Foraging decisions in a digestively constrained long-distance migrant, the red knot (Calidris canutus)
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Reinterpretation of gizzard sizes of red knots world-wide emphasises overriding importance of prey quality at migratory stopover sites

Jan A. van Gils, Phil F. Battley, Theunis Piersma and Rudi Drent
The size of digestive organs can be rapidly and reversibly adjusted to ecological circumstances, but such phenotypic flexibility comes at a cost. Here, we test how the gizzard mass of a long-distance migrant, the red knot (Calidris canutus), is adjusted to (i) local climate, (ii) prey quality, and (iii) migratory fuelling demands. For eight sites around the world (both wintering and stopover sites), we assembled data on gizzard masses of free-living red knots, the quality of their prey, and the local climate. Using an energetic cost-benefit approach, we predicted the gizzard size required for fastest fuelling (net rate-maximisation, expected during migration) and the gizzard size required to balance daily energy budgets (satisficing, expected in wintering birds) at each site. Measured gizzards matched the net rate-maximising predictions at stopover sites and the satisficing predictions at wintering sites. To our surprise, due to the fact that red knots selected stopover sites with prey of particularly high quality, gizzards at stopovers and at wintering sites were nevertheless of similar size. To quantify the benefit of minimising size changes in the gizzard, we constructed a model incorporating size-dependent costs of maintaining and carrying a gizzard. The model showed that by selecting stopovers containing high quality prey, metabolic rates are kept at a minimum, reducing the spring migratory period by a full week. Red knots appear to time their stopovers so that they hit local peaks in prey quality, that coincide with the reproductive seasons of their intertidal benthic prey.
Introduction

The realisation that size, structure, and function of digestive organs can be fine-tuned rapidly and reversibly to local/temporal ecological circumstances (phenotypic flexibility; reviewed by Piersma & Lindström 1997; Piersma & Drent 2003), raises the question of the costs that such adjustments entail. For example, as a response to increased energy demands through cold exposure, house wrens (Troglodytes aedon) increased the length of their small-intestines (Dykstra & Karasov 1992). Quail (Coturnix japonica) increased gizzard size, intestine length and mucosal surface when food quality was reduced (Starck & Rahmaan 2003; and see López-Calleja & Bozinovic 2003 for a similar effect in hummingbirds). When fuelling for migration, garden warblers (Sylvia borin) increased their digestive tract size (Hume & Biebach 1996).

Long-distance migrants encounter a variety of climates and food qualities through the year, and have different energy demands during nonbreeding and migration seasons. These factors result in seasonal changes in food requirements (e.g. Piersma 2002). Given the empirical relationships between digestive organ size and intake rate (Van Gils et al. 2003), migrants provide an excellent model for studying how organ size is optimised in relation to external and internal energy demands.

It is increasingly realised that much of the reproductive success of long-distance migrant birds may depend on the ecological conditions encountered long before arrival on the breeding grounds (Ebbinge & Spaans 1995; Drent et al. 2003). In a world where many stopover sites are under threat, this gives the study of the selection pressures during migration more than academic interest. Arguments for the safeguarding of stopover sites usually come from observations of large concentrations (Wetlands International 2002), their provision of ample food (Myers et al. 1987), or theoretical arguments based on issues of speed of migration (Alerstam & Hedenström 1998). Here we combine these factors in a single argument based on the organ architecture of a shorebird species during different times of the year in relation to diet quality, energy expenditure and migratory phase.

We examine gizzard flexibility in the red knot (Calidris canutus), a medium-sized shorebird that undertakes non-stop long-distance flights (1,400-6,500 km) between high-arctic breeding grounds and temperate, or tropical non-breeding grounds (Piersma et al. 2004). At these intertidal wintering sites, red knots feed primarily on hard-shelled prey that are generally poor quality (i.e. low ratio of digestible to indigestible matter). Over the past decade, studies on red knots have quantified (i) the energetic costs of living in (Wiersma & Piersma 1994; Bruinzeel & Piersma 1998), and travelling
between (Kvist et al. 2001) sites with contrasting climates (reviewed by Piersma 2002), (ii) the energetic costs and benefits of feeding on prey of different quality (Piersma et al. 2003; Van Gils et al. 2003), and (iii) fuelling rates at different sites around the world (Gudmundsson et al. 1991; González et al. 1996; Piersma et al. 2004). Recent advances in a non-invasive technique (ultrasonography; see Dietz et al. 1999) enabled us to reveal flexibility in the size of a digestive organ, the muscular gizzard, enforced by experimental changes in prey quality (Dekinga et al. 2001; Van Gils et al. 2003). This organ is vital in the feeding ecology of the knot as the hard-shelled prey, that provide most of their diet, are ingested whole and crushed in the gizzard (Piersma et al. 1993b). Changes in gizzard size, which can occur rapidly and reversibly (50% within a week; Dekinga et al. 2001), are likely to have an impact on the knot’s energy budget (Piersma et al. 2003; Van Gils et al. 2003). As rates of shell crushing increase with gizzard size, energetic benefits increase with gizzard size (Van Gils et al. 2003). However, as larger gizzards require larger maintenance and transport costs, energetic costs also increase with gizzard size (Piersma et al. 2003; Van Gils et al. 2003).

In this paper we predict optimal gizzard sizes at different sites on the basis of energy demand and prey quality. Energy demand varies with (i) local climate and (ii) ‘internal’ energy demands for migratory fuelling. Prey quality affects the amount of bulk material that must be processed to meet the daily energy demand. Optimal gizzard size depends on whether birds are balancing energy intake and expenditure (‘satisficing’; Nonacs & Dill 1993; expected during winter when there is no change in body mass), or maximising the net energetic benefit (intake minus expenditure; ‘net rate-maximisation’; Stephens & Krebs 1986; expected during spring when rapidly fuelling for migration). We tested this for five of the six recognised subspecies of knot (Piersma & Davidson 1992; Tomkovich 2001), for which data on climate, prey quality and gizzard size are available. These are canutus breeding at Taymyr Peninsula and wintering in West- and SW-Africa, islandica breeding in N-Greenland and NE-Canada and wintering in NW-Europe, rufa breeding in the central Canadian arctic and wintering in S-Patagonia and Tierra del Fuego, rogersi breeding at Chukotskiy Peninsula and wintering in New Zealand and SE-Australia, and piersmai breeding at the New-Siberian islands and wintering in NW-Australia (Figure 4.1). We considered shellfish-eaters only, but we will discuss exceptions later (horseshoe crab-egg-eating rufa knots during stopover in Delaware Bay; see Castro & Myers 1993). The links not specifically covered in this paper, due to lack of data, are the movements of roselaaari and the 6,900-km journey linking the S-Africa canutus wintering sites with W-African sites.
Material and methods

MODELLING COST-BENEFIT AS A FUNCTION OF GIZZARD SIZE

So-called ‘satisficing’ gizzards balance gross energy income with energy expenditure on a daily basis. So-called ‘net-rate maximising’ gizzards maximise net energy income on a daily basis (gross energy income minus energy expenditure). Of what size these two types of gizzards turn out to be, depends on how energetic benefits and energetic costs scale with gizzard mass $G$. These relations are clarified in Figure 4.2A.

In order to model energetic benefits as a function of $G$ we relied on the observation that the amount of shell material that can be crushed and processed per unit time increases quadratically with gizzard mass ($10^{4.293}$ g shell mass/s per g$^2$ gizzard mass; Van Gils et al. 2003). Rates of metabolizable energy intake ($\text{MEIR}; W$) can therefore be lifted by increasing gizzard size ($G$; g) and/or selecting prey with high flesh-to-shell ratios ($= \text{prey quality} Q$; J

Figure 4.1. A map of the world with the flyways and breeding and wintering grounds of the five subspecies of knots treated here. Distances (km) travelled between main wintering and breeding grounds are 9,000 (canutus), 4,680 (islandica), 15,000 (rufa), 15,000 (rogersi), and 10,400 (piersmai). The movements not specifically covered in this paper, are those of roseaari and the 6,900-km journey linking the S-Africa canutus wintering sites with W-African sites.

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Figure 4.2. Daily energy expenditure and daily metabolizable energy intake as a function of gizzard size to demonstrate the two optimal gizzard sizes. (A). Intake increases quadratically with gizzard mass (Van Gils et al. 2003) up to a level constrained by other processes in the physiology of digestion (Kirkwood 1983; Kvist & Lindström 2003). Since expenditure starts off higher but increases more slowly with gizzard mass than intake, the optimal satisficing gizzard mass is at the intersection of the two curves, indicated by the solid, left arrow. Net daily energy intake (i.e. intake minus expenditure) is maximised when (gross) daily intake hits the Kirkwood-Kvist/Lindström constraint; the open, right arrow indicates the optimal net rate-maximising gizzard mass. The parameters in this example are given standard values for thermoregulatory cost (TRC; 1 W) and prey quality (1 kJ/g DMshell). (B). An enhanced intake (through a higher digestive prey quality of 2 kJ/g DMshell instead of 1 kJ/g DMshell) decreases both the satisficing and the net rate-maximising gizzard mass. (C). An increased expenditure level (through a higher TRC of 2.5 W instead of 1 W) increases the satisficing gizzard mass but not the net rate-maximising gizzard mass. Note that costs scarcely increase at the lowest gizzard sizes because all of the HIF produced by small gizzards is assumed to substitute for TRC.
metabolizable energy/g shell mass). This can be formalised to MEIR = 10^{-4.293} \cdot G^2 \cdot Q (Van Gils et al. 2003). See Figure 4.2B for effects of prey quality on optimal gizzard size.

Prey quality Q was determined as precisely as possible by selecting only prey species and sizes fed upon by knots (see Appendix for diet composition and Table 4.1 for resulting values of Q). Since knots ingest their shelled, largely indigestible prey whole, their faeces reveal much about their diet. Shell fragments can usually be identified to species-level and hinge-sizes allow reconstructions of prey size (Dekinga & Piersma 1993). We reconstructed digestive prey quality in this way for each subspecies at most sites, except for four sites where Q was extracted from the literature (islandica at wintering site from Van Gils et al. (2003) and at stopover from Alerstam et al. (1992), and canutus and rufa at stopover from respectively Van Gils et al. (2003) and González et al. (1996)). Flesh and shell mass for each bivalve prey species, and where possible each relevant size class, were determined. This was done by removing the flesh from the shells, drying both flesh and shell for three days to constant mass at 60°C, and finally measuring dry masses to the nearest 0.1 mg (yielding respectively DM\text{flesh} and DM\text{shell}). Next, the dried flesh was incinerated for 2 h at 550°C to determine ash-free dry mass (AFDM\text{flesh}). After averaging AFDM\text{flesh} and DM\text{shell}, we calculated Q as

\[
Q = \frac{a \cdot d \cdot \text{AFDM}_{\text{flesh}}}{\text{DM}_{\text{shell}}}
\]

where a denotes assimilation efficiency (0.8; Kersten & Piersma 1987, Piersma 1994), and d denotes energetic density of the flesh (22 kJ/g AFDM\text{flesh}; Zwarts & Wanink 1993).

In order to model energetic costs as a function of G, we used the linear relation between basal metabolic rate BMR and lean body mass L (BMR = 0.0081 \cdot L - 0.046; Piersma et al. 1996), and assumed that L equals 100 g + G + intestine mass (Van der Meer & Piersma 1994), and that gizzard mass scales to intestine mass in a 1-to-1 isomorphic relationship (Piersma et al. 2003), or formally L = 100 + 2G. The metabolic rate due to flying MR_{fly} (W) scales to body mass B as MR_{fly} = 100.39 \cdot B^{0.35-0.95} (Kvist et al. 2001). Metabolic rate due to walking MR_{walk} scales to body mass B in the following manner:

\[
MR_{\text{walk}} = v \cdot 840 \cdot \left(\frac{B}{1000}\right)^{2.90}
\]

(Bruinzeel et al. 1999), where v denotes a walking speed of 0.072 m/s (Piersma et al. 2003). In order to equate these mass-dependent equations as a function of gizzard mass, we assume that B = L (i.e. no fat is assumed; as fat
Table 4.1. Site and sample data for the five sub-species of red knot, with predicted thermoregulatory costs (TRC in W), average digestive prey quality \( (kJ/g \text{ DM}_{\text{shell}}) \), expected satisficing and net rate-maximising gizzard masses (g), the number of gizzards sampled, and the observed gizzard masses (g; mean ± SE). References are to detailed studies at the particular site.

<table>
<thead>
<tr>
<th>Sub-species</th>
<th>Migratory phase</th>
<th>Site</th>
<th>Month</th>
<th>TRC (W)</th>
<th>Prey quality ( (kJ/g \text{ DM}_{\text{shell}}) )</th>
<th>Exp. satisficing gizzard mass (g)</th>
<th>Exp. net rate-maximising gizzard mass (g)</th>
<th>N gizzards sampled</th>
<th>Obs. mean gizzard mass ± SE (g)</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>canutus</td>
<td>Wintering</td>
<td>Banc d’Arguin, Mauritania</td>
<td>December</td>
<td>1.49</td>
<td>0.89</td>
<td>10.51</td>
<td>16.64</td>
<td>6</td>
<td>9.89 ± 0.53</td>
<td>1</td>
</tr>
<tr>
<td>canutus</td>
<td>Stopover</td>
<td>Wadden Sea, NW-Europe</td>
<td>May</td>
<td>1.99</td>
<td>3.74</td>
<td>5.73</td>
<td>8.14</td>
<td>2</td>
<td>8.00 ± 0.30</td>
<td>2</td>
</tr>
<tr>
<td>islandica</td>
<td>Wintering</td>
<td>Wadden Sea, NW-Europe</td>
<td>January</td>
<td>2.93</td>
<td>2.10</td>
<td>8.49</td>
<td>10.86</td>
<td>60</td>
<td>8.75 ± 0.18</td>
<td>2</td>
</tr>
<tr>
<td>islandica</td>
<td>Stopover</td>
<td>Selvogur, SW-Iceland</td>
<td>May</td>
<td>2.26</td>
<td>2.35</td>
<td>6.33</td>
<td>9.45</td>
<td>8</td>
<td>7.95 ± 0.48</td>
<td>3,4</td>
</tr>
<tr>
<td>rufa</td>
<td>Wintering</td>
<td>Tierra del Fuego, S-Argentina</td>
<td>February</td>
<td>1.82</td>
<td>2.03</td>
<td>7.21</td>
<td>11.04</td>
<td>13</td>
<td>8.09 ± 0.20</td>
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</tr>
<tr>
<td>rufa</td>
<td>Stopover</td>
<td>San Antonio Oeste, E-Argentina</td>
<td>March</td>
<td>1.35</td>
<td>3.50</td>
<td>5.09</td>
<td>8.41</td>
<td>7</td>
<td>8.17 ± 0.20</td>
<td>5</td>
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<tr>
<td>rogersi</td>
<td>Wintering</td>
<td>Northern New Zealand</td>
<td>March</td>
<td>1.30</td>
<td>0.82</td>
<td>10.64</td>
<td>17.32</td>
<td>10</td>
<td>10.42 ± 0.58</td>
<td>6</td>
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<tr>
<td>piersmai</td>
<td>Wintering</td>
<td>Roebuck Bay, NW-Australia</td>
<td>Jan.-April</td>
<td>0.67</td>
<td>2.22</td>
<td>5.91</td>
<td>10.55</td>
<td>24</td>
<td>5.94 ± 0.36</td>
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</tbody>
</table>

is metabolically inactive this assumption only affects the calculations through the relatively small transport costs). Metabolic rate due to probing equals 0.47 W (Piersma et al. 2003), and heat increment of feeding (HIF) amounts to 5.2 kJ per g AFDM flesh digested (Piersma et al. 2003).

Finally, thermoregulatory cost (TRC) is estimated on the basis of Wiersma & Piersma (1994), who provide (1) direct estimates for islandica and canutus and (2) an estimate of thermal conductance that we used to translate ambient temperatures into TRC for the other three subspecies (listed in Table 4.1; using data in Stans et al. 1972). This aspect of cost is exemplified in Figure 4.2C. We assume that some heat-generating sources can contribute towards TRC, which makes life in the cold considerably cheaper. Since BMR and HIF generate heat in the core of the body, 100% of this heat can potentially substitute for TRC (BMR-heat is the lower stable value in the classical ‘Scholander-curve'; Scholander et al. 1950). Since walking generates heat much closer to the skin, only 30% of this heat can substitute for TRC (Bruinzeel & Piersma 1998).

To complete the calculations on the daily energy budget, we multiplied these expenditure and intake rates with daily time allocations to foraging, flying and resting. Red knots feed at exposed intertidal mudflats during day and night, and therefore have daily foraging periods of 12 hours on average (Piersma et al. 1994; Van Gils & Piersma 1999; Van Gils et al. 2000). This value was used for all subspecies at all sites except for islandica stopping over at Iceland, which has been observed to extend its daily feeding period to 14.2 h by feeding higher up the beach in the seaweed during incoming and outgoing tide (Alerstam et al. 1992). For all subspecies at all sites we further assumed that 0.5 h per day was spent in flight (mainly to commute between roosts and feeding grounds), except for knots living in the Wadden Sea (islandica in winter and canutus during stopover) that were assumed to fly for 1 h per day due to larger daily foraging ranges compared to other sites (Piersma et al. 1993a). The remainder of the day was spent in rest.

Satisficing gizzard sizes were predicted from these parameters by solving for G while equating total expenditure and income on a daily basis (i.e. net energy gain = 0; Figure 4.2). Net rate-maximising gizzards were predicted by rewriting the quadratic intake-rate function (given above) to:

$$ G = \sqrt{\frac{\text{MEIR}_{\text{max}}}{Q \cdot 10^{-4.293}}} $$

(4.3)

Here, MEIR_{max} equals maximum metabolizable energy intake rate of 12.6 W when feeding for 12 h a day (i.e. 544 kJ/day such as in Figure 4.2), as based on the empirical estimates by Kirkwood (1983) and Kvist & Lindström (2003).
OBSERVED GIZZARD SIZES

Fresh masses of gizzards were determined either directly through dissections of carcasses (N = 50), or indirectly through ultrasonography on live birds (N = 80; see Dietz et al. 1999 for detailed methodology, Dekinga et al. 2001 and Van Gils et al. 2003 for results). Most carcasses were collected as catching casualties (N = 42); a few were obtained through shooting (N = 8; islandica at the Iceland stopover; see Piersma et al. 1999). The birds that were measured by ultrasound were caught with mistnets (N = 60; islandica at its wintering site) or with cannon-nets (N = 20; the majority of the piersmai-individuals). Table 4.1 gives the details on catch site, sample size and date. For islandica stopping over on northward migration in Iceland, to ensure that only actively fuelling birds were analysed, we selected birds from the middle of the stopover period (10 May). Likewise, for rogersi in New Zealand, to ensure that only non-fuelling birds were analysed, we excluded adult birds with more than 50 g of fat (see Battley & Piersma 1997).

Results

MODEL PARAMETERS AND PREDICTIONS

For each site, we predicted the optimal satisficing and rate-maximising gizzard mass based on climate, energy demand and prey quality (Table 4.1; exemplified in Figure 4.3A). In Figure 4.3, optimal gizzard size (right axis) follows from the daily amount of shell material that must be processed (left axis), which, in turn, follows from the daily amount of energy that is required (horizontal axis; equal to the Kirkwood/Kvist-Lindström constraint for fuelling birds) and the amount of metabolisable energy per g of shell material (= prey quality given by dashed lines). Due to low prey qualities for wintering sites, we predict relatively large satisficing gizzards, especially so in the case of canutus and rogersi (> 10 g; Figure 4.3B). Satisficing gizzards of overwintering islandica are predicted to be relatively large due to the combination of low quality prey at high TRC (Figure 4.3B). By contrast, due to high prey qualities for stopover sites, we predict relatively small net-rate maximising gizzards. This pattern holds for each subspecies of which we have stopover-data available (islandica, canutus, and rufa; Table 4.1; Figure 4.3B). Through this shift in prey quality, knots are predicted to keep their gizzards more or less at the 'satisficing-in-winter size' when fuelling at stopovers (grey large arrows in Figure 4.3B).
Figure 4.3. Daily energy requirement (kJ; horizontal axis) and prey quality (kJ/g DM<sub>shell</sub>; diagonal lines) predict the daily mass of shell material processed (g; left vertical axis) and thus predict the required gizzard size (g; right vertical axis). In (A), this prediction is made for satisficing and rate-maximising C. c. canutus, both at its wintering (filled squares) and at its stopover site (open squares). Arrows indicate expected change in gizzard mass when changing from wintering/satisficing conditions to wintering/rate-maximising or to stopping-over/rate-maximising conditions. (B). Similar to (A), but now for all subspecies (and ignoring rate-maximisation during winter). The message is that, due to an increase in prey quality, knots need hardly change gizzard size when moving up from wintering to stopover site (arrows). Note that gizzard scale is based on 12 h of foraging per day, which holds for all cases except for islandica at its stopover site (14.2 h). Therefore, in this case gizzard mass is predicted to be 8% below that indicated on the scale (indicated by small arrow on the Kirkwood/Kvist-Lindström-bar).
Observed gizzard sizes

Observed individual gizzard masses varied between 3.7-12.9 g, and were smallest in wintering piersmai and largest in wintering rogersi (Figure 4.4; Table 4.1). Gizzards at wintering sites were close to the predicted satisficing sizes (difference ± SE = 0.19 ± 0.14 g; N = 113; P > 0.15) and were smaller than the predicted net rate-maximising sizes (-3.41 ± 0.20 g; P < 0.0001; Figure 4.4; Table 4.1). Conversely, gizzards at stopover sites were closest to predicted net rate-maximising sizes (-0.82 ± 0.52 g; N = 17; P > 0.1) and were larger than the predicted satisficing sizes (2.30 ± 0.35 g; P < 0.0001; Figure 4.4; Table 4.1). However, these stopover gizzards were of similar size to the wintering gizzards (P > 0.1, taking differences between subspecies into account, N = 130, R² = 0.449).

Discussion

Gizzards at stopovers and gizzards at wintering sites were of similar size (Figure 4.4). This may seem counterintuitive, especially since ‘stopover gizzards’ were of rate-maximising size while ‘wintering gizzards’ were of satisficing size (Figure 4.4; Table 4.1). However, prey qualities at stopovers were on average twice those at wintering sites (Figure 4.3B; N = 8; P <
0.05). This enabled gizzards of the same size to accommodate a maximal fuelling mode (arrows in Figure 4.3B). When migrating northwards, the increase in prey quality for canutus is of such magnitude (from 0.89 to 3.74 kJ/g DM_{shell}) that fuelling ‘spring gizzards’ are predicted and observed to be 2-g smaller than satisficing ‘winter gizzards’. With an increase in prey quality from 2.03 to 3.50 kJ/g DM_{shell}, it seems as if rufa uses its relatively nearby stopover in San Antonio Oeste (‘only’ 1,400 km away from the wintering grounds at Tierra del Fuego) as a springboard to escape from the Patagonian wintering grounds. The increase in prey quality is smallest in the temperate-zone wintering islandica (from 2.10 to 2.35 kJ/g DM_{shell}), but in this case fuelling with relatively small gizzards seems feasible by foraging longer than 12 h (Alerstam et al. 1992), although not at maximal rates (see Figure 4.4).

Apparently, red knots only utilise the stopover sites that harbour prey of high quality. This agrees with theoretical predictions (Alerstam & Lindström 1990), observations on shorebirds (Gudmundsson et al. 1991), and with recent studies on Bewick’s swans (Cygnus bewickii; Beekman et al. 2002): poor-quality stopovers ought to be, and are, skipped. In an attempt to quantify the benefits of selecting high-quality stopovers, we modelled total duration of migration as a function of stopover selection (Figure 4.5). The model builds on our previous calculations, but now includes fattening. Fuelling birds deposit up to 100 g of fat at a biosynthesis-cost of 0.33 J per J of tissue (Ricklefs 1974).

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Due to their thick shell, the spat of giant bloody cockle (Arca senilis; 3-6 mm) are amongst the poorest-quality prey fed upon by knots in West-Africa. Photo: Jan Drent.
The next step in our model is their long-distance flight. During long-distance flight, the burning of 1 g of fat yields 40 kJ. To take into account the instantaneous changes in energetic costs with changing amounts of fat (increasing when fuelling and decreasing when flying), the model runs at discrete time steps of 1 second. Across any prey quality, net-rate maximising gizzards always yield a gross rate of energy gain that equals the upper physiological limit as empirically derived by Kirkwood (1983) and Kvist & Lindström (2003; grey bar in Figure 4.2). However, as net-rate maximising gizzard size declines with increasing prey quality (Figure 4.5A cf. Figure 4.2C), the overall cost of transport and maintenance declines likewise with increasing prey quality (Figure 4.5B).

**Figure 4.5.** The effect of digestive prey quality at stopovers on overall speed to migrate 15,000 km from wintering to breeding grounds. (A). Expected net-rate maximising gizzard mass declines with prey quality (curved line; see eq. 4.3). Given the observed frequency distribution of prey qualities among sites (bars at horizontal axis), knots only select stopovers that harbour the highest prey qualities (light grey bars; darker bars represent wintering sites). As predicted, gizzards observed at stopovers are therefore distributed around 8-g (bars at vertical axis). Mean stopover gizzard mass vs. mean stopover prey quality is given by open dot (bars are SD). (B). Metabolic rates increase as a function of gizzard size, especially during flight. (C). Through these higher energetic costs, the total length of the migratory period increases with increasing gizzard size, i.e. declines with increasing prey quality. Grey band across the three figures shows that stopping over in the best instead of in the worst sites reduces length of migratory period by about a week. Including the option of flexibly reducing gizzard size before flight (down to 6-g with no time or energy costs of transformation), accounts for only a minor reduction of the migratory period (dashed line in B and C).
This cost-reduction by minimising gizzard size brings two advantages that reduce overall duration of migration (by about one day per gram decline in gizzard mass; Figure 4.5C). Firstly, at the stopovers, higher net rates of energy gain (= gross gain minus costs) are achieved, leading to shorter stopover times ($P_{\text{dep}}$ increases, using the terminology of Hedenström & Alerstam 1998). Secondly, during flight, metabolic rate is reduced and thus longer distances can be travelled per gram of stored fat, which reduces required stopover time per distance travelled ($P_{\text{flight}}$ decreases, using the terminology of Hedenström & Alerstam 1998). Even though this second effect is stronger than the first on an instantaneous basis (given by differences in slopes in Figure 4.5B), overall, most energy is saved at stopovers, since much more time, and thus energy, is spent at stopovers than in flight (cf. Wikelski et al. 2003). Summarising, overall speed of migration improves by selecting stopovers that harbour high-quality prey. The overall speed of migration expected by the model (15,000 km in 91 days = 165 km/day) approaches the value of 175 km/day actually observed in red knots (Hedenström & Alerstam 1998).

We extended the model by including the flexibility to further reduce gizzard size just before the onset of a long-distance flight down to 6-g (as observed by Battley & Piersma 1997 and Piersma et al. 1999). We assumed such transformations incur no time or energy costs (which indeed may be minor; Overgaard et al. 2002). Due to the fact that fuelling gizzards are relatively small (8-g), such flexibility only marginally improves overall speed of migration through small reductions in $P_{\text{flight}}$ (by about a single day over the full distance of 15,000 km; dashed line in Figure 4.5B-C; overall speed of migration = 167 km/day); the great effect of prey quality remains.

Prey is of best quality (high amounts of flesh) in the reproductive phase just before the release of gametes (Gabbot 1983; Zwarts 1991; Honkoop & Van der Meer 1997). In temperate zones, reproduction of marine invertebrates is seasonally synchronised and takes place in spring (see references in Zwarts 1991), which is reflected in the peak in prey quality during spring (Van Gils et al. 2003). Keeping in mind that the boreal spring, and thus prey reproduction, starts later in the year with increasing latitude (Piersma et al. 1994), spring-migrating knots seem to follow a northwards ‘wave’ in prey quality. We therefore suggest that knots locate and time their stopovers such that they coincide with the local peaks in the prey’s reproductive periods. This idea has been suggested earlier with respect to increased availability of benthic prey (Piersma et al. 1994) and for arctic-breeding waterfowl tuning their migration to plant growth (‘the green wave hypothesis’; Drent et al. 1978).

In tropical regions, prey reproduction is much less synchronised and occurs throughout the year so that a distinct seasonal peak in prey quality
may be absent (De Goeij et al. 2003). Therefore, rapid fuelling may be impossible around the equator. This might explain why tropical regions are probably skipped as stopovers by knots wintering in the Southern Hemisphere (rufa and rogersi). Tropically wintering knots (canutus and piersmai) may have a hard time fuelling and leaving these sites, a suggestion that has been made before (Ens et al. 1990; Piersma et al. 2004). Indeed, rates of fuelling are lower (N = 14, R² = 0.29, P < 0.05), and length of fuelling periods are longer (N = 14, R² = 0.61, P = 0.001) in tropical than in temperate regions (data from Piersma et al. 2004). West-African wintering canutus may face the severest problems. If their prey in spring would be of the low quality observed in winter (0.89 kJ/g DMshell), rates of fuelling would be maximised at gizzards of approximately 17-g (Figure 4.3A; Table 4.1). In addition to higher maintenance and transport costs associated with such huge gizzards, ‘space’ for fat deposition might be limited in such muscular bodies. Indeed, knots departing from Banc d’Arguin (168 g) are relatively light-weighed (N = 14; P < 0.05; data from Piersma et al. 2004). Possibly, canutus manages with gizzards smaller than 17-g by extending the low tide period beyond the ‘usual’ 12 h/day (Zwarts et al. 1990; this has been observed for islandica in the Wadden Sea and at Iceland; Alerstam et al. 1992; Van Gils et al. 2004).

Fuelling in the Southern Hemisphere takes place during the austral autumn, a time of year long past the peak in prey quality in the (austral) spring (Wilson & Hodgkin 1967; Wilson 1969). Our ‘prey-reproduction’ hypothesis would therefore predict that among sites in temperate regions, fuelling and consequently speed of northward migration should proceed faster in the Northern Hemisphere than in the Southern Hemisphere. Using data published by Piersma et al. (2004), this prediction is upheld, both with respect to fuelling rates (N = 11, R² = 0.39, P < 0.05), and with respect to lengths of fuelling periods (N = 11, R² = 0.36, P = 0.05).

The approach used here, predicting optimal gizzard sizes from a prey’s flesh-to-ballast ratio, is only applicable to knots that feed on hard-shelled mollusk prey. Applying the model to rufa feeding on the super-high quality eggs of horseshoe crabs (Limulus polyphemus) at its stopover in Delaware Bay (N-America), predicted net-rate maximising gizzards of about 1-g. The fact that observed gizzards were much larger than that (mean ± SE = 7.0 ± 0.2 g, N = 61), hints that the grinding of horseshoe crab eggs is a fundamentally different process than the crushing of the outer shells of mollusks. Only in red knots from Delaware Bay do gizzards contain small stones, which may be used to grind the leathery surface of the eggs (T. Piersma, unpubl. data; see Piersma et al. 1993b). Direct experimentation is called for to clarify this.

Summarising, variation in gizzard mass of wintering red knots is large
(from 6-g in piersmai to 10-g in canutus and rogersi). The variation appears to reflect the best possible size adjustments to global variations in prey quality and climate in order to balance energy budgets on a daily basis. Variation in gizzard mass is, by contrast, small in migrating knots (around 8-g in all populations). By the selection of stopover sites with high quality prey, red knots maximise fuelling rates and overall speed of migration using relatively small gizzards. This idea generates testable predictions on the prey quality at stopover sites still unexplored, such as those of rogersi and piersmai along the East Asian-Australasian Flyway. Given the extremely late departure from their NW-Australian wintering site (Battley et al. 2003), piersmai is likely to encounter ‘super-food’ at its stopover in the Yellow Sea, such that gizzards can be kept small and migration can speed up (see box X in chapter 11).

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Appendix

Observed Diet Compositions

The diet of wintering islandica mainly comprised Hydrobia ulvae (1-9 mm) and small proportions of Macoma balthica and Cerastoderma edule (Van Gils et al. 2003). During stopover, islandica fed on Littorina spec. (4-15 mm) and Mytilus edulis (8-23 mm) and to a lesser extent on polychaetes and chironomid larvae (Alerstam et al. 1992). The diet of wintering canutus comprised Bittium spec. (3-10 mm) and Arca senilis (3-6 mm), and to a lesser extent Veneridae spec., Modiolus spec., Rissoa spec., and Hydrobia ulvae (in decreasing order of occurrence; P. J. van den Hout unpubl. data). During stopover, canutus mainly consumed Macoma balthica (7-19 mm), and occasionally Hydrobia ulvae, Mya arenaria, and Cerastoderma edule (Van Gils et al. 2003). The following bivalves predominated in the diet of wintering piersmai: Nucula spec., Anodontia omissa, Anomalocardia squamosa, Tellina
exotica, Tellina piratica, Siliqua pulchella, and Tellina capsoides (in decreasing order of occurrence; D. I. Rogers unpubl. data). The diet of wintering rogersi in the North Island, New Zealand, was assumed to be equivalent to that on Farewell Spit, at the top of the South Island: mainly Amphidesma australale (2-15 mm) and to a lesser extent Chione stuchburiy (P.F.B. unpubl. data). Finally, rufa fed on the intermediate size classes (10-20 mm) of Mytilus edulis at their wintering site in Tierra del Fuego (G. B. Escudero unpubl. data), and on Brachidontes rodriguezi (4-18 mm) at their stopover (González et al. 1996).

References


Red knots ingest their bivalve prey whole. Therefore energy assimilation rates are generally not bottlenecked by the relative short handling times but rather by the internal processing of bulky shell material. Photo: Jan van de Kam.