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

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Summary

1. 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.

2. The red knot *Calidris canutus* shows tremendous inter- and intra-individual variation in maximum rates of digestion due to variation in the size of the processing machinery (gizzard and intestine), which makes it a suitable species to study the effects of digestive processing rate on foraging decisions.

3. 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.

4. Using the digestive rate model, we a priori modelled patch use, prey choice, and daily foraging times as a function of gizzard mass. Focusing 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.

5. 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.

6. 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 realize 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.

7. 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.

Key-words: digestive constraint, foraging, gizzard, patch use, prey choice, time constraint.

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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-minimizing foragers that only require a given daily amount of energy (Schoener 1971). Ever since they have been developed (see review by Jeschke, Kopp & Tollrian 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, 2005; Zharikov & Skilleter 2003; Van Gils & Piersma 2004; Karasov & McWilliams 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, Karasov & Caviedes-Vidal 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, Gudmundsson & Lilliendahl 1999; Van Gils *et al.* 2003a). One of these organs, the muscular gizzard, crushes the generally hard-shelled prey, which are ingested whole (Piersma, Koolhaas & Dekinga 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; Fig. 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 (Fig. 1B; Van Gils *et al.* 2003a, 2005). This leads to gizzard-size dependent patch use whenever high-quality prey is collected at a slower rate than low-quality prey (Fig. 1B). In that case, birds with small gizzards maximize their energy intake rate in the
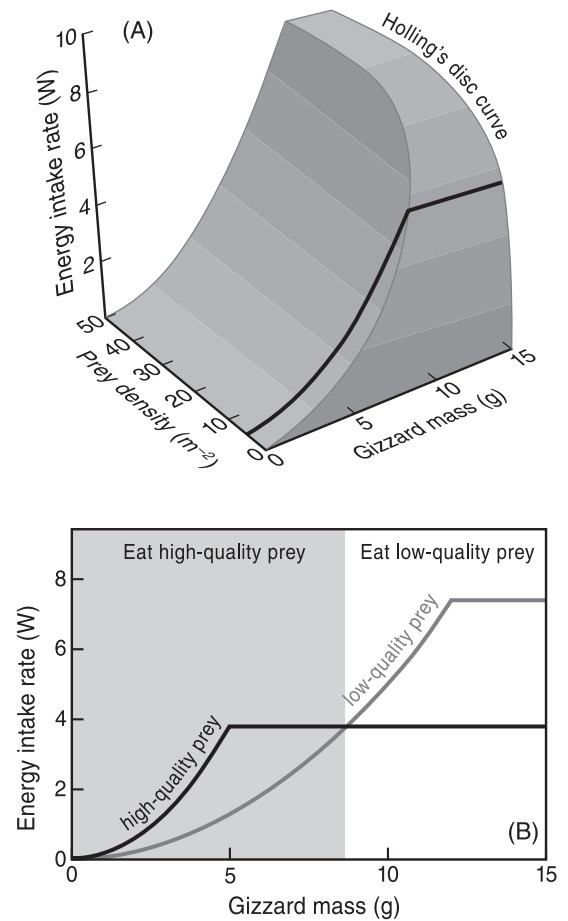
Fig. 1. (A) Functional response on a single prey type as a function of prey density and gizzard mass. At large gizzard masses and/or at low prey densities, energy intake rate is not constrained by rate of digestive processing (i.e. gizzard mass) but by rate of collection and follows the well-known Holling's 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 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-maximizing 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.

patch containing the slowly collected high-quality prey, while birds with large gizzards maximize their energy intake rate in the patch containing the rapidly collected low-quality prey (Fig. 1B).

Applying the above-mentioned digestive rate model (DRM; Hirakawa 1995; Van Gils *et al.* 2005) 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

Table 1. Available prey biomass and percentage of soft-bodied prey per patch per year. Biomass is expressed as g flesh ash-free dry mass per m²

	Patch A		Patch B	
Year	mean ± SE	% soft-bodied	mean ± SE	% soft-bodied
1997	5·12 ± 1·41	7	1·57 ± 0·30	25
1998	6·79 ± 2·79	0	0·73 ± 0·19	41
1999	6·45 ± 1·48	22	3·53 ± 0·69	39
2000	8·67 ± 4·95	0	1·76 ± 0·22	28

(400 ha) containing low prey 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.

Materials 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 (Fig. 2A; western Dutch Wadden Sea; 53°15′N, 5°15′E). We intensively monitored prey densities and the occurrence of red knots in these two patches (1998), the birds' diet composition (1997–98), 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 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 six (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 three 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 the case of *Hydrobia*).

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
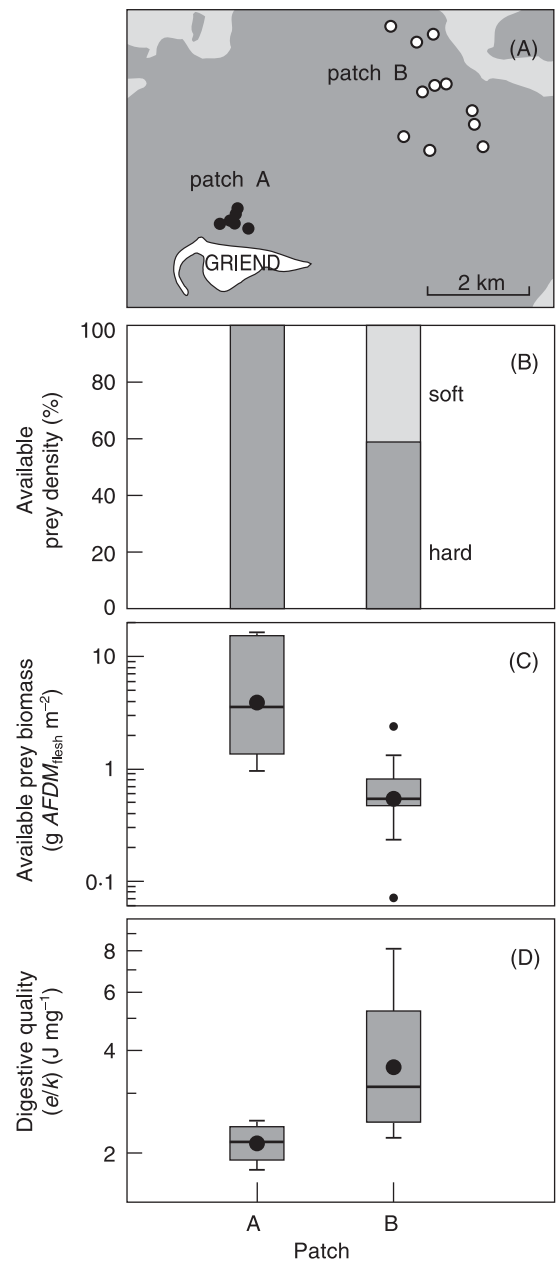
Fig. 2. Prey densities in 1998. (A) Map of prey sampling spots (dots) within the two patches. (B) Virtually all prey in patch A were hard-shelled, while in patch B about half were soft-bodied (calculated on the basis of available biomass). (C) Available prey biomass (g $AFDM_{flesh}$ m⁻²) in patch A was about five to 10 times higher than in patch B. These box-and-whisker plots give mean (large dot), median (horizontal line within box), inter-quartile 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.

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 experiment 1 in Van Gils *et al*. 2005 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). *Calidris canutus 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 northwestern 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 (Telemetrics, Arnhem, the Netherlands; see also Van Gils *et al*. 2000; Green *et al*. 2002; Battley *et al*. 2003). Handheld systems were used in 1997–98 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 (one station), 1998 (six stations), 1999 (14 stations), and 2000 (13 stations). At each station, a receiver (ICOM ICR10) was connected to a nondirectional antenna (1·2 m) and, through an interface, to a palm-top computer. Each bird was scanned every 10–15 min. The system recorded background noise and signal strength and detected valid signals up to about 1 km. An additional 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.

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 August–September 1997 and was repeated in August 1998. Each dropping sample contained six to 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). As food retention times

in digestive tracts of knots are relatively short (20–50 min, Piersma 1994) compared with 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 (August 1997–2000). Once they have left their roost, knots feed for most of their time (Piersma 1994; Van Gils *et al*., unpublished).

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 Zwarts & Blomert (1992) and Piersma *et al*. (1993a). 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 Fig. 1B, where only a single prey type occurs per patch. For details on applying the DRM to multiple-prey patches we refer to Hirakawa (1995) and Van Gils *et al*. (2005); here we will only explain the main steps.

First, 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^{-1}). For this purpose, we applied a searching efficiency a of 10·5 cm^2 s^{-1} (experiment 2 in Van Gils *et al*. 2005). 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 s (Zwarts & Blomert 1992). We used estimates for h for *Hydrobia*, *Crangon*, and *Carcinus* as obtained by Van Gils *et al*. 2005 (experiment 1). From prey items collected throughout Grienderwaard in August–September 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*. 2005 (experiment 1).

Secondly, applying the digestive constraint c (mg s^{-1}) on ballast intake rate as a function of gizzard mass G (g; Van Gils *et al*. 2003a; $c = 0.05 \times G^2$), we derived the maximum energy intake rate as a function of gizzard mass for each patch. Likewise, assuming maximization of instantaneous rates of energy assimilation (i.e. across search, handling, and digestion times; see Van Gils *et al*.

2005), we derived optimal patch and prey choice and daily foraging times as a function of gizzard mass. The assumption of rate-maximization seems valid, even for birds that aim to balance their daily energy budget on a daily basis but aim to minimize 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 Fig. 1 in Van Gils *et al.* 2005).

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

$$\frac{ADMR}{MEIR} \qquad \text{(eqn 1),}$$

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 maximize 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

$$\frac{9 \cdot 6 BMR}{MEIR} \qquad \text{(eqn 2).}$$

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*; Fig. 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*; Fig. 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 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 five to 10 times higher in patch A than in patch B (Fig. 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 (Fig. 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 Fig. 3A scaled on vertical and upper horizontal axis). Using the constraint on processing ballast mass set by gizzard size, enabled us to derive energy intake rates (vertical axis in Fig. 3A) as a function of gizzard mass (lower horizontal axis in Fig. 3A). This shows that birds with gizzards of least 7 g maximize their energy intake rate in patch A, while birds with smaller gizzards maximize their energy intake rate in patch B (Fig. 3A).

PATCH CHOICE

Of 42 birds radio-tagged in 1998, 16 visited patch A and/or patch B. Gizzard masses varied with patches visited ($P = 0.001$; $R^2 = 0.65$; GLM). Confirming the optimality predictions of the DRM as stated above, birds that only visited patch A had larger gizzards (7·72 g; $n = 4$; Fig. 3B) than birds that visited both patches (5·23 g; $n = 10$; $P < 0.005$; Bonferroni pairwise comparison; Fig. 3B) and than birds that only visited patch B (3·99 g; $n = 2$; $P < 0.005$; Bonferroni pairwise comparison; Fig. 3B).

Table 2. Observed $\log_{10}$–$\log_{10}$ relationships for the flesh ash-free dry mass $AFDM_{flesh}$ (mg) and ballast dry mass k (mg) as a function of size (mm) of relevant prey species collected in August–September 1998 at Grienderwaard. Metabolizable energy content e (J) is calculated as $0.725 \times 22 \times AFDM_{flesh}$ (mg; see Van Gils *et al.* 2005)

Species	Part	Constant	Slope	*n*	R^2	*F*-ratio	*P*
Macoma	$AFDM_{flesh}$	−2·457	3·402	285	0·837	1450·001	< 0·001
Macoma	k	−2·216	3·999	269	0·784	969·144	< 0·001
Cerastoderma	$AFDM_{flesh}$	−2·743	3·564	89	0·498	86·276	< 0·001
Cerastoderma	k	−1·556	3·545	93	0·759	287·234	< 0·001
Hydrobia	$AFDM_{flesh}$	−1·142	2·076	216	0·473	191·937	< 0·001
Hydrobia	k	−0·381	1·926	216	0·575	289·449	< 0·001
Carcinus	$AFDM_{flesh}$	−0·943	2·303	20	0·865	115·561	< 0·001
Carcinus	k	−0·838	2·486	20	0·905	170·723	< 0·001
Crangon	$AFDM_{flesh}$	−1·593	1·866	11	0·346	4·765	< 0·1
Crangon	k	−1·692	1·931	11	0·341	4·667	< 0·1
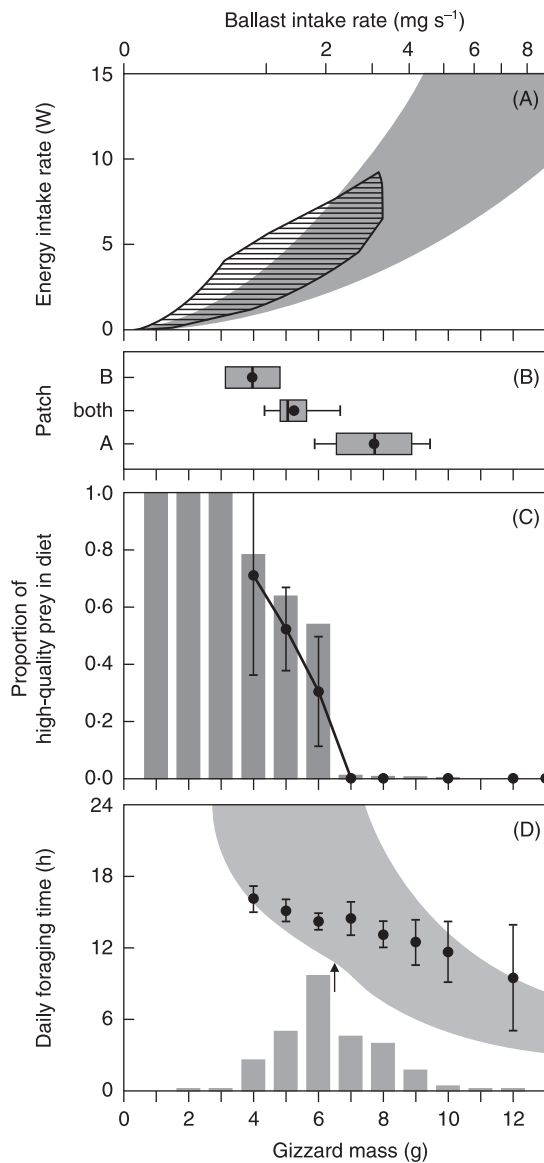
Fig. 3. (A) State–space of feasible short-term intake rates in terms of energy (vertical axis) and in terms of ballast mass (upper horizontal axis) in patch A (grey-shaded area; which continues beyond the scale of the graph) and in patch B (dashed area). Gizzards that can process more than 2 mg ballast s^{-1} obtain the highest energy intake rates in patch A (i.e. gizzards ≥ 7 g as indicated on lower horizontal axis), while smaller gizzards maximize their energy intake rate in patch B. Assuming rate-maximization, 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 with birds that only visited patch B, and compared with birds that visited both patch A and B (box-and-whisker plots are explained in Fig. 2C). (C). Observed diet compositions as a function of gizzard mass (mean ± SE, indicated by dots ± bars) match well with the predicted values (grey bars). Number of radio-tagged birds per gizzard class is two (4 g), two (5 g), two (6 g), one (7 g), one (8 g), one (10 g), one (12 g), and one (13 g). (D) Observed daily foraging time declines as a function of gizzard mass (mean ± 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 line in grey surface, where the arrow marks the transition from patch B to A, affecting the minimal daily foraging time); the second

PREY CHOICE

The proportion of high-quality, soft-bodied prey in the diet declined as a function of gizzard mass (Fig. 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 Fig. 3C).

DAILY FORAGING TIMES

Daily foraging times declined as a function of gizzard mass ($P = 0.019$; Fig. 3D; upper line in Table 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 line in grey surface in Fig. 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 line in grey surface in Fig. 3D indicating a limit of $9.6 \times$ BMR). The question why some birds must operate with a much smaller gizzard than others will be explored further in the discussion.

Discussion

TESTING THE DIGESTIVE RATE MODEL

In agreement with the predictions of the 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 (Fig. 3B). Thus, the observed patch choices imply that the birds were maximizing 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

gives the maximum daily foraging time set by upper limits to daily metabolizable energy gain ($9.6 \times$ BMR; upper line in 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 July–August ($n = 103$; grey bars) suggests that most birds presumably have a slightly positive daily energy balance.

Table 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 in bold are significant

Dependent variable	Slope (h g^{-1})	Regression SS	Residual SS	n	R^2	P
Daily foraging time	−0·71	217·01	1305·77	38	0·14	**0·019**
Departure from Richel	+0·05	1·61	126·25	46	0·01	0·458
1st arrival at Grienderwaard	−0·18	19·44	56·26	45	0·26	**< 0·001**
1st departure from Grienderwaard	−0·17	11·62	42·42	35	0·22	**0·005**
2nd arrival at Grienderwaard	−0·29	37·96	63·52	37	0·37	**< 0·001**
Arrival at Richel	−0·29	54·42	111·94	38	0·33	**< 0·001**

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*. 2005).

Prey choice within each patch also agreed well with the DRM predictions (Fig. 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 (Fig. 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 (Fig. 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) insure against unpredictability in supply and demand during winter (Johnson 1985; Piersma 1994; Piersma, Koolhaas & Jukema 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 inter-continental long-distance flights, while they have larger gizzards during the fuelling phase at stopovers (Piersma *et al*. 1999) or at their wintering grounds (Van Gils *et al*. 2003a). Such changes are likely the outcome of an underlying optimization 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).
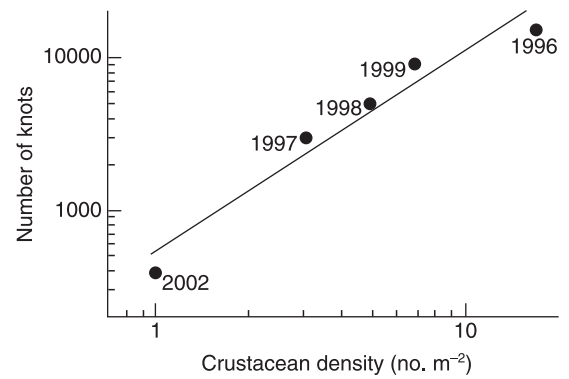
Gizzards are smallest after a period on the tundra breeding grounds where red knots feed on relatively soft-bodied arthropod adults and larvae (Battley & Piersma 2004) and after the southward flight to coastal staging and/or wintering grounds. Upon arrival, gizzards grow back to 'normal' proportions with rates of about 0·2 g day^{-1} (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^{-1}; 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 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 (Fig. 3B,C). The abundance of such soft-bodied prey items is highest when most birds arrive, which is during late July and early August (Fig. 4A). Owing to depletion and to dispersal to deeper water (Spaargaren 2000), crustacean densities decline rapidly over the following weeks (Fig. 4A). By then, all knots switch to hard-shelled mollusc prey (Van Gils *et al*. 2003a) and grow larger gizzards to cope (Fig. 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 as these small-gizzard birds have no spare feeding time left; their 17-h working day (Fig. 3D) is the absolute maximum that can be achieved in a tidally regulated system where flats are exposed for
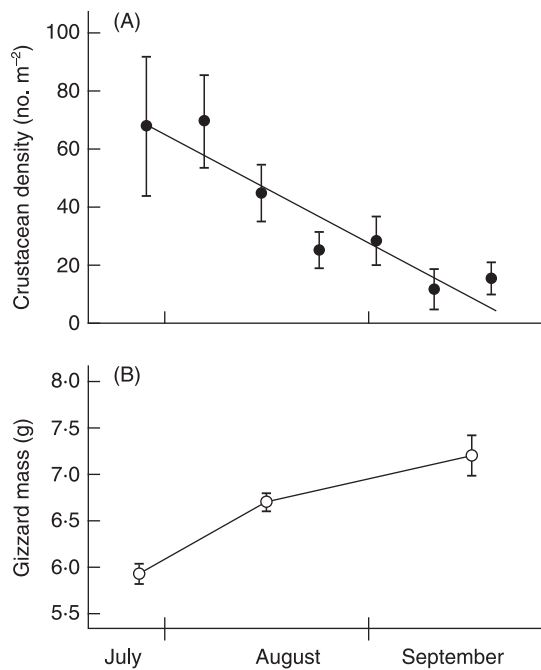
Fig. 4. (A) Crustacean density declines throughout the season (mean ± SE; patch B in 1998). (B) At the same time, gizzard mass increases gradually (mean ± SE; 813 gizzards measured during 1985–2002).


Fig. 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.

12 h day^{-1} (see below). This study adds to the growing evidence that delayed migration bears fitness costs (e.g. Schneider & Harrington 1981; Zwarts, Blomert & Wanink 1992; Kokko 1999; Drent *et al.* 2003).

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 (Fig. 5; $P = 0.005$; $R^2 = 0.95$; GLM), with more than 10 000 birds present in rich years and only a 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 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 (Fig. 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 UP 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 with the cycle 30 km further east (Fig. 6B). 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^{-1} to 16–17 h day^{-1}. Given their daily time away from the roost, we suggest that red knots do so, especially those with small gizzards (Fig. 6A).

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 (Fig. 6C). Indeed, all birds showed a strong west–east movement during the outgoing tide and many birds ended up feeding at the most eastern parts of Grienderwaard or even at Ballastplaat (see Fig. 6D for map). Consistent with the variation in the length of the working day, the passage
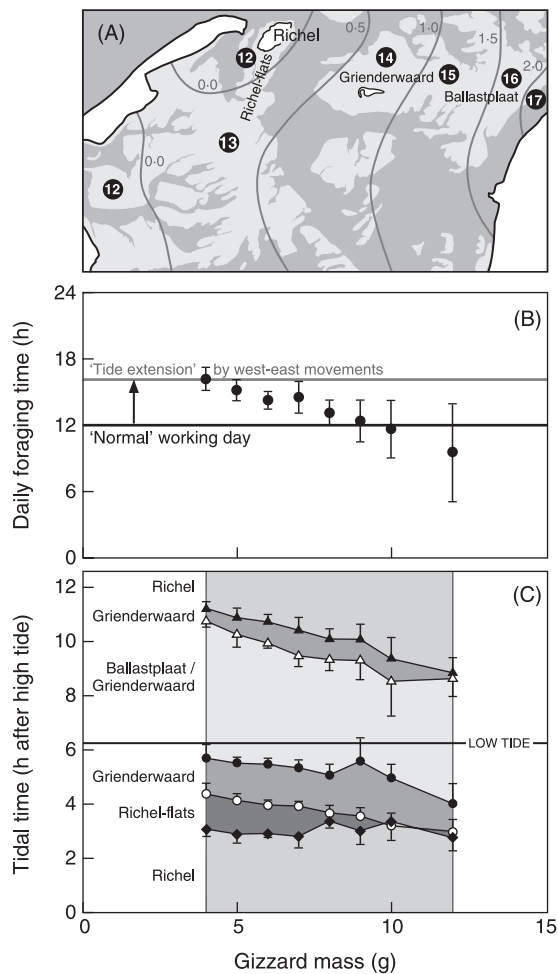
Fig. 6. (A) In the east of our study area, low tide occurs 2 h later than in the west (indicated by numbers at grey lines). By travelling along with the moving tide, red knots roosting at Richel can feed up to 17 h day⁻¹ (indicated by encircled numbers). This contrasts with feeding for only 12 h day⁻¹ 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 Fig. 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 to feed on the freshly exposed Grienderwaard (open circles; 169 observations on 45 individuals). This differential timing with respect to gizzard mass remains throughout the low tide period when leaving Grienderwaard for Ballastplaat (filled circles; 103 observations on 35 individuals; note that individuals do not always leave Grienderwaard), when coming back from Ballastplaat (open triangles; 115 observations on 37 individuals), and when coming back at the roost at Richel (filled triangles; 136 observations on 38 individuals).

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 (Fig. 6C). Small-gizzard birds arrived at Ballastplaat almost 2 h later. Almost 3 h 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.

In theory, knots could move even further east and extend their daily foraging time beyond 17 h day⁻¹. 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.*, unpublished).

Acknowledgements

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through different foraging sites varied significantly with gizzard mass (Fig. 6C; Table 3). During receding tides, birds with large gizzards left for Grienderwaard straight from their roost at Richel, while birds with

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