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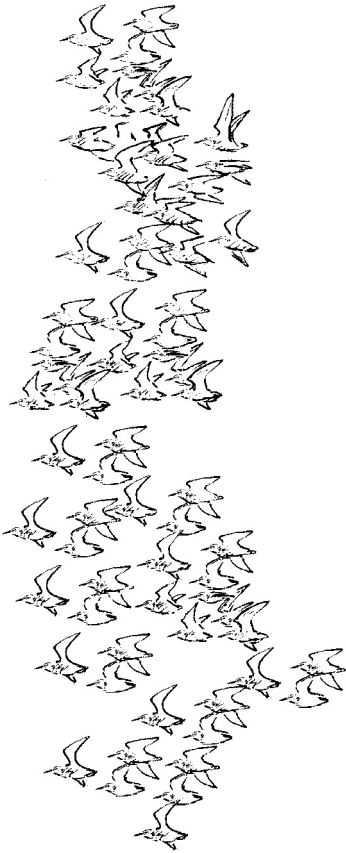
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Modelling phenotypic flexibility: an optimality analysis of gizzard size in Red Knots *Calidris canutus*

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van Gils J.A., Piersma T., Dekinga A. & Battley P.F. 2006. Modelling phenotypic flexibility: an optimality analysis of gizzard size in Red Knots *Calidris canutus*. *Ardea* 94(3): 409–420.

Reversible phenotypic changes, such as those observed in nutritional organs of long-distance migrants, increasingly receive the attention of ornithologists. In this paper we review the cost-benefit studies that have been performed on the flexible gizzard of Red Knots *Calidris canutus*. By varying the hardness of the diet on offer gizzard mass could experimentally be manipulated, which allowed quantification of the energetic costs and benefits as a function of gizzard size. These functions were used to construct an optimality model of gizzard mass for Red Knots on migration and during winter. Two possible currencies were assumed, one in which Knots aim to balance their energy budget on a daily basis (satisficers), and one in which Knots aim to maximise their daily energy budget (net rate maximisers). The model accurately predicted variation in gizzard mass that we observed (1) between years, (2) within years, and (3) between sites. Knots maintained satisficing gizzards during winter and rate-maximising gizzards when fuelling for migration. The model-exercise revealed the importance of digestive constraints and quality of prey in the life of Knots.

Key words: *Calidris canutus*, digestive constraint, gizzard, migration, optimisation, phenotypic flexibility

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INTRODUCTION

Organisms respond adaptively to short-term changes in their environment by behavioural, physiological, and morphological adjustments (Piersma & Lindström 1997, Piersma & Drent 2003). For example, in order to increase digestive

efficiency, tadpoles grow longer guts when competition with other tadpoles strengthens (Relyea & Auld 2004). If such intra-individual changes are reversible, we generally speak of 'phenotypic flexibility' (Piersma & Drent 2003). Recently, there has been increasing attention paid to phenotypic flexibility, notably for reversible size changes of nutri-

tional organs (Overgaard *et al.* 2002, Bozinovic *et al.* 2003), and especially so among ornithologists (Starck 1999, McWilliams & Karasov 2001, Guglielmo & Williams 2003, López-Calleja & Bozinovic 2003, Tieleman *et al.* 2003, McWilliams & Karasov 2005). For example, long-distance avian migrants are able to breakdown their digestive system before take-off in the course of just a week, while they rapidly build-up these organs again when fuelling along the route (Piersma 1998, Piersma & Gill 1998).

Now that documentation of flexibility in the digestive system is accumulating for a wide range of taxa, the time seems ripe to study this phenomenon from an optimality point of view. Thinking of phenotypic flexibility as 'physiological decision-making' should yield insights into the currencies and constraints underlying organ size changes, just as looking at foraging from an optimality perspective has, over the past four decades, taught us a great deal about the currencies and constraints underlying foraging decisions (reviewed by Stephens & Krebs 1986, Perry & Pianka 1997, Vásquez & Kacelnik 1998, Stephens *et al.* 2007). Specifically, with respect to flexible adjustments of the gastrointestinal tract, the more recently developed optimal digestion theory (Perry & Jumars 1987, Jumars 2000, Logan *et al.* 2002) may become the predictive framework for empirically oriented studies on flexible digestive systems.

Central to each optimality problem are the costs and benefits associated with each possible option. Here, the subject of study itself, reversible phenotypic variation, comes as a powerful tool to be used in experimental studies (Sinervo & Basolo 1996, Piersma & Drent 2003). By manipulating and (ideally) tracking size changes in digestive organs within individuals, (energetic) costs and benefits can elegantly be expressed as a function of variation in organ size within individuals (comparable to manipulative foraging studies mentioned above).

Red Knots *Calidris canutus*, medium-sized shellfish-eating shorebirds, are an ideal species upon which to undertake such optimality analyses of digestive organs. During the non-breeding

phase of life (10 months a year), they dwell on intertidal mudflats, feeding on hard-shelled molluscs, which they ingest whole (Piersma *et al.* 1993, Fig. 1). Because of this particular feeding habit, they possess a large muscular gizzard, which they use to crush their heavily armoured prey (Battley & Piersma 2005). Opposing evolutionary forces, favouring temporary reductions in gizzard and gut size (Piersma *et al.* 1999), are their long-distance migrations, which they undertake twice a year between breeding and non-breeding grounds (5000–15 000 km, one-way). Knots can be kept in captivity quite easily, and in recent years, experiments with captive birds have shown the ability to measure gizzard sizes in live birds using ultrasonography (Dietz *et al.* 1999), to manipulate gizzard size by the food on offer (Dekinga *et al.* 2001), and to measure the costs (Piersma *et al.* 2003, 2004) and benefits (van Gils *et al.* 2003a, 2003b, 2004, 2005a, 2005b, 2005c, van Gils & Piersma 2004) of feeding and digestion.

In this paper, we will review the optimality analyses that we performed on the gizzards of Knots. We do so by presenting the crucial experiment that mechanistically revealed the dependence of digestive processing rate on gizzard mass (experiment 1 in van Gils *et al.* 2003a). Subsequently, we formalise the observed relationships between gizzard masses and their associated energetic costs and benefits. We suggest two mutually exclusive currencies that may underlie the observed seasonal shifts in gizzard mass. Finally, the resulting optimality model is tested using field data on gizzard masses of Red Knots collected over different temporal and spatial scales (between years, within years, and between sites).

METHODS

An experiment on digestive processing rates

Six captive Red Knots, caught in the Dutch Wadden Sea in 1994–99, were randomly assigned to two flocks of each three individuals (experiment performed in August 2000). In order to manipulate gizzard size we followed the procedures out-



Figure 1. Red Knots ingest their mollusc prey whole and therefore need a relatively large gizzard in order to crush this hard-shelled food (photo by Jan van de Kam).

lined by Dekinga *et al.* (2001), who found that, in the course of a single week, Knots enlarge their gizzards when offered hard-shelled prey, while Knots reduce their gizzards when offered soft food. Based on these results, the flock that was intended to develop large gizzards was given hard-shelled Edible Cockles *Cerastoderma edule*, while the flock that was supposed to maintain small gizzards was given soft trout pellets (Trouvit, Produits Trouw, Vervins, France). These specific staple foods were offered to the birds three weeks before the actual experiment started.

At three times we used an ultrasound to estimate gizzard mass (Pie 200 ultrasound, Pie Medical Benelux BV, Maastricht, The Netherlands; see Dietz *et al.* 1999 for detailed methodology):

first, before gizzard manipulation started, in order to confirm similarity in gizzard mass between the two groups ($P > 0.3$); second, at the onset of the experiment, and third just after the experiment had ended, both in order to confirm the success of gizzard-size manipulation ($P < 0.01$; HLM with 6 level-2 observations).

The experiment consisted of 36 trials (6 birds \times 6 trials/bird), where in each trial a single Knot was offered a single prey type *ad libitum* (such that intake rate would not be constrained by searching). In total, we offered 6 prey types, hence 6 trials per bird (3 size classes of Edible Cockles and Baltic Tellins *Macoma balthica*; size classes were 5–7 mm, 9–11 mm, and 13–15 mm of shell length). Each trial lasted about 40 minutes, which

was enough to consume on average about 40 prey items. As shell crushing usually commences after 3–9 prey ingestions, the duration of the trials was sufficient for intake rates to be potentially constrained by rates of shell crushing. Trials were performed in random order with respect to bird and prey type.

Each trial was videotaped, using a Hi-8 video camera. We used 'The Observer' package (Noldus Information Technology 1997) to analyse prey intake in full detail. Replaying the tapes at 1/5 of the recording speed, we scored each prey intake and the time it took to handle each prey item (to the nearest 0.04 s). Handling times were measured in order to test for the hypothesis that intake rates were constrained by rates of handling rather than by rates of digestive processing (see van Gils *et al.* 2003a).

We took samples from the six prey types that we offered, in order to measure dry shell mass (DM_{shell}). We did so by taking out all fleshy parts of individual prey items before drying the shells for three days in a ventilated oven at 55–60°C, where after DM_{shell} was determined to the nearest 0.1 mg.

Each trial yielded one datum on intake rate (prey s^{-1}). Data were normalised by log-transformation and were analysed using the GLM-procedure in SYSTAT 10 (Systat Software Inc.). As in some trials birds ingested no prey at all, we added 0.001 prey s^{-1} to each intake rate in order to enable log-transformation of 0 values (following Berry 1987). A series of GLM-models were run, testing whether handling time or DM_{shell} constrained rate of prey intake. Here we will only present the most parsimonious model that remained, in which intake rate varied only with gizzard mass and DM_{shell} but not with handling time. For more details about the statistical analyses and further methodology we refer to van Gils *et al.* (2003a; experiment 1).

An optimality model on gizzard size

Using the outcome of the experiment described above enabled us to model maximal digestive processing rate (g $DM_{\text{shell}} s^{-1}$) as a function of gizzard mass. Subsequently, knowing a prey type's

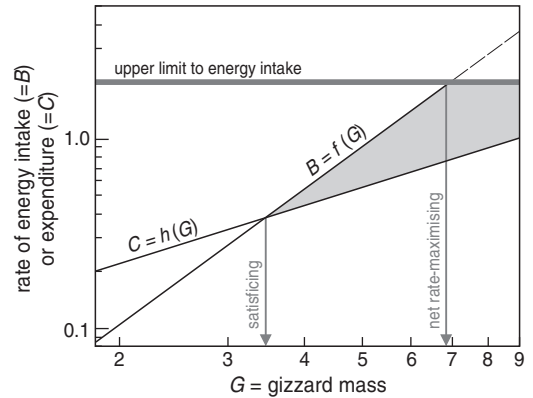


Figure 2. Abstraction of rate of energy intake B as a function f of gizzard mass G and rate of energy expenditure C as a function h of G . A so-called 'satisficing' gizzard is found when B and C intersect. A so-called 'net rate maximising' gizzard is found when $B - C$ (indicated by grey surface when positive) is maximal. This is where B starts to level off due to an upper limit to rate of energy uptake (horizontal grey bar).

metabolisable energy content per g DM_{shell} allowed us to model metabolisable energy intake rate as a function of gizzard mass under a digestive bottleneck (for a fictive example of such a function see Fig. 2). These energetic benefits B as a function f of gizzard mass G can formally be equated as:

$$B = f(G) \quad (1)$$

Function f will be parameterised in the current paper.

Along the same lines, we can formalise metabolic costs C as a function h of gizzard mass G (Fig. 2):

$$C = h(G) \quad (2)$$

For the parameterisation of function h we refer to the appendix in van Gils *et al.* (2003a). Basically, C increases with an increase in G because maintenance and transport costs and heat increments of feeding are larger in larger gizzards (see also Piersma *et al.* 2003).

Next, we define two reasonable currencies and optimise G with respect to B and C (Fig. 2). Firstly, we imagine so-called satisficing foragers, which aim to maintain energy balance on a daily basis

(i.e. keep body mass stable), hence:

$$B - C = 0 \quad (3)$$

Secondly, we envisage so-called *net-rate maximising* foragers, which aim to maintain a daily energy budget as positive as possible (i.e. fuel at maximum rate), hence:

$$\max(B - C) \quad (4)$$

We expect Red Knots to behave as *satisficers* during times when body mass is relatively stable (at the wintering grounds, long before the onset migration), while we expect Knots to behave as *rate-maximisers* when fuelling for migration (either at wintering grounds or at stopovers).

Field data on gizzard masses

The optimality model was tested using field data on gizzard masses collected over the years. Basically, we gathered three types of data on gizzard masses in Red Knots. (1) Data collected for several years (1998–2002) in late summer (late July–August) in the Dutch Wadden Sea ($n = 564$ gizzards, which were all obtained through ultrasonography on live birds). (2) Data collected during different times of the annual cycle in the Wadden Sea (1984–2002; $n = 920$, of which 73 were obtained through dissection of carcasses and the rest through ultrasonography on live birds). (3) Data collected worldwide at several wintering grounds and stopover sites on five out of the six recognised subspecies of Knots (Piersma & Davidson 1992, Tomkovich 2001; *canutus* at Mauritanian wintering ground, $n = 6$; *canutus* at Wadden Sea stopover, $n = 2$; *islandica* at Wadden Sea wintering ground, $n = 60$; *islandica* at Icelandic stopover, $n = 8$; *piersmai* at NW-Australian wintering ground, $n = 24$; *rogersi* at New Zealand wintering ground, $n = 5$; *rufa* at Tierra del Fuego wintering ground (S-Argentina), $n = 13$; *rufa* at San Antonio Oeste stopover (E-Argentina), $n = 7$; ultrasonography was used on all wintering *islandica* and 20 *piersmai* individuals, all other gizzard masses were obtained through carcass analysis). Carcasses were either collected as catching casualties, or recovered from poachers (*rogersi*), or obtaining by shooting under license (*islandica* in Iceland).

RESULTS

An experiment on digestive processing rates

Intake rates I (prey s^{-1}) increased with gizzard mass G (g) and decreased with the amount of shell mass per prey DM_{shell} (mg) ($n = 36$, $R^2 = 0.82$, $P < 0.00001$). In the most parsimonious GLM-model, the coefficients of log-transformed G and DM_{shell} did not deviate from 2 and -1 respectively ($P > 0.9$ and $P > 0.1$; see van Gils et al. 2003a for the results of more complicated GLM-models). Therefore, once backtransformed, the observed relationship can be formalised as:

$$I = c \frac{G^2}{DM_{shell}} \quad (5)$$

where c is constant at $0.05 \text{ mg } DM_{shell} \text{ s}^{-1} \text{ g}^{-2}_{gizzard}$. The inverse relation between I and DM_{shell} suggests that the rate at which shell mass is digestively processed ($\text{mg } DM_{shell} \text{ s}^{-1}$) is constant for a given gizzard mass. Therefore, if we define shell mass processing rate as:

$$P = I \times DM_{shell} \quad (6)$$

we can simplify equation (5) to:

$$P = c \times G^2 \quad (7)$$

For clarity we have calculated shell mass processing rate P in each trial and plotted its dependence on gizzard mass G (Fig. 3).

Fine-tuning the gizzard model with empirical insights

Now we know that digestive processing rate relates in a rather simple manner to gizzard mass and a characteristic of the prey (shell mass DM_{shell}), constructing the optimisation model of gizzard size is, at least from the benefit side of the coin, a rather straightforward exercise. If we define m as a second characteristic of the prey, namely the amount of metabolisable energy per g shell mass (from now on this ratio will be called prey quality), equation (7), describing digestive processing rate P in terms of shell mass per unit time, can be expressed as E in terms of metabolisable energy uptake per unit time:

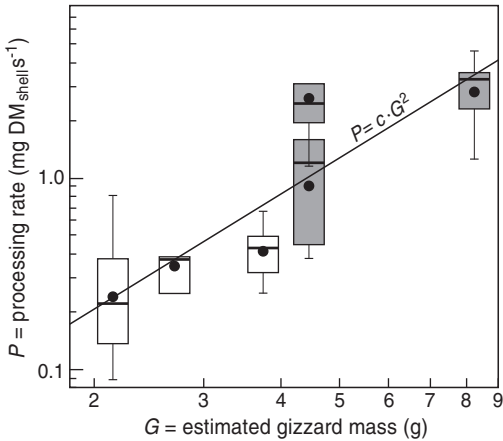


Figure 3. Rate P at which shell mass is digestively processed increases quadratically with estimated gizzard mass G , where diagonal line represents least-square regression line ($P = c \cdot G^2$; where $c = 0.05 \text{ mg DM}_{\text{shell}} \text{ s}^{-1} \text{ g}^{-2}_{\text{gizzard}}$). Each box represents data per individual bird, where grey-shaded boxes represent the three individuals from the large-gizzard group and open boxes represent the three individuals from the small-gizzard group. Such box-and-whiskers plots give mean (filled dot), median (horizontal line within each box), interquartile range (box), and range (bars outside each box).

$$E = m \times P \tag{8}$$

hence (combining equations 7 and 8):

$$E = m \times c \times G^2 \tag{9}$$

This latter equation forms the heart of the optimisation model, as it couples the energetic benefits to the cost-component of the calculations. Namely, under the assumption of *satisficing*, E should equal metabolic rate in order to keep body mass constant (when calculated on a daily basis). Thus, if we define E_{required} as metabolisable energy intake rate *required* to maintain energy balance, we can, by rewriting equation (9), calculate the gizzard mass G_{required} required to achieve this:

$$G_{\text{required}} = \sqrt{\frac{E_{\text{required}}}{mc}} \tag{10}$$

A graphical example on how E_{required} and m lead to a predicted G_{required} for *satisficers* is given in Fig. 4 (filled dot).

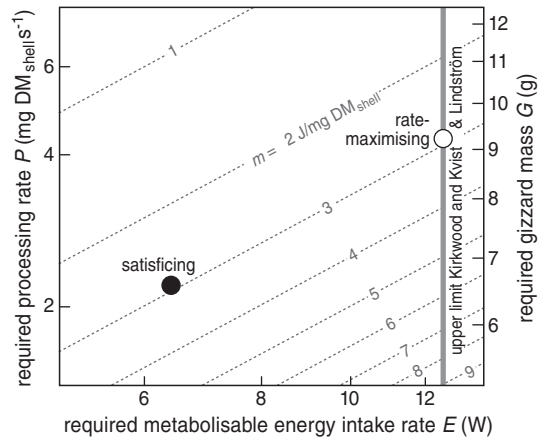


Figure 4. Predicting gizzard mass required to maintain energy balance (*satisficing*; filled dot) or to maximise net energy gain (*rate-maximising*; open dot). The example given here is for *islandica* Knots staging in the western Dutch Wadden Sea in April. In this particular case, Knots spend about 3 W on a daily basis and therefore, when feeding is possible for 12 h d⁻¹ only, require a metabolisable energy intake rate of approximately 6 W in order to maintain a balanced energy budget (filled dot). Given the quality of their food in April, which amounts to about 3 J per mg of shell mass (lines of equal prey quality m are given by dashed diagonal lines), Knots require a processing rate of $6/3 = 2 \text{ mg shell mass per s}$ (left vertical axis). From the experimental results (Fig. 3) we can deduce the gizzard size that this processing rate requires (6.6 g; right vertical axis). However, in order to fuel at maximum rates, Knots would need a larger gizzard (9.2 g; open dot). In that case, shell mass can be processed fast such that rate of metabolisable energy intake hits the upper limit to energy intake (12.6 W when feeding for 12 h d⁻¹), as empirically observed by Kirkwood (1983) and Kvist & Lindström (2003). Given that *islandica* Knots aim to rapidly gain body mass in order to fuel their spring migration, we expect them to possess large, *rate-maximising* gizzards during this time of year.

Along the same lines, under the assumption of rate-maximisation, E_{required} can be thought of as the upper limit to metabolisable energy intake rate (544 kJ d⁻¹; based on empirical estimates by Kirkwood (1983) and more specifically for Red Knots by Kvist & Lindström (2003)). In that case, equation (10) can be used to calculate the gizzard mass G_{required} required to maximise metabolisable energy intake rate (open dot in Fig. 4).

Comparing model predictions with field data

Based on the literature and occasionally on unpublished data, we estimated m and $E_{required}$ for each specific site and time of year where we had data on gizzard masses available (see van Gils *et al.* 2003a, 2005a, 2006a for references). Estimates of m were made by combining prey type-specific values for m with estimates of diet composition as determined by dropping analysis (Dekinga & Piersma 1993). $E_{required}$ basically varied with expected thermoregulatory costs (using Wiersma & Piersma 1994) and with time available for foraging (12–16 h depending on time of year and site). We assumed *satisficing* during overwintering and *rate-maximising* when stopping over and when fuelling to depart from the wintering grounds.

In all three comparisons (between years, within years, between sites), the fit between observations (y) and predictions (x) was strong (Fig. 5; between years: $n = 564$, $R^2 = 0.15$, $P < 0.00001$, $y = 0.00 + 1.00x$; within years: $n = 920$, $R^2 = 0.23$, $P < 0.00001$, $y = 0.44 + 0.94x$; between sites: $n = 125$, $R^2 = 0.35$, $P < 0.00001$, $y = 1.42 + 0.83x$). As predicted, gizzards were generally small (5–7 g) in *islandica* wintering in the Wadden Sea in late summer (especially in the first years of the dataset), and in *piersmai* wintering in NW-Australia (Roebuck Bay). Gizzards were large (10–11 g) in *islandica* fuelling in the Wadden Sea in early spring, and in *canutus* wintering in Mauritania (Banc d'Arguin).

Two issues are worth pointing out here. Firstly, largest deviations from expectations (underestimations by 1.6–2.0 g) were found in *islandica* in the Wadden Sea in early winter (Oct–Dec), which is when we assumed *satisficing* as a currency. Secondly, to our initial surprise, *rate-maximising* gizzards are not larger than *satisficing* gizzards in the 'between-sites' comparison ($R^2 = 0.45$, $P > 0.1$, taking subspecies into account).

DISCUSSION

This study shows that modelling costs and benefits that come with the size of a certain organ can be

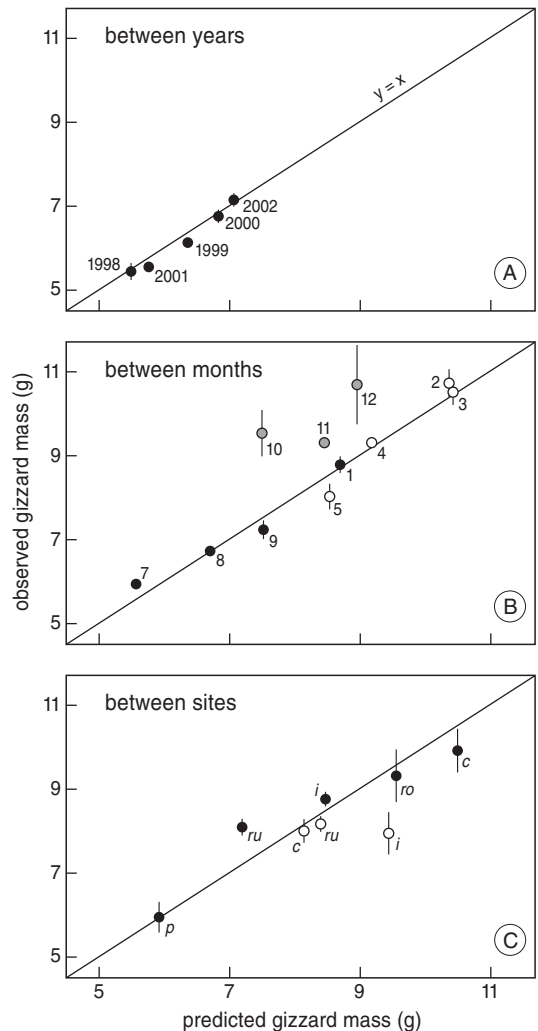


Figure 5. Relation between observed gizzard mass and predicted gizzard mass at various temporal and spatial scales: (A) between years (Dutch Wadden Sea during late summer); (B) between months (Dutch Wadden Sea; number indicates month) and (C) between sites (worldwide; letter indicates subspecies: c = *canutus*, i = *islandica*, p = *piersmai*, ro = *rogersi*, and ru = *rufa*). In all plots, black dots indicate samples from wintering periods when *satisficing* gizzards are predicted; in (B) and (C) open dots indicate fuelling periods when *rate-maximising* gizzards are predicted; additionally, in (B), grey-filled dots indicate those months when Knots build up a small peak in body mass (see Discussion). Diagonal lines give $y = x$ lines and bars give standard errors.

effective. We took advantage of phenotypic flexibility by experimentally manipulating gizzard size in order to measure its performance over a size-range. This performance function formed the basis of our optimality model, which successfully predicted gizzard masses of Red Knots at various temporal and spatial scales. Just as tests of optimality models in behavioural ecology yield insights into the currencies and constraints underlying a behavioural decision (Stearns & Schmid-Hempel 1987, Mitchell & Valone 1990; see van Gils *et al.* 2006b for an application), our tests generate evidence for the currencies and constraints underlying the physiological decision to adjust gizzard size.

With respect to currencies, we found that Knots behave as so-called satisficers throughout most of the year and only behave as rate-maximisers during fuelling. In the light of their seasonal changes in body mass this truly makes sense, but it may come as a surprise to foraging theoreticians who assume rate-maximisation, and not satisficing, to be the rule rather than the exception (e.g. McNamara *et al.* 1993, but see Ward 1992). In this perspective, it is worth pointing out that *islandica* Knots during early winter follow a sort of intermediate currency: their gizzards are larger than required for balancing the energy budget (0.8–2.0 g larger; grey dots in Fig. 5B), while they are smaller than required for maximising the energy budget (on average, respectively 1.4 g smaller in October, 2.3 g smaller in November, and 1.4 g smaller in December; see van Gils *et al.* 2003a for more details). In agreement with this is the observation that *islandica* shows some increases in body mass in early winter (presumably as a way to cope with increased unpredictability in food supply and demand during midwinter; Piersma 1994, see also van Gils *et al.* 2006).

With respect to constraints, this study comes with overriding evidence that intake rates in Red Knots are constrained by rates of digestion. Our calculations suggest that, throughout their annual cycle, Knots continuously adjust the capacity of their digestive machinery such that it is just sufficient to process the daily required amount of energy (be it in order to balance or in order to

maximise the energy budget). Again, this sheds new light on many classic and current perspectives on foraging, which have, by taking Holling's disc equation as a basis (Holling 1959), assumed (interference-free) intake rates to be constrained by rates of encounter and handling (Piersma *et al.* 1995, Norris & Johnstone 1998, Caldow & Furness 2001, Gill *et al.* 2001, van Gils *et al.* 2004; but see recent reviews by Jeschke *et al.* 2002 and Karasov & McWilliams 2005). Not only does this 'Holling-point-of-view', at least in the case of Red Knots, lead to biased predictions on intake rates (van Gils *et al.* 2003a), it also leads to a misunderstanding of the mechanism driving prey selection (van Gils *et al.* 2005b). In a multiple prey environment, prey selection according to Holling's model is based on prey profitability, i.e. only feed on those prey types whose energy content per unit handling time exceeds long-term energy intake rate (Pulliam 1974, Charnov 1976). However, when digestively constrained, prey should not be picked out on the basis of profitability, but rather on the basis of prey quality, i.e. the amount of energy content per g indigestible matter (Hirakawa 1995).

Along an expanding spatial scale, prey selection drives patch selection and possibly even (stopover-) site selection and therefore a proper mechanistic understanding of prey selection is of critical importance in distributional ecology. Indeed, differential patch selection by individual Red Knots in the Wadden Sea could be explained by the fact that digestively constrained individuals selected patches containing prey of high quality, while digestively unconstrained individuals selected patches on the basis of prey profitability (van Gils *et al.* 2005c). And indeed, at the largest spatial scale, migratory Knots even seem to pick out their stopover sites on the basis of prey quality (van Gils *et al.* 2005a). By stopping over at such 'hotspot' stopover-sites, fuelling at maximal rate is feasible with relatively small gizzards (all around 8 g; Fig. 5C). This saves them costly time, involved in adjusting gizzard size (Dekinga *et al.* 2001). As Knots fly with ultra-light gizzards (usually around 6 g; in order to minimise maintenance and transport costs), the selection of a hotspot will enable

them fuel at full speed after relatively little 'gizzard-adjustment-time'. And, upon departure from the hotspot, they would lose little time shifting back to a 'cheap-flight gizzard'.

So, besides maximum rate of digestion itself, the time it takes to enlarge digestive capacity such that maximum rates of digestion can be achieved seems to be an important additional constraint (Karasov & McWilliams 2005, McWilliams & Karasov 2005). With respect to post-breeding *islandica* arriving in the Wadden Sea in late summer, we found that survival chances critically relate to this 'gizzard-adjustment time'. Upon arrival, gizzards are often undersized (i.e. $G < G_{satisficing}$). The energy budget of Knots with undersized gizzards is negative and therefore the time available for adjusting gizzard mass depends on the amount of energy stores left. From field data on 'gizzard growth rates' (Piersma *et al.* 1999), we calculated that Knots arriving with undersized gizzards have fat stores left that allow them to regrow their gizzards by one gram only. Using data on gizzard masses upon arrival, we could therefore predict the proportion of birds that would be able to survive on a given prey quality: only those birds arriving with a gizzard mass $G \geq G_{satisficing} - 1$. As an increase in prey quality leads to a decrease in $G_{satisficing}$ (Fig. 4), we expected the proportion of birds surviving to increase with prey quality. Indeed, calculated from resighting rates of colour banded Knots (using MARK-software), annual survival rates (range: 0.45–0.72 year⁻¹) matched our quantitative predictions and increased with inter-annual variation in prey quality (range: 1.78–2.61 J mg⁻¹ DM_{shell}) in a way which suggests that, upon arrival, there is room for flexibly increasing gizzard size by one gram only (van Gils *et al.* 2006a).

To conclude, the study presented here shows that modelling the physiological decision underlying organ-size shifts can be effective and insightful. It leaves many open questions, which are relevant to address in the future. Firstly, given the importance of the time course of reversible organ-size changes, we need to know the factors determining rates of change in gizzard mass. Why did gizzards under well-nourished laboratory condi-

tions (Dekinga *et al.* 2001) grow by more than an order of magnitude faster than those observed in the field (Piersma *et al.* 1999)? Secondly, given that survival chances seem to depend on gizzard mass upon arrival, we need to know what sets arrival gizzard mass. Length of migration and availability of potential stopover sites along the route play critical roles (Piersma 1998, Piersma *et al.* 2005), but also stochasticity in environmental conditions should matter. For example, what is the effect of expected prey quality at the next stopover? Here, modelling techniques such as stochastic dynamic programming (Houston & McNamara 1999, Clark & Mangel 2000) can help us elucidating how digestive organ size during long-distance flights should be optimised with respect to such unpredictability *en route*.

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REFERENCES

- Battley P.F. & Piersma T. 2005. Adaptive interplay between feeding ecology and features of the digestive tract in birds. In: Starck J.M. & Wang T. (eds) *Physiological and ecological adaptations to feeding in vertebrates*: 201–228. Science Publishers, Enfield, New Hampshire.
- Berry D.A. 1987. Logarithmic transformations in ANOVA. *Biometrics* 43: 439–456.

- Bozinovic F., Gallardo P.A., Visser G.H. & Cortes A. 2003. Seasonal acclimatization in water flux rate, urine osmolality and kidney water channels in free living degus: molecular mechanisms, physiological processes and ecological implications. *J. Exp. Biol.* 206: 2959–2966.
- Caldow R.W.G. & Furness R.W. 2001. Does Holling's disc equation explain the functional response of a kleptoparasite? *J. Anim. Ecol.* 70: 650–662.
- Charnov E.L. 1976. Optimal foraging; attack strategy of a mantid. *Am. Nat.* 110: 141–151.
- Clark C.W. & Mangel M. 2000. *Dynamic state variable models in ecology*. Oxford University Press, New York.
- Dekinga A. & Piersma T. 1993. Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the knot *Calidris canutus*. *Bird Study* 40: 144–156.
- Dekinga A., Dietz M.W., Koolhaas A. & Piersma T. 2001. Time course and reversibility of changes in the gizzards of red knots alternatively eating hard and soft food. *J. Exp. Biol.* 204: 2167–2173.
- Dietz M.W., Dekinga A., Piersma T. & Verhulst S. 1999. Estimating organ size in small migrating shorebirds with ultrasonography: an intercalibration exercise. *Physiol. Biochem. Zool.* 72: 28–37.
- Gill J.A., Sutherland W.J. & Norris K. 2001. Depletion models can predict shorebird distribution at different spatial scales. *Proc. R. Soc. Lond. B* 268: 369–376.
- Guglielmo C.G. & Williams T.D. 2003. Phenotypic flexibility of body composition in relation to migratory state, age, and sex in the western sandpiper (*Calidris mauri*). *Physiol. Biochem. Zool.* 76: 84–98.
- Hirakawa H. 1995. Diet optimization with a nutrient or toxin constraint. *Theor. Pop. Biol.* 47: 331–346.
- Holling C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91: 385–398.
- Houston A.I. & McNamara J.M. 1999. *Models of adaptive behaviour*. Cambridge University Press, Cambridge.
- Jeschke J.M., Kopp M. & Tollrian R. 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecol. Monogr.* 72: 95–112.
- Jumars P.A. 2000. Animal guts as ideal chemical reactors: maximizing absorption rates. *Am. Nat.* 155: 527–543.
- Karasov W.H. & McWilliams S.R. 2005. Digestive constraints in mammalian and avian ecology. In: Starck J.M. & Wang T. (eds) *Physiological and ecological adaptations to feeding in vertebrates*: 87–112. Science Publishers, Enfield, New Hampshire.
- Kirkwood J.K. 1983. A limit to metabolizable energy intake in mammals and birds. *Comp. Biochem. Phys. A* 75: 1–3.
- Kvist A. & Lindström Å. 2003. Gluttony in migratory waders – unprecedented energy assimilation rates in vertebrates. *Oikos* 103: 397–402.
- Logan J.D., Joern A. & Wolesensky W. 2002. Location, time, and temperature dependence of digestion in simple animal tracts. *J. Theor. Biol.* 216: 5–18.
- López-Calleja M.V. & Bozinovic F. 2003. Dynamic energy and time budgets in hummingbirds: a study in *Sephanooides sephanooides*. *Comp. Biochem. Phys. A* 134: 283–295.
- McNamara J.M., Houston A.I. & Weisser W.W. 1993. Combining prey choice and patch use: what does rate-maximizing predict? *J. Theor. Biol.* 164: 219–238.
- McWilliams S.R. & Karasov W.H. 2001. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comp. Biochem. Phys. A* 128: 579–593.
- McWilliams S.R. & Karasov W.H. 2005. Migration takes guts. In: Marra P. & Greenberg R. (eds) *Birds of two worlds*: 67–78. Johns Hopkins Univ. Press, Baltimore.
- Mitchell W.A. & Valone T.J. 1990. The optimization research-program – studying adaptations by their function. *Q. Rev. Biol.* 65: 43–52.
- Noldus Information Technology. 1997. *The Observer; Support package for video analysis*. Reference manual version 4.0 for Windows edition. Wageningen, The Netherlands.
- Norris K. & Johnstone I. 1998. The functional response of oystercatchers (*Haematopus ostralegus*) searching for cockles by touch. *J. Anim. Ecol.* 67: 329–346.
- Overgaard J., Andersen J.B. & Wang T. 2002. The effects of fasting duration on the metabolic response to feeding in *Phyton molurus*: an evaluation of the energetic costs associated with gastrointestinal growth and upregulation. *Physiol. Biochem. Zool.* 75: 360–368.
- Penry D.L. & Jumars P.A. 1987. Modeling animal guts as chemical reactors. *Am. Nat.* 129: 69–96.
- Perry G. & Pianka E.R. 1997. Animal foraging: past, present and future. *Trends Ecol. Evol.* 12: 360–364.
- Piersma T. & Davidson N.C. 1992. The migrations and annual cycles of five subspecies of knots in perspective. *Wader Study Group Bull.* 64: 187–197.
- Piersma T., Koolhaas A. & Dekinga A. 1993. Interactions between stomach structure and diet choice in shorebirds. *Auk* 110: 552–564.
- Piersma T. 1994. Close to the edge: Energetic bottlenecks and the evolution of migratory pathways in knots. Uitgeverij het Open Boek, Den Burg.
- Piersma T., van Gils J.A., de Goeij P. & van der Meer J. 1995. Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. *J. Anim. Ecol.* 64: 493–504.

- Piersma T. & Lindström Å. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends Ecol. Evol.* 12: 134–138.
- Piersma T. 1998. Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight. *J. Avian Biol.* 29: 511–520.
- Piersma T. & Gill Jr. R.E. 1998. Guts don't fly: small digestive organs in obese bar-tailed godwits. *Auk* 115: 196–203.
- Piersma T., Gudmundsson G.A. & Lilliendahl K. 1999. Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird. *Physiol. Biochem. Zool.* 72: 405–415.
- Piersma T., Dekinga A., van Gils J.A., Achterkamp B. & Visser G.H. 2003. Cost-benefit analysis of mollusc-eating in a shorebird. I. Foraging and processing costs estimated by the doubly labelled water method. *J. Exp. Biol.* 206: 3361–3368.
- Piersma T. & Drent J. 2003. Phenotypic flexibility and the evolution of organismal design. *Trends Ecol. Evol.* 18: 228–233.
- Piersma T., Gessaman J.A., Dekinga A. & Visser G.H. 2004. Gizzard and other lean mass components increase, yet basal metabolic rates decrease, when red knots *Calidris canutus* are shifted from soft to hard-shelled food. *J. Avian Biol.* 35: 99–104.
- Piersma T., Rogers D.I., González P.M., Zwarts L., Niles L.J., De Lima Serrano do Nascimento I., Minton C.D.T. & Baker A.J. 2005. Fuel storage rates before northward flights in Red Knots worldwide: facing the severest ecological constraint in tropical intertidal environments? In: Greenberg R. & Marra P.P. (eds) *Birds of two worlds: ecology and evolution of migration: 262–273*. Johns Hopkins University Press, Baltimore.
- Pulliam H.R. 1974. On the theory of optimal diets. *Am. Nat.* 108: 59–75.
- Relyea R.A. & Auld J.R. 2004. Having the guts to compete: how intestinal plasticity explains costs of inducible defenses. *Ecol. Lett.* 7: 869–875.
- Sinervo B. & Basolo A.L. 1996. Testing adaptation using phenotypic manipulations. In: Rose M.R. & Lauder G.V. (eds) *Adaptation: 149–185*. Academic Press, New York.
- Starck J.M. 1999. Phenotypic flexibility of the avian gizzard: rapid, reversible and repeated changes of organ size in response to changes in dietary fibre content. *J. Exp. Biol.* 202: 3171–3179.
- Stearns S.C. & Schmid-Hempel P. 1987. Evolutionary insights should not be wasted. *Oikos* 49: 118–125.
- Stephens D.W. & Krebs J.R. 1986. *Foraging theory*. Princeton University Press, Princeton.
- Stephens D.W., Brown J.S. & Ydenberg R.C. 2007. *Foraging*. University of Chicago Press, Chicago.
- Tieleman B.I., Williams J.B., Buschur M.E. & Brown C.R. 2003. Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? *Ecology* 84: 1800–1815.
- Tomkovich P.S. 2001. A new subspecies of red knot *Calidris canutus* from the New Siberian Islands. *Bull. Brit. Orn. Club* 121: 257–263.
- van Gils J.A., Piersma T., Dekinga A. & Dietz M.W. 2003a. Cost-benefit analysis of mollusc-eating in a shorebird. II. Optimizing gizzard size in the face of seasonal demands. *J. Exp. Biol.* 206: 3369–3380.
- van Gils J.A., Schenk I.W., Bos O. & Piersma T. 2003b. Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. *Am. Nat.* 161: 777–793.
- van Gils J.A. 2004. Foraging decisions in a digestively constrained long-distance migrant, the red knot (*Calidris canutus*). PhD Thesis, University of Groningen, Groningen.
- van Gils J.A., Edelaar P., Escudero G. & Piersma T. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. *Oikos* 104: 197–204.
- van Gils J.A. & Piersma T. 2004. Digestively constrained predators evade the cost of interference competition. *J. Anim. Ecol.* 73: 386–398.
- van Gils J.A., Battley P.F., Piersma T. & Drent R. 2005a. Reinterpretation of gizzard sizes of red knots worldwide emphasises overriding importance of prey quality at migratory stopover sites. *Proc. R. Soc. Lond. B* 272: 2609–2618.
- van Gils J.A., de Rooij S.R., van Belle J., van der Meer J., Dekinga A., Piersma T. & Drent R. 2005b. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. I. Prey choice. *J. Anim. Ecol.* 74: 105–119.
- van Gils J.A., Dekinga A., Spaans B., Vahl W.K. & Piersma T. 2005c. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. II. Patch choice and length of working day. *J. Anim. Ecol.* 74: 120–130.
- van Gils J.A., Piersma T., Dekinga A., Spaans B. & Kraan C. 2006a. Shellfish dredging pushes a flexible avian top predator out of a marine protected area. *PLoS Biol.* 4: e376.
- van Gils J.A., Spaans B., Dekinga A. & Piersma T. 2006b. Foraging in a tidally structured environment by red knots (*Calidris canutus*): ideal, but not free. *Ecology* 87: 1189–1202.
- Vásquez R.A. & Kacelnik A. 1998. Animal foraging: more than met the eye. *Trends Ecol. Evol.* 13: 110–111.
- Ward D. 1992. The role of satisficing in foraging theory. *Oikos* 63: 312–317.
- Wiersma P. & Piersma T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. *Condor* 96: 257–279.

SAMENVATTING

Er bestaat een toenemende belangstelling onder ornithologen voor omkeerbare fenotypische veranderingen, in het bijzonder voor grootteveranderingen in het maagdkanaal van langeafstandstrekkingen. In dit artikel presenteren we een overzicht van de kosten-batenanalyses die we maakten van de flexibele spiermaag van de Kanoet *Calidris canutus*. Door de hardheid van het aangeboden voedsel te variëren, manipuleerden we de grootte van de spiermaag. Dit stelde ons in staat de energetische kosten en baten van foerageren uit te drukken als functie van de spiermaaggrootte. Deze functies maakten het mogelijk de optimale spiermaaggrootte te modelleren, zowel voor Kanoeten op trek als

tijdens de winter. We namen hierbij aan dat Kanoeten of (i) probeerden hun dagelijkse energiebudget in balans te houden, of (ii) probeerden hun dagelijkse energiebudget te maximaliseren. Het model voorspelde nauwkeurig de variatie in spiermaaggrootte die we vonden (1) tussen jaren, (2) binnen jaren en (3) tussen plekken. Het bleek dat de magen van Kanoeten in de winter geschikt waren om het energiebudget in balans te houden, terwijl ze in de opvetperiodes voor de wegtrek groot genoeg waren om het budget te maximaliseren. Deze toetsing van het magenmodel geeft het belang aan van verteringsbeperkingen en prooikwaliteit in het leven van Kanoeten.

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