetic costs of foraging (Piersma et al. 2003), travelling (Bruinzeel et al. 1999; Kvist et al. 2001) and thermo-regulation (Wiersma & Piersma 1994; Bruinzeel & Piersma 1998), and water turnover as a function of diet (Visser et al. 2000) have all been quantified. In addition, free-living individual knots roaming
through vast intertidal areas can be successfully tracked using radio-telemetry (Van Gils & Piersma 1999; Nebel et al. 2000; Van Gils et al. 2000; Battley et al. 2004).

Using this vast base of knowledge and experience, we here predict and analyse how red knots cope with spatial and, tidally caused, temporal variability in food abundance in the western Dutch Wadden Sea in terms of patch use and daily foraging routines (i.e. intensity of foraging). By focussing on the islandica-subspecies (Piersma & Davidson 1992) at the onset of its over-wintering period (end of July and August), we ensure that preparations for reproduction or long-distance migrations, such as fattening, can safely be ignored. In order to capture the dynamic nature of patch selection throughout a tidal cycle, we constructed a spatially explicit, stochastic dynamic programming model (SDP; Houston & McNamara 1999; Clark & Mangel 2000), which generated predictions on optimal itineraries along a set of food patches and on the intensity of feeding. Main input values in the model are expected energy intake rates per patch, which are computed from fine-scaled measurements on prey densities and prey qualities. The model’s predictions were tested on radio-marked (itineraries) and unmarked (intensity of foraging) red knots.

Red knots arriving at their roost on Griend. The finding that Griend-roosting knots are generally lighter and possess smaller gizzards than Richel-roosting individuals may reflect a trade-off between safety and proximity to the best feeding grounds. Photo: Jan van de Kam.
Material and methods

Spatial distribution of the prey
Each year in 1996-2000 during the end of July and August, prey densities in the western Dutch Wadden Sea (Figure 7.1A; 53° 14’ N, 05° 11’ E) were sampled at fixed stations as a grid with 250-m intervals (Figure 7.1B). In the selected sites (bordered by thick straight lines in Figure 7.1, which excludes stations that were sampled in the most recent years only), an average of 1,880 stations was sampled yearly. These stations were located using hand-held Global Positioning System devices (GPS; Garmin 45; Garmin Corporation, Lenexa, KS). At each station, one sediment core (1/56 m²) was taken down to a depth of 20-cm. In order to distinguish accessible from inaccessible prey, the top layer (0-4 cm) was separated from the bottom layer (4-20 cm; knots have bills of 3-4 cm) and both layers were subsequently sieved over a 1-mm mesh. Mudsnailes (Hydrobia ulvae) were sampled by sieving smaller cores (1/267 m²) over a finer mesh (0.5-mm). All potential prey items that retained on the sieve were stored in the freezer for later analysis.

In order to distinguish ingestible prey from prey that were too large to be swallowed, each prey item was identified with respect to species and size (to nearest mm or, in case of H. ulvae, to nearest 0.5-mm). A prey is considered to be available when its both accessible and ingestible (Zwarts & Wanink 1993). Maximally ingestible lengths were taken from Piersma et al. (1993a) and Zwarts & Blomert (1992). In order to determine metabolizable energy content and amount of indigestible ballast mass, we removed the soft, fleshy parts from the indigestible shell, and dried both flesh and shell to constant mass for three days in a ventilated oven at 55-60°C, where after shell mass was determined using an electronic balance (to nearest 0.1-g). Subsequently, the dried flesh was incinerated at 550°C for 2 h, after which flesh ash-free dry mass (AFDM_{flesh}) was determined (to nearest 0.1-g). Metabolizable energy content was calculated as AFDM_{flesh} · energetic density · assimilation efficiency; the latter two were assumed to be constant at respectively 22 kJ/g AFDM_{flesh} (Zwarts & Wanink 1993) and 0.725 (Piersma 1994). As soft parts could not be separated from hard parts in case of the non-bivalve species, we determined dry mass and ash-free dry mass of entire specimens and assumed that 12.5% of organic matter resides in the hard parts of H. ulvae (Dekker 1979), and 30% in those of crustaceans (Zwarts & Blomert 1990). See Piersma et al. (1993a, 2001) for more details on the benthic-sampling programme.
FROM PREY DENSITIES TO EXPECTED ENERGY INTAKE RATES

Per year per fixed station in the 250-m grid, an expected energy intake rate was calculated from the measured available prey density by using a multiple prey-species functional response. This particular functional response is based on the rate-maximising prey selection model of Hirakawa (1995), who generalised the classical ‘prey model’ (Pulliam 1974; Charnov 1976) to situations in which rates of ballast intake are subject to a digestive constraint. Whether a prey type is included in the diet, does not only depend on its energy content and required handling time (the classical model), but also on its amount of ballast mass. For details of the model we refer to Hirakawa (1995). Due to their habit of ingesting and thus processing their bulky bivalve prey whole (Piersma et al. 1993b), this model explained diet choice by knots significantly better than the classical prey model (see Van Gils et al. 2004b).

Functional response parameters were based on observed values. Searching efficiency was set to 5 cm$^2$/s for all prey types (Piersma et al. 1995). Size-specific handling times for Carcinus maenas, Crangon crangon, and Hydrobia ulvae were taken from Van Gils et al. (2004b), those for Macoma balthica and Cerastoderma edule from Piersma et al. (1995). Handling times for Gammaridae were assumed to be similar to those for C. crangon, while those on relatively rare bivalve species (Abra tenuis, Ensis directus, Mya arenaria, Mytilus edulis, and Tellina tenuis) were assumed to be similar to those for M. balthica. Since knots handle their prey quickly relative to the rate of finding and internal processing, the predicted intake rate is rather insensitive to natural variations in handling time (Van Gils et al. 2004b). The upper rate of processing ballast material (mostly shell mass) was set to 1.83 mg/s, a value that is specific for knots with the most frequent fresh gizzard mass of 6-gram (Van Gils et al. 2003a). Besides this gizzard-size-related constraint on rates of shell crushing, rates of energy intake were subjected to an additional constraint on rates of digestion in the gut as measured by Kvist & Lindström.

Figure 7.1. Maps of the study area, the western Dutch Wadden Sea. (A). Thick lined areas border the four sites in which prey were yearly sampled (Richel-area, “West”, Grienderwaard, and Ballastplaat). Main roosts are given in italic (Schorren, Hengst, Vliehors, Richel, and Griend). (B). All prey sampling stations (250-m spaced apart), given by small symbols, sized to predicted intake rate averaged across all years (intake rate is zero at open squares). In the SDP-model, sample stations are grouped into 55 blocks of 2 by 2-km, given by the larger squares. (C). Position and range of automated radio-tracking systems, given by filled dots encircled by solid-lined circles. Triangles encircled by dashed-lined circles indicate position and range of detection of handheld radio-receivers (most westerly-positioned circle represents mobile handheld station at RV Navicula). Numbered dots give positions of tidal-height stations (1 = Vlieland harbour; 2 = Inschot; 3 = Harlingen; station West-Terschelling is north of Griend, just beyond the scale of the map).
FORAGING IN AN INTERTIDAL HABITAT

A West Schorren

B Vliehors Richel-area

C Grienderwaard Ballastplaat

RICHEL

GRIEND

Ballastplaat

West

5 km
Birds that hit this constraint are forced to take digestive breaks such that intake rate over total time equals the upper rate of flesh digestion (McNamara & Houston 1997; Van Gils et al. 2003b).

**The Stochastic Dynamic Programming Model**

The fixed stations in the 250-m grid were grouped into 55 blocks of 2 by 2-km (Figure 7.1B). Such 4-km² blocks contained 7-64 sample stations (Figure 7.1B). The minimum of 7 samples per block yields standard errors in prey density estimates of 30% of the mean or smaller (based on Piersma et al. 1993a). These 55 blocks form the spatial units in our stochastic dynamic programming model. The predicted energy intake rate in each block was (i) year-specific, (ii) constant within a year (i.e. we assumed no seasonal depletion), and (iii) known to the forager.

A block can be available (exposed during low tide) or unavailable (inundated during high tide) for foraging. We calculated this for each 50-minute time step in the model by comparing each block’s elevation (using fine-scaled data collected in a grid by RIKZ, The Netherlands in 1992-1999) with measurements of water height collected at regular 10-minute intervals at the nearest out of four different stations (Inschot, Harlingen, Vlieland-harbour and West-Terschelling; Figure 7.1C; DONAR; http://www.waterbase.nl).

Five different types of tidal cycles could occur in the model (where type is indicated by w; Figure 7.2), each with a different probability p_w. The values of p_w were based on the frequency distribution of tidal cycle types observed during late summer 2000 (DONAR). They were 10% for very good tides (with many blocks available for feeding; w = 1, represented by the tide observed at 26 Aug 2000), 35% for good tides (w = 2; 12 Aug 2000), 30% for intermediate tides (w = 3; 10 Aug 2000), 20% for bad tides (w = 4; 8 Sep 2000), and 5% for very bad tides (w = 5; 6 Sep 2000). We assume that the foragers know (i) the values of p_w, (ii) the current cycle’s type w, and (iii) the availability of each block throughout the cycle for each type w. They therefore know how feeding opportunities will change throughout the rest of the current cycle. However, as the value of w in the next cycles behaves stochastically, they do not know this for future cycles.

For all tidal cycles availability was set to 0 for all 55 blocks during a cycle’s final time step (Figure 7.2), while the availability of the roost was set to 1 at all time steps. This forced foragers to roost at least during a cycle’s final time step, while they could go to roost as early as they ‘liked’. The roost was either located at Richel or at Griend (Figure 7.1A), which are the two most frequently used roosts in the western Wadden Sea (Piersma et al. 1993a).
reasons of simplicity, however, model birds could never switch roost and were therefore categorised as either ‘Richel-roosters’ or ‘Griend-roosters’.

We model fitness-maximising foragers, where fitness is defined as the probability to survive until some defined final time. Mortality occurs either through starvation or predation. In this sense, our model is similar to the so-called ‘small-bird-in-winter’-models (e.g. Houston & McNamara 1993; McNamara et al. 1994; Houston et al. 1997; Pravosudov & Lucas 2001), and seems appropriate for red knots at the beginning of their non-breeding period. Starvation occurs when the energy stores $x$ reach a critical level $X_{\text{crit}}$. Energy stores vary from 0 ($= X_{\text{crit}}$) to 100-g (Piersma et al. 2004), in discrete steps of 5-g. Predation only occurs during foraging with a probability of 0.0001 if a full time step is spent foraging; resting or having digestive breaks incurs no predation risk. The assumption that foraging is more dangerous than resting is backed up by the observations that feeding knots are more frequently disturbed by raptors than roosting knots (when expressed per individual bird; B. S., pers. comm.).

Time proceeds in discrete steps of 50 minutes. As tidal cycles last 12.5 h, they are made up of 15 such time steps ($t = 1...T$, where $T = 15 = \text{high tide}$; $t$ will be referred to as ‘tidal time’). We consider a sequence of 50 tidal cycles, and use $d$ to indicate cycle number ($d = 1...D$, where $D = 50$; see below as to why we selected a value of 50). The full time period thus consists of $50 \times 15 = 750$ time steps = 26 days. At each time step the forager makes two

![Figure 7.2. Number of 4-km$^2$ blocks available for feeding in the course of a tidal cycle, plotted for five different types of cycles (indicated by w).](image.png)
'sequential decisions' (Clark & Mangel 2000). At the onset of a time step it decides whether it will feed or rest, at the end of a time step it decides which 4-km$^2$ block to go to next. Which action is optimal, i.e. which action maximises the chance to survive until the final time, depends on the actions taken in the future; this problem should therefore be solved using dynamic programming by working backwards in time (Houston & McNamara 1999; Clark & Mangel 2000). We therefore start with the final time step in the whole sequence, where $t = T$ and $d = D$. Obviously, the chance to survive until the final time when at the final time equals 1 for all individuals that have energy stores $x > X_{\text{crit}}$. Thus, the so-called ‘terminal reward function’ is given by:

\[
F(x, s, D_w, T) = \begin{cases} 
1 & \text{for } x > X_{\text{crit}} \\
0 & \text{for } x = X_{\text{crit}} 
\end{cases}
\]  

(7.1a)

(7.1b)

where $s$ indicates the bird’s location (which is at the roost for $t = T$; see above) and subscript $w$ indicates the type of tidal cycle $d = D$ ($w = 1..5$; see above and Figure 7.2). The chance to survive until final time for all other time steps $t$ at $d_w$ is the maximum of the survival value of all possible actions taken at $t$ at $d_w$, assuming that the animal behaves optimally from $t+1$ at $d_w$ onwards (note that this is an assumption made in all dynamic programming models; Houston & McNamara 1999; Clark & Mangel 2000):

\[
F(x, s, d_w, t) = \max_{i,k} V_{ik}(x, s, d_w, t)
\]  

(7.2)

where

\[
V_{ik}(x, s, d_w, t) = (1 - m_{isk}) F(x + \Delta x, s', d_w, t + 1)
\]  

(7.3)

In these equations, $V$ indicates the survival value of actions $i$ (feed or rest) and $k$ (block to go to for the next time step). These two actions lead to a change in energy store by $\Delta x$ (see Appendix) and a new location $s'$ at the next time step ($d_w, t+1$), contingent on the probability not to be taken a predator during the current time step ($d_w, t$). In order to make $x + \Delta x$ discrete, we used ‘linear interpolation’ (Clark & Mangel 2000). As predation can only occur when foraging, predation risk $m$ depends on the time spent actively feeding. Obviously, $m$ then depends on whether it chooses to feed or rest (indicated by $i$). Through foraging time loss to digestive breaks (which is safe from predation), $m$ also depends on where it currently is (indicated by $s'$). And finally, through foraging time loss to travelling time to the next block (which is safe from predation), $m$ also depends on where it moves to next (indicated by $k$).
Note that \( V \) at the last time step \( t = T \) in tidal cycle \( d \) is ‘sequentially coupled’ (Clark & Mangel 2000) to the first time step \( t = 1 \) in the next tidal cycle \( d + 1 \). As the value of \( w \) (cycle type from 1..5; see above) of cycle \( d + 1 \) is a stochastic variable, \( V \) at \( t = T \) is calculated for each value of \( w \), and subsequently averaged across all values of \( w \) (weighed for the probability \( p_w \) of occurrence of \( w \); given above):

\[
V_{ik}(x,s,d_w,T) = \sum_{w=1}^{5} p_w(1-m_{isk})F(x + \Delta x, s, d_w + 1, 1) \quad (7.4)
\]

Because of this stochasticity in feeding opportunities generated by uncertainty about the types of cycles to expect in the future, our model shows strong backward convergence (Houston & McNamara 1999). This means that survival probability as a function of both states (energy store and current location) becomes independent of the terminal reward initially assumed (eq. 7.1) at times well before the final time \( (d << D) \). In other words, no matter what terminal reward assumed, the predictions of the model will always be the same at times well before the final time. We checked this by varying the terminal reward and found that 50 tidal cycles are enough to generate convergence (tested over 1,000 cycles), which is why we used \( D = 50 \) (see above).

For each roost (Richel and Griend), we performed 1,000 Monte Carlo forward iterations (Clark & Mangel 2000). In order to avoid any influence of the applied shape of the terminal reward (eq. 7.1), we only analysed the results in cycle \( d = 1 \). The initial distribution in energy stores \( x \) was extracted from a distribution of body masses of birds caught in the Wadden Sea in July-September 1985-2002 (\( N = 811 \)) by assuming a lean mass of 92-g.

The model ran for each year separately (both back- and forward), with years only being different in the distribution and quality of the food. In order to compare the relatively fine-scaled model results on patch use with the relatively large-scaled empirical data on patch use (especially those collected by handheld radio-receivers; see below), we categorised the 4-km\(^2\) blocks into four large sites (Figure 7.1).

**PATCH USE**

Each year in 1996-2000 at the end of July or in August, we mist-netted red knots near Richel (53° 17’ N, 05° 07’ E), the main high-tide roost of red knots in the western Dutch Wadden Sea. Of each bird, we measured body mass (to nearest g) as a measure of energy stores (Van der Meer & Piersma 1994). Using ultrasonography (Dietz et al. 1999), we estimated gizzard size of the birds that we radio-tagged after 1996 as a measure of digestive processing.
capacity (Van Gils et al. 2003a). Before release, each bird was fitted with a small radio-transmitter glued to its back (1.4 g; 172-173 MHz; Holohil Systems Ltd., Carp, Ontario, Canada; following Warnock & Warnock 1993 but using superglue, see Nebel et al. 2000). Subspecific identity was based on the presence or absence of active primary moult (islandica changes primaries in NW-Europe, while the subspecies that uses the Wadden Sea as its stopover, canutus, changes primaries in West-Africa; Nebel et al. 2000), the presence of bare broodpatches on the belly (regrown at the first stopover in Iceland in islandica while usually still completely bare in canutus that arrive directly from the Siberian tundra), and body mass (in the Wadden Sea, islandica usually weighs less than 160 g in early autumn; Piersma 1994). The number of islandica that were radio-tagged each year were 11 (1996), 13 (1997), 7 (1998), 45 (1999), and 45 (2000).

A fully automatic radiotracking station at Grienderwaard. Each year, a maximum of 14 such solar panel powered systems were erected at strategic places in our study area. Photo: Jan van Gils.
Daily movements of radio-tagged birds were followed using a combination of handheld radio-receivers (TRX-2000S, Wildlife Materials Inc., Carbondale, Illinois, USA; see also Van Gils & Piersma 1999; Nebel et al. 2000) and automated radio-tracking systems (Telemetronics, Arnhem, The Netherlands; see also Van Gils et al. 2000; Green et al. 2002; Battley et al. 2004). Handheld systems were used in 1996-1998 at two fixed stations (Griend and Richel) and at a mobile station (research vessel Navicula). At each station, a directional three-element Yagi-antenna was mounted on a mast (3-4 m), which enabled radio-signals to be detected up to distances of 4-8 km. Each bird was scanned at half- or hourly intervals. If a valid radio-signal was detected, direction and time was recorded. Automated systems were used in 1997 (1 station), 1998 (6 stations), 1999 (14 stations; see Figure 7.1C), and 2000 (13 stations). At each station, a receiver (ICOM ICR10) was connected to a non-directional antenna (1.2 m) and, through an interface, to a palmtop computer. Each bird was scanned every 10-15 minutes. The system recorded

A flock of red knots leaving the high tide roost at Richel to feed near Griend. Using a directional Yagi antenna, such flocks were always checked for the presence of radio-tagged individuals. Photo: Jan van Gils.

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background noise and signal strength and detected valid signals up to 1-km. The system used in 1997 was of a different type (Aktiv500, GFT-Gesellschaft fur Telemetriesysteme mbH; described in Exo et al. 1992), connected to a three-element Yagi and with a detection range of about 3-km. Because available prey densities change seasonally through depletion, shell growth and changes in burying depth (Piersma et al. 1993a; Zwarts & Wanink 1993; De Goeij et al. 2001), we restricted the analyses of movement data to the time period when prey sampling was ongoing, which was during the end of July and August.

FORAGING INTENSITY
During low tide (1988-2000; mostly in August), groups of 2-4 observers covered tidal flats during low tide in search for flocks of knots. Upon encounter of a flock, time of day was noted and individual birds were observed through a telescope at a distance of 60-100 m. By means of scan sampling (Martin & Bateson 1993), behaviour (foraging or non-foraging) and abdominal profile (only in 1997 and 2000) was scored instantaneously for a number of individuals (mostly 100). Abdominal profile, which provides an estimate of an individual’s total fat mass and body mass, was scored on a nominal scale from 1-5 (cf. Wiersma & Piersma 1995). Due to small sample sizes in the heaviest classes, we pooled profile classes 3, 4 and 5 before analysis. Using calibrations provided by Wiersma & Piersma (1995), we calculated body mass from abdominal profile in order to make data and model predictions comparable. Note that due to the inability to distinguish islandica from canutus in the field, the data on foraging intensity are, in contrast to the radio-tracking data, partly collected on the fuelling canutus, especially those from the end of July and early August (Nebel et al. 2000).

Results

PATCH USE
The stochastic dynamic programming model predicted that Richel-roosters would be more prone to leave the vicinity of their roost during low tide than Griend-roosters (Figures 7.3A-B). This prediction was verified by the observations on the radio-tagged birds. Somewhat more than half of the knots roosting at Richel left the vicinity of the roost during low tide (Figure 7.3C; 4,985 observations on 67 individuals in 512 tidal cycles), while only a small proportion of the birds roosting at Griend did so (Figure 7.3D; 1,565 obs. on 37 ind. in 164 cycles). In agreement with model predictions (Figure 7.3A),
Richel-roosters that left the vicinity of their roost were mostly tracked at Grienderwaard (Figure 7.3C). As expected by the model (Figures 7.3A-B), birds that left the vicinity of their roost had a lower chance to be found at the rich feeding grounds of Ballastplaat when roosting at Richel (Figure 7.3C) than when roosting at Griend (Figure 7.3D).

**Figure 7.3.** Site use throughout the tidal cycle, predicted for (A) birds roosting at Richel and for (B) birds roosting at Griend. In contrast to Griend-roosters, the majority of Richel-birds are expected to leave the vicinity of their roost (mainly for Grienderwaard). Also note that the proportion of birds feeding at the best site, Ballastplaat, is expected to be twice as high for Griend-roosters compared to Richel-roosters. (C). Conforming to these predictions, a major part of the Richel-roosters were observed to leave Richel-area for Grienderwaard (4,985 obs. on 67 ind. in 512 cycles), and (D) almost all Griend-roosters stayed at Grienderwaard in the vicinity of their roost (1,565 obs. on 37 ind. in 164 cycles). The proportion of birds feeding at Ballastplaat was found to be twice as high for Griend-roosters compared to Richel-roosters.
FORAGING INTENSITY

Intensity of foraging was lowest during high tide and peaked during low tide, both in the model (bars in Figure 7.4A) and in the observations (dots in Figure 7.4A; 1,124 obs. on a total of 367,950 birds). On average, this led to an observed total daily period of active foraging of 12.8 h (which does not differ from the predicted 13.0 h; $R^2 = 0.0; P > 0.4$). As predicted (Figure 7.4B), intensity declined with energy stores as represented by body mass (Figure 7.4C; 40 obs. on a total of 2,490 birds), though the heaviest class (body mass > 150 g) fed somewhat more intense than predicted (compare Figures 7.4B and 7.4C).

Discussion

PATCH USE

Observed shifts in patch use throughout the tidal cycle were in agreement with the expectations of the stochastic dynamic programming model (Figure 7.3). This invites speculations on underlying mechanistic explanations for the observed patterns, which we conceptualised and simplified in Figure 7.5 for birds roosting at Richel. Although commuting between the roost at Richel and the neighbouring Richel-flats is obviously cheap in terms of time and energy (Figure 7.5B), birds roosting at Richel are likely to leave the vicinity of their roost around low tide (Figure 7.3C). Energy intake rates are much better elsewhere (Figures 7.1B and 7.5A), and visiting the nearby Grienderwaard seems the best compromise between travel distance and energy gain. In fact, it seems the only option that yields a positive energy balance on a daily basis (Figure 7.5B). This trade-off between travel costs and energetic benefits seems to be the reason that Ballastplaat, yielding even better intake rates than Grienderwaard but at a greater distance (Figures 7.1B and 7.5), is not used very often (Figure 7.3C). On average, feeding only at Ballastplaat when roosting at Richel yields a slightly negative energy budget (Figure 7.5B). Birds that do visit Ballastplaat usually combine this with a visit to Grienderwaard during the tidal times Ballastplaat is unavailable. This is a profitable policy since (i) Ballastplaat is near Grienderwaard and (ii) low tide at Ballastplaat occurs 1-2 h later than at Grienderwaard, which allows for an extension of the daily feeding period (see Van Gils et al. 2004a for details on ‘tide extension’). The idea of a trade-off between energy gain and travel costs is supported by the theoretical and empirical observations that birds roosting nearby (Griend) are more likely to visit Ballastplaat than birds roosting further away (Richel; Figure 7.3). An additional disadvantage of feeding at Ballastplaat is the
Figure 7.4. Foraging intensity throughout the tidal cycle (expressed as h after high tide). (A). Conform the predictions by the SDP-model (bars), observed foraging intensity peaks during low tide and is minimised during high tide (dots with SE-bars; 1,124 obs. on a total of 367,950 birds). (B). Foraging intensity is predicted to decline with body mass (energy store; 3 classes; legend as in C). (C). Conform these predictions, observed foraging intensity declines with body mass (40 obs. on a total of 2,490 birds).
relatively short time its flats are available (Figure 7.5A), especially during the worst tides (type 4 and 5 in Figure 7.2). In other words, available feeding times at the profitable Ballastplaat are often too short to cover the high travel-costs (Figure 7.5).

**FORAGING INTENSITY**

Observed foraging intensity as a function of ‘tidal time’ and body mass was in agreement with the expectations of the stochastic dynamic programming model (Figure 7.4). Foraging was most intense around low tide, and lean birds fed more intensely than fat birds. The model suggests that, especially for heavy birds (> 150 g), foraging only pays off when the best patches are available, which is the case around low tide. Only lean birds (< 115 g) seem to benefit from foraging in the generally poorer patches that are the only ones available.

![Figure 7.5](image_url)

**Figure 7.5.** How intake rate, available foraging time, and distance to the Richel-roost determine daily net energy gain for red knots, that feed in either one out of four sites (Ballastplaat [B], Grienderwaard [G], Richel-area [R], or “West” [W]). (A). Daily metabolizable energy intake (kJ; vertical axis) is the product of metabolizable energy intake rate (W; horizontal axis) and daily available foraging time (h; diagonal lines) and is therefore highest at Grienderwaard (long daily available foraging period) and at Ballastplaat (high metabolizable energy intake rate). (B). In this conceptual model (based on flight costs reported by Kvist et al. 2001), daily energy expenditure (kJ; lower horizontal axis) is a linear function of the distance that needs to be travelled daily between roost and feeding site (km; upper horizontal axis; ignoring variable foraging costs for the moment). With daily metabolizable energy intake (kJ) on the vertical axis, the y=x line represents a balanced daily energy budget. Obviously, net daily energy gains are maximised (and positive) at Grienderwaard.
around high tide. The reason for this is straightforward (at least in the model): lean birds experience higher starvation risks, and therefore accept higher predation risks through increased foraging. This result agrees with the general notion that the marginal value of energy increases with a decrease in energy stores, which causes leaner birds to accept higher predation risks (Brown 1988; Houston & McNamara 1999). In line with this reasoning, Dierschke (2003) recently observed that predators mostly kill lean passerine birds. With respect to the fattest birds (> 150 g), the model somewhat underestimates the intensity of foraging (Figures 7.4B-C). Possibly, this is due to the fact that some observations may be collected on canutus-individuals that aim to raise body mass up to 200-g in order to migrate to their west-African wintering grounds (Nebel et al. 2000; note that in the field, islandica cannot be distinguished from canutus). As the model is based on islandica that at this time of year simply aim to keep body mass above a starvation threshold, it predicts foraging to be somewhat less intense (Figure 7.4B).

CONCLUSIONS AND FUTURE DIRECTIONS

Patch use and length and intensity of foraging by red knots depends on the spatial distribution of the prey in relation to the location of the roost and the availability of patches set by the tide. To reduce time and energy lost to travelling, knots apparently feed as close to their roost as possible, as long as intake rates coupled with available foraging times are sufficient to cover the daily energy expenditure (summarised in Figure 7.5). Within these environmental constraints, birds with modest amounts of energy stores seem to cope by feeding more intensely (Figure 7.4C).

As the position of the roost seems so important, a relevant question is what determines the choice for a given roost (see Rogers et al. 2003). A preliminary analysis suggests that both energy stores and digestive processing capacity play a role, as the proportion of high tides spent at Griend relative to Richel declines with body mass and gizzard mass (P < 0.01; R² = 0.152; N = 66 birds; arcsine-transformed and weighed for the number of observations per bird; see Van Gils et al. 2003a for the relation between digestive processing capacity and gizzard mass). Possibly, this differential roost choice is a reflection of a trade-off between energy gain and predator-avoidance. Comparing both roosts, Griend is obviously nearest to the best feeding grounds, Grienderwaard and Ballastplaat (Figures 7.1 and 7.5). However, due to surprise attacks by raptors likely being more successful at Griend than at Richel (due to the presence of a dike at the former island), it has been suggested that roosting at Griend incurs at a higher risk of predation than roosting at Richel (Piersma et al. 1993a). As birds with fair amounts of energy
stored or high digestive capacities experience lower marginal values of energy (Brown 1988; Houston & McNamara 1999), they aim to minimise predation risk by roosting at the safer, but energetically more costly, Richel over Griend.

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**Appendix**

**On the calculation of \( \Delta x \)**

The change \( \Delta x \) in energy store \( x \) per 50-minute time step equals gross energy gain \( B \) minus energy cost \( C \), or formally:

\[
\Delta x = B - C \quad (A7.1)
\]

We assume that storing 1-g of fat costs \( 40/0.75 = 53.3 \text{ kJ} \) and burning yields \( 40 \text{ kJ} \) (Ricklefs 1974).

Gross energy gain \( B \) is the product of gross energy gain rate (predicted from the observed prey densities in a block as described in the main text) and time spent feeding in the 50-minute time interval (which is determined by whether it is feeding or resting and the travel time to the patch in the next time interval; see below). It therefore depends on respectively the current location \( s \), the current action \( i \), and the location \( k \) in the next time step.
Energy cost $C$ is determined by current action $i$ (foraging is more costly than resting), the time lost to travelling which is a function of current patch $s$ and patch $k$ chosen in the next time interval (travelling is more costly than foraging), and by energy store $x$ (metabolic rates during travelling and during foraging are mass-dependent). More specifically, metabolic rate while resting is set to 1.63 W (Piersma et al. 2003 taking into account a gizzard mass of 6-g). On top of this comes a thermoregulatory cost of 0.69 W, which is typical for knots living in the western Dutch Wadden Sea in August (Wiersma & Piersma 1994). When foraging, a constant component of 0.47 W is added due to probing (Piersma et al. 2003), and a mass-dependent component is added due to walking (Bruinzeel et al. 1999; expressed in W):

$$60 \left( \frac{92 + 5x}{1000} \right)^{2.9}$$

which assumes a walking speed of 0.072 m/s as observed by Piersma et al. (2003). As an energetic saving, 30% of the heat produced during walking substitutes for thermostatic heat (Bruinzeel & Piersma 1998). In addition, a variable digestion cost is added, which amounts to 5,195 J/g AFDM$^{flesh}$ digested (Piersma et al. 2003), where we assume that 100% of this heat increment of feeding (HIF) substitutes for thermostatic heat (cf. Van Gils et al. 2003a). When travelling between current patch $s$ and future patch $k$, the following mass-dependent flight cost is added (Kvist et al. 2001; expressed in W):

$$10^{0.39(92 + 5x)^{0.35} - 0.95}$$

Time devoted to travelling is calculated by assuming a flight speed of 15 m/s (cf. Kvist et al. 2001; truncated at a maximum of 50 minutes) and is subtracted from the foraging or resting time in the current patch $s$. 
References


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Red knots usually feed in dense flocks, almost shoulder to shoulder. Occasionally, this leads to short fighting bouts. As long as digestion proceeds at full speed during such interference interactions then the time cost of interference competition may be negligible.

Photo: Jan van de Kam.