

Behavioural compensation reduces energy expenditure during migration hyperphagia in a large bird

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Summary

1. Bird migration is often seen as the summit of animal performance. Because higher foraging effort associated with fuelling and increased flight activity should generate maximum level of energy turnover, we expect the migratory process to be constrained by energy, whether it is energy expenditure or energy intake.

2. We used implanted data loggers to continuously monitor foraging effort, flight activity and heart rate (as a proxy for rate of energy expenditure), in a wild migratory sea duck before and after moult migration to test the energy budget limitation hypothesis.

3. We show that despite the fact that departing birds forage at three times the level observed during post-migration, daily energy expenditure (DEE) remains the same when periods before and after migration are compared.

4. In an attempt to determine how the birds achieve such a feat, we compared heart rate when active (feeding and flying) for the periods before and after migration and found no significant difference for feeding and flight heart rate. However, heart rate during periods of inactivity was significantly lower during fuelling which together with a reduced time spent flying completely counteracted the observed high energy costs of foraging.

5. The time spent active represented a tiny proportion (8–20%) of the 24-h time budget suggesting that energy minimization and an optimization process may be at work here, confounding any apparent support for the energy budget limitation hypothesis. We thus concluded that similar DEE before and after migration could be owing to the bird's inability to increase energy expenditure over a certain limit or to the survival costs associated with a certain level of physical exertion. Nevertheless, our results indicate that behavioural, and possibly physiological, compensation may be used as a mechanism to reduce the overall energy cost of fuelling in migrating birds.

Key-words: activity budget, daily energy expenditure, foraging effort, heart rate method, migration, oxidative stress, *Somateria mollissima*

Introduction

Not only is the level of flight activity achieved during migration a formidable feat, it is preceded by an unsurpassed feeding intensity occurring just before departure that is known as migratory hyperphagia (Odum 1960). During these episodes, birds ingest large amounts of food daily to gather the fuel (mostly in the form of fat) required for the journey. As increased foraging activity should generate a higher daily energy expenditure (DEE) and because such a process may last several days, hyperphagia is thought to be

the main cost component of the whole migration energy budget (Lindström 2003; Newton 2008).

Although reversible organ size and body mass variation (Biebach 1998; Piersma 1998; McWilliams & Karasov 2001) are indications of the extraordinary flexibility of migrating birds, our understanding of migration strategies is limited without integrated measurements of energy expenditure and time budgets. Estimates of the DEE have the potential to incorporate positive and negative effects of energy demands whereas time budget analysis is likely to identify some of the mechanisms leading to the variation in energy expenditure. However, measurements of time budget and energy expenditure of animals in the field are challenged by many technical difficulties, which is especially true for birds diving for food

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and moving over large distances (Robinson *et al.* 2009). Recent technological advances have allowed investigators to quantify foraging and flight activity, together with rate of energy expenditure, by measuring heart rate and hydrostatic pressure. Using multi-purpose data loggers, sampling rate is high and continuous, and a complete account of the time spent flying (TSF) and diving for a long period of time is now possible (Guillemette *et al.* 2007; Pelletier *et al.* 2007, 2008; Portugal *et al.*, in press).

Because locomotion, digestion of food and thermoregulation may vary over the seasons, it might be expected that the total energy budget of a wild bird would covary with any variation of these components. For example, increasing the time spent to search, catch and process food, such as during pre-migratory hyperphagia, should increase DEE of a migrating bird. However, there might be a limit to which energy can be consumed or expended. Comparisons of maximum metabolic rate with DEE at the interspecific level suggest that endotherms may well work on a daily basis close to the maximum allowed by their metabolic machinery (Kirkwood 1983; Daan, Masman & Groenewold 1990; Weiner 1992). In such a case, we might expect DEE to stay relatively constant when the workload is high. One of the predictions of the energy budget limitation hypothesis is that birds will reorganize their time-energy budget when faced with an increase in energy demand (Pelletier *et al.* 2008) or will use metabolic compensation to keep the rate of energy expenditure within certain limits (Deerenberg *et al.* 1998). Here we test the energy budget limitation hypothesis by continuously monitoring feeding and flying behaviour and by measuring heart rate together with estimates of DEE before and after migration in a large diving bird, the common eider *Somateria mollissima*.

Materials and methods

MODEL SPECIES AND POPULATION STUDIED

Common eiders are large (2 kg) sea ducks that dive for food. The population studied is breeding in the Baltic and moult in the Kattegat sea (Rigou & Guillemette 2010) and can be characterized as a short-distance migrant (600–1200 km) compared to other sub-species where the maximum distance covered by any population between breeding and wintering habitats is no more than 3000 km (Rigou & Guillemette 2010). Thus, the migratory ability of this species seems to be relatively poor when compared to that of migrants such as shorebirds and seabirds that cross continents and oceans to cover the world in search of safety, abundant food supplies and a comfortable thermal environment (Shaffer *et al.* 2006; McKinnon *et al.* 2009). Perhaps, such a relatively poor migratory ability is related to flight costs, which are excessive in common eider ducks (Pelletier *et al.* 2008), most probably related to their short pointed wings and high wing-loading (Rayner 1988; Guillemette & Ouellet 2005).

During migration, eider ducks usually follow the coast and do not fly over areas of unsuitable feeding habitats as they exploit habitats composed of abundant and widespread food supply (Guillemette 2001). As with many other species of waterfowl, common eiders undergo a moult migration in late summer.

They move from breeding habitats to their moulting areas where they lose their wing feathers all at once leading to a period of flightlessness that last 36 days on average; the time interval between migration and the beginning of the moult (flightless) period is about 42 days (Guillemette *et al.* 2007). The flightless period is associated with a high metabolic rate and preceded by a low level of energy expenditure (Guillemette *et al.* 2007). Before and after moult migration, eiders most probably feed on blue mussel (*Mytilus edulis*), a common prey species (Öst & Kilpi 1998), which dominates the benthic community in both the Kattegat (Larsen & Guillemette 2000) and the Baltic (Guillemette *et al.* 2004).

The study was performed on Christiansø Island (55°19'N, 15°12'E), an old Danish fortress located in the southern Baltic Sea, 18 km from the Danish island of Bornholm. The general approach of our work involved the monitoring and deployment of data loggers on breeding females, partitioning of heart rate data and using heart rate to estimate the energy costs of flight and foraging.

DEPLOYMENT OF DATA LOGGERS

We studied the breeding biology of common eiders by monitoring about 100 nests every year on the study plot (1999–2006). Nests of banded females were identified by numbered wooden sticks. In spring 2003, 20 females were surgically implanted with heart rate data loggers (DLs). We obtained a licence from Dyreforsøgtilsynet (Royal Veterinarian Corporation) in Denmark and birds were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care. All surgical procedures were conducted indoors 100 m from the experimental plot. The 20 DLs were 36 mm long (\pm SD = 0.5) \times 28 mm (0.2) wide \times 11 mm thick (0.3) and weighed 21 g (0.3), that is 1.2% of body mass at implantation (Guillemette *et al.* 2007).

Eighteen (90%) of the experimental females returned to the study area 1 year later, which is similar to previously reported survival rate in that species (Coulson 1984). This is most likely related to the fact that implanted DLs do not alter aerodynamic and hydrodynamic properties of experimental individuals (Guillemette *et al.* 2002). However, the number of days with available information in the present study was uneven (ranging from 45 to 220 days), likely due of battery failure. The sixteen individuals used in the present study had loggers recording continually for about 3 months which covered the moult migration (occurring the 12th of July in average), ranging from 8 June to 31 July 2003.

TIME ACTIVITY BUDGET AND PARTITIONING OF HEART RATE DATA

The time budget data involved calculating the daily time (i) spent flying, (ii) spent feeding and (iii) spent inactive (i.e. neither feeding nor flying). The partitioning of heart rate data involved (iv) calculating the number of heart beats associated with each of these aforementioned categories of behaviour, (v) counting the number of heart beats occurring in 1 day (daily heart beats) and (vi) subsequently converting these values into estimates of energy expenditure (see below). For every day (24 h) of sampling, hydrostatic pressure and heart rate were sampled every 2 s. Flight schedules (number and duration of flights) were compiled for each bird following the method described by Pelletier *et al.* (Pelletier *et al.* 2007). This method is based on the dramatic increases and decreases of heart rate upon take-offs and landings, respectively, and a plateau phase during flight where heart rate is

typically three to four times the resting level. For every female, the daily TSF was obtained by summing the duration of all flights that occurred during 1 day.

In birds, dives are usually performed in series, where time spent submerged alternates with time breathing at the surface, which constitute a dive cycle (Guillemette *et al.* 2004). A feeding bout (> 1 dive) is defined as the succession of dive cycles, and the daily time spent feeding (TSFe) was obtained by summing all feeding bouts occurring in 1 day. In benthic foragers, the time spent submerged is composed of time travelling back and forth from the surface and bottom time where the bird actually searches for and swallows prey items (Guillemette *et al.* 2004). Eiders feed on a very abundant but low-quality food, blue mussels and ingest a large number of whole mussels (including shells) during each dive (Guillemette 1994). We assumed the amount of food ingested during each dive is proportional to bottom time. For this reason, we performed a similar analysis with both bottom time [average before-after difference = 82.7 min \pm (95% CI) 42.7 min] and TSFe and, as the results were similar, we only present data dealing with TSFe. Finally, the daily time spent 'inactive' (TSI) was obtained for each day and each female sampled by subtracting the time spent active (feeding + flying) from 1440 min (the total in 24 h). From visual observations, we know that 'inactive' behaviour is composed of swimming, preening and resting (Guillemette 2001).

The heart rate data were partitioned into quantities like feeding heart rate (FeHR), flight heart rate (FHR) and inactive heart rate (IHR). Thus, for every category of behaviour and for every female, we summed the total number of heart beats associated with each behaviour and divided this by the number of minutes spent doing that activity. Thus, we obtained averages of FHR, FeHR and IHR for the sixteen females. A similar procedure was followed for the total (daily) heart rate by dividing the total number of heart beats obtained in 1 day by 1440 min. A customized written computer program was run to calculate all these quantities from the raw data.

DEFINING MIGRATION AND HYPERPHAGIA

Both the daily frequency of flight and the average flight duration increase during migrations of female common eiders and are easily recognized on a plot of TSF in relation to calendar days (Pelletier *et al.* 2008). These authors used a frequency distribution plot of flight duration occurring during a period of 7 months and revealed that 99% of all flights were shorter than 30 min. We used this value as a cut-off point to differentiate migrating from non-migrating birds. Moulting migration lasted on average (mean \pm SD) 2.5 \pm 1.2 days with a mean TSF during migration days of 204 \pm 65.4 min per day. Using the mean observed flight speed of eiders (83.5 km h⁻¹) during migration (Day *et al.* 2004), we estimate the average distance covered during moulting migration to be 710 km.

Hyperphagia is defined as a state of intensive feeding associated with an increase in body mass (Guillemette 2001). We could not monitor body mass of the instrumented females once they departed from the colony, although we know from other populations (Gorman & Milne 1971; Korschgen 1977) that females at this time recover from incubation fast and prepare for moulting migration when body mass increases on average 10 g per day (Korschgen 1977). The annual average time spent diving per day is 91.4 \pm 5.5 (95% CI) min in this population, which correspond to the feeding time required to achieve energy balance on a yearly basis (Rigou & Guillemette 2010). Therefore, we considered females that dive 100 min or more during 3 consecutive days to be hyperphagic. Using this benchmark value for all

females included in our study, pre-migratory hyperphagia lasts about 3 weeks, and we used this time period in our analysis (for the before and after periods). The 3-week period was chosen as a compromise between discarding some hyperphagic days for some individuals and including a number of days without any hyperphagia for others. Choosing a shorter time interval for our before-after analysis does not change our conclusions (see Fig. 1).

CONVERSION OF HEART RATE INTO ENERGY EXPENDITURE

Several studies have shown that the HR method provides a valid approximation of energy expenditure as HR is strongly and positively related to oxygen consumption in various animal species (reviewed by Butler *et al.* 2004; Green 2011). We used the calibration study of Hawkins *et al.* (2000) to convert HR data into mass-specific metabolic rate (sMR). Hawkins *et al.* (2000, Table 4) related HR (beats min⁻¹) and mass-specific rate of oxygen consumption, $s\dot{V}O_2$ (ml O₂ kg⁻¹ min⁻¹) for six common eiders that were monitored continuously for 2 days on a water flume during the experiments, exercised at various speeds for up to 6 h per day and fed with water-fowl diet pellets. The functional (reduced major axis) relationship was $s\dot{V}O_2 = 0.146HR + 9.677$ ($r = 0.868$, $P = 0.023$). One litre of oxygen consumed was multiplied by 20.083 kJ (Schmidt-Nielsen 1997) to obtain sMR of birds.

A different procedure was required to estimate flight costs as it has been shown that both heart rate and stroke volume increase during flight (Bishop *et al.* 2002; Ward *et al.* 2002). Using the second model of Bishop (1997), Pelletier *et al.* (2008) estimated mass-specific flight costs of flight to be 79.5 W kg⁻¹ and this estimate was used in the present study. Finally,

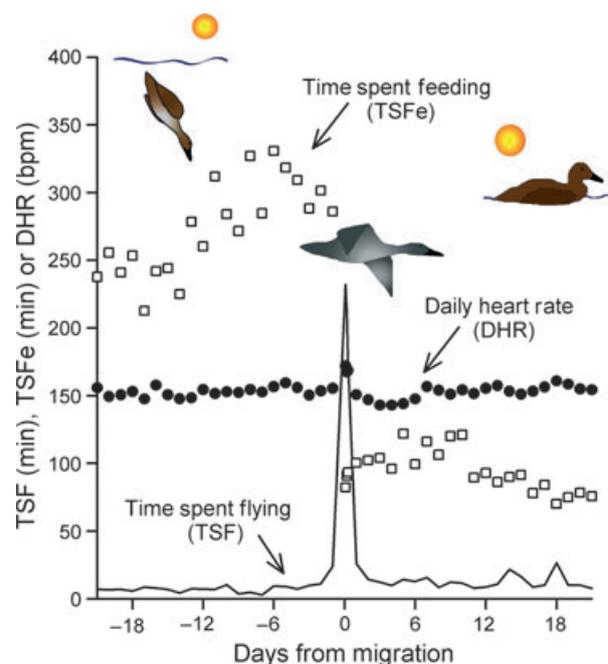


Fig. 1. Mean values of time spent flying (TSF), time spent feeding (TSFe) and daily heart rate (DHR) for female common eider ducks ($N = 16$) 3 weeks before and after moulting migration. Measures are from implanted data loggers that record daily the total number of heart beats and the total duration of diving and flight time for each female (see Methods).

mass-specific DEE (sDEE) was obtained by summing the sMR of birds while flying, feeding and being inactive.

As already indicated above, when the heart rate data are converted into DEE, a mass-specific estimate of energy expenditure is obtained (sDEE). It would be relevant to compare the absolute DEE before and after migration as body mass is reduced during migration (see Discussion). Unfortunately, we did not know the body mass of individuals upon departure. However, we can back-calculate an estimate of body mass at departure based on the body mass of females on the moulting areas (1.82 kg, Korschgen 1977) and the energetic cost of a typical migration day (3170 kJ) by summing the absolute energetic cost of flying, feeding and inactive behaviours. Our estimate is based on the observation that mostly fat (95%) is consumed during migration flights and only a small proportion of protein is (5%) used (Jenni & Jenni-Eiermann 1998; Klaassen, Kvist & Lindström 2000), giving an average energy density of 36 kJ g⁻¹.

DATA ANALYSIS

We used a before-after approach for our analysis. For each individual, we summed the total number of heartbeats (or any other variable) for the period of interest (e.g. before migration, after migration). Then, we subtracted the value obtained after migration from that obtained before migration and the difference (Δ) enabled us to compare the two periods. By repeating this overall individuals sampled, we obtained the average difference (over the 16 individuals) for which we calculated 95% confidence intervals using the bootstrap method and ten thousand re-samplings. Inspection of the sampling distribution resulting from that procedure demonstrated that, in all cases, the distribution was symmetric. Thus, we were able to use the Student's *t* version of the bootstrap (Lunneborg 2000) to compare period of interest. When the 95% confidence intervals of the average difference excluded 0, the difference was declared significant at the 5% level, otherwise it was concluded that no difference could be detected between the periods being compared. A similar approach was used for the time budget. Because time budget observations generate compositional data by definition, the various categories (summing to 1440 min) are interrelated and the confidence interval approach was used only with TSFe (to limit type II error).

Results

TIME BUDGET

Both TSFe and TSF varied substantially in relation to migration (Fig. 1). The time spent feeding before migration averaged (\pm SD, standard deviation) 280 \pm 151 min and was significantly greater, by 181 min (CI = 109 and 253), than TSFe after migration (98 \pm 52 min, Fig. 2a). In contrast, the TSI before migration (1152 \pm 150 min) was lower than that after migration (1328 \pm 53 min), giving an average difference of -176 min, which mirrored the increase in TSFe (Fig. 2a). The average TSF before migration (8 \pm 5 min) was also lower than that after migration (13 \pm 8 min). Thus, the percentage of the day (24 h) spent active (feeding + flying) during hyperphagia was only 20% (Fig. 2a).

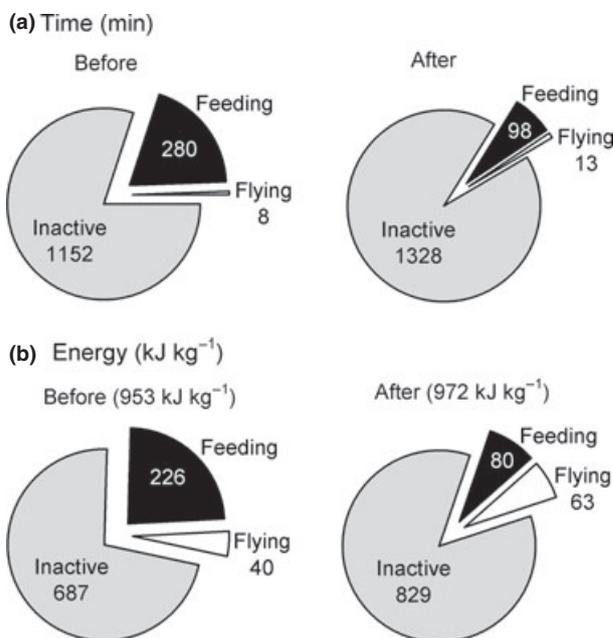


Fig. 2. Time and energy budget of female common eider ducks ($N = 16$) before and after moult migration. (a) The time budget is obtained from continuous recordings of flight and feeding (see Methods) whereas inactive behaviour was obtained by subtracting active time (flying + feeding) from 1440 min (24 h). (b) The energy budget was estimated from conversion of heart rate data into mass-specific daily energy expenditure (sDEE) (see Methods).

HEART RATE

Daily heart rate (DHR) was strikingly similar before and after (Fig. 3) migration [153 ± 31 beats min⁻¹ (mean \pm SD) and 153 ± 27 beats min⁻¹, respectively] despite a substantial difference in foraging effort (Fig. 1). A similar situation exists when FeHR (209 ± 38 beats min⁻¹) and FHR (308 ± 22 beats min⁻¹) before migration are compared to

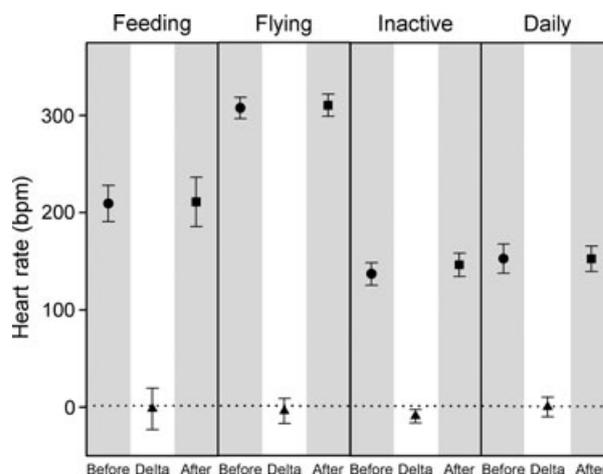


Fig. 3. Average (\pm 95% CI) feeding, flying, inactive and daily heart rate for female Common Eiders ($N = 16$) before (circles) and after (squares) moult migration. Each triangle (delta) represents the mean difference between the before-after periods, which are declared significantly different when their 95% CI exclude zero (see Methods).

those observed after migration (Fig. 3), indicating that no physiological adjustment occurred at this level. However, IHR was significantly higher (Fig. 3) after migration (146 ± 25 beats min^{-1}) than that before migration (137 ± 24 beats min^{-1}). Although the difference is small in terms of IHR, it is substantial in terms of daily heart beats, as the time spent inactive dominated the time budget of pre- and post-migrating eider ducks (Fig. 2a).

ENERGY EXPENDITURE

When the heart rate and activity budget data are converted into a comprehensive energy budget (Fig. 2b), we found mass-specific DEE to be similar before and after moult migration despite the fact that female eiders spent an additional 146 kJ kg^{-1} foraging before migration (226 kJ kg^{-1}), compared to after migration (80 kJ kg^{-1}). Therefore, the increased foraging effort before migration corresponds to 15.3% of the total pre-migration energy budget (953 kJ kg^{-1}). We found the extra energy expended during foraging before migration was almost completely compensated by reductions of IHR (Fig. 3) and TSI (Fig. 2a). For instance, the saving is equivalent to 142 kJ kg^{-1} per day or 14.9% of the total pre-migration energy budget (953 kJ kg^{-1}). In addition, common eiders reduced the TSF, resulting in a saving of 23 kJ kg^{-1} per day (Fig. 2).

Because body mass decreases during migration, we were interested in knowing if the similar values of sDEE would be mirrored by absolute daily energy expenditure (aDEE), so we estimated body mass of female eiders upon departure from known body mass on the moulting grounds and the cost of migration (see Methods). We considered three different assumptions for our calculations. The first analysis corresponds to a minimum estimate and assumes that eiders do not lose body mass during migration, giving an estimate of absolute DEE of 1734 kJ per day before migration and 1769 kJ per day after migration, that is a -2.0% difference. This estimate is unlikely to apply given that DEE during migration days increases 83% and because eiders feed in average 89 min during migration days (Fig. 1), which is about half the time spent feeding in average during a full annual cycle (Rigou & Guillemette 2010). The second analysis assumes that eiders consume body fuel at a maximum rate and do not feed during migration (body mass loss of 220 g), giving an estimate of absolute DEE of 1944 kJ before migration compared to 1769 kJ per day after migration, that is a difference of 9.0%. This estimate is also unlikely to apply, for the reason stated above, as eiders do feed during migration days. That is why we consider an intermediate estimate, assuming that inactive and feeding behaviours were fuelled by energy intake during the journey and that only flight consumed stores of body fuel, as the most realistic estimate of body mass loss (123 g) and absolute DEE. Our intermediate estimate of aDEE before migration (1851 kJ) was 4.4% higher than after migration (1769 kJ). Thus, the increase of aDEE from hyperphagia to post-migration was small, at least compared to the additional energy spent foraging before migration (15.3%).

Discussion

Although observations of body mass variations of migrating birds ought to translate into various levels of energy expenditure, it is surprising that no studies have examined time budgets of migrants, because behaviour might be expected to react promptly to changes in energy demands. However, until recently it has been difficult to obtain accurate data from birds during migration. Using multi-purpose data loggers, we present here for the first time intensive recordings of time spent feeding (TSFe) and TSF, together with estimates of DEE before and after the migration of a large diving bird, and show how the time-energy budget was adjusted in relation to changes in metabolic demands.

Our estimates of mass-specific and absolute DEE before and after migration indicate that they were similar (Fig. 2b). Intuitively, we would expect that extra foraging activities of an animal will incur a higher level of energy expenditure. Our study showed that female eiders compensate or even over-compensate in relation to an increase in their workload associated with pre-migration hyperphagia. Similarly, studies with captive birds (Bautista *et al.* 1998; Deerenberg *et al.* 1998; Wiersma & Verhulst 2005) and wild birds (Moreno *et al.* 1999; Welcker *et al.* 2010) testing the effect of increasing workload found no evidence of associated increases of DEE. One study found that workload elicit physiological compensation (a decrease in resting metabolic rate during the night, Deerenberg *et al.* 1998) and another had a negative effect on reproductive output (Moreno *et al.* 1999). Also, most of these studies found that birds lost body mass during the experimental trials, indicating that individuals were consuming body reserves as a means to cope with the increased workload. This is in stark contrast with pre-migrating birds which lay down fuel reserves and improve their condition before departure.

To cope with an increase in workload during the pre-migratory foraging period, female common eiders reduced both IHR and time spent flying (TSF, Figs 2 and 3). Thus, we may wonder if the mechanism involved is behavioural or physiological compensation? Evidence of physiological compensation during migration is found in barnacle geese (*Branta leucopsis*) and blackcaps (*Sylvia atricapilla*) that become hypothermic during migration (Butler & Woakes 2001; Wojciechowski & Pinshow 2009), and it has been speculated that hummingbirds use hypothermia to enhance fuel deposition rate before and during migration (Carpenter & Hixon 1988; Hiebert 1993). Unfortunately, we did not record body temperature in our study. However, behavioural flexibility of birds has been observed when facing increases in reproductive costs, thermoregulatory challenges and food limitation (reviewed by Vezina & Salvante 2010). Because behavioural adjustments are energetically cheaper and faster than physiological adjustments, we might expect behaviour to be the first response to an increase in metabolic demands. Visual observations of focal eiders during spring hyperphagia support this view, as the time spent feeding was inversely related to comfort, swimming and resting activities (Guillemette 2001), which are grouped in the present study under 'inactive'

behaviour. Therefore, the various components of the time and energy budget would be inherently related and the reduction of IHR would be driven by a shift from high-cost (comfort) to low-cost behaviour [resting, see Supplementary Information (in Pelletier *et al.* 2007)]. We therefore consider behavioural compensation as the most parsimonious interpretation of our results, although we cannot rule out the possibility that compensation may also have been physiological.

We believe our results have important implications for the understanding of migration strategy, as they unravel an important mechanism that may facilitate migration of birds. By reducing the energetic contribution of non-foraging components of the time budget, migrating birds may circumvent an important cost associated with hyperphagia. If other migrating birds use this strategy, it would indicate that behavioural adjustments play a major role in the bioenergetics of migration. In two recent reviews (Lindström 2003; Newton 2008), it was argued that reducing energy expenditure to enhance fuel deposition rate was probably not an important strategy for migrants. Thus, the implicit view assumes that fuelling contributes to an increase of DEE. One major disadvantage of such a strategy would be that extra foraging costs require additional feeding time, which need to be paid back whether it is by a higher percentage of time spent feeding every day or alternatively by increasing the duration of the pre-migratory period.

The present study was designed to test the energy budget limitation hypothesis by selecting a period of high energy turnover and by comparing DEE before and after moult migration. Because DEE was similar before and after migration, results of the present study support that hypothesis. Recent investigations on energy budget limitations have focused on whether upper levels of metabolism are determined by central processing limits or by peripheral limits or by limits to dissipate heat (reviewed by Weiner 1992; Bacigalupe & Bozinovic 2002; Speakman & Król 2005, 2011). These various mechanisms have been elucidated from careful manipulative experiments performed mostly on small laboratory rodents and are beyond the scope of our study. However, there is an alternative interpretation to the notion that physiological functions may limit the energy budget of animals: behavioural compensation and similar DEE before and after migration observed in the present study may be the result of an optimization process. One surprising result of this study is how little time each day eiders spent feeding and flying: only 20% (288 min of 1440 min) during pre-migratory hyperphagia and 8% (111 min of 1440 min) after migration. Energy minimization may be the underlying principle of time allocation in birds (Daan, Deerenberg & Dijkstra 1996). Therefore, it may be possible that increasing DEE over a certain level would be associated with a decrease of survival rate and that, according to the oxidative stress theory of ageing (an imbalance between anti-oxidants and pro-oxidants in favour of the later), energy minimization would be the best strategy to follow (Wolf & Schmid-Hempel 1989; Daan, Deerenberg & Dijkstra 1996). This theory of ageing suggests that a high level of energy expenditure would be associated with the

production of reactive oxygen species contributing to an acceleration of senescence (Ramsey, Harper & Weindruch 2000; Speakman *et al.* 2002; Hulbert *et al.* 2007; Monaghan, Metcalfe & Torres 2009).

Although it is clear that physical activity affects oxidative balance [reviewed in (Leeuwenburg & Heinecke 2001; Powers & Jackson 2008; Fisher-Wellman & Bloomer 2009)], numerous studies conducted on humans have shown that exercise may or may not increase oxidative damage, and even in some cases be beneficial to health, leading to the so-called exercise paradox. It seems apparent, however, that exercise of longer duration or higher intensity may be associated with a higher probability of oxidative damage (Leeuwenburg & Heinecke 2001; Fisher-Wellman & Bloomer 2009). Recent studies have shown that oxidative stress is increased under flight activities in homing pigeons (Costantini, Dell'Arciccia & Lipp 2008) and captive budgerigars (Larcombe *et al.* 2008), but we are not aware of any study that has investigated the impact of foraging level on oxidative stress. One of the best treatments to manipulate life span in animals is caloric restriction and it has been shown repeatedly that this increases life span of animals through a reduction of oxidative damage (Sohal & Weindruch 1996; Ramsey, Harper & Weindruch 2000). Increasing DEE during hyperphagia would increase further caloric intake (see above).

We conclude that it is difficult or impossible to discriminate the energy budget limitation hypothesis from the energy minimization hypothesis in our study as both hypotheses predict that the time-energy budget would be rearranged when metabolic demands increase. The similar DEE before and after migration could be owing to the bird's inability to increase energy expenditure over a certain limit (metabolic ceiling) or to the survival costs associated with a certain level of physical exertion. We suggest that only experimental manipulations will likely be successful at discriminating these two hypotheses in future studies. Nevertheless, our results indicate that the benefits obtained from increased foraging effort while maintaining DEE constant are important mechanisms for saving energy and we predict that such a strategy is used by other migratory birds. Another implication of our study is that an increase in the activity level of animals does not necessarily imply an increase in energy expenditure as is very often assumed in the ecological literature.

Acknowledgements

Thanks to Dr. Annette Flagstad from Royal Veterinary School of Denmark for performing the surgeries on experimental birds and Torben Anderson and Ina Jørgensen for lending a very convenient surgery room. Thanks to Yves Rigou and Peter Lyngs for their indispensable help in the field. Many thanks to Jean-Marc Grandbois who designed the computer software used in this study and to David Pelletier who performed the analysis on flight behaviour. Thanks to Dr. Michal Wojciechowski, two anonymous reviewers and the associate editor for their constructive and helpful comments. We thank Fonds Québécois de la Recherche Nature et technologie (FQRNT) for the post-doctoral fellowship to S. E. R. This study was done in collaboration with the National Environmental Research Institute of Denmark and was funded through the Canadian Natural Sciences and Engineering Research Council (NSERC) discovery and equipment grants to M. G.

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Received 3 May 2011; accepted 16 March 2012

Handling Editor: Jonathan Blount