Diet selection in a molluscivore shorebird across Western Europe
Quaintenne, Gwenael; van Gils, Johannes; Bocher, Pierrick; Dekinga, Anne; Piersma, Theun; Webb, Tom

Published in:
Journal of Animal Ecology

DOI:
10.1111/j.1365-2656.2009.01608.x

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2010

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.
Diet selection in a molluscivore shorebird across Western Europe: does it show short- or long-term intake rate-maximization?

Gwenael Quaintenne, Jan A. van Gils, Pierrick Bocher, Anne Dekinga and Theunis Piersma

Laboratory Littoral Environnement et Sociétés, UMR6250, CNRS-ULR, University of La Rochelle 17000 La Rochelle, France; Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands; and Animal Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

Summary

1. Studies of diet choice usually assume maximization of energy intake. The well-known ‘continuity model’ (CM) additionally assumes that foraging animals only spend time searching or handling prey. Despite considerable empirical support, there are many foraging contexts in which the CM fails, but such cases were considered exceptions rather than the rule.

2. For animals constrained by the rate at which food is digested, CM does not necessarily lead to maximal energy intake rates because the time for digestion is not part of the selection criteria. In the main model developed to explain diet choice under a digestive constraint, the ‘digestive rate model’ (DRM), time lost to digestive breaks is minimized so that energy intake over total time (searching, handling, digestive breaks) is maximized.

3. It is increasingly acknowledged that most animals may face digestive constraints as prey capture rates vary over time and as it would be a waste to carry around heavy digestive machinery that can rapidly process food under all circumstances: this is only needed in times of high demand, provided that enough food can be found.

4. In molluscivore shorebirds ingesting hard-shelled prey such as red knots (Calidris canutus), the predictions of DRM were held up so far, whereas those of CM were rejected. However, most tests were carried out under controlled experimental conditions. Red knots overwinter in coastal areas over much of Western Europe and we capitalized on this variation by comparing, during a single winter, observed diet composition with predictions of DRM, CM and a null model assuming no prey selection (‘no-selection model’, NSM).

5. The observed diets were best predicted by DRM followed by CM. NSM poorly predicted observed diet choice. Under the present conditions, diet choice based on DRM would on average have yielded an energy intake rate twice as large as one based on CM. By adjusting the size of their gizzard (held constant in the present simulations), red knots could have lifted their energy intake rate further. We suggest that application of the DRM can help many diet studies forward, especially those previously seen as exceptions to the classical CM-based rule.

Key-words: digestive constraint, food intake rate, molluscivory, optimal foraging, prey selection

Introduction

It is usually assumed that natural selection ensures that free-living animals adopt strategies of food selection that minimize time and energy spent for a given quantity of food ingested (Stephens & Krebs 1986). The original, and still most frequently used, optimal prey-selection model is the so-called ‘continuity model’ (CM) (Charnov 1976; Stephens & Krebs 1986). CM assumes that prey items are selected according to the energy intake per unit handling time (an expression called profitability), i.e. encountered prey items are only included in the diet when their profitability exceeds...
the forager’s long-term energy intake rate. In their review, Sih & Christensen (2001) concluded that most empirical tests of this simple optimal diet choice model have achieved successful quantitative and qualitative fits. However, they show that particularly in herbivores, successful prey-selection models include additional criteria that account for nutritional and/or digestive constraints.

An animal that is able to find and capture prey items faster than it can process them is said to be ‘digestively bottlenecked’. Jeschke, Kopp & Tollrian (2002) propose that most foragers face a digestive constraint, whereas Verlinden & Wiley (1989), Hirakawa (1997) and Whelan & Brown (2005) present diet choice models that include both the handling and the digestion of prey. In these ‘digestive rate models’ (DRM), maximum intake rate is limited by rates of digestion and prey items are selected on the basis of digestive quality (i.e. energy content per unit indigestible bulk mass) rather than profitability. In this way, an animal can spend more time searching for items of higher digestive quality instead of losing time to digestive pauses. Nevertheless, the question of whether to use CM or DRM, even in digestively constrained animals, may depend on the time horizon over which energy intake is maximized. When digestively constrained foragers aim to maximize their long-term intake rate, they should ‘obey the rules’ of DRM, but the same animals should follow the CM in case they aim to maximize their intake rate during active foraging only (i.e. searching and handling), the so-called short-term or instantaneous intake rate (Farnsworth & Illius 1998; Bergman et al. 2001; Fortin, Fryxell & Pilote 2002). So-called ‘time-minimizers’ aim to maximize short-term intake rate, as they only require a certain amount of (daily) energy and aim to minimize the daily time devoted to collect (i.e. search and handle) this food (Schoener 1971).

A common molluscivore shorebird wintering in Western Europe (Van de Kam et al. 2004), the red knot Calidris canus tus islandica, ingests its hard-shelled prey whole and is therefore easily digestively constrained (Van Gils et al. 2003a). Red knots have relatively large muscular gizzards (up to 10% of fresh body mass) and a similarly large intestine that is able to withstand the stress of rapidly passing shell fragments (Piersma, Koolhaas & Dekinga 1993b; Piersma, Gudmundsson & Lilliendahl 1999; Battley & Piersma 2004). It has been experimentally established that the maximum long-term food intake rate in red knots is determined by the rate at which shell mass can be processed (Van Gils et al. 2003a). Despite their trophic specialization (Piersma et al. 1998), red knots feed on a variety of molluscs and crustaceans that differ in profitability as well as digestive quality (Van Gils et al. 2005c). This variation makes it possible to distinguish between the predictions of CM and DRM (Verlinden & Wiley 1989; Van Gils et al. 2005b,c), and is the basis to explore whether overwintering red knots behave as long-term rate-maximizers or as time-minimizers.

So far, tests of diet choice criteria were based on a rather limited range of conditions, a range that certainly did not do justice to the variable foods encountered by red knots in Europe (Bocher et al. 2007). Here, we used data on food availability and diet choice collected during a single winter at eight feeding sites covering much of the European wintering range. We compared diet choice with predictions based on CM, DRM and a ‘no-selection-model’ (NSM; Fig. 1). Predicted intake rate realized over the total foraging time (searching, handling and digestive pauses) by the three models are also compared. We will discuss which costs and benefits and constraints induce overwintering red knots to adopt either a ‘time-minimization’ or ‘energy-maximization’ strategy, with special consideration of the temporal scale over which foraging decisions are made.

Materials and methods

STUDY SITES

Study sites were chosen to cover as much as practically possible of the winter range of red knots along the European Atlantic coast. The British estuaries, the Dutch Wadden Sea and France harbour respectively 64%, 20% and 6% of the wintering population (Stroud et al. 2004). In the Dutch Wadden Sea, eastern England and the French coast north and south of Brittany, eight major feeding sites were selected (Fig. 2), the details of which are assembled in Table 1.

The Dutch Wadden Sea is a shallow coastal sea bordered by the Friesian barrier islands. Two major feeding grounds on sandflats were selected: (i) Griend, a core area in the western Wadden Sea (Piersma et al. 1993a); and (ii) Engelsmanplaat, 60 km eastward. The Wash is a large intertidal bay in eastern England, where we focused on two major feeding grounds: (iii) breast Sand, a slightly muddy to muddy sandflat in the south; and (iv) Stubborn Sand, a slightly muddy sandflat in the eastern part of the bay (Goss-Custard, Jones & Newbery 1977). Mont-Saint-Michel Bay is the third main wintering
ground for red knots in France (Deceuninck & Maheô 2000). It is located along the North French Channel coast at the boundary between Brittany and Normandy. Feeding of red knots is concentrated in the south-western part of the bay (Le Dréan-Quénechdu 1999), where we established (v) Cherrueix, a slightly mucky sandflat study site. Pertuis Charantais et Breton, the southernmost wintering area of *islandica*-knots in Europe, is located between Loire and Gironde estuaries. In the north, (vi) Aiguillon Bay is the second main wintering area for knots in France (Deceuninck & Maheô 2000). Moêze-Oléron Bay is situated 40 km south of Aiguillon Bay and is the most important French wintering area. This bay was subdivided into two feeding sites: (vii) Moêze, a bay with sandy mudflats on mainland coast; and (viii) Oléron, seagrass-covered flats bordering the east coast of Oléron island.

**Benthos Sampling and Treatment**

Study sites were sampled between 25 November 2003 and 24 March 2004 (Table 1). Macrofauna was sampled systematically at stations arranged in a grid of 250-m interval (Bocher et al. 2007; Kraan et al. 2007, 2009). Stations were localized using a handheld gos (Garmin 45 and 12; Garmin International, Lenexa, Kansas, USA) with WGS84 as the geographic coordinate system. Across all eight study sites, a total of 2041 stations were visited. Most sampling stations were reached by foot during low tide (70%), except for stations in Engelsmanplaat, Aiguillon Bay and Moêze, which were visited by boat during high tide. At each station reached by foot, we took one sediment core of 15 cm diameter down to a depth of 20–25 cm. The upper 4 cm was separated from the rest of the core to distinguish prey that were accessible from prey that were not accessible to red knots that can probe up to 4 cm with their 3.5-cm long bill (Zwarts & Blomert 1992). Subsequently, these two parts were sieved over a 1-mm mesh.

Hydrobia ulvae, a small gastropod which is potentially present in very high densities, was sampled by taking a core of 7 cm diameter down to a depth of 4 cm and subsequently sieved over a 0.5-mm mesh. At stations reached by boat, we took two cores of 10 cm diameter down to a depth of also 25–40 cm. One score was subsequently sieved over a 1-mm mesh and the other over a 0.5-mm mesh (the latter was used

---

Fig. 2. Study sites along the European Atlantic coast, which have been selected such that they cover the large geographical scale of the red knots’ wintering distribution.
to also sample *H. ulvae*. As for the samples collected on foot, living molluscs were collected and stored in a freezer (–20 °C).

In the laboratory, molluscs were identified to species level, counted and size (length) was measured with a precision of 0.1 mm. After separating the flesh from the shell, each individual’s flesh ash-free dry mass (AFDM_flesh) and shell dry mass (DM_shell) was determined with a precision of 0.1 mg (Piersma et al. 1993a; Kraan et al. 2007).

### RECONSTRUCTION OF DIET FROM DROPPING SAMPLES

Near the stations at which we sampled the macrofauna, we also collected droppings of red knots. Each dropping sample consisted of 25 droppings and was geo-referenced using a GPS. In total, 204 dropping samples were collected across all study sites (Table 1). In the laboratory, diet was reconstructed from these samples following the protocol of Dekinga & Piersma (1993). Briefly, shell fragments of bivalves and gastropods were retrieved from the dried droppings and the shell lengths of prey ingested could be reconstructed using predictive allometric equations between shell length and hinge height (or width of first turn in the case of gastropods). The relative DM_shell-contribution of each prey species in the diet followed from the weighted shell fragments sorted by species. Subsequently, the size- and species-specific AFDM_flesh-to-DM_shell ratios, determined per study site, were used to calculate the relative AFDM_flesh-contribution of each prey species.

### MODELLING DIET SELECTION

We tested the CM using our field data on diet composition by considering each mm-length class of each species as a prey type *k*, each with a unique value for energetic contents *e*_k (equivalent to AFDM_flesh), handling time *h*_k and encounter rate *i*_h (being the product of type-specific searching efficiency and density). Searching efficiencies and handling times were similar to the ones used in Van Gils et al. (2005c) (for parameter details see Tables S1–S4). Prey selection for the CM is modelled by the standard algorithm (Charnov 1976) in which prey types are ranked in decreasing order of their profitability (*e*_k/*h*_k_). In this order, prey types are then added to the diet until:

\[
\frac{e_{j+1}}{h_{j+1}} < \frac{\sum_{i=1}^{j} e_i h_i}{1 + \sum_{i=1}^{j} \lambda_i h_i}
\]  

(eq1)

The first *j* types are included in the diet and all other types are excluded (the so-called ‘zero-one rule’; Stephens & Krebs 1986).

In addition to the parameters included in the CM, the DRM takes account of each prey type’s ballast mass * λ* (equivalent to DM_shell). In this model, long-term energy intake rate is constrained by the long-term ballast intake rate, the latter cannot exceed a specific limit. Under this constraint, DRM predicts a selection based on the ranking of prey type in which digestive quality outweighs the importance of profitability, where digestive quality is expressed as the energy content per unit indigestible bulk mass (*e_/*h_). It is beyond the scope of this study to explain the mathematics underlying the optimal diet selection; we refer to Hirakawa (1995) or Van Gils et al. (2005c). However, Hirakawa (1995) developed a nice graphical procedure to explain the functioning of the DRM, which we have illustrated in Fig. 3.

In red knots, the limit upon long-term ballast intake rate goes up quadratically with increasing gizzard mass (Van Gils et al. 2003a). Here, we applied a gizzard mass of 9 g, which more or less represents the average gizzard mass found in red knots overwintering in Western Europe (Van Gils et al. 2003a, 2005a; Battley & Piersma 2004).

As a null-model, we included the case where foragers accepted each prey they encountered. In this so-called ‘no-selection model’ (NSM), diet composition (expressed as the relative contribution to the total amount of flesh mass consumed) simply depends on the encounter rate *i_h* of each prey type.
Because of the spatial heterogeneity in prey distribution within each study site, there will be some heterogeneity in diet selection as well. For this reason, we chose to analyse our benthos data at a spatial scale smaller than the scale of an entire site, and selected benthos samples that were collected within 500 m from a dropping sample as input into the different models. Thus, data from a maximum of nine nearest benthos sampling stations were used. Only available (i.e. accessible and ingestible; Zwarts & Blomert 1992) prey densities were used as input. Prey too large to be ingested were at least 15 mm long for Cerastoderma and at least 18 mm long for Macoma (Piernma et al. 1993a). Density, DMshell and AFDMflesh were consequently averaged per prey type (i.e. by species-specific 1-mm length classes) around each dropping sample. Therefore, the predictions were made specific for each dropping sample.

To test the goodness of fit to observations for each observation, we calculated the Euclidian distance across the three main prey species (equivalent to the 'root mean-squared deviation') method proposed by Kobayashi & Salam 2000:

$$E_{\text{obs-pred}} = \sqrt{(Cer_{\text{obs}} - Cer_{\text{pred}})^2 + (Hyd_{\text{obs}} - Hyd_{\text{pred}})^2 + (Mac_{\text{obs}} - Mac_{\text{pred}})^2};$$

(eqn 2)

where $Cer$ is the proportion of AFDMflesh in the diet observed (obs) or predicted (pred) for Cerastoderma edule, $Hyd$ denotes Hydrobia ulvae and $Mac$ denotes Macoma balthica. Note that we only concentrated on these three species as they made up 98% of the average diet, except for the Oleron site, where M. balthica was replaced by Scrobiculariaidae (as values for searching efficiency and handling times were not available for Scrobiculariaidae, we assumed them to be similar to the values in the more or less similarly shaped $M. balthica$). Euclidian distances were log-transformed to normalize them before testing the goodness of fit between models by paired t-tests.

We compared the long-term energy intake rates predicted by the three models, i.e. a situation in which the long-term energy intake rate is constrained by the specific limit (called $C$; Fig. 3) upon long-term ballast intake rate set by a 9-g gizzard. Thus, in those cases where a CM-diet or an NSM-diet would lead to a digestive constraint, the actual long-term energy intake rate (asterisks in Fig. 3) equals the ‘unconstrained’ long-term energy intake rate (small triangles in Fig. 3) multiplied by the ratio between $C$ and the ‘unconstrained’ long-term ballast intake rate (this ratio thus represents the proportion of time that CM- and NSM-foragers can devote to active foraging; the rest of their time is lost to digestive breaks).

**Results**

Most of the diet was made up of three mollusc species: the bivalves Baltic tellin $M. balthica$ (average contribution to AFDM in observed diets ± SE: 20 ± 4%) and edible cockle $C. edule$ (23 ± 4%) and the mudsnail $H. ulvae$ (55 ± 4%) (Fig. 4: left most histograms ‘observed diet’). Two other bivalves, Scrobicularia plana and Abra tenuis (both Scrobiculariidae) were only found in droppings from Oleron. Diet composition varied not only between sites, but also within sites (Fig. 4). *Hydrobia* dominated the diet at Moëze and Oleron with respectively 87 ± 5% and 80 ± 9%. On Engelsmanplaat, Breast Sand and Aiguillon Bay, *Hydrobia* contributed c. 70% of the estimated biomass intake (respectively 72% ± 10%, 69 ± 5%, 73 ± 24%). *Macoma* was the dominant prey at Cherrueix with 87 ± 5% of the energy intake. At Stubborn Sand, Cerastoderma dominated the diet (88 ± 9%) and in the Wadden Sea Cerastoderma and *Hydrobia* were selected in similar proportions with respectively 40 ± 14% and 54 ± 14% in the average diet.
Fig. 4. Comparison of observed diet against predicted diet for each of the three models on each of the eight study sites. In the histograms, the percentages refer to the relative contribution of AFDM consumed of the following species: Cerastoderma edule (cer); Hydrobia ulvae (hyd); Macoma balthica (mac); Scrobicularidae (scr) is represented by Scrobicularia plana and Abra tenuis for the Oléron-site. Error bars represent SE, denoting the variation between dropping samples within each site. For the three models, bars are filled when a model shows the significantly shortest Euclidean distances to the observations, bars are not filled otherwise (Table 2). In the most right column, box plots represent long-term energy intake rate (mg AFDM/s) as predicted by the three prey-selection models. Bottom boundary of the box indicates the 25th percentile, line within box marks the median, and top boundary of the box indicates the 75th percentile. Errors bars above and below indicate 90th and 10th percentiles. Horizontal lines in the top of these graphs indicate significant differences (at the 0.05 level) between the intake rates predicted by the different models.
Across all study sites, DRM-based predictions of diet showed significantly shorter Euclidean distances to the observed diets than CM-based diets (average ± SE Euclidean distances: 0.23 ± 0.02 vs. 0.48 ± 0.04, t-test, P < 0.0001; Table 2), while CM-based diets were closer to the observed diets than random (NSM) diets (0.48 ± 0.04 vs. 0.54 ± 0.03; t-test: P = 0.009; Table 2). At six of eight sites, DRM-based predictions were significantly nearer to observed diets than CM-based predictions (t-test: Engelsmanplaat, P = 0.027; Breast Sand, P < 0.0001; Cherrueix, P = 0.027; Aiguillon Bay, P = 0.024; Mœze, P = 0.035; Oléron, P = 0.012). At Griend and Stubborn Sand, Euclidean distances to the true diets did not differ significantly between DRM and CM (t-tests, respectively P = 0.371 and P = 0.222). On Stubborn Sand, distances did not also differ significantly from those of the NSM prediction (t-tests: vs. DRM: P = 0.178; vs. CM: P = 0.378).

On average, a diet based on DRM would permit an energy intake rate over total feeding time that is twice that obtained for a CM-instructed diet (t-test: P < 0.0001; right most column of graphs in Fig. 4). A diet based on DRM would yield long-term intake rates as much as 2 times higher than those based on NSM (t-test: P < 0.0001). Also a CM-diet yields a 1.2 times higher long-term intake rate than an NSM-diet (t-test: P < 0.0001). Within each study site, except for Stubborn Sand, DRM-based diets yielded a significantly higher intake rate over total time than a CM-based and an NSM-based diet. At four sites (Griend, Breast Sand, Cherrueix and Oléron), a CM-based diet yielded a significantly higher long-term intake rate than an NSM-based diet.

**Discussion**

From the comparison between the observed diets and the predicted diets, we can conclude that the DRM best predicted diet composition, followed by the CM, which in turn was followed by the NSM. Given that red knots are digestively constrained most of the time (for a knot with a gizzard of 9 g, we predict a digestive bottleneck at 98% of the sampling stations; Fig. 5a), adherence to the rules of the DRM maximized their long-term intake rate.

Although the average knot in winter carries a gizzard of c. 9 g, there is much inter-individual variation, certainly at the vast spatial scale of W-Europe (Piersma et al. 1993b; Van Gils et al. 2003a; Dietz & Piersma 2007). Therefore, we performed a sensitivity analysis to explore the effect of gizzard size on the goodness of fit of the DRM model. We did so by varying gizzard size between 1 and 20 g (which covers the natural range in gizzard masses; M.W. Dietz, A. Dekinga & T. Piersma, unpublished data) in steps of 1 g (Fig. 5). This shows that, not surprisingly, the percentage of sampling stations at which knots would face a digestive constraint fell from 100% (1 g gizzard) to 51% (20 g gizzard; Fig. 5a). More importantly and encouragingly, based on the analysis of the Euclidian distances, the DRM performs best at a modelled gizzard mass of 9–10 g (Fig. 5b), the most frequently observed values in overwintering islandica-knots. This is consistent with our conclusion that a DRM-based diet best reflects reality. For gizzard sizes larger than 9–10 g, a DRM diet starts to mimic a CM diet (relating this to the conceptual plot in Fig. 3; the vertical line C indicating the digestive constraint would shift to the right and thus the optimal diet line ODL would become more horizontal). DRM foragers with a gizzard size smaller than 9–10 g would only select the highest quality prey. At very tiny gizzards (2 g), a DRM-based diet would be so narrow and specialized that the DRM would be outcompeted in performance by the CM, and even by the NSM (with respect to Fig. 3: the digestive constraint would shift to the left and thus the optimal diet line ODL would have a very steep slope). We also analysed the sensitivity of

Table 2. Sample sizes, means and standard errors of Euclidian distances between predictions of each of the three prey-selection models and diet observations on the eight study sites

<table>
<thead>
<tr>
<th>Area sites</th>
<th>Sample size</th>
<th>Digestive rate model</th>
<th>Contingency model</th>
<th>No selection model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n Dropping locations</td>
<td>n Benthos stations</td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>All Sites</td>
<td>73</td>
<td>340</td>
<td>0.23 ± 0.02</td>
<td>0.48 ± 0.04</td>
</tr>
<tr>
<td>Dutch Wadden Sea</td>
<td></td>
<td></td>
<td>0.30 ± 0.07</td>
<td>0.68 ± 0.10</td>
</tr>
<tr>
<td>Engelsmanplaat</td>
<td>7</td>
<td>33</td>
<td>0.26 ± 0.07</td>
<td>0.20 ± 0.06</td>
</tr>
<tr>
<td>Griend</td>
<td>9</td>
<td>55</td>
<td>0.11 ± 0.04</td>
<td>0.13 ± 0.07</td>
</tr>
<tr>
<td>The Wash</td>
<td></td>
<td></td>
<td>0.27 ± 0.05</td>
<td>0.58 ± 0.04</td>
</tr>
<tr>
<td>Stubborm sand</td>
<td>7</td>
<td>33</td>
<td>0.25 ± 0.06</td>
<td>0.55 ± 0.15</td>
</tr>
<tr>
<td>Breast sand</td>
<td>29</td>
<td>107</td>
<td>0.16 ± 0.06</td>
<td>0.56 ± 0.16</td>
</tr>
<tr>
<td>Mont-Saint-Michel Bay</td>
<td></td>
<td></td>
<td>0.12 ± 0.04</td>
<td>0.66 ± 0.12</td>
</tr>
<tr>
<td>Cherrueix</td>
<td>9</td>
<td>41</td>
<td>0.10 ± 0.03</td>
<td>0.36 ± 0.07</td>
</tr>
<tr>
<td>Pertuis Charentais</td>
<td>4</td>
<td>24</td>
<td>0.16 ± 0.04</td>
<td>0.56 ± 0.16</td>
</tr>
<tr>
<td>Aiguillon Bay</td>
<td>3</td>
<td>13</td>
<td>0.12 ± 0.04</td>
<td>0.66 ± 0.12</td>
</tr>
<tr>
<td>Mœze</td>
<td>5</td>
<td>34</td>
<td>0.10 ± 0.04</td>
<td>0.36 ± 0.07</td>
</tr>
</tbody>
</table>

Mean is printed bold when a model yielded the significantly lowest distance among the models (paired t-test).
the model output to variation in the other parameters (handling time, energy content, shell mass and encounter rate). As shown in Fig. S1, the DRM performed best across the entire range of parameter values studied (followed, in almost all cases, by the CM).

The majority of foraging studies have obtained data consistent with long-term rate-maximization (Stephens & Krebs 1986; Sih & Christensen 2001), and our results are no exception. However, as overwintering knots only require a certain amount of energy per day to maintain energy balance, a priori we may have expected overwintering knots to be time-minimizers, in which case they should have obeyed the CM-based rules. Also with respect to the observed gizzard sizes in winter, we might expect a time-minimizing strategy: the observed 9–10 g gizzard seems to be the size required to maintain energy balance; only during late winter/spring, when fuelling before commencing their non-stop long-distance flights, do knots further enlarge their gizzard such that the rate of storing fuel is maximized (Van Gils et al. 2003a, 2005a). As digestive breaks are generally not mutually exclusive with other activities (Fortin, Boyce & Merrill 2004; Van Gils & Piersma 2004), why did knots then not follow a time-minimizing strategy that would minimize their time devoted to active foraging bouts (e.g. these multiple short breaks amounted to 80% of total foraging time in Van Gils et al. 2003b). Thus, the effect of minimizing total foraging time for a knot is that total time on the mudflat is minimized, whereby daily time on the roost is maximized. This may be a relatively safe option due to risk dilution and shared predator detection (Clark & Mangel 1986; Cresswell 1994; Fernandez-Juricic, Siller & Kacelnik 2004; Caro 2005) as flock sizes are largest on the roost (Piersma et al. 1993a; Van den Hout, Spaans & Piersma 2008), in addition to thermostatic costs being relatively low on roosts (Wiersma & Piersma 1994). We have strong indications that knots aim to maximize their roosting time: daily time off the roost decreased strongly as a function of gizzard mass, from 16 h (4 g gizzard) to 9 h (12 g; Van Gils et al. 2005b), and it has been suggested earlier that just-arrived knots grow somewhat larger gizzards to minimize the total foraging time (Van Gils et al. 2007).

The implications of our study may be wide-ranging. Digestive constraints are faced by many more species than just red knots. It has been suggested that rates of digestion, rather than rates of encounter and handling, delimit the intake rate in many foragers during much of their live (Jeschke et al. 2002). And this makes much sense from an optimization point of view. Food encounter rates vary widely in time and space, and it would be costly and wasteful to maintain and carry large digestive organs (e.g. Piersma et al. 2003) that can process food faster than any rate at which food is encountered and ingested. Rather, maintaining a somewhat smaller digestive machinery is cheaper and outweighs the costs of facing regular digestive constraints. This study shows that
the costs of facing a digestive constraint can be kept to a minimum when sticking to the rules of the digestive rate model.

Acknowledgements

The sampling of the eight study sites was only possible with the precious help of numerous people from the three involved countries. We would like to thank the staff of ONCFS for providing additional help: H. Audebert, M. Claise, T. Dodin, A. François, D. Gaillard, Y. Limouzin, P. Malassagne, J. Marquis, J. Moreau and G. Puaud. We thank D. Lamoise and M. Allain for their participation in the sorting of droppings. Logistic help, including the provision of Weld accommodation, was generously arranged or provided by P. L. Ireland, P. Atkinson, N. Alligier, N. Clark, E. Feunteun and P. Miramand. We are especially grateful to the managers of the nature reserves in Aiguillon Bay, F. Meunier of the Ligue pour la Protection des Oiseaux (LPO) and E. Joyeux of the Office National de la Chasse et de la Faune Sauvage (ONCFS), as well as the manager of Moeze-Oléron, P. Delaporte of LPO. Financial support was received from the Conseil Général de Charente-Maritime, the Programme Environnement, Vie et Société CNRS Micropolluants Marennes-Oléron, Zone Atelier du Mont Saint-Michel (PEVS CNRS), Réserve Naturelle de la Baie de l’Aiguillon (LPO) and the bilateral Van Gogh programme administered by the Netherlands Organisation for Scientific Research (NWO) and the French Ministry of Foreign Affairs. Finally, we thank the editors and two anonymous reviewers for important feedback on the study.

References


Received 20 April 2009; accepted 11 July 2009

Handling Editor: Tom Webb