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Optimal digestion strategies in seabirds: A modelling approach

Geoff M. Hilton, Graeme D. Ruxton,* Robert W. Furness and David C. Houston

Ornithology Group, Division of Environmental & Evolutionary Biology, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK

ABSTRACT

It has been shown that there can be marked differences between seabird species in gut retention times and digestive efficiencies, even when eating the same amounts of the same foods. We use mathematical modelling to explore the relationship between optimal avian digestion strategy and various ecological factors. The key factor determining the performance of a given digestive strategy is an 'ingestion bottleneck', which forces individuals to reduce their ingestion rate once their gut is full of digesta. The severity of the bottleneck is related to the retention time of digesta, with the result that an individual's optimal time and energy management differs according to digestive physiology. The model predicts that rapid (and thus inefficient) digestion is likely to be favoured when the energy cost of commuting between feeding and nesting sites is large, whereas slow (but efficient) digestion is preferable when these costs are small.

Keywords: digestion strategy, digestive efficiency, modelling, retention time, seabirds.

INTRODUCTION

It is well known that diet type influences gut retention time, digestive efficiency and gut morphology (e.g. Warner, 1981; Demment and Van Soest, 1985; Karasov and Diamond, 1988; Castro *et al*., 1989; Karasov, 1990, 1996). During experiments on digestion in both birds of prey (Barton and Houston, 1993a,b, 1994) and seabirds (Jackson, 1992; Hilton *et al*., in press), marked variation in digestion parameters among species feeding on the same diet have been observed. For birds of prey, Barton and Houston (1993a,b, 1994) explained this variation in terms of differences between the feeding ecologies of the study species. They argued that a key feature of the digestive process was the cost of carrying ingested food, whether expressed as reduced prey capture rates, increased energy expenditure in flight or increased predation risk. Calder *et al*. (1990) showed that male hummingbirds may keep the gut nearly empty for much of the day, even when food is abundant, apparently to improve flight performance. Similarly, if retention time determines the rate at which new food can be eaten, then digestion may affect time and energy budgets (Kenward and Sibly, 1977; Diamond *et al*., 1986; Zwarts and Dirksen, 1990; Kersten and Visser, 1996).

* Author to whom all correspondence should be addressed. e-mail: g.ruxton@bio.gla.ac.uk

The 'digestion paradigm' (Sibly, 1981; Karasov, 1996) predicts that the proportion of available energy that is absorbed from a meal is a function of the time that the digesta is held in the gut. This means that digestive efficiency is causally related to gut retention time, in what can be considered a trade-off: long retention times result in high digestive efficiency, but may have associated costs; short retention times give rise to low digestive efficiency, but may have associated benefits.

Here, we model some of these effects for seabird species, and determine how aspects of fitness vary according to how this trade-off is manifested. Specifically, we develop time–energy budgets during the chick-rearing period for two contrasting holarctic seabird species – the Common Murre, *Uria aalge*, and the Herring Gull, *Larus argentatus*. We use an experimentally derived relationship between gut retention time and digestive efficiency in these and six other seabird species (Hilton *et al.*, in press) to define a range of plausible digestion strategies, where a strategy is defined as a point on this trade-off relation. We then quantify the effect of varying excretion rate (and, because of the trade-off, necessarily varying digestive efficiency also) on daily energy expenditure and foraging time. For each species, we determine the optimal digestion strategy under a range of realistic foraging conditions. We aim to elucidate the ecological factors that are likely to lead to selection for a given digestion strategy.

We selected the two modelled species for several reasons: they are similar in size and have similar gut capacities, and yet they differ significantly in both gut retention time and digestive efficiency when given the same quantities of the same diets (G. Hilton, unpublished data). Herring Gulls had slower but more efficient digestion than Common Murres when fed on two fish species that regularly occur in the diet of both species in the north-east Atlantic. Furthermore, the two species' ecologies differ considerably. Both species make discrete commuting trips to feeding sites that are removed from the nest territory. However, Herring Gulls are generalist foragers, consuming a wide variety of food types, frequently including low-quality items (i.e. low energy density or resistant to digestion; Cramp and Simmons, 1983). They have low wing loadings (Pennycuick, 1987) and frequently use gliding flight, and so have relatively low flight energy expenditure (Pennycuick, 1989). They carry large quantities of food back to a brood of up to three chicks, which fledge at adult mass. By contrast, Common Murres are specialist piscivores, eating mainly small shoaling fish (Bradstreet and Brown, 1985; Cramp, 1985) which are relatively energy dense (Wallace and Hulme, 1977; Montevecchi and Piatt, 1984; Hislop *et al.*, 1991) and easy to digest (Hilton *et al.*, 1998). Their wing loading is among the highest of any flying bird (Pennycuick, 1989), and they frequently make long flights to the feeding grounds (Bradstreet and Brown, 1985; Phillips *et al.*, in press). They carry only very small quantities of food back to a single chick, which fledges at one-third of adult mass (Harris and Birkhead, 1985).

METHODS

In a study of eight North Atlantic seabird species, Hilton *et al.* (in press) found a negative relationship between digestive efficiency, measured as the nitrogen-corrected true metabolizable energy coefficient ($TMEC_N$; Miller and Reinecke, 1984), and mean retention time of digesta. We adapt this interspecific relation to approximate the likely trade-off between the two conflicting beneficial traits – rapid digestion and high digestive efficiency – within individuals of our model species. Clearly, using a relation derived from average

values for species to estimate the trade-off that would be experienced by an individual is not ideal. However, it is extremely difficult to study this trade-off empirically within a species or within an individual. As with most trade-offs between conflicting beneficial traits, a negative intraspecific relationship between the traits is unlikely to be detected, because it is likely to be confounded by individual quality: high-quality birds can achieve both rapid digestion *and* high digestive efficiency. In many studies of evolutionary trade-offs, individuals are manipulated to remove the confounding quality effect. One could manipulate the digestion rate of individuals by acclimating them to diets of differing digestibilities, or administering drugs that alter gastrointestinal motility (see Afik and Karasov, 1995). This may provide convincing evidence that a trade-off exists, but the effects of the manipulation on digestive function mean that this is most unlikely to quantify the trade-off satisfactorily, hence our adoption of a relationship obtained by interspecific comparison.

For each of the eight species, a negative exponential curve was fitted to plots of cumulative wet excreta production against time after a meal, and from the fitted curves we calculated Δ, the specific excretion rate (% wet meal mass excreted per second). $TMEC_N$ was related to Δ in the following relationship:

$$TMEC_N = 0.628 \times \Delta^{-0.043} \qquad (F_{1,6} = 7.5;\ r^2 = 0.56;\ P = 0.03) \qquad (1)$$

which was used in the model to define the resultant digestive efficiency for any given specific excretion rate (see Miller and Reinecke, 1984, for a full discussion on different measures of digestive efficiency).

Model overview

The model derives those combinations of number and duration of foraging trips that allow the bird to balance its energy budget over a 24 h period, while delivering enough food to the chick(s). These combinations were calculated for a rapid digester (high specific excretion rate) and a slow digester (low specific excretion rate), under a range of plausible combinations of food energy density and foraging range. Thus we compare a hypothetical slow-digesting Common Murre with a rapid-digesting individual of the same species, and consider the impact on a Herring Gull of adopting a rapid digestion strategy versus a slow digestion strategy. We consider two separate optimization criteria: first, 'time minimization', in which the bird aims to minimize the time spent away from the nest; and, secondly, 'energy minimization', in which the bird aims to minimize its daily energy expenditure.

Optimization criteria

Minimizing time spent on feeding trips is a means of maximizing time spent at the nest. This is likely to reduce the risk of predation on the chick or chicks – a major cause of mortality in both species (Hatchwell, 1991; Bukacinska *et al*., 1996) – and strengthen pair bonds, which is an important behaviour in species such as these that pair for life (Nelson, 1988). Minimizing daily energy expenditure is a means for an individual to maximize its residual reproductive value (Daan *et al*., 1990). When feeding conditions are favourable, Common Murres do not increase chick provisioning; instead, they spend more time resting at the colony (Burger and Piatt, 1990; Monaghan *et al*., 1994). This is consistent with the suggestion that, once the threshold for healthy chick growth has been reached, they seek to minimize time away from the nest and/or their own energy expenditure.

Model definition

Strategy

The strategy of a pair of birds is defined by the number of feeding trips (n) which each bird makes, and its specific excretion rate (Δ). We assume that each bird in the pair makes the same number of trips. We further assume that the total time available to the pair for feeding trips (T) is 18 h (86,400 s) per day, since neither species regularly forages in darkness during the chick-rearing period (Sibly and McLeery, 1983; Harris and Wanless, 1985). In Common Murres, it is normal for one parent to attend the chick at all times (Wanless *et al.*, 1988). Therefore, in the model, we allow each member of the pair 9 h per day in which to forage, and assume that the birds alternate feeding trips. Time limits are less strict for Herring Gulls: pairs of this species with large chicks often leave them unattended, so we allow each member of the pair up to 18 h per day of feeding trip time. Thus, for Common Murres, trip durations cannot exceed t_{max} seconds, where

$$t_{max} = \frac{T}{2n} \tag{2}$$

If we measure time of day (t_{day}) starting from dawn, then one bird will begin its trips at times $t_{day} = 0$, $2t_{max}$, $4t_{max}$, etc., whereas its partner will begin at $t_{day} = t_{max}$, $3t_{max}$, etc. This alternation will continue until one bird is due to leave at time $t_{day} = T$. For Herring Gulls, trip durations cannot exceed

$$t_{max} = \frac{T}{n} \tag{3}$$

Energy needs

Let us assume that the daily energy requirements of the brood is given by a constant E_{chick}, and the daily requirements of an adult which remains at the nest are given by E_{adult} (both measured in kilojoules). We assume that, on each feeding trip, sufficient assimilable energy is gathered to cover the extra costs incurred during the feeding trip and to gather extra energy equivalent to

$$\frac{E_{chick}}{2n} + \frac{E_{adult}}{n} \tag{4}$$

The extra energy costs of the feeding trip can be broken down into the flight costs of commuting to and from the foraging grounds, and the costs incurred at the feeding site.

Outward flight

The extra power required for powered flight with different payloads can be calculated from Pennycuick (1989). A key component of our model is that flight costs are a function of mass. Specifically, for a Common Murre of mass W (g), the cost of flapping flight (in watts) is given by

$$F(W) = 0.0018\,W^{1.6} \tag{5}$$

For Herring Gulls, this becomes

$$F(W) = 0.0012\,W^{1.5} \tag{6}$$

Furthermore, we assume that, while Common Murres use flapping flight exclusively, Herring Gulls flap for 50% of the time and glide for the remainder (Norstrom *et al.*, 1986). The energy costs of gliding flight are generally considered to be twice the resting metabolic rate (RMR; Baudinette and Schmidt-Nielsen, 1974). Hence, the actual extra costs of flight in a Herring Gull are given by

$$F(W) = 0.0006W^{1.5} + \mathrm{RMR} \tag{7}$$

We assume that every time a bird begins its foraging trip, all food from previous trips has been processed, so the bird's mass is simply a constant 'empty mass', W_e. Thus, if the foraging area is a distance D (km) from the nest, and the bird flies at a constant speed V (in $\mathrm{m \cdot s^{-1}}$), then the extra energy used in the outbound flight, E_{out} (kJ), is given by

$$E_{out} = \frac{F(W_e)\mathrm{D}}{V} \tag{8}$$

Feeding and excretion rates

While at the feeding site, the bird eats food at a variable rate S ($\mathrm{g \cdot s^{-1}}$). As it forages, the mass of food it carries (W_f) increases. If the mass of food carried is lower than maximum capacity of the gut (W_{max}), then the feeding rate is unconstrained by digestive considerations and proceeds at a constant rate (S_{max}). However, if the bird's digestive tract is full, then it is forced to ingest food at a (generally lower) rate (denoted S_{min}) equivalent to the rate at which mass is excreted.

To describe time at the feeding site (t seconds), we now define the time that the bird arrives at the feeding site as $t = 0$. The bird begins filling its digestive tract at this time at rate S_{max}. However, no food is excreted until after a fixed (transit) time $t_{transit}$ (estimated from direct observation during digestion trials to be 60 min for Herring Gull and 70 min for Common Murre). Sibly (1981) argued that the rate at which mass is output from digestive chambers is generally proportional to the mass of digesta in the chamber. Hence, we assume that excretion rate is solely dependent on gut contents, regardless of the length of time that food is retained in the gut (with the exception that no excretion occurs until $t = t_{transit}$). From the moment that $t \geq t_{transit}$, excretion is proportional to gut contents. Specifically, the excretion rate (in $\mathrm{g \cdot s^{-1}}$) is given by the product of the mass of food in the digestive tract (W_f) and the specific excretion rate (Δ) defined earlier. This means that food particles take variable times to pass through the bird. This distribution of times is bounded below, since excretion rate is never greater than the ingestion rate while the bird is feeding. Implicitly, this means that all food particles take at least time $t_{transit}$ to pass through the bird. Mathematically, we can define how the feeding rate changes under different circumstances as follows:

$$S = \begin{cases} S_{max} & \text{if } W_f < W_{max} \\ 0 & \text{if } W_f = W_{max} \quad \text{and} \quad t < t_{transit} \\ S_{min} & \text{if } W_f = W_{max} \quad \text{and} \quad t \geq t_{transit} \end{cases} \tag{9}$$

where $S_{min} = \Delta W_f$.

The amount of food in the digestive tract starts at zero, when $t = 0$, increases due to feeding and decreases due to excretion. The feeding rate (S) will depend on gut fullness and whether or not excretion is occurring (see equation 9). Excretion begins after the bird has

been feeding for a time t_{transit}, after which it occurs at a rate $S_{\min} = \Delta W_{\text{f}}$. Thus the weight of food in the gut changes according to the following equation:

$$\frac{\mathrm{d}W_{\text{f}}}{\mathrm{d}t} = \begin{cases} S & \text{if } t < t_{\text{transit}} \\ S - S_{\min} & \text{if } t \geq t_{\text{transit}} \end{cases} \tag{10}$$

This equation ensures that $W_{\text{f}} \leq W_{\max}$. After the gut becomes full, equation (9) ensures that feeding either stops (i.e. S is set to zero) if excretion has not started, or occurs at the same rate as excretion ($S = S_{\min}$), such that the gut is always kept full.

Cost of foraging

We can also calculate the extra energy spent at the feeding site (E_{forage}) (kJ). We assume that the bird divides its time between resting on the water (which costs an extra R_{water} watts above RMR) and actively feeding (which costs an extra R_{feeding} watts above RMR). Specifically, E_{forage} starts at zero when $t = 0$ and increases as follows:

$$\frac{\mathrm{d}E_{\text{forage}}}{\mathrm{d}t} = \frac{R_{\text{water}} + S(R_{\text{feeding}} - R_{\text{water}})/S_{\max}}{1000} \tag{11}$$

The factor of 1000 occurs since we measure E_{forage} in kilojoules but measure R_{water} and R_{feeding} in watts, which are joules per second.

Flight back to nest

We need to calculate the cost of the homeward flight. This is more complicated than for the outbound trip because an individual's mass will decrease through excretion during the flight. If the bird leaves the feeding site at a time t_{L} (measured from the point of arrival), then the energy cost of the homeward flight (in kJ) will be given by

$$E_{\text{back}} = \frac{\int_{t_{\text{L}}}^{t_{\text{L}} + D/V} F(W_{\text{e}} + W_{\text{f}}(t))\mathrm{d}t}{1000} \tag{12}$$

where, from time t_{L}, W_{f} changes according to

$$\frac{\mathrm{d}W_{\text{f}}}{\mathrm{d}t} = \begin{cases} 0 & \text{if } t < t_{\text{transit}} \\ -S_{\min} & \text{if } t \geq t_{\text{transit}} \end{cases} \tag{13}$$

Energy gathered

The last quantity we need to define is the total energy gathered during a feeding period (E_{in}) in kilojoules. This starts at zero when the bird arrives at the feeding site ($t = 0$) and increases according to

$$\frac{\mathrm{d}E_{\text{in}}}{\mathrm{d}t} = \begin{cases} QS & \text{if } E_{\text{in}} < E_{\text{chick}} \\ eQS & \text{if } E_{\text{in}} \geq E_{\text{chick}} \end{cases} \tag{14}$$

where Q is the energy density of the food ($\text{kJ} \cdot \text{g}^{-1}$ wet weight), e is TMEC_{N} ($0 < e < 1$) and S is the variable rate at which food mass is ingested (given by equation 9). The energy which the bird gathers for the chick is not assimilated, so is not subjected to losses incurred in this

process. In reality, the bird probably gathers this food for the chick at the end of its feeding period. Here, for mathematical convenience, it is gathered at the start, but this has no effect on the model's predictions.

Time spent at feeding site

Using the equations above, we can calculate the energy gathered (E_{in}) for any given time interval at the feeding site (t). We can also calculate the fixed energy requirements (E_{adult}, E_{chick} and E_{out}) and the costs of feeding for a time (t), $E_{forage}(t)$, and of flying back to the nest after this time, $E_{back}(t)$. To find the unique value of t (t^*) where the individual gathers exactly enough energy to cover its costs, we solve

$$E_{in}(t^*) = \frac{E_{adult}}{n} + \frac{E_{chick}}{2n} + E_{out} + E_{forage}(t^*) + E_{back}(t^*) \tag{15}$$

Providing that the bird can gather assimilable energy faster than it expends energy during foraging, this equation has a unique solution: this is the time that we assume the bird spends at the feeding site. We find this time for every possible value of daily feeding trip numbers (n) that can be accomplished within the time limit, that is, for which

$$t^* + \frac{2D}{V} \leq t_{max} \tag{16}$$

From this subset, we find the value of n which optimizes one of our two criteria (see earlier). This is the optimal strategy, for which we can determine the time spent and the energy expended over a whole day.

An alternative energy-minimizing strategy – 'sit and wait'

Consider an alternative strategy whereby the bird saves flight energy costs on the return journey to the nest by sitting on the water for as long as it can before flying back to the nest just within the maximum trip duration restriction. If the individual forages for a time t, then it can wait on the water for a time

$$t_{max} - t - \frac{2D}{V} \tag{17}$$

before flying back. We assume that there is an added cost (measured in kJ) to resting on the water compared to the protected micro-climate of the nest. This is given by

$$E_{sit} = R_{water}\left(t_{max} - t - \frac{2D}{V}\right) \tag{18}$$

However, the bird's flight energy costs will be reduced because it will have been losing mass according to equation (13) during the time that it remained on the water at the feeding site. As before, we find the unique foraging time (i.e. the time beteween arriving in the foraging area and finally quitting feeding), t^*, under the assumption that the bird will then sit on the water as long as possible before flying back. This t^* is obtained by solving

$$E_{in}(t^*) = \frac{E_{adult}}{n} + \frac{E_{chick}}{2n} + E_{out} + E_{forage}(t^*) + E_{sit} + E_{back}(t^*) \tag{19}$$

Model runs

For Common Murres, model runs simulate commonly observed foraging ranges (D) of 0–100 km, food energy densities (Q) of 4–8 $kJ \cdot g^{-1}$ wet weight, and maximum ingestion rates (S_{max}) of 0.037 $g \cdot s^{-1}$. For Herring Gulls, these parameters become $D = 0$–30 km, $Q = 3$–7 $kJ \cdot g^{-1}$ wet weight and $S_{max} = 0.067\ g \cdot s^{-1}$. The Appendix gives published information on plausible foraging conditions and other parameter values adopted in the model. For each species and set of foraging circumstances, we consider both a slow ($\Delta = 0.0015\%$ meal mass $\cdot s^{-1}$) and a rapid ($\Delta = 0.011\%$ meal mass $\cdot s^{-1}$) digestion strategy. This corresponds to the range of values observed in our experimental studies, and allows $TMEC_N$ to vary between 0.76 and 0.83.

RESULTS

Patterns of energy gain

Figure 1 compares the cumulative assimilable energy gain of a slow digester with a fast digester over the course of a feeding period, and is key to the outcomes of the model. Initially, the rate of energy gain is determined by the rate at which food can be ingested, and the efficiency with which that food is then digested. During this period, energy gain is rapid for both strategies, but is slightly higher for the slow digester, because it has higher digestive efficiency. This period of rapid energy gain continues until the gut is full. From this point, food can only be ingested if space is created in the gut by excretion, and therefore ingestion rate is limited by excretion rate. If gut fill is reached before excretion starts, then ingestion must cease completely until excretion commences. Thereafter, ingestion rate

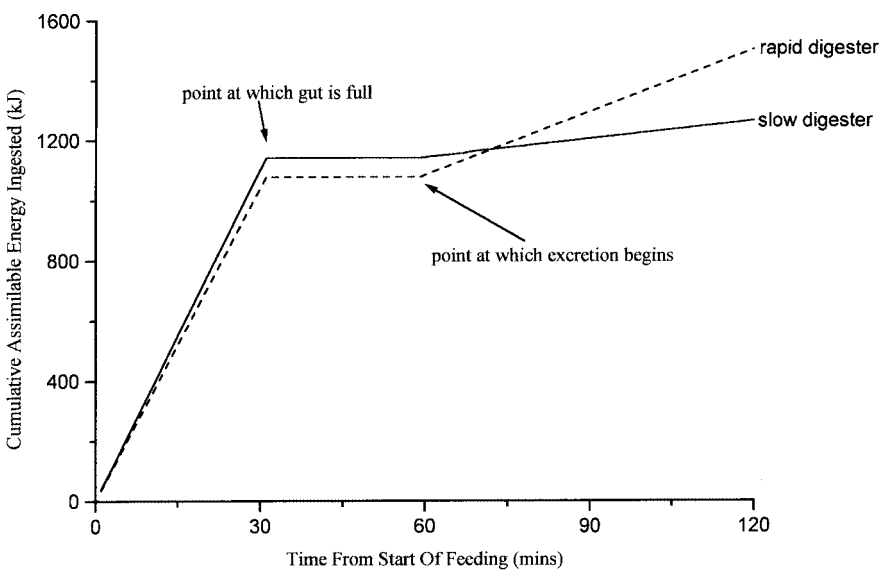

Fig. 1. Cumulative energy assimilation curves during a feeding period for a low excretion rate and a high excretion rate strategy.

is equal to excretion rate. The crucial point is that the rate of excretion of both fast and slow digesters is much lower than the unconstrained rate of ingestion. Thus, following gut fill there is a major 'ingestion bottleneck' on energy assimilation, and the severity of this bottleneck is determined by the excretion rate: its impact is much greater for slow digesters than for fast digesters.

Time minimization

For any digestion strategy, there are two key behavioural tactics which aid the minimization of daily foraging time. First, birds should avoid the ingestion bottleneck by terminating feeding periods at or before gut fill, because after gut fill, energy gain is relatively slow, and therefore this is very time-inefficient. Secondly, each feeding trip incurs a fixed time penalty – flight time between nest and feeding grounds – so that infrequent trips with long feeding periods should be favoured. There is, however, conflict between these two tactics; the former favours a limited feeding period on each trip and the latter favours long feeding periods. The optimal strategy balances these pressures to give the shortest possible time away from the nest.

Where the balance lies is dependent on both the digestion strategy and the foraging conditions. Figures 2a and 2b show the optimal number of feeding trips per day for rapid- and slow-digesting Common Murres and Herring Gulls eating high- and low-quality food, at a range of foraging distances. Feeding trip frequency decreases as food energy density increases, simply because less food must be gathered to assimilate the required amount of energy. Avoidance of the ingestion bottleneck is more important for slow digesters, as can be seen in Fig. 1, and therefore they tend to make more and shorter feeding trips than rapid digesters under many combinations of food energy density and foraging range. Under foraging conditions where rapid digesters do make fewer trips, rapid digestion is almost always the time-minimizing strategy (Figs 3a,b). Under those foraging conditions where the optimal trip frequency does not differ between digestion strategies, slow digestion is the time-minimizing strategy, but by small margins only.

For Common Murres, rapid digestion is the time-minimizing strategy under most realistic foraging conditions, often by a large margin of up to 200 $\text{min} \cdot \text{day}^{-1}$ (Fig. 3a). For Herring Gulls, slow digestion is the time-minimizing strategy when foraging conditions are more favourable (high food energy density and/or short foraging range), and rapid digestion is favoured when conditions are more severe, but the difference between the strategies is never more than about 50 min and rarely more than 15 min (Fig. 3b).

As foraging conditions deteriorate (foraging range increases and food energy density decreases), the minimum time away from the nest increases until a threshold is reached, beyond which the bird is unable to achieve energy balance within the time available. It must presumably then either use body reserves to meet the energy deficit or neglect the chicks. An important prediction of the model is that rapid digesters achieve energy balance within the time limit under more severe foraging conditions than slow digesters. This is illustrated in Fig. 4, which shows the threshold foraging range–food quality combinations (where energy balance can just be obtained) for fast- and slow-digesting Common Murres. For Herring Gulls, we assumed that the absolute limit to daily foraging time is 18 h (see Methods), and this time limit was exceeded only under the harshest of foraging conditions.

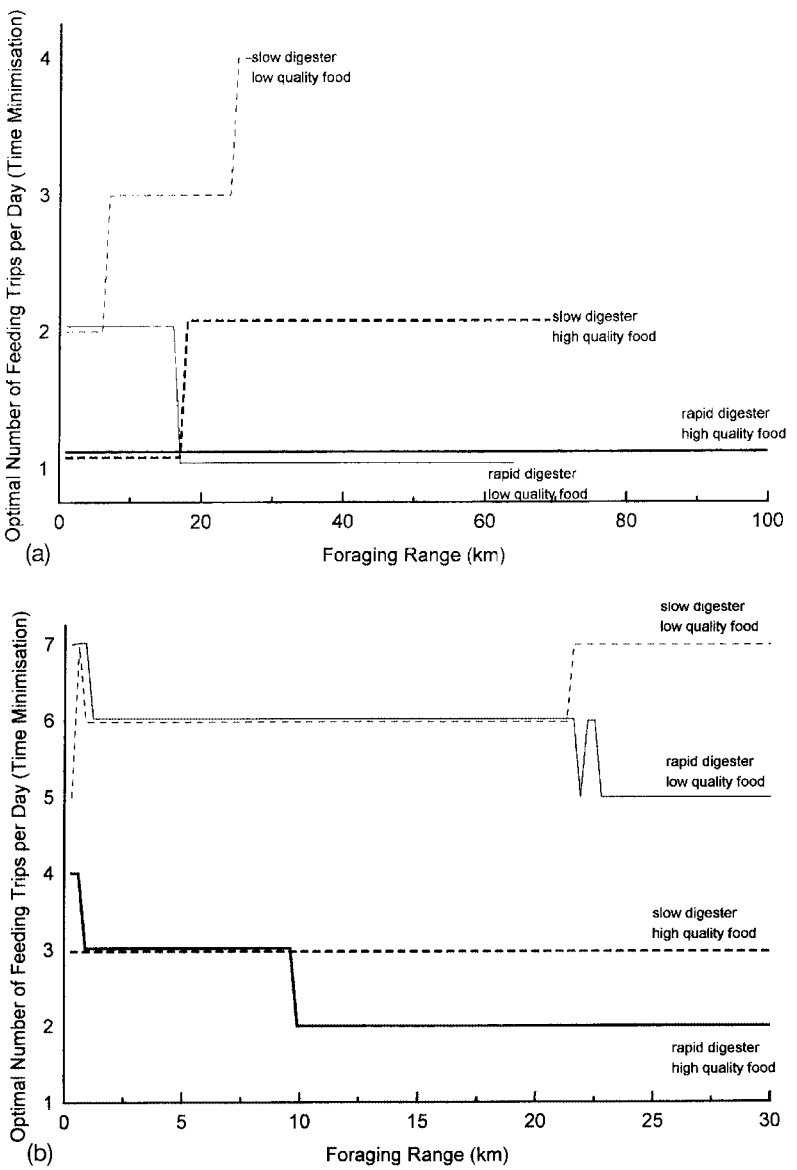

Fig. 2. Optimal feeding trip frequency for minimizing daily foraging time, as a function of foraging range. (a) Common Murre: dashed line = slow digestion ($\Delta = 1.5^{-3}$); solid line = rapid digestion ($\Delta = 0.011$); narrow lines = low-quality food (4 kJ · g^{-1}); thick lines = high-quality food (8 kJ · g^{-1}). (b) Herring Gull: dashed line = slow digestion ($\Delta = 1.5^{-3}$); solid line = rapid digestion ($\Delta = 0.011$); narrow lines = low-quality food (3 kJ · g^{-1}); thick lines = high-quality food (7 kJ · g^{-1}).

Energy minimization

When the minimization of energy expenditure is the optimization criterion, the optimal feeding trip frequency is always the lowest that can be achieved within the constraints of

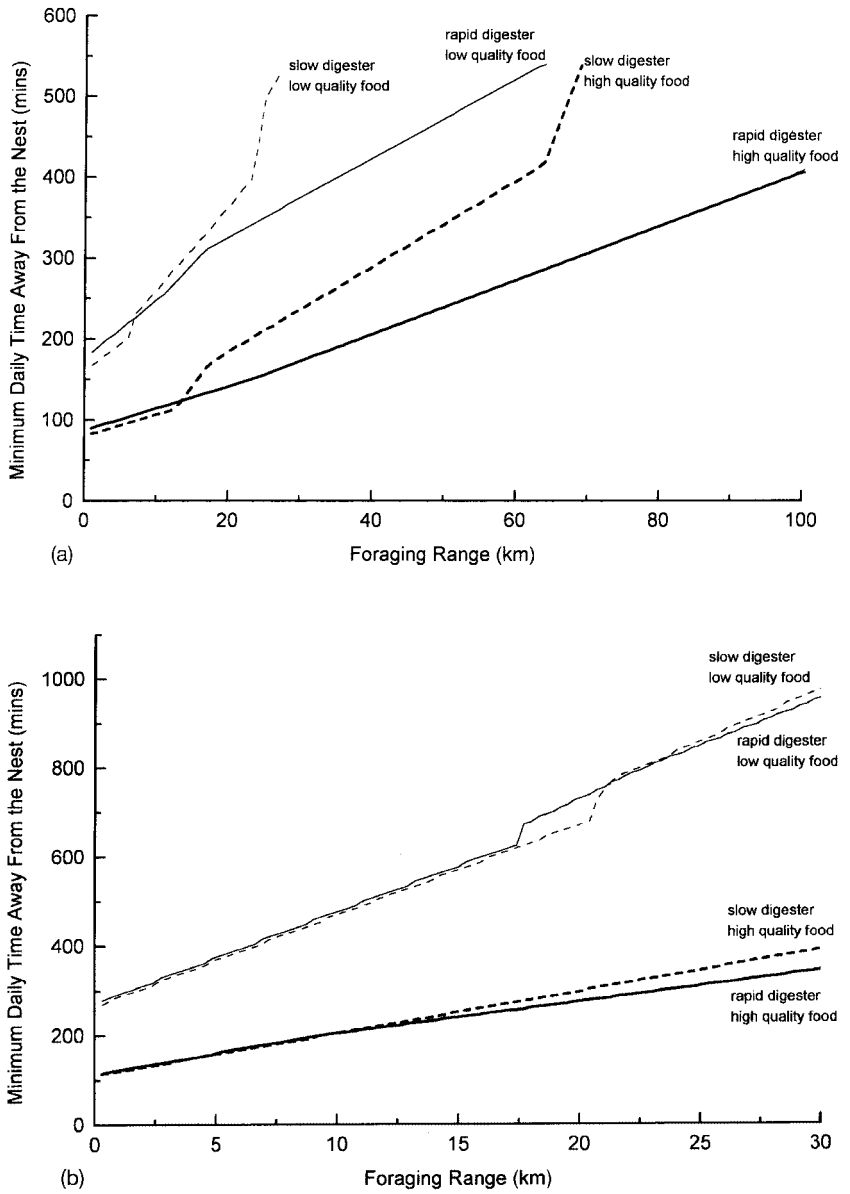

Fig. 3. Minimum daily foraging time as a function of foraging range. (a) Common Murre: dashed line = slow digestion ($\Delta = 1.5^{-3}$); solid line = rapid digestion ($\Delta = 0.011$); narrow lines = low-quality food (4 kJ · g^{-1}); thick lines = high-quality food (8 kJ · g^{-1}). (b) Herring Gull: dashed line = slow digestion ($\Delta = 1.5^{-3}$); solid line = rapid digestion ($\Delta = 0.011$); narrow lines = low-quality food (3 kJ · g^{-1}); thick lines = high-quality food (7 kJ · g^{-1}).

chick provisioning. This is because for each feeding trip made, there is a fixed energy cost – the cost of flying to the feeding site. In contrast to the time-minimizing strategy, there is almost no cost associated with continuing to feed after the ingestion bottleneck sets in. The

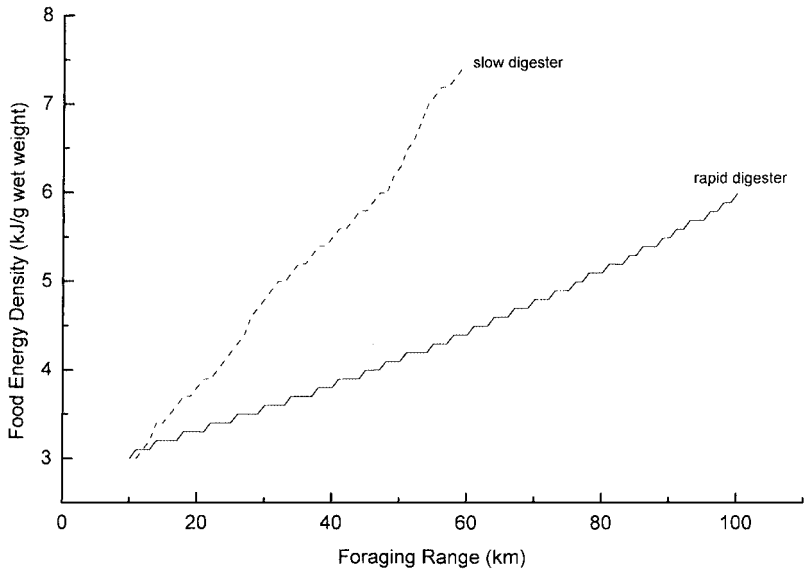

Fig. 4. Threshold combinations of food energy density and foraging range for achieving energy balance in the Common Murre, as a function of digestion strategy. The curves depict the food energy density–foraging range combinations at which the bird meets energy balance in 540 min, the daily time available for foraging. At greater foraging ranges, and/or lower food energy densities, the bird must neglect the chick or accept negative energy balance. Dashed line = slow digestion ($\Delta = 1.5^{-3}$); solid line = rapid digestion ($\Delta = 0.011$). The rapid digester is able to achieve energy balance under much more severe foraging conditions.

difference arises because we assume that when the bird is constrained to reduce its ingestion rate to equal the rate of excretion, it spends the 'spare' time at the feeding site resting on the water surface, which is only marginally more energetically expensive than resting at the nest site (Croll and McLaren, 1993).

The number of feeding trips per day for energy minimization frequently exceeds one, however. If all the daily energy requirements are gathered on a single feeding trip, then a large amount of food must be ingested on that trip, which tends to mean that the feeding period is continued well after the onset of the ingestion bottleneck. Doing this is so time-inefficient that it frequently results in the bird exceeding the maximum daily time away from the nest (9 h and 18 h for Common Murre and Herring Gull, respectively). Thus more and shorter feeding trips must be made to avoid the ingestion bottleneck and meet the time constraints. Also, for the Herring Gull, it is often not possible to carry the entire chick requirements in a single load, due to gut capacity limitations, so extra feeding trips must be made purely to maintain chick provisioning.

As discussed above, rapid digesters have a higher energy assimilation rate after the ingestion bottleneck sets in. This means that, for a given feeding trip frequency, the rapid digester is more likely than the slow digester to be able to achieve energy balance before the time limit is reached, and so avoid having to make an extra feeding trip. Rapid digestion is the energy-minimizing strategy by a considerable margin in those circumstances where the

rapid digester is able to make fewer feeding trips than the slow digester. This is illustrated in Figs 5 and 6, which show optimal number of feeding trips for energy minimization, and minimum daily energy expenditure, for the two species.

There is, however, a counter-advantage to slow digestion. The increased digestive efficiency of this strategy means that less food must be ingested to assimilate the same amount of energy. This can result in energy savings, because less effort must be expended in foraging for that food. Thus, under foraging conditions where minimum feeding trip frequencies are the same for both fast and slow digesters, slow digestion is the energy-minimizing strategy, but only by a small amount.

The model runs indicate that rapid digestion is likely to be favoured for energy minimization in the Common Murre, except where food is of a high quality and the foraging range is small (Fig. 6a). However, under most circumstances, slow digestion is the energy-minimizing strategy for the Herring Gull, the exception to this being under conditions of low food quality and long foraging range (Fig. 6b).

Lastly, for Common Murres, we explored another potential energy-minimizing strategy, which we term 'sit and wait'. Figure 7 illustrates the energy savings that can be made by operating this strategy compared with simply flying back to the nest immediately the feeding period ends (which is the situation we have modelled in the time-minimizing and energy-minimizing sections). The energy savings are proportional to the foraging range and for the larger foraging ranges are considerable, up to about 10% of daily energy expenditure.

DISCUSSION

Which digestion strategy is favoured?

As observed in digestion trials (Hilton *et al.*, 1998, in press), the model successfully predicts that rapid digestion is optimal for Common Murres. For this species, slow digestion appears to be favoured only under conditions of very high food quality and a short foraging range. The model predictions suggest that, under demanding foraging conditions, this species may find it difficult to gather enough energy in the time available for foraging, and therefore a time-minimizing rapid digestion strategy will be very strongly selected. We have also shown that, as Gabrielsen (1996) proposed, a 'sit-and-wait' strategy of remaining at the feeding site can reduce energy expenditure, because excretion of part of the ingested food reduces flying mass.

In contrast, according to the model, neither strategy is clearly better for the Herring Gull, which had longer retention times in digestion trials (Hilton *et al.*, in press). For both optimization criteria, there is a tendency for slow digestion to be favoured when foraging is easy, and for rapid digestion to be favoured when conditions are more severe.

Both species are unlikely to simply have a pure strategy. Individuals will be balancing chick neglect (a time-minimizing consideration) with energy expenditure and chick feeding (energetic considerations). The extent to which any one of these applies at any given moment depends on ecological conditions (e.g. food availability). For guillemots, the last of the three would almost never be dominant – if food was ever that scarce, they would abandon breeding. For gulls, all three could be dominant at different times.

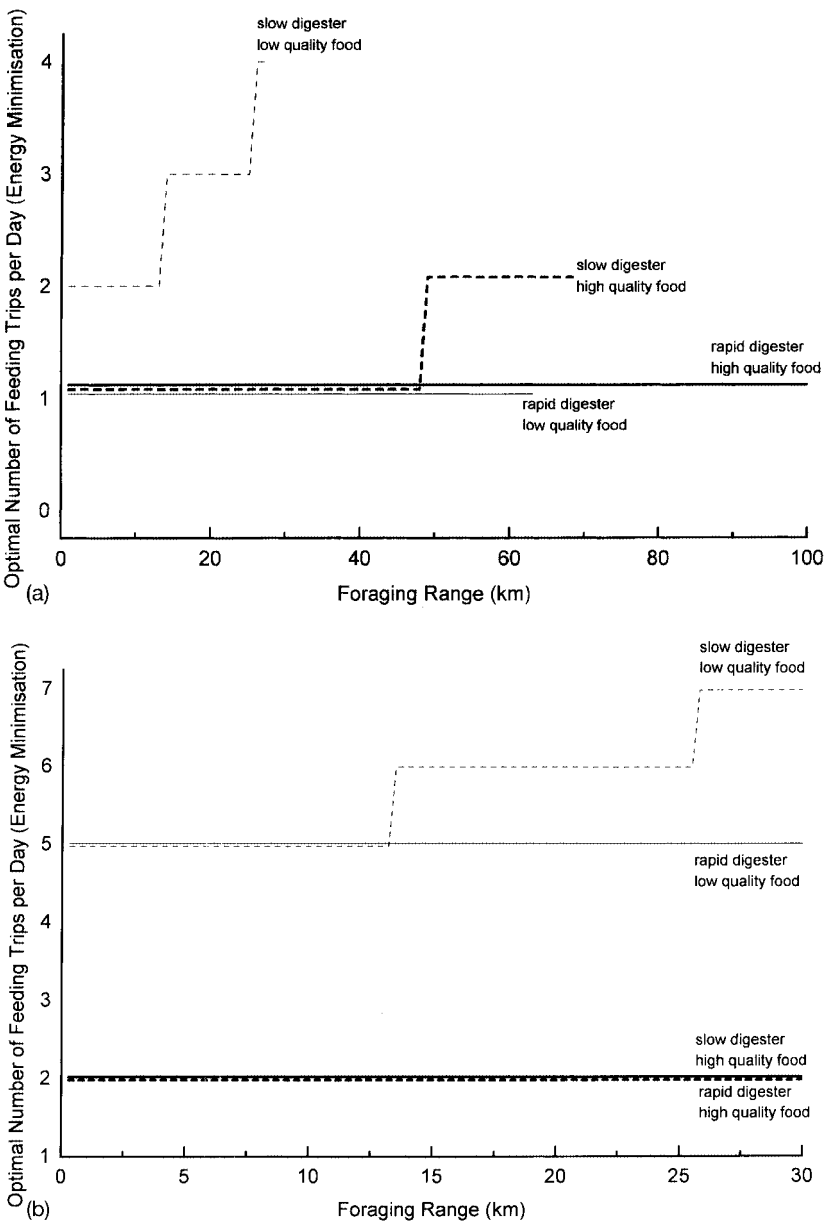

Fig. 5. Optimal feeding trip frequency for minimizing daily energy expenditure, as a function of foraging range. (a) Common Murre: dashed line = slow digestion ($\Delta = 1.5^{-3}$); solid line = rapid digestion ($\Delta = 0.011$); narrow lines = low-quality food (4 kJ · g^{-1}); thick lines = high-quality food (8 kJ · g^{-1}). (b) Herring Gull: dashed line = slow digestion ($\Delta = 1.5^{-3}$); solid line = rapid digestion ($\Delta = 0.011$); narrow lines = low-quality food (3 kJ · g^{-1}); thick lines = high-quality food (7 kJ · g^{-1}).

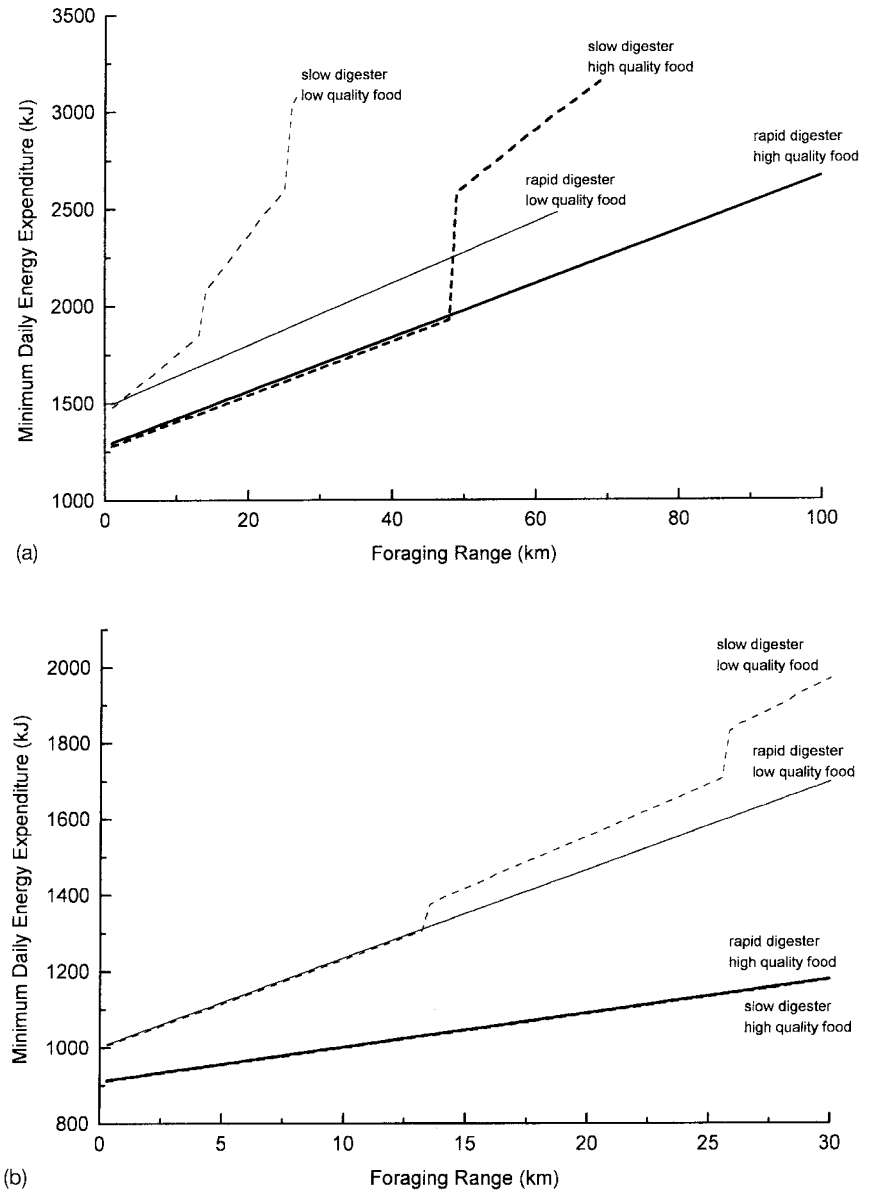

Fig. 6. Minimum daily energy expenditure as a function of foraging range. (a) Common Murre: dashed line = slow digestion ($\Delta = 1.5^{-3}$); solid line = rapid digestion ($\Delta = 0.011$); narrow lines = low-quality food (4 $kJ \cdot g^{-1}$); thick lines = high-quality food (8 $kJ \cdot g^{-1}$). (b) Herring Gull: dashed line = slow digestion ($\Delta = 1.5^{-3}$); solid line = rapid digestion ($\Delta = 0.011$); thin lines = low-quality food (3 $kJ \cdot g^{-1}$); thick lines = high-quality food (7 $kJ \cdot g^{-1}$).

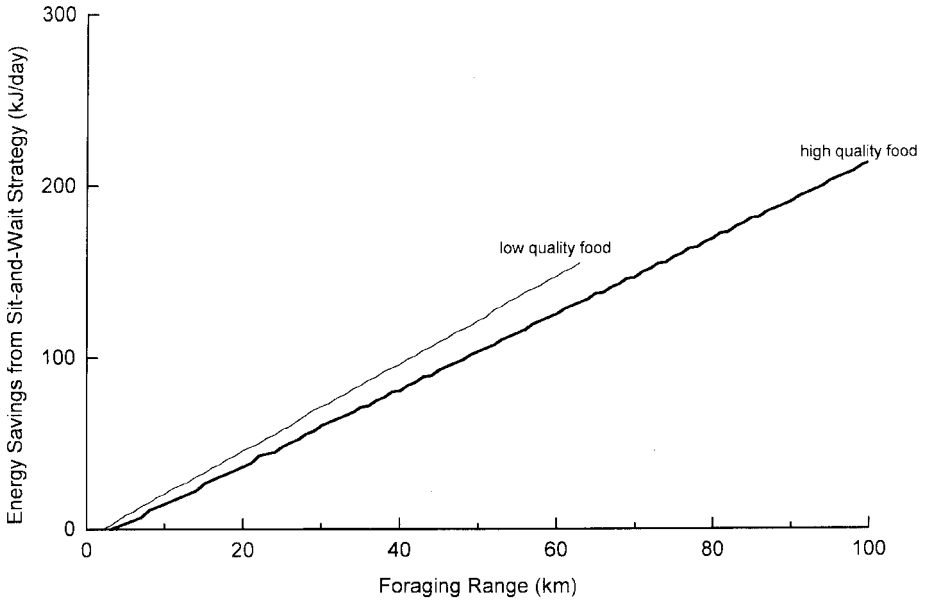

Fig. 7. Daily energy savings that can be achieved by Common Murres adopting the 'sit-and-wait' strategy. Values are $kJ \cdot day^{-1}$ saved, compared to adopting a conventional energy-minimizing strategy of flying back to the nest immediately the foraging period ends. Dashed line = low-quality food (4 $kJ \cdot g^{-1}$); solid line = high-quality food (8 $kJ \cdot g^{-1}$). Both curves represent rapid digestion.

Other factors affecting favoured digestion strategy

Energy assimilation bottlenecks

There has been much interest in the idea that the processing capacity of the gut sets an upper limit to the amount of food an animal can eat and, therefore, to the energy that an animal can metabolize (Kirkwood, 1983; Weiner, 1989, 1992; Suarez, 1996; Hammond and Diamond, 1997). The Common Murre has to eat a large amount of food because it has a high daily energy expenditure (Cairns *et al.*, 1987; Gabrielsen, 1996); the Herring Gull (although it has a lower daily expenditure) will also frequently have to consume large amounts of food because it generally eats food of low energy density (Pons, 1994; Pierotti and Annett, 1987). If an animal has a high food processing requirement, then either gut capacity must be increased or gut retention time must be decreased (Karasov, 1996). Is it possible, therefore, that the digestion rate of our modelled species is influenced by processing capacity limitations?

Following Kersten and Visser (1996), we calculated the maximum energy assimilation of our study species as a function of their excretion rate. To calculate the mass of food processed, we assumed that, over the whole day, the gut was kept on average half-full (i.e. containing approximately 100 ml of digesta). Thus, the daily mass of excreta produced is the specific excretion rate (percent meal mass excreted per second) $\times$ 100 ml $\times$ 86,400 s. The mean ($\pm$ S.D.) asymptotic proportion of wet meal mass excreted by seabird species in

digestion trials was 0.60 ± 0.14, so the total wet mass of food processed (g) is mass excreted ÷ 0.6. Energy assimilated (kJ) from this food mass is

$$\text{food processed} \times \text{food energy density} \times \text{digestive efficiency} \quad (20)$$

where digestive efficiency is $TMEC_N$, calculated from the excretion rate–digestive efficiency trade-off curve.

The models predicted maximum daily energy requirements under harsh foraging conditions of around 2000 kJ · day^{-1} for Herring Gulls and 3000 kJ · day^{-1} for Common Murres (Fig. 6). Figure 8 shows the calculated maximum daily energy assimilation as a function of specific excretion rate for three different food energy densities. When specific excretion rate is very low, daily energy assimilated is below predicted energy requirements, especially where food energy density is low. Avoiding an energy assimilation bottleneck might, therefore, be a factor in selecting against the slowest excretion rates. However, except in these rather exceptional circumstances, maximum energy assimilation seems to exceed energy requirements by a fairly large margin.

Prey capture rate and temporary flightlessness

Barton and Houston (1994) argued that pursuit-foraging raptors adopt a rapid digestion strategy because their flight performance, and hence their hunting ability, is strongly mass-dependent (Andersson and Norberg, 1981), and rapid excretion is a means of rapidly

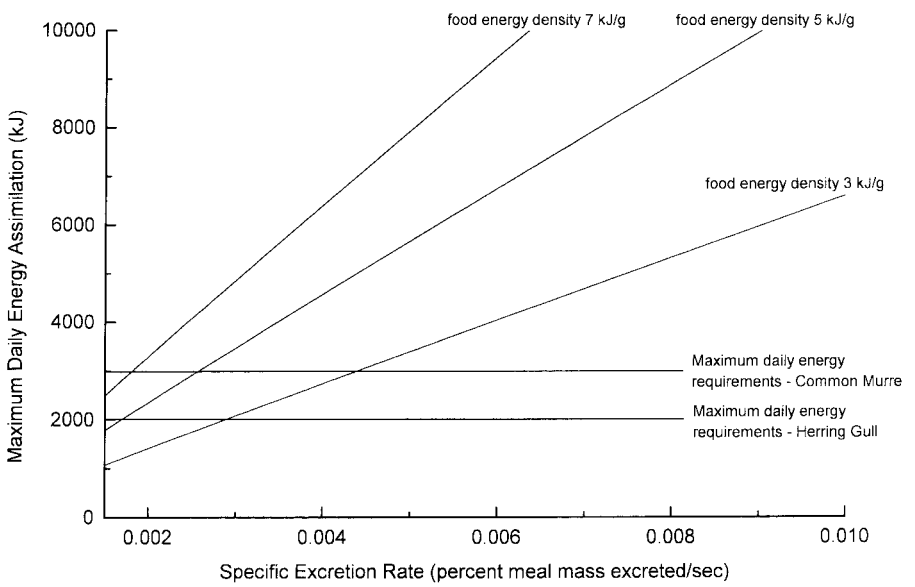

Fig. 8. Maximum daily energy assimilation (kJ) as a function of specific excretion rate, for three different food energy densities. Horizontal lines at 2000 and 3000 kJ indicate approximate maximum daily energy requirements of Herring Gulls and Common Murres respectively, taken from the energy-minimizing model outcomes. Where maximum daily energy requirements exceed maximum daily energy assimilation, an energy assimilation bottleneck may occur.

reducing mass after a meal (Sibly, 1981). This selection pressure on pursuit predators is distinct from those that we have modelled. However, its importance in seabirds is unclear: the effects of mass on underwater pursuit performance, as practised by the Common Murre, are entirely unknown; Herring Gulls rely little on flight or diving performance for their foraging success.

Birds such as the Common Eider, *Somateria mollissima*, which eat very heavy meals relative to their body mass, and/or have small load carrying abilities, may potentially be rendered temporarily flightless after feeding (Guillemette, 1994). In this case, there may be strong selection pressure to digest food rapidly. Wing loadings of Common Murres are among the highest recorded in flying birds (Pennycuick, 1987), and they are further disadvantaged by the task of taking off from water, suggesting that temporary flightlessness may occur in this species. Herring Gulls, which have a much lower wing loading than Common Murres, are unlikely to be flightless even when the gut is filled to capacity.

CONCLUSIONS

The driving force behind the often large differences in time and energy budgets between different digestion strategies is the ingestion bottleneck that arises when the gut is full. It is the same phenomenon, but distinct in its effects, as the digestive bottleneck that limits energy assimilation in several taxa (e.g. hummingbirds: Diamond *et al.*, 1986; pigeons: Kenward and Sibly, 1977), by enforcing resting periods between feeding bouts to clear the gut. Here we have shown that such bottlenecks can have a profound influence on time and energy budgets, quite apart from simply constraining the maximum energy assimilation rate. The reason for this is the extreme time-inefficiency of prolonging feeding bouts once the gut is full. The onset of the bottleneck could be delayed by increasing gut capacity, but presumably this would also have costs: flying mass would be higher, causing greater energy expenditure (Pennycuick, 1989), and the metabolic cost of maintaining the gut would be greater (Cant *et al.*, 1996).

The key advantage of rapid digestion is the reduced feeding trip frequency, relative to slow digestion, that can be achieved in some foraging conditions. This reduction occurs under a wider range of modelled foraging conditions for the Common Murre than for the Herring Gull. This is because flight energy costs tend to be lower, and flight times shorter, for Herring Gulls, so that making extra trips to avoid the ingestion bottleneck is favoured, even in rapid digesters for which the bottleneck is less severe. Furthermore, in the Herring Gull, even when a slow digester does have to make more trips than a rapid digester, the cost is relatively small because flight is inexpensive in time and energy. A general conclusion can be drawn here: where flight costs per trip are small (whether the currency is time or energy), then the balance will tip towards slower digestion. Slow digesters can assimilate less energy per day, because their lower food processing rate is not fully compensated by their higher digestive efficiency. However, during a feeding period, slow digestion actually gives the highest rate of assimilable energy gain, until the gut is filled (Fig. 1). Therefore, in some circumstances, slow digestion may allow the speediest return to the nest site carrying a given quantity of assimilable energy. Another outcome of the model is that high digestive efficiency does not necessarily correspond to high energetic efficiency (energy assimilated/energy expended in foraging; Kacelnik, 1984). Since slow digesters frequently have to make more foraging trips per day than rapid digesters, and hence have greater flight energy expenditure, they are relatively inefficient foragers.

The model outcomes suggest that selection pressure on digestion strategy may differ according to foraging conditions, particularly for the Herring Gull. We may expect to find large variations in digestive strategy in this species. Indeed, it is notable that several of the traits which we suspect might have an influence on optimal digestion rates are not fixed within a species. Among seabird species, foraging range, diet and food acquisition rate vary widely between colonies (Furness and Monaghan, 1987). Given the flexibility of digestive traits in many animals (see Karasov, 1996), it is possible that between-individual variation in gut retention time can in part be explained by variations in feeding ecology.

It might be expected that pressure to reduce flight mass would result in selection for rapid digestion, particularly in Common Murres, which have extremely high flight costs. However, in our model, the birds nearly always make the return flight to the nest with a gut filled to capacity, so there is no mass difference between fast and slow digesters. It is not mass savings that favour rapid digestion, but rather a reduction in the food ingestion bottleneck. Only when the 'sit-and-wait' strategy is used do significant energy savings arise because of mass loss through excretion.

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APPENDIX: CALCULATION OF FORAGING PARAMETER VALUES

Calculation of energetic costs

Energy requirements of adults at the nest (E_{adult})

Common Murre: We assume that, when not on a foraging trip, the bird consumes energy at $2 \times$ RMR. This allows for activities such as preening, interactions with partners or conspecifics, and chick feeding, which will increase energy expenditure above resting rate. Five published values of RMR were measured under similar conditions (Johnson and West, 1975; Croll and McLaren, 1993; Bryant and Furness, 1995; Gabrielsen, 1996; G.W. Gabrielsen, personal communication). Regression of these values on body mass yields the relationship RMR ($kJ \cdot day^{-1}$) = $0.007 \times$ body mass $(g)^{1.9979}$ ($F_{1,3} = 17.85$, $r^2 = 0.86$, $P = 0.02$). For a Common Murre of mass 888 g, this gives a RMR of 544 $kJ \cdot day^{-1}$; hence E_{adult}, the daily energy expenditure of an adult at the nest, is 1088 $kJ \cdot day^{-1}$.

Herring Gull: Published RMR values are 432 and 415 $kJ \cdot day^{-1}$ (Bennett and Harvey, 1987; Bryant and Furness, 1995), with a mean of 424 $kJ \cdot day^{-1}$. As for the Common Murre, we assume that E_{adult} is $2 \times$ RMR, hence $E_{adult} = 848$ $kJ \cdot day^{-1}$.

Energy requirements of the brood (E_{chick})

Common Murre: We use the mean energy received by chicks in wild colonies = 286 kJ per chick per day (see Harris and Wanless, 1985, and references therein; Birkhead and Nettleship, 1987; Harris and Wanless, 1988).

Herring Gull: Data are available from captive chick rearing experiments (G. Hilton, unpublished data). At close to fledging mass, chicks were fed an average 1348.5 $kJ \cdot day^{-1}$, and were growing at a similar rate to healthy chicks in the colony. For a three-chick brood, this gives $E_{chick} = 4046\ kJ \cdot day^{-1}$.

Energy cost of feeding ($R_{feeding}$ *and* R_{water})

Common Murre: Croll and McLaren (1993) measured energy expenditure during dive bouts as 15.3 W. However, their experiment was conducted in a warm (20°C) pool. De Leeuw (1996) showed that, for each 1°C fall in water temperature, the metabolic cost of diving in Tufted Ducks, *Aythya fuligula*, increased by 0.23 W. Applying this effect to Common Murres gives an energy expenditure of 17.6 W at a water temperature of 10°C. In addition, De Leeuw (1996) demonstrated that incorporating the energy costs of thermogenesis and dive-associated preening following a dive increases the overall energy expenditure by a factor of 2.8 above that measured simply within the dive-pause cycle in Tufted Ducks at 10°C. Therefore, for Common Murres, we set the rate of energy expenditure during active feeding ($R_{feeding}$) to 50 W (= *c*. 2.8×17.6). Croll and McLaren (1993) determined energy expenditure of Common Murres resting on water as 17.39 – (temperature (°C) × 0.6) $W \cdot kg^{-1}$. We use this to estimate the rate of energy expenditure while resting on the water (R_{water}) as 12.8 W.

Herring Gull: Use a wider variety of feeding methods than Common Murres, but most of these involve relatively low cost activities, with rather little flying or diving (Verbeek, 1977; Cramp and Simmons, 1983; Pierotti and Annett, 1987; Pons, 1994). We therefore assume an $R_{feeding}$ of $4.0 \times RMR$, = 19.6 W, and we estimate R_{water} as $2 \times RMR = 10$ W.

Energy cost of flight ($F(W)$)

Program 1 (version 2) of Pennycuick's (1989) flight power calculation programs was used to estimate the power required for flapping flight in watts (F), as a function of mass in g (W). We calculated the function $F(W)$ for flight at predicted minimum power velocity, which is very close to the observed flight speed of these species (Pennycuick, 1987). Wing span, wing area and aspect ratio data for the two species were taken from Pennycuick (1987); other parameter values were the default settings for the program.

Calculation of foraging parameters

Foraging range (D) *and flight speed* (V)

Common Murre: Foraging ranges during chick rearing have been estimated at many sites, and fall between 1.1 and 110 km (for reviews, see Bradstreet and Brown, 1985; Phillips *et al.*, in press). To estimate the time required to fly these distances, we use a flight speed of 17.9 $m \cdot s^{-1}$ (Pennycuick, 1987).

Herring Gull: Foraging ranges during this period largely fall between 2 and 30 km (Verbeek, 1977; Pierotti and Annett, 1991; Phillips *et al.*, in press). We use a flight speed of 11.3 $m \cdot s^{-1}$ (Pennycuick, 1987) to estimate the flight time required to cover these foraging ranges.

Energy density of diet (Q)

Common Murre: Predominantly piscivorous (Bradstreet and Brown, 1985). In general, the fish available as food to these birds fall within the range 4.0–8.0 $kJ \cdot g^{-1}$ wet weight (Wallace and Hulme, 1977;

Harris and Hislop, 1978; Montevecchi and Piatt, 1984; Hislop *et al*., 1991), and Q is varied within this range.

Herring Gull: Eats a wider variety of foods, including items with much lower energy density, for example earthworms, *Lumbricus* spp., 2.97 $kJ \cdot g^{-1}$; shore crabs, *Carcinus* spp., 3.35 $kJ \cdot g^{-1}$; starfish, *Asterias* spp., 2.64 $kJ \cdot g^{-1}$ (Hunt, 1972); and Blue Mussels, *Mytilus edulis*, 1.8 $kJ \cdot g^{-1}$ (Bustnes and Erikstad, 1990; Kersten and Visser, 1996); together with domestic refuse (7.8 $kJ \cdot g^{-1}$, Pons, 1994) and fish. We allow Q to vary between 3 and 7 $kJ \cdot g^{-1}$ wet weight for Herring Gulls.

Rate of food acquisition (S)

Common Murres: Cairns *et al*. (1990) estimated that Common Murres in eastern Newfoundland eat 511 g of fish per day. They must also obtain about 18 g of food per day for the chick (see Harris and Wanless, 1985, and references therein; Birkhead and Nettleship, 1987; Harris and Wanless, 1988). Cairns *et al*. (1990) estimated that 117 $min \cdot day^{-1}$ is spent diving. Given that 63% of a foraging bout is spent underwater (Wanless *et al*., 1988), this gives a total foraging bout time of 186 $min \cdot day^{-1}$, hence $S_{max} = 0.047\ g \cdot s^{-1}$.

The daily energy expenditure calculated from time budgets given in Monaghan *et al*. (1994) suggest daily energy expenditures of 1822 and 1118 kJ in 1990 and 1991 respectively (using the activity-specific energy values used in this paper). At a $TMEC_N$ of 0.79 (Hilton *et al*., in press), and a food energy density of 7.4 $kJ \cdot g^{-1}$ (calculated from Hislop *et al*., 1991, for Sandlance, *Ammodytes* spp., of the size eaten in the study by Monaghan *et al*., 1994), this gives 312 and 191 g eaten per day in 1990 and 1991 respectively, plus 18 g chick meals. Time spent in foraging bouts = 318 and 89 min in 1990 and 1991 respectively, giving $S_{max} = 0.016$ and $0.036\ g \cdot s^{-1}$ for the two years. Averaging the results of these studies, we assume a value for S_{max} of $0.037\ g \cdot s^{-1}$.

Herring Gull: The rate of food acquisition appears to vary considerably between sites and food types (Verbeek, 1977; Sibly and McLeery, 1983; Pierotti and Annett, 1987). Values appear to lie between about 0.017 and $0.117\ g \cdot s^{-1}$. We thus allowed S_{max} to vary between 0.017 and $0.117\ g \cdot s^{-1}$, but present results for an intermediate value of $0.067\ g \cdot s^{-1}$.

Gut capacity constraints

The gut capacity of Common Murres and Herring Gulls was measured by dissection. The foregut (oesophagus and stomach) was excised and digesta removed by flushing. The small intestine was clamped at the pylorus and the foregut suspended from a clamp stand. We measured the volume of water that the foregut could hold. The capacity of the small and large intestine was measured by calculating volume from length and width measurements. We assume that digesta has a density of $1\ g \cdot ml^{-1}$. Total gut capacity of Common Murres and Herring Gulls was 192 ml (S.D. = 20.2) and 212 ml (S.D. = 21.1) respectively. For the Herring Gull, which regurgitates food for the chick, there is an additional constraint: the chick meal can be no bigger than foregut capacity of 154 ml (S.D. = 13.1). Common Murres carry (very small) chick meals in their bill.