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Thermoregulatory use of heat increment of feeding in the tawny owl (*Strix aluco*)

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Abstract

The heat increment of feeding (HIF) was investigated in the tawny owl (*Strix aluco*) in central Norway (63°N, 10°E), close to the northern limit of its distribution. HIF was measured as the increase in heat production (measured as oxygen consumption) after force-feeding the owls with laboratory mice at thermoneutral conditions (20 °C) and during cold-exposure (5 °C and −5 °C). The basal metabolic rate of the owls (mean mass 419 g) was 4.39 kJ h^{-1} and the lower critical temperature was approximately 16 °C. During cold conditions, HIF substituted for thermogenesis, and at an ambient temperature of −5 °C the substitution was complete. Calculations indicate that the substitution by HIF may save the owls as much as 60% of their daily thermoregulatory costs. This corresponds to about 10% of their total daily energy budget.

Keywords: Heat increment of feeding; *Strix aluco*; Tawny owl; Thermoregulation

1. Introduction

The energy cost of processing a meal is commonly referred to as the 'heat increment of feeding' (HIF), and is observed as a postprandial increase in metabolic rate. The major part of HIF stems from the postabsorptive biochemical transformation of carbohydrates, lipids and proteins to ATP, although the mechanical processing of food is also involved (Blaxter 1989). Although HIF may be regarded as an unavoidable loss of ingested energy, several authors have suggested that HIF may substitute for thermogenic heat production in cold-stressed endotherms. Such a substitution would lower the need for thermoregulatory heat production and accordingly function as an energy-saving mechanism when the animal is exposed to low ambient temperatures.

In both mammals and birds, results have been conflicting as to whether HIF may actually constitute such a benefit. While substitution by HIF has been documented in some species of mammals (e.g. Jensen et al., 1999; MacArthur and Campbell, 1994; Šimek, 1975), other studies have not found a substitution (e.g. Campbell et al., 2000; Rosen and Trites 2003). Also studies on birds have given conflicting results. Studies on incubating starlings (*Sturnus vulgaris*, Biebach, 1984), house wren chicks (*Troglodytes aedon*, Chappell et al., 1997), granivorous song birds (Meienberger and Daubersch-midt, 1992) and Japanese quail chicks (*Coturnix coturnix japonica*, Marjoniemi, 2000) conclude that there is a substitution at low ambient temperatures. On the other hand, in kestrels (*Falco tinnunculus*) the substitution was only partial (Masman et al., 1989) and in Arctic tern

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chicks (*Sterna paradisea*) there was no substitution at any ambient temperatures (Klaassen et al., 1989).

The magnitude of HIF depends on the composition of the food, and is greatest after intake of a protein-rich diet, as compared to a carbohydrate- or lipid-rich diet. Hence, one would expect a greater potential for a thermoregulatory substitution by HIF in predominantly protein-digesting animals. In the present study we investigate whether HIF offer any thermoregulatory benefit during cold exposure in a medium-sized bird of prey, the tawny owl (*Strix aluco*). The tawny owl is a nocturnal species that is active almost exclusively between dusk and dawn. In Norway small rodents constitute as much as 74% of their prey items (Hagen, 1952). The species occurs in most parts of Europe, and our study site in the middle of Norway is close to its northernmost limit in Europe (Sunde et al., 2001). Since the species is mainly resident, the individuals in these northernmost parts of its range are usually exposed to temperatures below their thermoneutral zone during the winter. This feature, in addition to the fact that it normally digest whole preys at irregular intervals, makes the tawny owl an ideal species for experimental studies of the effects of heat increment of feeding.

The specific aim of the present study is hence to determine whether there is a substitution by HIF for thermoregulatory needs in the tawny owl exposed to cold. The existence of such an effect will be evaluated by comparisons of metabolic rates in fed and fasted individuals at ambient temperatures within and below the thermoneutral zone.

2. Materials and methods

The study was performed in central Norway during 2000 and 2001. Two fledgling tawny owls were taken from their nests in the vicinity of Trondheim (63°N, 10°E) during June 2000 and raised in captivity. During the initial period of captivity (approximately 1 month) they were hand fed 2–3 times per day with different types of meat. After this period they were able to feed by themselves and were mainly fed with dead day-old chicks. The raising of the owls in this way ensured that they became accustomed to being handled, and could easily be force-fed during the subsequent experiments. However, they never became 'tame'. Experiments were carried out when the birds were fully grown, from November 2000 to May 2001, e.g. at an approximate age of 7–13 months. In a first series of experiments, the metabolic rate was measured at ambient temperatures between −15 °C and 30 °C in order to estimate the lower critical temperature (T_{lc}). In a second series of experiments, HIF was measured as the increase in the metabolic rate after feeding the owls with dead, rewarmed, laboratory mice (*Mus musculus*; body mass 9–37 g). Feeding experiments were carried out at thermoneutral conditions (20 °C) and during cold-exposed conditions (5 °C and −5 °C). When not used in experiments the owls were kept individually in large indoor aviaries, at an ambient temperature of 20 °C and a relative humidity of 45%. Light was turned on at 07:30 and off at 20:00. However, also in the dark period there was a dim light to prevent total darkness.

The metabolic rate was measured indirectly as oxygen consumption using open flow-through respirometry. Dry fresh air was pumped through a 24 L metabolic chamber with an air flow rate of approximately 1.5 L/min. Actual flow rates were measured using a calibrated mass flowmeter (Bronkhorts high-tech). An aliquot of the effluent air was dried and the oxygen concentration was measured using an oxygen analyser (Servomex, series 1100). The oxygen analyser was calibrated using dry outside air (set to 20.95% oxygen) and pure stock nitrogen. Rates of oxygen consumption (VO_2) were calculated using formula 3A given by Withers (1977), assuming a respiratory exchange ratio of 0.71, and corrected for wash-out delay in the system by the method described by Niimi (1978). In this way, instantaneous rates of oxygen consumption were obtained. The ambient temperatures (T_a) during the experiments were measured using a copper–constantan thermocouple (California Fine Wire, type 0.005) placed inside the metabolic chamber. All readings of T_a, as well as the output from the oxygen analyser and the mass-flowmeter, were recorded at one-minute intervals and stored on a datalogger (Grant Squirrel, Type 1203) and later transferred to a computer for analyses.

The birds were fasted for a minimum of 12 h prior to both types of experimental runs to ensure a post-absorptive state (Duke et al., 1976). All experimental runs were initiated between 09:00 and 10:00 (e.g. at the beginning of the resting phase for this nocturnal species). The metabolic experiments (for determining T_{lc}) lasted for about 8 h, while the feeding experiments lasted for about 24 h (at thermoneutrality, 20 °C) or about 13 h (at cold exposure, 5 °C or −5 °C). Before and after each experimental run the birds were weighed to the nearest 0.1 g. A linear change in body mass was assumed when calculating mass-specific metabolic rates. In the first series of experiments the birds were exposed to two different T_a's during the same experimental run. The ambient temperature was generally changed after about 4 h, but not before the bird had remained quiescent for at least 1 h. In the feeding experiments the same temperature was maintained during the whole experimental period. Feeding of the birds took place after about 4 h of resting in the metabolic chamber. The mice fed to the birds in the feeding experiments were heated to approximately 40 °C to avoid a rise in oxygen consumption due to the energetic cost of heating a meal (Wilson and Culik, 1991). The energy content of the

food was calculated using a calorific equivalent of 2.14 kcal/g for mice (Brisbin, 1970). This calorific value is found to be generally valid for mice with body mass over 5 g (Brisbin, 1970). A few sham-feeding experiments, performed at all three T_a's, did not induce any increase in VO_2, except for a short transient activity-related increase. Hence, the increases in VO_2 observed in the feeding experiments were assumed to relate to feeding.

Values of resting VO_2, in the non-feeding experiments, were calculated from the lowest recorded values of oxygen consumption calculated over a 25-min interval during exposure to a certain ambient temperature. In the feeding experiments, apparent HIF was obtained by subtracting the resting VO_2 (BMR) from the post-prandial VO_2. Peaks in oxygen consumption due to periods of activity were deleted and replaced using a bisquare smoothing function for the whole curve (see results). The areas below the curves were calculated using Sigma Plot (Sigma Plot 2000, SPSS Science). Values of metabolic rates were calculated from VO_2 using a conversion factor of 20,08 kJ per L O_2.

We are fully aware of the limitation in obtaining data from two individuals only. However, the procedure of hand-raising the owls was time-consuming, and it is hardly likely that we will be able to obtain data from more individuals. In addition, the results are clear cut and convincing, warranting publication of the obtained results.

3. Results

For the estimation of the lower critical temperature 25 metabolic measurements were performed at ambient temperatures between −15 °C and 30 °C (Fig. 1). Neither the thermoneutral VO_2 nor the relationship between VO_2 and T_a below T_{lc} differed significantly between the two individuals. The average VO_2 within thermoneutrality was 3.64 ml O_2 min^{-1} corresponding to a BMR of 4.39 kJ h^{-1} (average body mass was 419 g). The T_{lc} was found to be approximately 16 °C (Fig. 1). Based on these results ambient temperatures of 20, 5 and −5 °C were chosen for the subsequent feeding experiments.

HIF was first measured at thermoneutrality (20 °C) after feeding the owls with mice of variable body mass (9.1–37.2 g). The two individuals did not differ in any respect when analysing the HIF-data, and data from both individual owls (14 measurements) were consequently analysed together. There was a significant positive relationship between the gross energy intake (EI) and the resultant HIF ($r^2 = 0.65$, $p < 0.001$, $n = 14$; Fig. 2) described by the equation: HIF = 1.11 + 0.07 * EI. Also, the duration of HIF was positively and significantly related to EI ($r^2 = 0.76$, $p < 0.001$, $n = 14$; Fig. 3), described by the equation: duration of HIF = 264.1 + 1.68 * EI. In contrast, the maximal level of

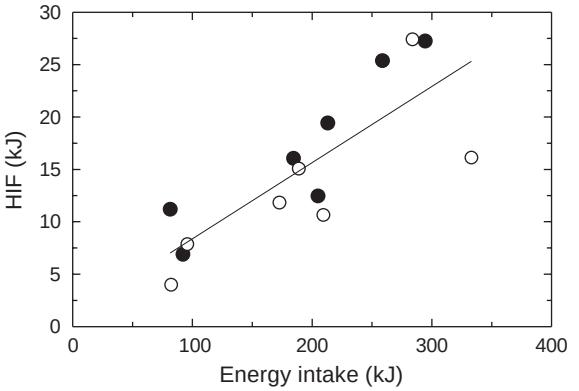

Fig. 2. Heat increment of feeding (HIF) as a function of energy intake (at T_a of 20 °C) in tawny owls. Different symbols denote different individuals.

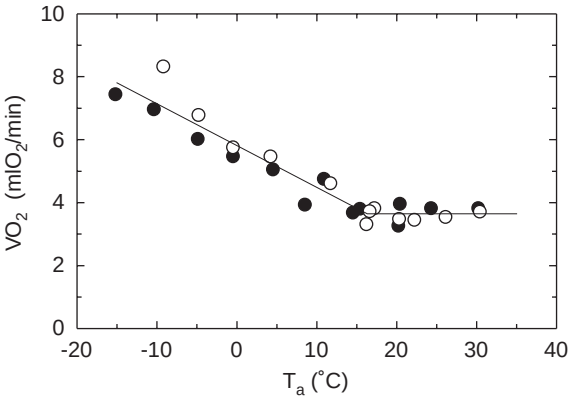

Fig. 1. Oxygen uptake as a function of ambient temperatures in tawny owls. Different symbol denote different individuals.

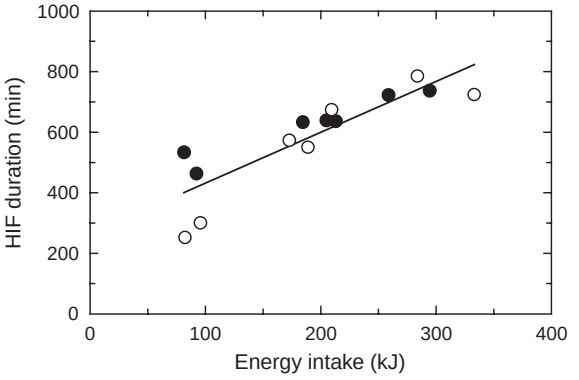

Fig. 3. The duration of HIF as a function of energy intake (at T_a of 20 °C) in tawny owls. Different symbols denote different individuals.

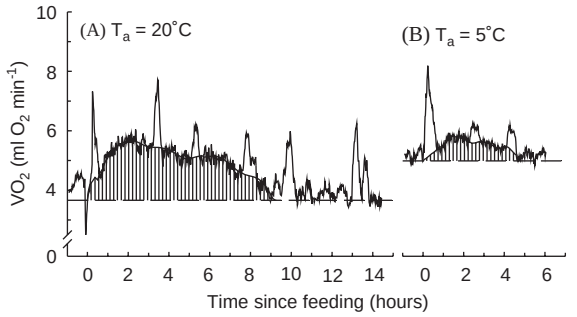

Fig. 4. Two examples of the changes in oxygen uptake as a function of time after feeding at 20 °C (A) and at −5 °C (B). The peak values of oxygen uptake are related to activity periods, which are excluded during the calculation of HIF. The shaded areas thus signify the measured HIF. The horizontal broken line denotes the BMR of the owls measured in separate experiments.

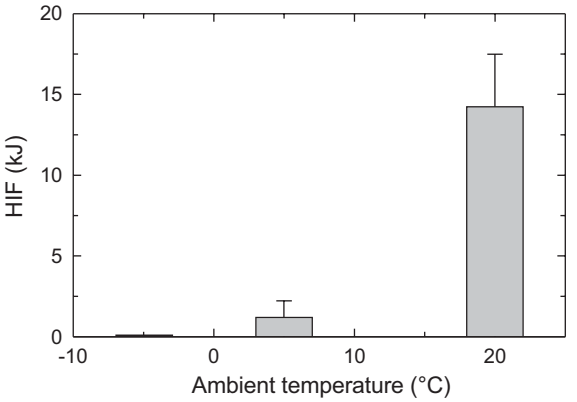

Fig. 5. The apparent, measured, HIF at the three experimental ambient temperatures in tawny owls. Each mean value is based on six measurements from two individuals. For the sake of visual clarity, the value at −5 °C is marked as a thin line, even though the value is zero.

metabolic rate reached during HIF was not significantly related to the ingested energy. Consequently, the increase in HIF due to an increase in energy intake mainly seems to be reflected in the duration rather than the maximal rate of HIF.

The magnitude of HIF, expressed as a percentage of the gross energy intake, was not significantly related to EI ($r^2 = 0.02$, $p = 0.660$, $n = 14$). On average HIF accounted for 8.0% (SD = 2.4%, $n = 14$; variation: 4.8–13.7%) of the ingested energy independent of the amount of food eaten.

To study the effect of ambient temperature on the resultant HIF, three feeding experiments were performed on each individual owl at each of the three ambient temperatures (−5 °C, 5 °C and 20 °C). The mass of the mice fed to the owls did not differ significantly between the experiments at the three T_a's (ANOVA: $F_{2,15} = 0.571$, $p = 0.577$), being on average 22.4 g corresponding to an energy content of 200 kJ. The feeding experiments showed an unmistakable substitution by HIF for regulatory thermogenesis at low ambient temperatures (Fig. 4). The mean apparent HIF measured at thermoneutrality (20 °C) was 14.2 kJ (SD = 3.3 kJ, $n = 6$), while at −5 °C it had decreased significantly and was only 1.2 kJ (SD = 1.0 kJ, $n = 6$). In feeding experiments at T_a of −5 °C measurements in either of the two owls did not reveal any increase in the metabolic rate following feeding and the apparent HIF consequently equalled zero (Fig. 5).

4. Discussion

The BMR reported for the tawny owls in the present study (4.39 kJ h^{-1}) is 75% of the BMR predicted for an owl of similar body mass (Hohtola et al., 1994). Similarly, calculation of the wet thermal conductance for the tawny owls in the present study gave values of 0.11 W kg^{-1} $°C^{-1}$, which is only about 71% of the predicted value for a bird of similar body mass (Aschoff, 1981). Hence, the thermal biology of the tawny owl seems to be characterized by low BMR, low thermal conductance (see also Massemin and Handrich, 1997) as well as a lower than expected T_{lc} (based on Calder and King, 1974). Taken together, these features suggest that the species is well adapted to a cold climate.

The magnitude of the HIF depends on the amount of food ingested as well as the food composition (Ricklefs, 1974). Different nutrients have different calorigenic effects and the metabolic increase following food intake will vary accordingly. In the present study we found that 8% of the gross energy intake appeared as HIF. This value is of a magnitude similar to the values reported in other studies on HIF. Hence, Campbell et al. (2000) reported HIF values of 8.7% for the Star-nosed mole (*Condylura cristata*), while in Harbour seals (*Phoca vitulina*) values of between 5.0 and 9.0% were reported (Markussen et al., 1994). In a study on kestrels fed mice, Masman et al. (1989) found an HIF value of 12.9%. Since small rodents also are the dominating food for tawny owls in Norway, our reported value of 8% for the HIF is thus likely to be close to what would be the case for free-living tawny owls.

The main result of the present study is a complete substitution of regulatory thermogenesis by HIF at low ambient temperatures. A similar substitution has been demonstrated in incubating starlings (Biebach, 1984), house wren chicks (Chappell et al., 1997), granivorous song birds (Meienberger and Dauberschmidt, 1992) and Japanese quail chicks (Marjoniemi, 2000). However, other studies on birds have failed to demonstrate any substitution for regulatory thermogenesis. In Arctic tern

chicks there was no substitution by HIF (Klaassen et al., 1989) while the substitution in kestrels was found to be only partial (Masman et al., 1989). The reason for this large variation in the degree of substitution is unknown. Rosen and Trites (2003) recently reviewed the available data and concluded that so far there was no relationship between either taxonomy, ecology, or developmental stage and the ability to substitute HIF for thermogenesis during cold exposure. Irrespective of the underlying physiological and evolutionary explanation for such species-specific variation, there is no doubt that our results have clearly demonstrated such an HIF substitution in the tawny owl. The following question then arises: what is the overall thermoregulatory benefit of such a substitution? Substitution of HIF clearly reduces the need for regulatory heat production in owls exposed to low ambient temperatures. Since shivering is the main mechanism for regulatory heat production in birds, a substitution of HIF for regulatory heat production will therefore result in less shivering. How much shivering is reduced depends on different factors, of which the temporal appearance of HIF is of obvious importance.

The amount of HIF is known to increase with the amount of energy ingested (Chappell et al., 1997; Secor and Phillips, 1997) and this was indeed also found in the present study. An increase in HIF, as a response to an increased meal size, could theoretically appear as an elevation in the maximal level of HIF or as an increase in the duration of HIF. Our results on tawny owls show clearly that increased HIF, due to increased meal size, is reflected mainly in the duration of HIF (Fig. 3). This is also in accordance with what was found in house wren chicks (Chappell et al., 1997). An increase in duration rather than peak level for larger HIF will obviously affect energy savings for those organisms in which HIF substitute for thermogenesis. When this is the case, such as for the tawny owls, foraging could preferably be at intervals of not less than the duration of HIF. Indeed, in a German study on the tawny owl, Ritter (1972) reported two peaks in hunting activity: one immediately after sunset and the other shortly before sunrise. An HIF duration of about 10 h (Fig. 3) would make the most of the energy saving due to HIF substitution. The HIF from food consumed immediately after sunset would last and substitute for thermogenesis for most of the night. HIF from feeding just before sunset would then last for additional hours into the day, lowering the need for energy used in thermoregulation. The temporal pattern of activity may, however, be different at more northern latitudes during certain times of the year, when hunting activity may merge into one, giving one peak just before midnight (Grönlund and Mikkola, 1979).

A rough estimate of the thermoregulatory benefit of HIF substitution is possible for the tawny owls in our study area. During late October the owls in the area of Trondheim typically experience ambient temperatures around 5 °C (Aune, 1993), which will give rise to a maintenance metabolism (BMR + thermoregulatory cost) of approximately 150 kJ day^{-1} (based on Fig. 1). Assuming maintenance metabolism to be 50% of the total daily energy expenditure (Walsberg, 1983), we can stipulate a total energy expenditure of about 300 kJ day^{-1}. If the owls have a feeding activity similar to what Ritter (1972) found, they will feed at sunset and then again at sunrise, which in late October in Trondheim is around 17:30 and 08:30, respectively. Eating a small rodent of about 20 g, with an energy content of around 180 kJ, twice a day, would in turn produce an HIF of approximately 28 kJ day^{-1}. Since the time interval between the two meals is about 9 h, the resulting HIF will only have a minimal overlap. Since over 90% of the HIF in addition will substitute for regulatory thermogenesis at T_a of 5 °C, we can calculate a total saving by HIF substitution of roughly 26 kJ day^{-1}. This corresponds to almost 60% of the thermoregulatory cost or about 10% of the total daily energy expenditure. Hence, the substitution of HIF for regulatory thermogenesis might reduce the tawny owls' need to shiver by more than half.

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