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Cite this article: Guillemette M, Woakes AJ, Larochelle J, Polymeropoulos ET, Granbois J-M, Butler PJ, Pelletier D, Frappell PB, Portugal SJ. 2016 Does hyperthermia constrain flight duration in a short-distance migrant? *Phil. Trans. R. Soc. B* **371**: 20150386. http://dx.doi.org/10.1098/rstb.2015.0386

Accepted: 4 July 2016

One contribution of 17 to a theme issue 'Moving in a moving medium: new perspectives on flight'.

Subject Areas:
biomechanics

Keywords:
avian, body temperature, eider ducks, heat dissipation, migration

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rstb.2015.0386 or via http://rstb.royalsocietypublishing.org.

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Does hyperthermia constrain flight duration in a short-distance migrant?

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While some migratory birds perform non-stop flights of over 11 000 km, many species only spend around 15% of the day in flight during migration, posing a question as to why flight times for many species are so short. Here, we test the idea that hyperthermia might constrain flight duration (FD) in a short-distance migrant using remote biologging technology to measure heart rate, hydrostatic pressure and body temperature in 19 migrating eider ducks (*Somateria mollissima*), a short-distance migrant. Our results reveal a stop-and-go migration strategy where migratory flights were frequent (14 flights day^{-1}) and short (15.7 min), together with the fact that body temperature increases by 1°C, on average, during such flights, which equates to a rate of heat storage index (HSI) of 4°C h^{-1}. Furthermore, we could not find any evidence that short flights were limited by heart rate, together with the fact that the numerous stops could not be explained by the need to feed, as the frequency of dives and the time spent feeding were comparatively small during the migratory period. We thus conclude that hyperthermia appears to be the predominant determinant of the observed migration strategy, and suggest that such a physiological limitation to FD may also occur in other species.

This article is part of the themed issue 'Moving in a moving medium: new perspectives on flight'.

1. Introduction

Long-distance bird migrants seem to be able to achieve the impossible, spending energy at an unmatched rate among vertebrates and dumping large amounts of heat produced while flying, all without dehydrating. Numerous wind-tunnel studies, laboratory and aviary experiments have shown that convection is the main mechanism by which a flying bird maintains heat balance, followed by radiation and evaporation [1–9]. Hyperthermia, a condition that develops when those mechanisms of heat dissipation are not sufficient to maintain heat balance, is barely mentioned as a potential constraint of performance in migrating birds (but see [4] and [10]).

Forty years ago, it was proposed that cheetahs (*Acinonyx jubatus*) might stop running upon reaching a critical body temperature (T_b) ([11], but see [12]), which was confirmed further with other mammal models, including rats, antelopes, goats and dogs [13–16]. Fatigue is a complex multi-faceted phenomenon and one interesting avenue that has been investigated in humans is how body temperature increases during exercise, leading to hyperthermia-induced fatigue [17]. The critical core body temperature hypothesis stipulates that exercise in the heat ceases at some critical body temperature independently of T_b at the start of exertion [18–20]. Here, the subjects are working at a constant rate until T_b reaches some unsustainable level, triggering then a 'safety' switch associated with a reduced recruitment of muscles as controlled by the brain [20]. The idea that body temperature may constrain prolonged exercise gained credence upon the experimental work of Danish researchers [18,21,22,23] showing that leg blood flow, altered muscle metabolism or skeletal muscle glycogen could not explain the termination of exercise, and that the attainment of critical T_b could severely alter homeostasis. A second hypothesis assumes instead that an exercising subject can modulate exercise intensity in an anticipatory fashion where they would eventually reduce the workload in order to avoid reaching some critical T_b [24,25]. Under this hypothesis, hyperthermia is considered as an evolving condition during exercise and is related to the existence of a continuous thermal signal. In this case, the rate at which heat is stored in the exercising body would be the monitored cue.

The core body temperature of pigeons (*Columbia livia*) during flight under captive conditions has been recorded as high as 43.1–44.4°C, and flight time is reduced during bouts of such high-temperature activity [26]. Such high temperatures in captive experiments may be a result of handling stress [27], and therefore are not necessarily an accurate reflection of body temperatures experienced by birds in flight under field conditions. As such, field experiments are pivotal to truly investigate body temperature changes during natural flight. Captive experiments have also demonstrated that individual birds are reluctant or refuse to fly once a high body temperature has been reached [2,26–33]. Many studies of body temperature during flight, however, have involved very short flights (less than 10 min) where birds were often tethered to trailing wires.

To identify how heat dissipation may constrain prolonged exercise, affect energy expenditure, and play a major determining role in shaping migration strategies, we studied a migratory population of common eiders (*Somateria mollissima*) (herein referred to as eiders), a large marine diving duck [34]. Here, our aim is to investigate if hyperthermia might influence the migration strategy of a large bird and test both the critical body temperature and anticipation hypotheses. Moreover, we investigate two other alternative hypotheses in this paper in order to substantiate further our interpretation, by testing the possibility that the migration strategy observed is limited by the working capacity of the heart or simply by the need to feed. Using remote biologging technology, we recorded heart rate (every 2 s), time spent diving (derived from a pressure sensor measuring dive depth every 2 s) and body temperature (16 s) regularly for every bird for a period of 4–12 months using internally implanted multi-channelled data loggers (DLs) [34–38]. The sampling rate of these measurements allows the identification of all periods of flight and the interaction between flight duration (FD) and body temperature to be examined at a level of detail not previously explored under natural conditions.

2. Material and methods

(a) Model species and methods

Common eiders (*S. mollissima)* are large (approx. 2 kg) sea ducks that dive for food. They are characterized by short-pointed wings resulting in high wing-loadings and high flight speeds [34–36]. The population studied here breeds in the Baltic and moults in the Wadden Sea [39] and can be characterized as short-distance migrants (200–1100 km) compared with other sub-species where the maximum distance covered by any population between breeding and wintering habitats could be up to 3000 km [39].

This 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 DLs on breeding females, using heart rate data to determine the start and the end of each flight, calculating the time spent diving from the depth sensor, and measuring variation of body temperature during flights. All instrumented females of this study were diving during the migratory process, indicating that they were following a coastal route (see Results). As with many other species of waterfowl, eiders undergo a moult migration in late summer. They move from breeding habitats to their moulting areas where they completely lose their wing feathers, leading to a period of flightlessness that lasts 36 days on average [35]. Such simultaneous moulting of the flight feathers has been shown to be energetically demanding in many species of waterfowl [35,39–42].

(b) Deployment of data loggers

On Christiansø Island, 45 common eiders were captured in 2003, 2004 and 2005 and implanted with DLs under license from Dyreforsøgtilsynet (Danish Royal Veterinarian Corporation) and the Canadian Council of Animal Care. All surgical procedures were conducted indoors according to the procedure described by Guillemette *et al.* [34]. The 45 DLs were 36 mm long (±s.d. = 0.5) × 28 mm (0.2) wide × 11 mm thick (0.3) and weighed 21 g (0.3), that is 1.2% of body mass at implantation [34]. The DLs were encased in biocompatible material with two asymmetrical leads protruding from them towards the heart. Thirty nine (87%) experimental females returned to the study area 1 year later, which is similar to previously reported survival rate in that species [43]. One year after the implantation, 36 females were re-captured of which 17, 7 and 12 (respectively for 2003, 2004 and 2005) had their DLs removed. For all studied years, DLs recorded pressure and heart rate every 2 s and body temperature every 16 s, except for 2003 females as the temperature sensor was not operational for that deployment. We thus analysed for this paper data from 19 females (2004 and 2005 deployment only).

(c) Time spent flying and feeding

Flight schedules (number and duration of flights) were compiled for each bird following the method described by Pelletier *et al.* [36]. This method is based on the dramatic increases during flight where heart rate is typically 3–4 times the resting level. For every female, the daily time spent flying (TSF) was obtained by summing the duration of all flight episodes that occurred during 1 day.

In benthic foragers, the time spent submerged is composed of time travelling back and forth from the surface, and the bottom time where the bird actually searches for and swallows prey items [44,45]. Eiders feed mainly on a very abundant but low quality food, blue mussels (*Mytilus edulis*), and ingest a large number of whole mussels (including shells) during each dive. The pressure sensor encased within the DL enables the identification of each dive performed by the experimental bird in relation to time. Thus, the daily time spent diving was computed by summing the underwater duration of all dives performed during a migration day for each female.

(d) Defining migration

Both the daily frequency of flights episodes and the average duration of flights episodes (FDs) increases during migrations of female common eiders and is easily recognized on a plot of TSF in relation to calendar days [36]. These migration events were associated with at least one flight of more than 30 min. We used the occurrence of such flights (30 min duration) as a cut-off point to differentiate migrating from non-migrating birds. FD was categorized in classes by doubling the upper limit (log 2 scale) of each class (e.g. 0–5 and 5–10 min) to ensure a more even number of flights in each category. A similar approach was used for flight segments (FS), defined as the time interval between two specific points (e.g. 0–5 and 5–10 min) in time during flight.

(e) Body temperature and heat storage index

For each flight episode, the starting (T_{bStart}) and ending (T_{bEnd}) body temperatures (T_{b}) were obtained together with the maximum value (T_{bMax}), whenever it occurred during each episode. We define the overall maximal T_{b} as the maximum T_{b} among all flights performed by one individual and averaged over all the 19 females. We used this overall maximal T_{b} as an approximation of a critical T_{b} for that species. We define the heat storage index (HSI) as the variation of T_{b} in relation to time (degrees celsius per hour). More specifically, we calculated a reduced major axis slope of T_{b} in relation to time for each flight performed by an individual. The T_{b} sensor time inertia was evaluated to be 3 min, as we observed changes in T_{b} only after 3 min of flight. Thus, all flights less than 3 min were excluded from our analysis ($n = 412$).

Three metrics of HSI were used. An average HSI was calculated for all flight episodes performed by an individual and averaged over the 19 females giving an $\mathrm{HSI}_{\mathrm{average}}$ of 4.1°C h^{-1} (s.d. = 1.9). A categorical HSI was also calculated for each flight and averaged over the 19 females within each FD category in turn (0–5 min, 5–10 min, etc.), which revealed that $\mathrm{HSI}_{\mathrm{category}}$ varied with FD. In order to reduce the variation due to FD, we also calculated an average individual HSI based on all 5–10 min segments (HSI_{5-10}) performed by an individual (all FDs). This was preferable than using a single value per individual as some FD categories were not performed by all individuals. We thus used HSI_{5-10} as an individual index of heat storage.

(f) Data analysis

Confidence intervals were computed for all delta T_{b} and HSI values using the bootstrap method and 10 000 re-samplings. We used the Student's *t* version of the bootstrap [46] to compare the period of interest. When the 95% confidence intervals of the average deltas 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. We used a two-way repeated measures ANOVA, with the Satterthwaite's approximation for degrees of freedom, to test the hypothesis that HSIs would vary with both FD and FS. More specifically, we tested the anticipation hypothesis by looking at the interaction term using $p = 0.05$ as the critical value. Finally, the level of significance of correlations were computed using a permutation test.

3. Results

The migration of this population of eiders involved a distance of 714 ± 286 km, taking, on average, 2.6 ± 1.0 days, from the central Baltic region to the Wadden Sea. For each day, the birds spent a total of 205 ± 81 min in flight (14.2% of total day), comprised of 13.7 ± 5.7 flights in total per day. Each individual flight averaged 15.7 ± 5.2 min, and of the 655 flights recorded from the 19 birds approximately only 10% lasted more than 40 min, with most (48%) flights being shorter than 5 min (figure 1*a*). These longer flights (more than 40 min) were most important in terms of contribution to migration effort (flight time of figure 1*a*).

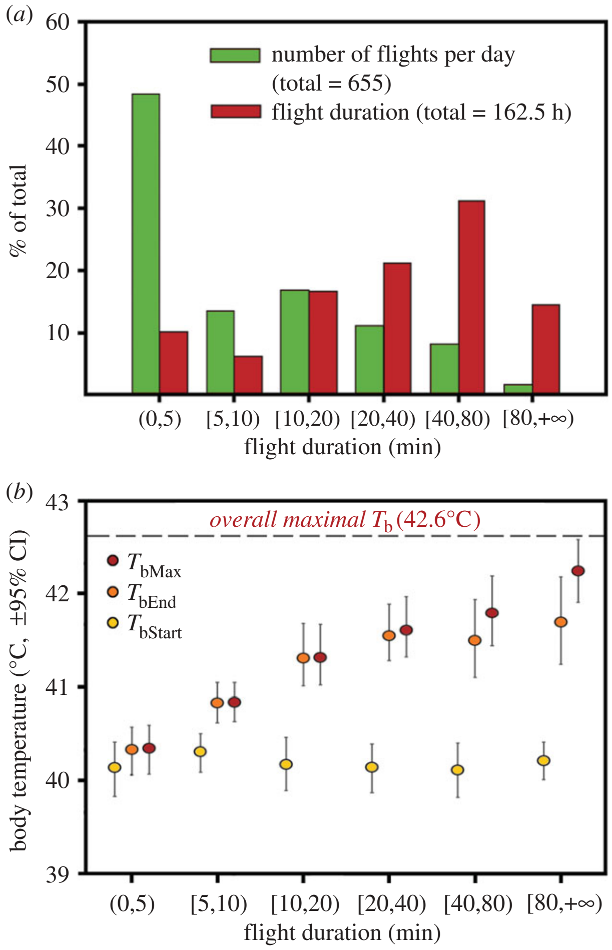

Figure 1. (*a*) Flight frequency and total flight time in relation to flight duration (FD). Most flights performed during moult migration were of short duration but those contributing the most to migration effort were long flights. (*b*) Mean body temperature (T_{b}) at the beginning (T_{bStart}) and at the end (T_{bEnd}) of a flight together with (T_{bMax}) while aloft in relation to FD. Errors bars depict 95% confidence intervals. Critical T_{b} was assessed as the overall maximal T_{b} among all flights performed by one individual and averaged over all the 19 females (42.6 ± (s.d.) 0.1°C).

(a) The critical body temperature hypothesis

During flights lasting up to 80 min, the maximum body temperature (T_{bMax}) recorded while the eiders are actively flying increases monotonously with FD (figure 1*b*). The overall maximal T_{b} recorded (see Methods) during such flights in the 19 eiders is 42.6 ± 0.1°C, thought to be the critical T_{b} limit (see Discussion). However, during longer duration flights (more than 80 min, up to 170 min), the patterns of heat gain are quite different from those observed during shorter duration flights. Body temperature, measured at the end of flight, increases linearly up to 30 min but then tends to level off, reaching 41.7 ± 0.9°C on average (figure 1*b*). This indicates that after reaching a peak body temperature within the first 30 min of flight, the rate of heat storage decreases as FD increases.

(b) Alternative hypotheses explaining short flights

Although reaching a high absolute level of body temperature is a likely signal to stop long flights, such a limit cannot explain why birds stop flying after only a few minutes. For instance, 59% of the 412 flights, lasting 14 min on average, were stopped while T_{b} was still increasing. Here, we test three alternative hypotheses. The first one is based on the idea that some anticipatory mechanism is used by the migrating birds based on the

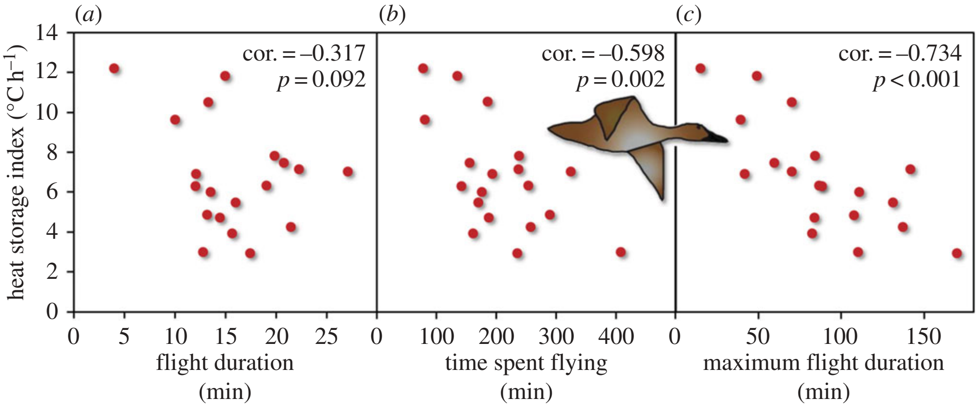

Figure 2. Scatterplot relating the individual (see Methods) heat storage index averaged over all flight segments (HSI_{5-10}) performed by an individual in relation to (*a*) average flight duration, (*b*) average daily time spent flying and (*c*) maximum flight duration (one flight per individual). Pearson's correlation coefficients are shown together with probability levels determined from permutation tests. (Online version in colour.)

Table 1. Average (bold) values of heat storage index (HSI in degrees celsius per hour), with 95% confidence intervals (CIs) in relation to flight durations (FD) and flight segments (FS), to test the hypothesis that long flights are characterized by a lower level of heat storage than short flights (see text). The table reads from left to right going through FD classes from a single FS class. Only late segments of flight for longer flights have HSI non-significantly different from zero (italicized values).

	flight duration classes (min)					
flight segments classes (min)	**(0,5)**	**[5,10)**	**[10,20)**	**[20,40)**	**[40,80)**	**[80, + ∞)**
(0,5)	**3.38**	**4.61**	**3.69**	**3.74**	**3.90**	**4.23**
CI −	2.37	3.67	2.77	2.76	2.86	2.59
CI +	4.39	5.56	4.61	4.73	4.92	5.87
[5,10)		**7.59**	**7.09**	**6.14**	**6.58**	**5.26**
CI −		6.44	6.17	4.86	5.54	3.62
CI +		8.74	8.02	7.56	7.60	6.91
[10,20)			**5.74**	**3.09**	**3.76**	**2.84**
CI −			4.74	2.10	2.12	1.19
CI +			6.76	4.08	4.19	4.49
[20,40)				**1.49**	***0.32***	***1.25***
CI −				0.38	*−0.71*	*−0.40*
CI +				2.60	*1.35*	*2.90*
[40,80)					***0.64***	***1.34***
CI −					*−0.46*	*−0.31*
CI +					*1.72*	*2.98*
[80, + ∞)						***1.06***
CI −						*−0.93*
CI +						*3.04*

rate of heat storage [24,25,47,48]. By partitioning each flight into FD segments, we were able to test the hypothesis that long flights would start with a lower rate of heat storage compared with shorter flights. This hypothesis was supported by our analysis of HSI values as the interaction between the duration of flight episodes (FD) and that of FSs was highly significant (repeated measures ANOVA, $F_{10,709} = 4.4$, $p < 0.0001$). Apart from the 0–5 FS, the HSIs of various FSs were generally higher for short flights than for longer flights (table 1).

From this, we expected migration effort to be modulated at the individual level by the rate of heat storage during flight (figure 2). HSI_{5-10} (see Methods) was negatively correlated with FD but not significantly so ($r = -0.317$, $p = 0.092$ from a permutation test). However, the rate of heat storage was significantly and inversely correlated with both the TSF ($r = -0.598$, $p = 0.002$) and maximum FD (FD_{max}, $r = -0.734$, $p < 0.001$).

The second alternative hypothesis is the cardiac drift hypothesis [49], which stipulates that the stop-and-go strategy of eider ducks may be caused by the limiting capacity of the heart while flying. Indeed, heat accumulation within the body might trigger an increase of blood perfusion to the periphery to enhance heat dumping, thereby causing a reduction of blood pumped at each heart beat. The increase in peripheric perfusion comes from a drop in peripheric

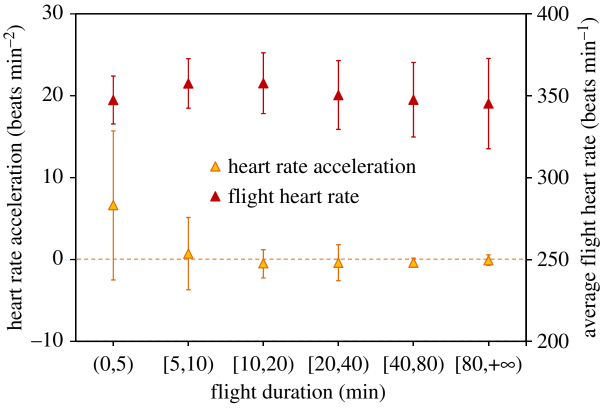

Figure 3. Mean flight heart rate (FHR $\pm$ 95% CI) and mean heart rate acceleration (HRA $\pm$ 95% CI) in relation to flight duration. HRA was calculated for each category as an average reduced major axis slope relating time and HR together with 95% CIs using the bootstrap approach. When a CI excludes the zero line, the average slope is considered to be significantly different from zero ($p < 0.05$).

resistance. This causes a drop in arterial pressure, and increase in cardiac output, but a decrease in muscle perfusion. More likely, cardiac output is unchanged but increased vasodilation in mucosal and cutaneous surfaces diverts more blood from flight muscles. Hence, an increase in heart rate as a compensation mechanism could have confounded our results. However, average flight heart rate (FHR) varied very little in relation to FD (figure 3) with an average of 351 bpm (s.d. $\pm$ 40) for all FD and individuals. This conclusion was confirmed by an analysis of heart rate acceleration within FD categories (heart rate acceleration is the rate at which heart rate changes its velocity (beats per min min^{-1} (beats min^{-2}))). Although heart rate (HR) acceleration of 0–5 min flights was highly variable with a positive tendency, it was not significantly different from zero for each flight category in turn (figure 3, CIs include zero).

A third and obvious hypothesis to explain the observed migration strategy is that short flights and the numerous stops could have been spent to fuel the high level of exertion. This was not the case as only 22% of the stops between flights ($n = 606$) were devoted to feeding. We thus discard the hypothesis that feeding was driving the stop and go strategy of this species during migration.

4. Discussion

Here, we have shown that during migratory flights, eiders experience hyperthermia, with body temperature increasing by, on average, 1.0°C at the end of a typical flight (16 min). This temperature increase equates to 4.1°C h^{-1}, and corresponds to the storage of a significant fraction (8.2%) of the body heat produced during flapping flight. Heat stress is a vital component to consider when evaluating migration physiology. Aside from having its own direct effect on flight physiology, hyperthermia will additionally have significant implications for overall body water balance, as it stimulates birds to increase their heat loss through evaporative cooling. Flight hyperthermia is a complex multi-faceted phenomenon, potentially altering homeostasis and causing a multitude of physiological problems. For example, hyperthermia can damage enzymes and other proteins, leading to mitochondrial dysfunction, oxidative stress and cell death in muscle as well as in other organs. This raises the possibility that flight induced hyperthermia is dictating FD.

(a) Flight and critical T_b

The observation that T_b increases during flight activity of captive or trained birds has been made several times [26–33]. Indeed, various experiments performed in captivity have shown that individuals birds are reluctant or refuse to fly once a high body temperature has been reached. Birds produced heat while flying at a level one order of magnitude higher than their resting rate, and they do so with a formidable level of insulation as their plumage may act as barrier to heat dissipation [50].

We determined the highest value of body temperature (T_{bMax}) for each female. The overall average of T_{bMax} among females, which we presumed to be the highest T_b tolerated (T_{bCrit}), was 42.6°C, 2.4°C higher than the average. An average T_{bCrit} of 43.7°C can be estimated ($n = 5$, range 43.1–44.5°C) for pigeons (*C. livia*) reluctant to fly in captive conditions [7,28,30,31], which is 1.1°C higher than our estimate of T_{bCrit} in eiders. However, it is well known that T_b of birds is inversely related to body mass [51], and pigeons, with a much lower body mass (340–369 g) should have a higher T_b compared with eider ducks. Moreover, T_{bCrit} during flight may be influenced by habitat features and the thermic regime of their environment [52]. Therefore, it is highly unlikely that a single value of T_{bCrit} might apply to all species and conditions. In a very different situation, captive eiders suffering handling stress experienced increase in body temperature of 2°C from 41.5°C, plateauing at 43.5°C [27]. More importantly, allowing body temperature to reach a point at which homeostasis is not maintained is expected to have negative survival consequences. We thus conclude that although it must be a critical T_b at which a bird stops flying, the notion of a critical T_b alone cannot fully explain the migration strategy of eider ducks.

(b) Flight and the rate of heat storage

The anticipation hypothesis, derived from experiments conducted on humans and other mammals, stipulates that an animal can modulate exercise intensity in an anticipatory fashion, where an individual would eventually reduce the workload in order to avoid reaching some critical T_b [24,25,53]. In this case, the rate at which heat is stored in the exercising body would be the monitored cue. As predicted by this hypothesis, the HSIs of various flight stages/durations were higher for short flights than for longer flights in eider ducks (table 1). The main underlying assumption of that hypothesis is that an individual should be able to regulate its working level, which in turn would stabilize or even decrease T_b while flying, and then avoid reaching some critical level of T_b. However, the ability of eider ducks to modulate their work level (see below) seems to be limited by their wing morphology and a high wing-load [54], which in turn produce one of the highest flight speeds among birds using flapping flight [55,56]. We thus suggest that the main avenue to vary the workload while flying for an eider duck is to stop flying. A second avenue would be to select favourable wind conditions that would minimize the workload and the rate of heat storage, for instance flights assisted by tail winds [55]. Thirdly, individual HSIs were negatively correlated with the daily TSF and maximum FD, suggesting that heat storage has the potential to shape migration strategy in this species.

(c) Alternative hypotheses to hyperthermia constrained flight duration

We could not find any evidence for the cardiac drift hypothesis (see Results) or any relationship between heart rate and T_b (figures 1*b* and 3). The latter is puzzling especially when compared to a recent study on bar-headed geese (*Anser indicus*) where FHR and T_b were apparently tightly related in four migrating individuals (figure 1, [57]). One possible reason to explain the apparent discrepancy is the high wing-loading of eider ducks compared with geese. In theory, the relationship between flight speed and power output is a U-shaped curve where low and high flight speeds would be associated with a high level of exertion. Following Bishop [58] & Pelletier [59], calculations of available power (P_{max}) over required power (P_{min}) suggest that the power margin, and the possibility to modulate (air) flight speed, is weak or almost null in eider ducks. In other words, eiders would have little aerobic capacity above their minimum requirements, which would reduce their capacity to modulate their working level while flying. In contrast with these theoretical considerations, FHR of eiders can vary notably within a FD category (figure 3) and it was observed that T_b can be down-regulated during long flights (figure 1*b*). Bowlin *et al.* [60] have shown the heart rate of wild thrushes (*Catharus spp.*), a passerine bird, to be tied to wing-beat frequency. Unfortunately, we did not record wing-beat frequency in this study and we suggest that without such information, it is difficult to test the main assumption of the anticipation model when applied to eider ducks. Nevertheless, we conclude again that the main option available to eider ducks to vary the work level during migration is to stop flying.

Another and final consideration is the observation that only 22% of the stops involved diving, thereby refuting the possibility that feeding was driving the stop-and-go strategy of migrating eiders. Indeed, the birds spent only 2.3% of their time (per 24 h) diving during the migration period compared with 6.3% of their time, on average, during a full annual cycle [39]. With the increase in energetic requirements due to the migratory flights [34], this time spent diving is likely to be insufficient to be replenishing lost fat stores, and the short dives probably perform an alternate function.

(d) What about other migratory birds?

This paper is the first report of direct and detailed measurements of the daily TSF and the time spent feeding of a migrating bird together with measurements of body temperature. We would like here to consider how our findings might apply to other bird species. We thus postulate that birds prone to hyperthermia during migration are associated with high wing-loadings, large body masses and frequenting aquatic habitats. First, hyperthermia during migration should apply to diving birds with high wing-loading and continuous, fast-flapping flight such as diving ducks and alcids because of their high wing-loadings dictating high flight costs [54–56], which would generate a large amount of heat while flying. The only other study we are aware of that measured T_b during flight of diving birds has been done with shags (*Phalacrocorax georgianus*, [61]), where the rate of T_b increase (16°C h^{-1}) was much higher than what we quantified for eider ducks; although this was only for short flights (less than 5 min). Second, birds exchange heat with their surroundings at rates proportional to their surface areas while heat storage is proportional to body mass [62], rendering heat storage more probable in large species, while the insulation level (low conductance) also increases with body mass [63]. We thus predict that the likelihood of hyperthermia will vary with body size, where large migratory birds are the most likely candidates to store heat while flying. Third, aquatic birds migrating over the water may be more inclined to let hyperthermia happen as the cooling power of water is much larger than that of air (in terrestrial habitats).

Finally, migration strategies are diverse and we expect birds to use various behavioural strategies to limit the extent of hyperthermia during migration. For example, three common strategies used by migratory birds are nocturnal travelling, flying at high altitudes and V-formation flocking [10,64–67]. This could lessen considerably the possible outcome of hyperthermia and facilitate the thermoregulatory balance during flight, particularly as nocturnal flight and altitude are associated with cooler air and an increase in convection. On the other hand, many other species of birds migrate during the day at low altitude [64]. We thus consider that only recent and future advances of biologging capabilities will offer the opportunity to determine the role that hyperthermia may play during flight and migration of these various species.

Ethics. This study was performed under the approval of the Canadian Council of Animal Care # CPA 16-03-07-01.

Data accessibility. Electronic supplementary materials are available with the paper http://dx.doi.org/10.1098/rstb.2015.0386.

Competing interests. No competing interest to declare.

Funding. This study was undertaken 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.

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. Final tanks to Dr Alain Caron for statistical advices. We are grateful to two anonymous reviewers for their insightful comments on the manuscript.

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