Foraging decisions in a digestively constrained long-distance migrant, the red knot (Calidris canutus)
van Gils, Johannes Adrianus

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Digestive bottleneck affects foraging decisions in red knots (Calidris canutus).
II. Patch choice and length of working day

Jan A. van Gils, Anne Dekinga, Bernard Spaans, Wouter K. Vahl
and Theunis Piersma
CHAPTER 6

Summary

When prey occur at high densities, energy assimilation rates are generally constrained by rates of digestion rather than by rates of collection (i.e. search and handle). As predators usually select patches containing high prey densities, rates of digestion will play an important role in the foraging ecology of a species. The red knot (Calidris canutus) shows tremendous inter- and intra-individual variation in maximum rates of digestion due to variation in the processing machinery (gizzard and intestine), which makes it a suitable species to study effects of digestive processing rate on foraging decisions. Here we report on patch use, prey choice, and daily foraging times as a function of gizzard size in free-ranging, radio-marked, red knots. As knots crush their bulky bivalve prey in their gizzard, the size of this organ, which we measured using ultrasonography, determines digestive processing rate. Using the digestive rate model (DRM), we a priori modelled patch use, prey choice, and daily foraging times as a function of gizzard mass. Focussing on two contrasting patches, birds with small gizzards were expected to feed on high-quality (soft-bodied) prey found in low densities in the one patch, while birds with large gizzards were expected to feed on low-quality (hard-shelled) prey found in high densities in the other patch. Assuming that red knots aim to balance their energy budget on a daily basis, we expected daily foraging time to decline with gizzard mass. Observed patch and prey choices were in quantitative agreement with these theoretical predictions. Observed daily foraging times were only in qualitative agreement: they declined with gizzard mass but less steeply than predicted. We discuss that red knots might be aiming for a slightly positive energy budget in order to (i) refuel their stores depleted during migration and (ii) to insure against unpredictability in supply and demand during winter. Red knots arriving from their breeding grounds with small gizzards are only able to realise this aim when densities of soft-bodied prey are high, which is the case in late July and early August. Rapidly declining soft-bodied prey densities throughout late summer pose a major penalty for individuals arriving late at their wintering grounds. The long daily foraging periods required by knots with small gizzards are only feasible through ‘tide-extension’. In our study area, birds can and do raise the daily low tide period from 12-h to almost 17-h by moving along with the tide in an easterly direction, subsequently flying back to their starting point at the high tide roost.
Introduction

In a patchy, multiple prey environment, patch choice cannot be understood without understanding prey choice (e.g. Tinbergen 1981), and vice versa (e.g. Brown & Morgan 1995). Through their effect on intake rate, these two decisions affect other decisions, such as the daily time devoted to foraging, at least in time-minimising foragers that only require a given daily amount of energy (Schoener 1971). Ever since they have been developed (see review by Jeschke et al. 2002), models of functional response have played a major role in understanding such foraging decisions (e.g. Fryxell 1991; Piersma et al. 1995; Stillman et al. 2002). In the best known functional response model, Holling’s disc equation (Holling 1959), energy intake rate is only delimited by the rate at which food is collected, i.e. the rate at which food is found and externally handled, and this ignores the maximum rate at which food can internally be digested. However, evidence for the significant role of digestive processing rate shaping functional responses and thus foraging decisions is rapidly gaining momentum (Kersten & Visser 1996; Zwarts et al. 1996; Jeschke et al. 2002; Van Gils et al. 2003a, b; Zharikov & Skilleter 2003; Van Gils & Piersma 2004; Karasov & McWilliams 2004; Van Gils et al. 2004). At the same time, it is increasingly acknowledged that digestive organs vary flexibly in size (Piersma & Lindström 1997; Piersma & Drent 2003), and it has recently been shown that digestive rates vary accordingly (Lee et al. 2002; Van Gils et al. 2003a). Through constraining effects on intake rates, organ flexibility is therefore likely to lead to differences in foraging decisions (Klaassen 1999). In this way, organ flexibility can be used as a tool to study the effects of digestive processing capacity on foraging decisions.

Red knots (Calidris canutus), medium-sized shorebirds that make a living by feeding on marine invertebrates, show tremendous flexibility in digestive organ size (Piersma et al. 1999; Van Gils et al. 2003a). One of these organs, the muscular gizzard, crushes the generally hard-shelled prey which are ingested whole (Piersma et al. 1993b). It has been verified experimentally that gizzard size constrains digestive processing rate in knots (Van Gils et al. 2003a). Growing a larger gizzard therefore yields a higher (gross) energy intake rate, up to a level where rate of collection delimits energy intake rate (i.e. when maximum processing rate > rate of collection; Figure 6.1A). As the digestive constraint acts on the rate at which shell mass can be processed (Van Gils et al. 2003a), selecting higher quality prey (i.e. amount of metabolizable energy per gram shell mass; indicating a prey’s ‘softness’), also yields a higher energy intake rate for a given gizzard size (Figure 6.1B; Van Gils et al. 2003a, 2004). This leads to gizzard-size dependent patch use whenever high-quality
prey is collected at a slower rate than low-quality prey (Figure 6.1B). In that case, birds with small gizzards maximise their energy intake rate in the patch containing the slowly collected high-quality prey, while birds with large gizzards maximise their energy intake rate in the patch containing the rapidly collected low-quality prey (Figure 6.1B).

Applying the above-mentioned digestive rate model (DRM; Van Gils et al. 2004; Hirakawa 1995) to red knots, we here predict patch use, prey choice, and daily foraging times as a function of digestive capacity (i.e. gizzard size). These predictions are based on prey density estimates in two contrasting patches in the western Dutch Wadden Sea in 1998; one patch (100 ha) containing high densities of low-quality prey, the other patch (400 ha) containing low densities of high-quality prey. Subsequently, we examine these predictions by using detailed data from a series of years (1997-2000) on the whereabouts of radio-tagged knots that varied in gizzard mass.

Material and methods

During late summer in 1997-2000, flocks of red knots frequently fed at two sites (patch A and patch B) in our study area the Grienderwaard (Figure 6.2A; western Dutch Wadden Sea; 53º 15’ N, 5º 15’ E). We intensively monitored prey densities and the occurrence of red knots in these two patches (1998), the birds’ diet composition (1997-1998), and the length of their foraging day (1997-2000). Across these years, summer prey densities at these sites were more or less constant as revealed by yearly sampling at fixed stations in a grid with 250-m intervals (Table 6.1; see Piersma et al. 2001 for detailed methodology).

- **Prey density.** In each of the two patches during late summer 1998, we sampled prey densities at spots where flocks of knots had been seen feeding. Each feeding spot was marked with a stick placed in the sediment, which enabled us to come back to the exact spot and resample it. Sampling was repeated every 3-6 days at 6 (patch A) and 11 (patch B) such feeding spots. Each sample was made up of 10 subsamples. Each subsample consisted of sediment taken to a depth of 20 cm with a core of 1/56 m². Subsequently, this sediment was sliced into a top layer (0-4 cm; containing the accessible prey) and a bottom layer (4-20 cm; containing the inaccessible prey), which were sieved separately over 1-mm mesh. Densities of *Hydrobia* were estimated from 3 subsamples taken with a smaller core (1/267 m²) and sieved with a finer mesh (0.5-mm). In the laboratory, we assorted all items into prey types; i.e. species and size (to nearest 1-mm or to nearest 0.5-mm in case of *Hydrobia*).
Figure 6.1. (A). Functional response on a single prey type as a function of prey density and gizzard mass. At large gizzard masses and/or at low prey densities, energy intake rate is not constrained by rate of digestive processing (i.e. gizzard mass) but by rate of collection and follows the well-known Holling’s disc equation. At small gizzard masses and/or at high prey densities, energy intake rate is constrained by rate of digestive processing and increases quadratically with gizzard mass. The black line indicates an example intake rate as a function of gizzard mass within a single patch (i.e. where prey density, and thus rate of prey collection, is fixed). (B). When there are two patches, each containing a different prey type, rate-maximising patch choice might depend on gizzard mass. This is the case when the high-quality prey occurs in lower densities than the low-quality prey. In such a scenario, birds with small gizzards (grey surface on the left) should feed in the patch containing low densities of high-quality prey, while birds with large gizzards (white surface on the right) should feed in the patch containing high densities of low quality prey.
Radio-telemetry. Each year in 1997-2000 at the end of July or in August, we caught red knots with mist-nets at Richel (53° 17' N, 5° 7' E), the main roost of waders in the western Dutch Wadden Sea. After attaching a small radio-transmitter (1.4 g; 172-173 MHz; Holohil Systems Ltd., Carp, Ontario, Canada) to their backs (following Warnock & Warnock 1993 but using superglue, see Nebel et al. 2000), ultrasonographically estimating their gizzard size (see exp. 1 in Van Gils et al. 2004 and Dietz et al. 1999 for methodology), and subspecific identification, the birds were released again. During late summer, two subspecies of knot occur in our study area (Piersma & Davidson 1992). C. c. islandica uses the area as its wintering grounds, while C. c. canutus uses it as its stopover on its way to its west-African wintering grounds. This distinct migratory behaviour is likely to lead to distinct foraging behaviour. We therefore restricted our analyses to the subspecies that we caught most, C. c. islandica (N = 110 individuals for 1997-2000). Subspecific identity was based on the presence or absence of active primary moult (islandica changes primaries in NW Europe, while 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 in early autumn, islandica usually weighs less than 160 g while canutus approaches masses up to 200 g; Piersma 1994).

Daily movements of radio-tagged birds, with special attention to the occurrence in patch A and B in 1998, 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 1997-1998 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 (day and night). 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), 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 background noise and signal strength and detected valid signals up to about 1-km. The system used in 1997 was of a different type (Aktiv500, GFT-Gesellschaft für Telemetriesysteme mbH; described in Exo et al. 1992), connected to a three-element Yagi and with a detection range of about 3-km.

- **Prey choice.** In both patches, we collected droppings of flocks of red knots that contained at least one radio-tagged individual. This was done in Aug-Sep 1997 and was repeated in Aug 1998. Each dropping sample contained 6-100 droppings (47 on average), and was analysed following Dekinga & Piersma (1993). We assorted shell fragments into different prey species, and reconstructed each species' size distribution from unbroken hinges (to nearest mm). Since food retention times in digestive tracts of knots are relatively short (20-50 minutes, Piersma 1994) compared to the times spent at feeding sites (often more than 1 h), dropping analysis reliably reveals what knots have been eaten locally.

- **Daily foraging times.** In order to estimate the daily time spent foraging, we analysed at what time radio-marked individuals left and arrived back at their main roost at Richel (Aug 1997-2000). Once they have left their roost, knots feed for most of their time (Piersma 1994; Van Gils et al. MS chapter 7).

- **Modelling gizzard-size dependent energy intake rates.** In order to predict the gizzard-size dependent energy intake rate that each patch potentially had on offer, we applied the DRM across a range of gizzard masses to the available prey densities observed in 1998. A prey is considered to be available when it is both accessible (see above) and ingestible (Zwarts & Wanink 1993). Maximally ingestible lengths were taken from Piersma et al. (1993a) and Zwarts & Blomert (1992). We only selected prey types of the five most abundant prey species, that together made up virtually all of the available biomass prey density in both patches (Baltic tellins Macoma balthica, edible cockles Cerastoderma edule, mudsnails Hydrobia ulvae, shore crabs Carcinus maenas, and common shrimps Crangon crangon). Note that applying the DRM
to such multiple-prey situations is more advanced than to the simple two-prey situation presented in Figure 6.1B, where only a single prey type occurs per patch. For details on applying the DRM to multiple-prey patches we refer to Van Gils et al. (2004) and Hirakawa (1995); here we will only explain the main steps.

Firstly, for all possible diet compositions in each patch, we calculated the expected intake rate, both in terms of energy (W) and in terms of ballast mass (mg/s). For this purpose, we applied a searching efficiency \( a = 10.5 \text{ cm}^2/\text{s} \) (experiment 2 in Van Gils et al. 2004). Size-specific handling times \( h \) for Cerastoderma and Macoma were taken from Piersma et al. (1995). For both prey species we took into account that handling buried bivalves requires at least 2 seconds (Zwarts & Blomert 1992). We used estimates for \( h \) for Hydrobia, Crangon and Carcinus as obtained by Van Gils et al. 2004 (experiment 1). From prey items collected throughout Grienderwaard in Aug-Sep 1998 as part of a larger survey (Piersma et al. 2001) we determined metabolizable energy content \( e \) and ballast mass \( k \) as described by Van Gils et al. 2004 (experiment 1).

Secondly, applying the digestive constraint \( c \) (mg/s) on ballast intake rate as a function of gizzard mass \( G \) (g; Van Gils et al. 2003a; \( c = 0.05 \cdot G^2 \)), we derived the maximum energy intake rate as a function of gizzard mass for each patch. Likewise, assuming maximisation of instantaneous rates of energy assimilation (i.e. across search, handling and digestion times; see Van Gils et al. 2004), we derived optimal patch and prey choice and daily foraging times as a function of gizzard mass. The assumption of rate-maximisation seems valid, even for birds that aim to balance their daily energy budget on a daily basis but aim to minimise the time devoted to foraging (Schoener 1971). Optimal prey choices were derived by drawing gizzard-size dependent ‘optimal diet lines’ in the state space of energy vs. ballast intake rate (see Hirakawa 1995 and Figure 5.1 in Van Gils et al. 2004).

Optimal daily foraging times were calculated for two policies. Birds that aim to balance their energy income with energy expenditure on a daily basis use the first policy. In this case, the proportion of the day that needs to be foraged equals

\[
\frac{\text{ADMR}}{\text{MEIR}} \tag{6.1}
\]

where ADMR gives the average daily metabolic rate and MEIR gives the metabolizable energy intake rate while feeding. Note that ADMR itself increases with daily foraging time (mainly though higher processing costs) and gizzard mass (through higher maintenance and transport costs; for details
on ADMR-calculations see Appendix in Van Gils et al. 2003a). Birds that aim to maximise their daily energy intake use the second policy. Besides the instantaneous digestive constraint set by gizzard size, daily energy income seems constrained by other physiological parameters (e.g. intestine size). Kvist & Lindström (2003) estimated that this additional constraint in red knots equals 9.6 times basal metabolic rate (BMR), which is the limit that we applied here (using BMR = 0.95 W; Piersma et al. 1996). In this case, the proportion of the day that can be foraged equals

\[
\frac{9.6 \text{BMR}}{\text{MEIR}}
\]  

(6.2)

Results

- **Prey density.** In 1998, patch A was dominated by low-quality, hard-shelled prey (Hydrobia ulvae, Macoma balthica, and Cerastoderma edule) and contained virtually no high-quality, soft-bodied prey (Carcinus maenas; Figure 6.2B). In contrast, almost half of the biomass in patch B comprised high-quality, soft-bodied prey (Carcinus maenas and Crangon crangon), while the rest comprised lower quality, hard-shelled prey (Macoma balthica, Hydrobia ulvae and Cerastoderma edule; Figure 6.2B).

- **Modelling gizzard-size dependent energy intake rates.** The allometric relationships for flesh and ballast mass, required to model intake rates, are presented in Table 6.2. From these equations and available prey densities it was calculated that (i) overall available prey biomass (g AFDM_{flesh} m^{-2}; where AFDM_{flesh} is flesh ash-free dry mass) was about 5-10 times higher in patch A than in patch B (Figure 6.2C), and that (ii) average digestive prey quality (e/k expressed as metabolizable energy per mg ballast mass) in patch A was about half of that in patch B (Figure 6.2D). Using these parameters on flesh and ballast mass in combination with available prey densities, searching efficiency and handling times, we reconstructed for both patches the range of feasible intake rates (in terms of energy and ballast mass; two loops in Figure 6.3A). Using the constraint on processing ballast mass set by gizzard size, enabled us to derive energy intake rates (vertical axis in Figure 6.3A) as a function of gizzard mass (lower horizontal axis in Figure 6.3). This shows that birds with gizzards of least 7-g maximise their energy intake rate in patch A, while birds with smaller gizzards maximise their energy intake rate in patch B (Figure 6.3A).
Figure 6.2. Prey densities in 1998. (A). Map of prey sampling spots (dots) within the two patches. (B). Virtually all prey in patch A were hard-shelled, while in patch B about half were soft-bodied (calculated on the basis of available biomass). (C). Available prey biomass (g AFDM flesh/m²) in patch A was about 5-10 times higher than in patch B. These box-and-whisker plots give mean (large dot), median (horizontal line within box), interquartile range (box), range (bars), and outliers (small dots). (D). Because of high abundance of soft-bodied prey in patch B, average digestive quality in this patch tended to be about twice as high as that in patch A.
**Patch choice.** Out of 42 birds radio-tagged in 1998, 16 visited patch A and/or patch B. Gizzard masses varied with patches visited (P = 0.001; R² = 0.65; GLM). Confirming the optimality predictions of the DRM as stated above, birds that only visited patch A had larger gizzards (7.72 g; N = 4; Figure 6.3B) than birds that visited both patches (5.23 g; N = 10; P < 0.005; Bonferroni pairwise comparison; Figure 6.3B) and than birds that only visited patch B (3.99 g; N = 2; P < 0.005; Bonferroni pairwise comparison; Figure 6.3B).

**Prey choice.** The proportion of high-quality, soft-bodied prey in the diet declined as a function of gizzard mass (Figure 6.3C; dropping samples were collected from 28 flocks that together contained 11 radio-tagged individuals). Birds with gizzards of least 7-g never fed on soft-bodied prey. These observations were in agreement with the predictions of the DRM (grey bars in Figure 6.3C).

**Daily foraging times.** Daily foraging times declined as a function of gizzard mass (P = 0.019; Figure 6.3D; upper line in Table 6.3; N = 123 observations on 38 radio-tagged individuals). Although steeper than observed, such a decline was predicted by the DRM applied to birds that aim to balance their energy budget on a daily basis (lower border of grey surface in Figure 6.3D).

### Table 6.2. Observed log₁₀-log₁₀ relationships for the flesh ash-free dry mass AFDMₙ (mg) and ballast dry mass k (mg) as a function of size (mm) of relevant prey species collected in Aug-Sep 1998 at Grienderwaard. Metabolizable energy content e (J) is calculated as 0.725 · 22 · AFDMₙ (mg; see Van Gils et al. 2004).

<table>
<thead>
<tr>
<th>Species</th>
<th>Part</th>
<th>Constant</th>
<th>Slope</th>
<th>N</th>
<th>R²</th>
<th>F-ratio</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macoma</td>
<td>AFDMₙ</td>
<td>-2.457</td>
<td>3.402</td>
<td>285</td>
<td>0.837</td>
<td>1450.001</td>
<td>&lt;0.001</td>
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<tr>
<td>Macoma</td>
<td>k</td>
<td>-2.216</td>
<td>3.999</td>
<td>269</td>
<td>0.784</td>
<td>969.144</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cerastoderma</td>
<td>AFDMₙ</td>
<td>-2.743</td>
<td>3.564</td>
<td>89</td>
<td>0.498</td>
<td>86.276</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cerastoderma</td>
<td>k</td>
<td>-1.556</td>
<td>3.545</td>
<td>93</td>
<td>0.759</td>
<td>287.234</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Hydrobia</td>
<td>AFDMₙ</td>
<td>-1.142</td>
<td>2.076</td>
<td>216</td>
<td>0.473</td>
<td>191.937</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Hydrobia</td>
<td>k</td>
<td>-0.381</td>
<td>1.926</td>
<td>216</td>
<td>0.575</td>
<td>289.449</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Carcinus</td>
<td>AFDMₙ</td>
<td>-0.943</td>
<td>2.303</td>
<td>20</td>
<td>0.865</td>
<td>115.561</td>
<td>&lt;0.001</td>
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<tr>
<td>Carcinus</td>
<td>k</td>
<td>-0.838</td>
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<td>20</td>
<td>0.905</td>
<td>170.723</td>
<td>&lt;0.001</td>
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<tr>
<td>Crangon</td>
<td>AFDMₙ</td>
<td>-1.593</td>
<td>1.866</td>
<td>11</td>
<td>0.346</td>
<td>4.765</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Crangon</td>
<td>k</td>
<td>-1.692</td>
<td>1.931</td>
<td>11</td>
<td>0.341</td>
<td>4.667</td>
<td>&lt;0.1</td>
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</tbody>
</table>
Figure 6.3. (A). State-space of feasible short-term intake rates in terms of energy (vertical axis) and in terms of ballast mass (upper horizontal axis) in patch A (grey-shaded area; which continues beyond the scale of the graph) and in patch B (dashed area). Gizzards that can process more than 2-mg ballast/s obtain the highest energy intake rates in patch A (i.e. gizzards ≥ 7-g as indicated on lower horizontal axis), while smaller gizzards maximise their energy intake rate in patch B. Assuming rate-maximisation, knots with large gizzards are
therefore expected to feed in patch A, while knots with small gizzards are expected to feed in patch B. (B). Confirming these expectations, birds that only visited patch A had larger gizzards compared to birds that only visited patch B, and compared to birds that visited both patch A and B (box-and-whisker plots are explained in Figure 6.2C). (C). Observed diet compositions as a function of gizzard mass (means ± SE, indicated by dots ± bars) match well with the predicted values (grey bars). Number of radio-tagged birds per gizzard class is 2 (4-g), 2 (5), 2 (6), 1 (7), 1 (8), 1 (10), 1 (12), and 1 (13). (D). Observed daily foraging time declines as a function of gizzard mass (means ± SE, indicated by dots ± bars; 123 observations on 38 individuals) and lies in between two theoretical predictions. The first gives the daily foraging time required to balance the daily energy budget (lower border of grey surface); the second gives the maximum daily foraging time set by upper limits to daily metabolizable energy gain (9.6 · BMR; upper border of grey surface). Small gizzards just seem able to balance their daily energy budget, while large gizzards approach the upper daily limit to metabolizable energy intake. Frequency distribution of gizzard masses found in Jul-Aug (N = 103; grey bars) suggests that most birds presumably have a slightly positive daily energy balance.

6.3D). It seems that birds with large gizzards feed longer than a balanced budget requires and that daily foraging times in the largest gizzards (12-g) are set by limits on daily metabolizable energy intake (upper border of grey surface in Figure 6.3D indicating a limit of 9.6 · BMR). The question why some birds must operate with a much smaller gizzard than others will be explored further in the discussion.

Table 6.3. General linear models of the effect of gizzard mass on departure and arrival times at Richel and Grienderwaard, weighed for the number of observations per bird. SS is sum-of-squares. P-values are bold printed when significant.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Slope (h/g)</th>
<th>Regression SS</th>
<th>Residual SS</th>
<th>N</th>
<th>R²</th>
<th>P</th>
</tr>
</thead>
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<td>Daily foraging time</td>
<td>-0.71</td>
<td>217.01</td>
<td>1305.77</td>
<td>38</td>
<td>0.14</td>
<td><strong>0.019</strong></td>
</tr>
<tr>
<td>Departure from Richel</td>
<td>+0.05</td>
<td>1.61</td>
<td>126.25</td>
<td>46</td>
<td>0.01</td>
<td>0.458</td>
</tr>
<tr>
<td>1st arrival at Grienderwaard</td>
<td>-0.18</td>
<td>19.44</td>
<td>56.26</td>
<td>45</td>
<td>0.26</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1st departure from Grienderwaard</td>
<td>-0.17</td>
<td>11.62</td>
<td>42.42</td>
<td>35</td>
<td>0.22</td>
<td><strong>0.005</strong></td>
</tr>
<tr>
<td>2nd arrival at Grienderwaard</td>
<td>-0.29</td>
<td>37.96</td>
<td>63.52</td>
<td>37</td>
<td>0.37</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Arrival at Richel</td>
<td>-0.29</td>
<td>54.42</td>
<td>111.94</td>
<td>38</td>
<td>0.33</td>
<td>&lt;0.001</td>
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</tbody>
</table>
Discussion

TESTING THE DIGESTIVE RATE MODEL

In agreement with the predictions of the digestive rate model (DRM), birds with small gizzards fed in the patch containing low densities of high-quality prey (patch B), while birds with large gizzards fed in the patch containing high densities of low-quality prey (patch A). Birds with intermediate gizzards were observed to alternate between both patches (Figure 6.3B). Thus, the observed patch choices imply that the birds were maximising their instantaneous rates of energy assimilation. The high rate at which the bulky, low-quality prey are found and handled in patch A is simply too high to be kept up by the digestive processing rate of birds with small gizzards. Such birds better search for high-quality prey containing less bulky material, even if they are found and handled at a much lower rate. Note that the better known prey choice model, the so-called ‘contingency model’ (Pulliam 1974; Charnov 1976; Stephens & Krebs 1986), would predict all birds, irrespective of gizzard size, to feed in the patch yielding the highest rates of prey collection (patch A). This is because processing constraints are ignored in the model. Instead, prey choices in this classic model are solely based on a prey type's profitability ($e/h$, metabolizable energy content over handling time; see also Van Gils et al. 2004).

Prey choice within each patch also agreed well with the DRM-predictions (Figure 6.3C). In the patch chosen by birds with small gizzards (patch B), the proportion of high-quality prey declined as a function of gizzard mass, while in the patch chosen by birds with large gizzards (patch A), the birds virtually ate no high-quality prey. By contrast, ignoring digestive constraints, the contingency diet model would have predicted a similar diet for all gizzard sizes.

As expected for birds that balance their energy budget on a daily basis, daily time spent foraging declined as a function of gizzard mass (Figure 6.3D). As digestive processing rates constrain energy gain rates across all gizzard sizes (even the largest classes), gross energy intake rates while feeding should continue to increase with increasing gizzard size. As this increase is steeper than the putative increase in metabolic costs associated with maintaining and carrying larger nutritional organs (Piersma et al. 2003a), net energy intake rates while feeding should increase with gizzard size. Therefore, the daily foraging time required to balance the energy budget should decline with increasing gizzard size. The fact that the observed decline is less steep than expected on the basis of this reasoning (Figure 6.3D) suggests that birds with larger gizzards obtain a slightly positive energy budget on a daily basis. Red knots might be aiming for a slightly positive energy budget in order to (i) refuel their stores depleted during migration, and (ii) to insure against...
unpredictability in supply and demand during winter (Johnson 1985; Piersma 1994; Piersma et al. 2003b). Having listed the advantages of maintaining a slightly positive energy budget, the question arises why we find knots with small gizzards. Birds with small gizzards are unable to obtain positive energy budgets as this would require daily foraging times in excess of the maximum our tidal system has to offer (17 h per day at most, see below).

**WHY DO KNOTS SOMETIMES HAVE SMALL GIZZARDS?**

The flexibility in digestive organ size seems partly related to the knot’s migratory life style (Piersma & Lindström 1997; Piersma 2002; Battley & Piersma 2004). Red knots possess small, atrophied gizzards just before, during, and just after their intercontinental long-distance flights, while they have larger gizzards during the fuelling phase at stopovers (Piersma et al. 1999b) or at their wintering grounds (Van Gils et al. 2003a). Such changes are likely the outcome of an underlying optimisation process (Van Gils et al. 2003a): digestive organs should be reduced whenever maintenance and transport costs outweigh benefits (i.e. during long-distance flights), while they should be enlarged whenever benefits outweigh costs (i.e. at intertidal feeding grounds).

Gizzards are smallest after a period on the tundra breeding grounds where red knots feed on relatively soft-bodied arthropod adults and larvae (Battley & Piersma 2004) and after the southward flight to coastal staging and/or wintering grounds. Upon arrival, gizzards grow back to ‘normal’ proportions with rates of about 0.2 g/day (calculated from changes in gizzard lean dry mass observed by Piersma et al. 1999; by contrast, well-nourished captive knots showed rates up to 0.5 g/day; Dekinga et al. 2001). In the current study, inter-individual differences in gizzard size are therefore likely due to differences in the timing of arrival. As most of the foraging data were collected in the first 10 days after catching (mainly due to birds disappearing from our

Great and red knots feeding during incoming tide. Note the colourbands and radio-transmitter on the most right red knot (photo taken in Roebuck Bay, NW-Australia).

Photo: Jan van de Kam.
study area), we assume that gizzard mass during these days has not changed much since the ultrasonographical measurements taken right after catching.

During their ‘small-gizzard’ phase the birds rely heavily on high-quality, crustacean prey (Figure 6.3B-C). The abundance of such soft-bodied prey items is highest when most birds arrive, which is during late July and early August (Figure 6.4A). Due to depletion and to dispersal to deeper water (Spaargaren 2000), crustacean densities decline rapidly over the following weeks (Figure 6.4A). By then, all knots switch to hard-shelled mollusc prey (Van Gils et al. 2003a) and grow larger gizzards to cope (Figure 6.4B; Van Gils et al. 2003a). This suggests a major problem for birds that arrive too late to join the crustacean feast. Such individuals might have a hard time keeping their energy budget balanced, let alone refuelling in order to gain mass. This problem is especially stringent since these small-gizzard birds have no spare feeding time left; their 17-h working day (Figure 6.3D) is the absolute maximum that can be achieved in a tidally regulated system where flats are exposed for 12-h per day (see below). This study adds to the growing evidence that delayed migration bears fitness-costs (e.g. Schneider & Harrington 1981; Zwarts et al. 1992; Kokko 1999; Drent et al. 2003).

![Figure 6.4](image_url)

**Figure 6.4.** (A). Crustacean density declines throughout the season (mean ± SE; patch B in 1998). (B). At the same time, gizzard mass increases gradually (mean ± SE; 813 gizzards measured during 1985-2002).
Possibly, these fitness-costs are highest for the canutus-subspecies, as it faces an abrupt dietary shift upon arrival directly from its breeding grounds. The other subspecies arriving in the Wadden Sea, islandica, has the potential to already build up some gizzard mass during its stopover at intertidal bays in Iceland (Piersma et al. 1999). For the Wadden Sea in late summer, it has been suggested that the numbers of canutus-knots fluctuate more than the numbers of islandica-knots (Nebel et al. 2000). In order to test whether this is related to the abundance of soft food, we analysed the yearly variation (1996-2002) in the abundance of Carcinus maenas and Crangon crangon, using data collected in the 250-m grid mentioned before (Piersma et al. 2001). We linked this variability to the number of knots staging in the western Dutch Wadden Sea during late July and the first week of August, which is the time when most knots in the Wadden Sea belong to the canutus-subspecies (Piersma & Davidson 1992). This number was estimated by taking the maximum number of knots roosting at Richel and at Griend, which are the two main roosts of knots in the western Dutch Wadden Sea. There appears to be a strong correlation (Figure 6.5; \( P = 0.005; R^2 = 0.95; \) GLM), with more than 10,000 birds present in rich years and only few hundred birds in poor years. This fact supports the hypothesis postulated by Nebel et al. (2000), which states that “canutus-knots may skip the western Dutch Wadden Sea in some years (females) or in most years (males)”. The authors found no evidence for canutus-males staging in the Wadden Sea and calculated that a flight directly

**Figure 6.5.** The number of knots visiting the western Dutch Wadden Sea during late July and the first of August correlates strongly with the abundance of soft-bodied crustaceans in the same area (represented by Carcinus maenas and Crangon crangon). Given the early timing, these knots probably belong to the canutus-subspecies. Line gives linear regression. Note the absence of data for 2000 and 2001.
from the breeding grounds to their West-African wintering grounds would be feasible. These new analyses suggest that (female) canutus-knots skip the Wadden Sea in years when soft-food is scarce and only stop by in years of plenty. The rapid decline in soft-food abundance in the course of late summer (Figure 6.4A) may explain why male canutus-knots almost always skip the Wadden Sea, as they are the sex taking care of the hatched young (Tomkovich & Soloviev 1996; Tulp et al. 1998) and thereby arrive in a Wadden Sea that has become unliveable for knots with small gizzards by virtue of the seasonal disappearance of the crustaceans.

**How can knots extend their working day to 17-h in a 12-h tidal system?**

In the western Dutch Wadden Sea, there are large spatial differences from west to east in the timing of the tidal cycle. The tidal cycle in the most western corners is 2-h ‘ahead’ compared to the cycle 30-km further east (Figure 6.6A). Therefore, western flats are exposed 2-h earlier than eastern flats, and by gradually moving eastwards during low tide, birds can ‘extend’ their low tide feeding period from the usual 12 h/day to 16-17 h/day. Given their daily time away from the roost, we suggest that red knots do so, especially those with small gizzards (Figure 6.6B).

Research vessel ‘Navicula’ has a very shallow draft, which made it an ideal ship for our yearly prey sampling efforts throughout the western Wadden Sea. Photo: Jan van Gils.
In order to evaluate this idea, we partitioned the working day into large-scale site use and analysed how long Richel-roosting knots stayed in different parts of the western Dutch Wadden Sea (Figure 6.6C). Indeed, all birds showed a strong west-east movement during outgoing tide and many birds ended up feeding at the most eastern parts of Grienderwaard or even at Ballastplaat. Consistent with the variation in the length of the working day, the passage through different foraging sites varied significantly with gizzard mass (Figure 6.6C; Table 6.3). During receding tides, birds with large gizzards left for Grienderwaard straight from their roost at Richel, while birds with small gizzards first fed near Richel before their move to Grienderwaard. By the time small-gizzard-birds arrived at Grienderwaard, large-gizzard-birds were about to leave Grienderwaard for Ballastplaat (Figure 6.6C). Small-gizzard-birds arrived at Ballastplaat almost two hours later. Almost three hours later, during incoming tide, the first birds to arrive back at Grienderwaard, and back at Richel-roost later on, had large gizzards, while the last birds to do so had small gizzards.

A flock of knots feeding on mussels. Photo: Jan van de Kam.
Figure 6.6. (A). In the east of our study area, low tide occurs 2-h later than in the west (indicated by numbers at grey lines). By travelling along with the moving tide, red knots roosting at Richel can feed up to 17 h/day (indicated by encircled numbers). This contrast to feeding for only 12 h/day if they would stay in the vicinity of Richel throughout the entire tidal cycle. (B). Daily foraging times increase with a decrease in gizzard mass (these are the same data as in Figure 6.3D), such that small gizzards extend their working day up to almost 17-h. This is only feasible by extending the low tide period by moving from west to east during the low tide period. (C). Composition of the working day, in terms of area use, as a function of gizzard mass, given for a full tidal cycle (expressed as hours after high tide on the vertical axis). Independent of gizzard mass, red knots leave their roost at Richel about 3 h after high tide to feed on the flats SSW of Richel (filled squares; bars are SE; 221 observations on 45 individuals). The smaller a knot’s gizzard, the later it leaves these flats
In theory, knots could move even further east and extend their daily foraging time beyond 17 h/day. However, the ability to do so might be constrained by increased flight costs (twice flying back and forth between Richel and Ballastplaat incurs a daily flight distance of about 70-km). How daily foraging time and flight costs are traded off and how an optimal daily feeding itinerary throughout the western Dutch Wadden Sea can be derived is examined elsewhere (Van Gils et al. MS chapter 7).

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The field station near Richel: when the tide was up, life was lived at just a few square meters. Photo: Jan Drent.

References


Red knots generally roost during high tide, though heavy birds extend their resting bouts well into the low tide period. Photo: Jan van de Kam.