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Gluttony in migratory waders – unprecedented energy assimilation rates in vertebrates

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Maximum energy assimilation rate has been implicated as a constraint on maximal sustained energy expenditure, on biomass production, and in various behavioural and life history models. Data on the upper limit to energy assimilation rate are scarce, and the factors that set the limit remain poorly known. We studied migratory waders in captivity, given unlimited food supply around the clock. Many of these waders assimilated energy at rates of seven to ten times basal metabolism, exceeding maximum rates reported for vertebrates during periods of high energy demand, for example during reproduction and in extreme cold. One factor allowing the high energy assimilation rates may be that much of the assimilated energy is stored and not concomitantly expended by muscles or other organs. The remarkable digestive capacity in waders is probably an adaptation to long and rapid migrations, putting a premium on high energy deposition rates. The upper limit to daily energy assimilation in vertebrates is clearly higher than hitherto believed, and food availability, total daily feeding time and, possibly, the fate of assimilated energy may be important factors to take into account when estimating limits to energy budgets in animals.

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Energy assimilation rates of animals are sometimes limited, not by food availability or ingestion rates, but by the rate at which energy from food can be digested and absorbed in the digestive tract (Diamond et al. 1986, Zwarts and Dirksen 1990, Kersten and Visser 1996). Maximum energy assimilation rates have been implicated as a constraint on maximal sustained energy expenditure and biomass production, and in various behavioural and life history models (Weiner 1992, Karasov 1996, Hammond and Diamond 1997). The proximate and ultimate causes of the upper limit to energy assimilation are poorly known and evidence indicating where this limit may lie are scarce (Kirkwood 1983, Weiner 1992, Karasov 1996, Johnson and Speakman 2001). High reported energy assimilation rates, as well as sustained rates of energy expenditure (per definition balanced by an energy assimilation rate of equal

size) in vertebrates range between 3 and $7 \times \text{BMR}$ (basal metabolic rate) and include lactating rodents, force-fed poultry and Tour de France cyclists (Kirkwood 1983, Weiner 1992, Hammond and Diamond 1997). However, very few studies report energy assimilation rates or sustained energy expenditures exceeding six times BMR (Hammond and Diamond 1997). In a recent study, a value of $7.7 \times \text{BMR}$ was reported for cold-exposed lactating mice, which to our knowledge is the highest value reported to date (Johnson and Speakman 2001).

In many studies showing high energy assimilation rates, animals were experimentally challenged by extreme cold, force-feeding, or extra young to nourish, or a combination of these (Kirkwood 1983, Weiner 1992, Hammond and Diamond 1997, Johnson and Speakman 2001). In contrast, birds fuelling for long migratory

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flights are naturally motivated to maximise energy assimilation without manipulation (Lindström and Kvist 1995, Klaassen et al. 1997, Karasov and Pinshow 2000). The natural urge to maximise intake rates may be due to the favoured strategy of maximising speed of migration (including both flight and fuelling phases, Alerstam and Lindström 1990). To achieve a fast migration, birds should maximise fuel deposition rates, which is best accomplished by maximising energy assimilation rates (Alerstam and Lindström 1990).

Some of the most impressive avian migrations are carried out by waders, flying up to 20 000 km yearly between breeding and wintering grounds, making them strong candidates for extreme adaptations in energy turnover rates. We studied captive waders fuelling for migratory flights and show that they can assimilate energy at rates by far exceeding the maximum found in birds during reproduction and extreme cold (Kirkwood 1983, Weiner 1992), and higher than those implied from the highest sustained energy budgets reported for vertebrates (Hammond and Diamond 1997, Johnson and Speakman 2001).

Material and methods

Migrating waders were trapped at Ottenby Bird Observatory, SE Sweden (56°12' N, 16°24' E) in late July to early September in 1995–1997. Birds were kept indoors in separate cages under a natural light regime. For details about housing conditions see Kvist and Lindström (2001). All birds were weighed every day between 1700 and 1800 local time and their fat stores scored (on a scale 0–6) according to Pettersson and Hasselquist (1985).

Basal metabolism

After capture, birds with higher fat scores (most birds) received limited food rations in order to gradually reduce their fat stores until they reached a fat score of 1–3. Birds with a low fat score at capture were given some food for one or two days to ensure that they would eat in captivity. Thereafter the birds had their basal metabolic rate (BMR) measured overnight by respirometry. For details about respirometry set-up and BMR measurement protocol see Kvist and Lindström (2001).

Energy assimilation

All birds had a continuous (24h) supply of food *ad libitum* (mealworms *Tenebrio* sp.) from about 0900 the morning following the BMR measurement. Monitoring of food intake did not start until 1700 on the same day

to give the birds time to fill their guts after the overnight fast. In this way we avoid overestimating assimilated energy during the first 24 h measurement period. We now had birds starting and ending each 24 h period with a full stomach. Between 1700 and 1800 on each of the following days remaining food was collected and weighed, and new food of a known amount was supplied. Energy assimilation rates were calculated as the gross intake of mealworms times the energy content of mealworms times the apparent efficiency of energy utilisation (see below) divided by time (24 h). Sporadic checks of the food trays showed that the birds fed at a high rate also during night. Only birds that increased in mass for at least three consecutive days were included in the analysis. This 3-day rule was chosen arbitrarily as an indication that the birds were clearly motivated for fuel deposition. In total 33 out of 124 tested birds were excluded from the analyses by this rule. The experimental protocol ended, and all birds were released, when they ceased to increase in mass. Maximum energy assimilation rate for each individual was taken as the highest daily (24 h) energy assimilation.

BMR changes substantially and rapidly in a bird during fuel deposition (Lindström et al. 1999, Kvist and Lindström 2001, Battley et al. 2001). The BMR of our birds was measured a few days before energy assimilation rates peaked. Therefore, when maximum energy assimilation rate is presented as a multiple of BMR, the BMR of that particular day was estimated by adjusting for body mass increase using an allometric scaling exponent of 1.19 (Kvist and Lindström 2001). The BMR of the day with peak energy assimilation rate (BMR_e) was calculated as:

$$BMR_e = BMR_m \times (Mass2/Mass1)^{1.19}$$

where BMR_m is the BMR measured, Mass2 is body mass when maximum energy assimilation was measured and Mass1 is body mass when BMR was measured. Further, we use Mass1 as an estimate of lean body mass (LBM) when calculating fuel deposition rates.

Apparent efficiency of energy utilisation

The apparent efficiency of energy utilisation (Hume and Biebach 1996) for waders eating mealworms was estimated for some of the birds (19 individuals of 6 species) on selected experimental days in 1996 and 1997. We assume that the droppings produced from food eaten before the selected experimental day started equalled the droppings that would have been produced from the food remaining in the digestive tract at the end of the day. Removable plastic trays, completely covering the floor, were placed in the cages when new food was supplied and all droppings were collected when remain-

ing food was collected. Energy content of each batch of mealworms and droppings were determined using a IKA C400 adiabatic bomb calorimeter at the Netherlands Institute of Ecological Research in Nieuwersluis, the Netherlands.

Apparent efficiency of energy utilisation was on average 0.815 and did not vary between species (ANOVA, $F_{5,13} = 0.63$, $p = 0.68$) or between batches of mealworms ($F_{3,15} = 0.95$, $p = 0.44$). The energy density of mealworms, however, varied significantly between batches ($F_{4,10} = 45.8$, $p < 0.001$, average: 11.2 kJ g^{-1} wet mass). Therefore the average apparent efficiency of energy utilisation and the batch-specific energy density of mealworms was used when calculating energy assimilation rates.

Results

The maximum energy assimilation rates, as measured over 24 h, was on average very high. The maximum rates exceeded $6 \times \text{BMR}$ in 12 of the 15 wader species in the analysis, and $7 \times \text{BMR}$ in five species (Fig. 1). High individual assimilation rates were found in many of the species studied: 33 of the 91 individuals (36%), representing eleven species, had assimilation rates of

more than $7 \times \text{BMR}$, and 21 of 91 individuals (23%) of ten species had assimilation rates higher than $7.7 \times \text{BMR}$. The highest average species value, $10.4 \times \text{BMR}$, was found in the red knot (*Calidris canutus*), and the second highest, $8.8 \times \text{BMR}$, was found in the common sandpiper (*Actitis hypoleucos*).

In addition, the birds were able to maintain very high intake rates for several consecutive days. The assimilation rate averaged over the experiment (3–5 days per bird) was on average only 18% lower than the maximum rate measured over 24 h.

The energy assimilation rates resulted in average rates of body mass increase of 9.6% of LBM per day. The two highest average values were 14.5% in the common sandpiper and 13.4% in the red knot.

Discussion

Energy assimilation and fuel deposition rates

The maximum daily energy assimilation of the migrating waders was very high in most species and unprecedented in species like common sandpiper and red knot (Kirkwood 1983, Weiner 1992, Hammond and Diamond 1997, Johnson and Speakman 2001). The assimi-

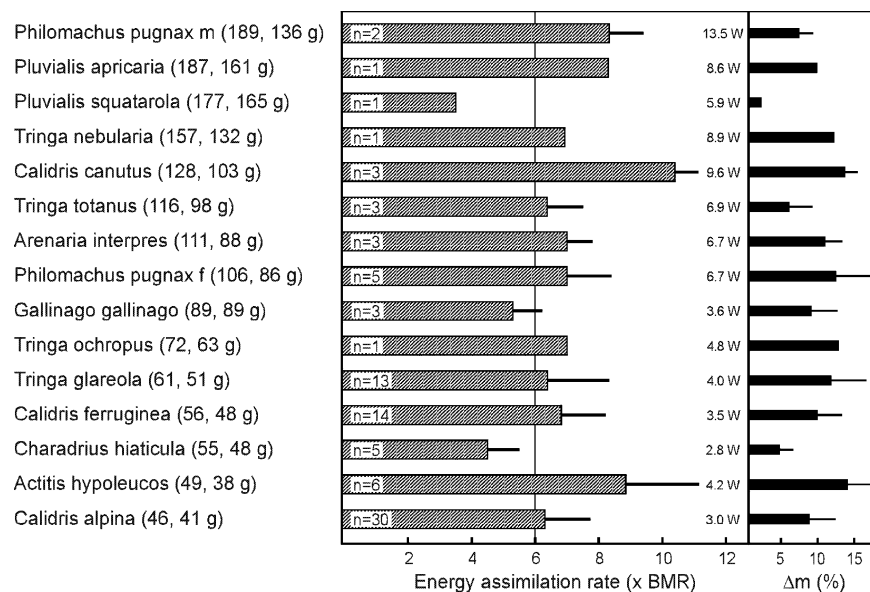


Fig. 1. Maximum energy assimilation and fuel deposition rates of captive waders, trapped on autumn migration at Ottenby in south Sweden. The first mass presented after the species name is the average body mass of the birds the day (24 h period, see text) when maximum energy assimilation rate was measured. The second mass is the average body mass when BMR was measured, which is the value we use as an estimate of lean body mass (LBM). Energy assimilation rates (gray bars to the left) are presented as multiples of BMR to normalise for differences in size and metabolic capacity between animals. Energy assimilation rates in Watt are presented to the right of the bars. The black bars to the right represent the mass increase per 24 h (Δm), the 24 h period with the maximum energy assimilation rate, expressed in % of LBM. Error bars represent standard deviation. Most species had energy assimilation rates higher than 6 times BMR (vertical line), a level rarely surpassed by vertebrates (Hammond and Diamond 1997).

lation rate of the red knot exceeded that of similarly sized broiler chicken by 120% (Visser 1991), it is 49% higher than the postulated limit of $7 \times \text{BMR}$ in animals (Hammond and Diamond 1997), and still 35% higher than the apparent record of $7.7 \times \text{BMR}$ presented by Johnson and Speakman (2001). Accordingly, the migratory waders we studied include some of the biggest gluttons described in the animal kingdom so far.

The accompanying mass increase rates (fuel deposition rates, FDR) of up to almost 15% of body mass per day are also very high. Free-living migrants of this size-range rarely have FDR above 7–8%, although a few values of 10–15% have been reported (Lindström 1991, 2002).

The aim of our study was to measure the maximum energy assimilation rates migratory waders can accomplish under ideal circumstances. In several species and individuals we found higher energy assimilation rates than previously measured in vertebrates. What relevance do our results from captive birds with ideal (?) feeding conditions then have for birds in the wild? Further, what implications do our results have on our understanding of wader migration specifically and vertebrate energetics in general?

First, mealworms are clearly not the normal food for waders. However, different bird species feeding on the same food type generally have similar assimilation efficiencies, and different food types within the same broad category (fish, meat, invertebrates, etc.) are generally assimilated at similar efficiencies (Castro et al. 1989, Bairlein 1999). Therefore, Castro et al. (1989) suggested that birds' digestive chemistries, with respect to assimilation efficiency, are not adapted to specific food types. This suggests that birds may also be able to achieve similar assimilation rates when feeding on different food types within the same broad category. In his review of avian energy assimilation efficiencies, Bairlein (1999) found that aquatic and terrestrial invertebrates are on average assimilated with the same efficiency. Thus, waders feeding on their natural invertebrate prey in the wild could probably also accomplish the high assimilation rates shown by our waders feeding on mealworms, in circumstances where the birds are motivated to maximise food intake, and when food availability and foraging conditions allow it.

Second, many animals in the wild are limited to feeding during only a part of the day, normally the daylight hours, or, as in waders, they may be constrained by tidal regimes (Alerstam et al. 1992). In an earlier experiment with passerine long-distance migrants, thrush nightingales (*Luscinia luscinia*), we found that the daily energy assimilation was linearly proportional to the time food was available for digestion and absorption by the gut (as measured over a span of 7 to 23 h per day, Kvist and Lindström 2000). The waders in the present study also fed both day and night. Do wild birds in natural circumstances ever forage around

the clock? Waders on migration are indeed known to forage during both day and night (Alerstam et al. 1992), so under non-tidal conditions, these birds could potentially forage around the clock. Also, at high latitudes in summer, where many of the species of the present study carry out a large part of their yearly migrations, there is daylight 24 h per day.

Third, our birds had food ad libitum. Situations with unlimited food supply in the wild are not uncommon for birds during migration (Lindström 1990). Further, red knots and other arctic-breeding shorebirds forage on apparently infinite masses of horse-shoe crab eggs in spring (Tsipoura and Burger 1999, T. Piersma pers. comm.), and turnstones (*Arenaria interpres*) on stopover in the northern Pacific were shown to feed on seemingly unlimited supply of blowfly larvae (Thompson 1974).

The extremely good feeding conditions experienced by our captive birds are probably not commonplace in the wild. However, they certainly do occur, and birds seem to have the capacity to make full use of them, as shown by some very high FDR recorded in the wild (Lindström 1991, 2002). A contributing factor to this high capacity is the rapid build-up of the digestive organs in the first phase of migratory fuelling, as shown, for example, by the red knot (Piersma et al. 1999).

What selective forces have turned migrating waders into the prime gluttons among vertebrates? Many waders, with the red knot as the champion, travel literally across the world and spend several months on migration each year. Most of this time is devoted to feeding, to fuel up for the energy consuming flights (Piersma and Jukema 1990, Hedenström and Alerstam 1997). To complete the migratory journeys within the appropriate seasons, the birds must fuel up rapidly, and therefore a premium is put on high energy assimilation capacity (Alerstam and Lindström 1990). Intake rates of up to $10 \times \text{BMR}$, resulting in fuelling rates of 8–10% of LBM per day, surely will allow very fast migration (Alerstam 2002). It is likely that the remarkable digestive capacity in waders is an adaptation to enable very long and rapid migrations. But also other types of migrants may prove to have this extraordinary capacity, should they be given the same conditions as the waders of our study (Bairlein 1998, Kvist and Lindström 2000).

Limits to energy assimilation rates

However high the measured intake rates are, there is eventually something that sets an upper limit to energy assimilation rates also in the waders. Given that animals feed at the highest rate their physiology allow (that is, lack of motivation is not an issue), energy assimilation rates may be limited either centrally by the

rate at which energy can be digested and absorbed by the energy-supplying organs such as the gut, or peripherally by the rate at which organs and tissues concurrently expend the energy. This is an issue yet to be fully answered (Kirkwood 1983, Weiner 1992, Karasov 1996, Hammond and Diamond 1997). During migratory fuel deposition, energy is not assimilated to meet concomitant demands for energy expenditure or growth, but is stored, mainly as lipids, for later use. The level of energy assimilation in our waders can therefore be limited either centrally by the gut or by the capacity to build up lipid stores in adipose tissue, but not by any peripheral energy consuming organs or the growth of complex biological structures (Weiner 1992, Hammond and Diamond 1997). Possibly, this may be one important reason why migrating waders show these high assimilation rates.

Johnson and Speakman (2001) suggested that reproducing mice may prefer to feed at sub-maximal levels because of a trade-off between current and future reproductive output. Although it is difficult to see why the animals would have a higher capacity than they actually use (not even under circumstances when really challenged), could such fitness trade-offs be limiting intake rates in waders? It seems unlikely, unless putting on fat at a high rate for waders has physiological repercussions not yet described.

We conclude that daily assimilation of energy in vertebrates can be much higher than hitherto believed, and that it can reach $10 \times \text{BMR}$. Food abundance and availability, total feeding time and, possibly, the fate of assimilated energy, are important factors to take into account when estimating limits to energy budgets in animals.

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