

SHORT COMMUNICATION

Daily energy expenditure in white storks is lower after fledging than in the nest

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ABSTRACT

Many juvenile birds turn into long-distance migrants within weeks of fledging. This transition involves upheavals in their energy management as major changes in growth and activity occur. Understanding such ontogenetic transitions in energy allocation has been difficult because collecting continuous data on energy costs in wild developing birds was previously largely impossible. Here, we continuously measured heart rate and fine-scale movements of 20 free-living juvenile white storks (*Ciconia ciconia*) using on-board biologgers to explore individual and environmental factors relating to daily mean heart rate. In addition, we explored which specific energy management strategy storks use during these crucial early life stages. We found that daily mean heart rate increased with overall movement activity, and increasing body temperature, but that it decreased with age. Further, we found that during the nestling period, when growth costs are high, activity costs are low, and post-fledging that activity costs are increased while maintenance costs are low, indicating a constraint on overall energy use in both phases. Our observations are consistent with the hypothesis that individuals invested more energy per unit time while still in the nest than after fledging despite the high costs of flight.

KEY WORDS: Energy management model, Daily energy expenditure, Heart rate, *Ciconia ciconia*, Ontogeny

INTRODUCTION

Energy is a limited resource due to its finite availability in the environment and/or the restricted ability of individuals to acquire/spend it. Thus, animals are forced to allocate it carefully between their different behaviours and metabolic processes, thereby influencing fitness and survival (e.g. growth, migration, reproduction; Stearns, 1992). Because of the constraints on the amount of energy spent per day (i.e. daily energy expenditure, DEE), there is a potential trade-off between the two components of DEE: resting metabolic rate (RMR) and activity energy expenditure (Careau and Garland, 2012; Mathot and Dingemanse, 2015; Portugal et al., 2016; Halsey et al., 2019). RMR is defined as the lowest metabolic rate of an endotherm (juvenile or adult) at rest

(Speakman et al., 2004); it corresponds to the costs of self-maintenance, including development, thermoregulation and immune functions. In recent years it has been shown that the minimum heart rate of an individual may serve as a proxy for RMR (Green, 2011). The difference between DEE, approximated by the average heart rate of an individual, and RMR represents energy spent specifically on energetically costly activities such as locomotion and/or foraging (Ricklefs et al., 1996; White et al., 2011). By examining the way in which the daily rate of energy expenditure, activity and RMR relate to each other, we may gain insights into an animal's energy management strategy and energy budget, and how these vary during different life stages. While many studies explore energy management strategies during a given life stage [e.g. breeding season (Hicks et al., 2018); moulting (Guillemette et al., 2007)], we also know that energy management patterns can change during different life phases, or as a result of environmental factors (Halsey et al., 2019).

Within the first few months of life, young migrant birds experience a drastic transition in their physiology and behaviour, as they develop from nearly immobile nestlings to high-performance long-distance migrants. Examining the metabolic rate of developing wild migrants allows us to not only establish the relationships between the different components of energy expenditure at within-species and even within-individual levels but also examine the energy management strategies during the transition between these important life-history stages. Because of variation in activity, we expect that DEE (approximated by mean heart rate) varies during different developmental periods, and that changes in DEE give insight into the constraints acting on patterns of energy use (Mathot and Dingemanse, 2015). Given variation in DEE, an animal could follow three possible models of energy management patterns. (i) The independent model in which the amount of energy spent on activity is not related to the (constant) amount of energy spent on maintenance processes (Ricklefs et al., 1996; Careau and Garland, 2012; Hicks et al., 2018). Increases in RMR are predicted to have a positive relationship with DEE, as the former is a component of the latter, but with a slope smaller than unity as there is no relationship between RMR and activity (Mathot and Dingemanse, 2015; Portugal et al., 2016). (ii) The constrained or allocation model assumes that an animal maintains its overall energy expenditure within a narrow range (Deerenberg et al., 1998; Welcker et al., 2015), so that an increase in activity results in a decrease of maintenance energy expenditure or vice versa. In this case, we expect to observe no covariation between overall and maintenance energy expenditure (slope <1). (iii) The performance model is defined by an intrinsic link between daily and background energy expenditure, such that an increase in one is associated with an increase in the other (Careau et al., 2008), and is represented by positive covariation between overall and maintenance energy expenditure with a slope greater than 1 (as RMR is part of DEE).

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Up to now, no continuous estimates of energy costs in wild birds that develop from fledgling to migrant have been collected, leaving a gap in our understanding of the energetic costs of this transition as well as of how birds may allocate their energy in this crucial life-history phase. Here, we examined long-term estimates of energy expenditure by looking at heart rate measurements as a qualitative proxy of energy expenditure rates (Green, 2011). We measured the heart rate and overall movements of wild white storks, *Ciconia ciconia* (Linnaeus 1758), to answer the following questions: which individual and environmental factors determine DEE during development?; how does DEE relate to RMR?; and what can this relationship tell us about different energy management strategies during the storks' early life stages?

MATERIALS AND METHODS

Ethics

Stork tagging in Poland was approved by Regional Directorate for Environmental Protection in Białystok (WPN.6401.50.2014.WL) and the Local Ethical Committee on Animal Experimentation in Białystok (73/2013). All methods conformed to the ASAB/ABS Guidelines for the Use of Animals in Research.

Dataset

Field work was conducted in the summers of 2014 and 2015 at the University of Białystok field station in Gugno, in Biebrza National Park (N 53°20'54.05", E 22°35'33.85"). We tagged storks in three villages (Gielczyn: N 53°13'49"; E 22°29'04"; Brzeziny: N 53°14'21"; E 22°32'06"; and Laskowiec: N 53°13'52"; E 22°33'22") located in the fork of the rivers Narew and Biebrza, close to the southern border of Biebrza National Park, northeast Poland. In order to record their movements, we equipped a total of 20 juvenile white storks (10 each year) with high-resolution, solar GSM-GPS-ACC loggers (e-Obs GmbH, Munich, Germany; Flack et al., 2016, 2018). All juveniles were taken from the nest to be fitted with the GPS logger (see Flack et al., 2016, 2018 for details) and a heart rate logger. We aimed to tag the birds approximately 1–2 weeks prior to fledging, but it was difficult to estimate precisely the age of the nestlings, so some birds took longer than 14 days to fledge. In addition, to measure heart rate, we implanted heart rate loggers into the abdominal cavity of the birds (9 g, 27×22×17 mm, e-Obs GmbH; see below). Every 20 min, the heart rate loggers recorded ECG (177.83 Hz) in bursts of 4.5 s (786 samples per burst) and abdominal temperature. GPS positions were recorded every 5 min. Tri-axial body acceleration was measured every 2 min (sampling details are given in Table S1). We recorded GPS locations, 3D body acceleration, body temperature (T_b) and an electrocardiogram (ECG) for 18 h a day (between 04:00 h and 22:00 h local time at the natal grounds). GPS transmitters (mass 54 g) were attached using a Teflon-nylon harness (mass ~12 g). GPS had a positional accuracy of ±3.6 m (i.e. when stationary, 50% of fixes remained within a radius of 3.6 m within 24 h). For each measurement, the loggers recorded heart rate through two electrodes, temperature through an internal sensor, and a time stamp.

Average mass of the birds was 3010 g (range 2300–3600 g). Implantations were performed by a veterinarian (I.M.) in the field station to which the birds were transported by car. We administered a pre-anaesthetic analgesic (Butorphanol, 1.5 mg kg⁻¹, intramuscular application) and Ringer's solution (at T_b , 20 ml kg⁻¹, subcutaneous application) to prevent dehydration during anaesthesia. Sterilized loggers were implanted under isoflurane inhalation anaesthesia by inserting them into the abdominal cavity via a 4 cm long midline incision through the skin and body wall. The two flexible electrodes

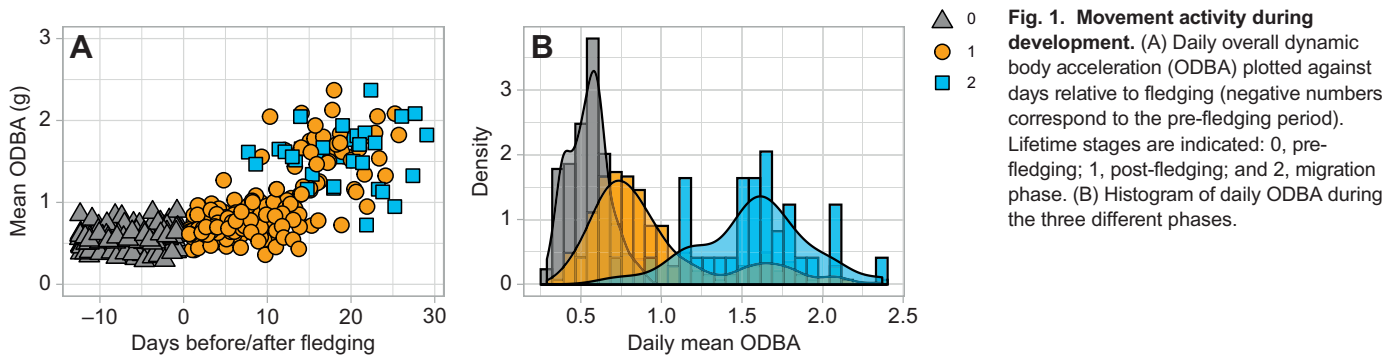
(diameter 3 mm, length 50 and 80 mm) were placed close to the heart. The strength of the signal was checked during implantation to achieve optimal position of the electrodes. The surgical incision was closed with a two-layer absorbable suture. Post-surgery, the birds received a non-steroidal anti-inflammatory analgesic (Meloxicam, 0.5 mg kg⁻¹ body mass). Aseptic techniques were adhered to wherever possible. Birds were returned to the nest after recovering from anaesthesia and T_b was checked remotely during the following days. None of the birds showed a fever reaction.

All GPS loggers had a Global System for Mobile Communications (GSM) unit that sent two short text messages (SMS) per day (limited to areas of cellular coverage) each containing five GPS locations recorded at 1 h intervals, providing low-resolution positional data. These low-resolution data allowed us to find the animals in the field to download data of all sensors via a UHF radio link from a distance of approximately 300 m. We obtained simultaneous recording of position, accelerometer and ECG for the pre-migration period for 17 individuals. We also received data from all sensors during migration of 6 individuals, covering between 103.4 and 2670.2 km. Of the 20 tagged individuals, we excluded three birds completely from the analyses because of failure of the heart rate logger (1), or because the birds died shortly after their first flight (2). We analysed a total of 49,886 heart rate recordings, 162,396 GPS locations and 337,044 accelerometer recordings.

Data analyses

All statistical analysis was performed using R version (3.5.2, R Foundation for Statistical Computing, Vienna, Austria). Raw acceleration data were converted from mV into m s⁻² using the moveACC package (<https://gitlab.com/anneks/moveACC>). To calculate overall dynamic body acceleration (ODBA), the three signals were first individually smoothed using means of the entire burst. Next, for each axis, the smoothed data were subtracted from the corresponding unsmoothed data; the sum of all three axes provided ODBA (Wilson et al., 2006). ECG data were post-processed to obtain heart rate values for each recorded ECG burst (f_H , beats min⁻¹) using a custom-written detection algorithm (eOBS GmbH), which we manually verified. We determined daily mean f_H for each 24 h period and individual as well as daily minimum f_H , which corresponds to the lowest burst value of each day. In addition, we determined activity f_H , defined as the difference between daily mean and daily minimum f_H (Ricklefs et al., 1996; Careau et al., 2008; Portugal et al., 2016). We discarded the first 72 h after device implantation because of potential interference from the surgical procedure. We also discarded the day of death (determined using criteria from Cheng et al., 2019). We examined the pre- and post-fledging phases separately with fledging being defined as the first of three consecutive days during which the maximum distance to the nest was larger than 500 m. Because some individuals took longer to fledge (they might have been younger during tagging), we cut the pre-fledging phase to the last 12 days prior to fledging to examine the same number of days for all individuals. The post-fledging phase ended with the first day of migration (i.e. first day with a latitudinal difference of -0.38°). We collected migration data for only a few individuals and days: a total of 34 migration days for 5 individuals.

We ran general linear mixed models with individual animal ID as a random factor to determine the environmental and individual factors that influenced daily mean f_H (DEE). Models were also implemented with a temporal autocorrelation structure (corAR1). For the final model, we selected only those factors that were retained in the four best GLMMs using the Akaike information criterion for small sample sizes (AICc) within the MuMIn library. Individual



features included in the models were daily mean T_b and mean movement activity (ODBA). In the post-fledging model, we also included distance travelled (beeline distance between the first and last point of each day). We also included days until (or after) fledging to correct for variation in f_H independent of individual and environmental conditions. We used the environmental-data automated track annotation (Env-DATA) system (Dodge et al., 2013) to annotate the tracking data with ambient atmospheric observations. Environmental conditions included mean ground temperature, mean precipitation, mean thermal uplift, mean wind support and mean cross-wind. Thermal uplift velocity estimates provided by Env-DATA were calculated using estimates of temperature, relative humidity, surface pressure, boundary layer height, and instantaneous moisture and surface heat fluxes using ECMWF data (Bohrer et al., 2011).

We assessed the use of alternative energy management patterns by examining the slope and 95% confidence intervals of regression between daily mean f_H and daily minimum f_H , and between minimum f_H and activity f_H . These regressions were generated from a single mixed model, including individual identity as a random effect to account for the repeated values representing each individual.

RESULTS AND DISCUSSION

First, we explored how individuals changed their movement activities during development. To do so, we calculated their daily mean ODBA to quantify the level of movement. ODBA was lowest when the birds had not yet fledged, ranging from 0.29 to 0.89

(Fig. 1B). It increased during the post-fledging phase (mean±s.d. daily ODBA 0.95 ± 0.41), and reached a maximum during migration (daily ODBA 1.57 ± 0.34 ; Fig. 1). In addition, daily mean ODBA was strongly positively correlated (GLMM, conditional $R^2=0.77$, $P<0.001$) with cumulative flight distance (Fig. S1), indicating that it is a reliable estimate of flight behaviour.

Next, we examined the costs of flight development by looking at daily mean f_H (our measure of DEE) and its influencing factors. We found that daily mean f_H decreased with time (Fig. 2A). In addition, it was positively influenced by daily mean ODBA (Fig. 2B), internal T_b (Fig. 2C) and daily travel distance (Fig. 2D; GLMM, marginal $R^2=0.38$; Table S2). Thus, although the movement activity of the juveniles increased as their development progressed (Fig. 1A), daily mean f_H was highest during their time in the nest (Fig. 2A).

Finally, because we clearly observed a change in daily activity levels and energy expenditure throughout juvenile development, we tested whether this decrease in DEE is also linked to changes in the energy management pattern. To do so, we examined the relationship between daily mean f_H and daily minimum f_H (a measure of maintenance energy) for the pre- and post-fledging phase (including migratory movements) separately. In both phases, before and after fledging, we observed a strong positive relationship between mean daily f_H and daily minimum f_H . The across-individual slopes between these values were lower than 1 during both life stages (pre-fledging: 0.64; post-fledging/migration: 0.67; Fig. 3, Table S3), indicating that there is a partial compensation of high maintenance or high activity energy expenditure. This means that high

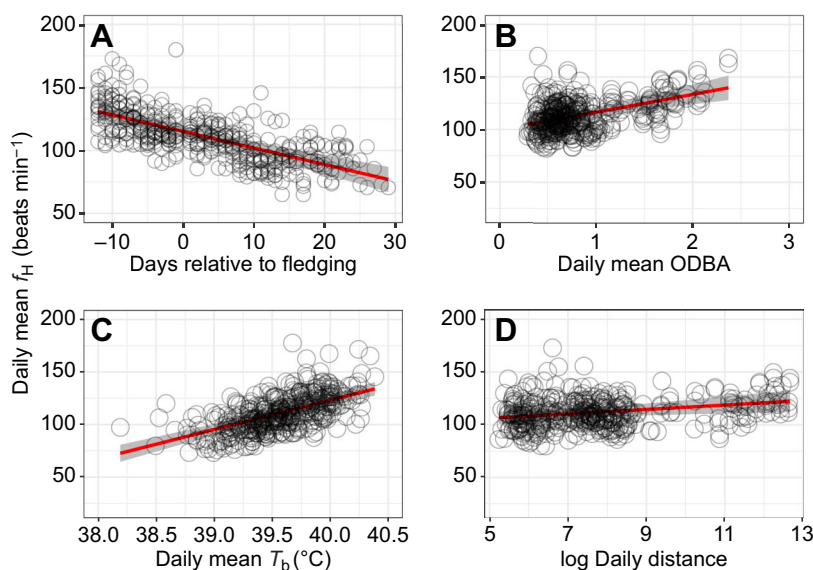


Fig. 2. Partial residual plots for the model examining the relationships between daily mean heart rate (f_H) and its predictors. See Table S2. The plots include the partial fits (red solid lines) and their 95% confidence intervals (shaded grey areas). Partial residuals are plotted for (A) days relative to fledging (negative numbers correspond to the pre-fledging period); (B) daily mean ODBA, (C) daily mean body temperature (T_b); and (D) cumulative daily distance (m ; log-transformed). Each fit is adjusted by the other covariates.

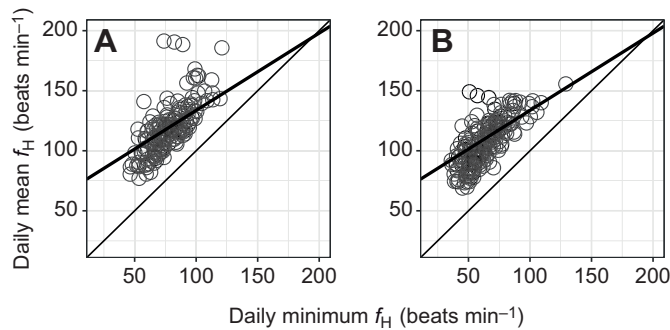


Fig. 3. Relationship between daily mean and minimum f_H at different life stages. (A) Pre-fledging and (B) post-fledging/migration. Daily mean f_H is a proxy for daily energy expenditure; daily minimum f_H is a proxy for daily maintenance energy expenditure. The individual slopes are clearly >0 and <1 (see Table S3). Open circles represent all observations (one data point per individual per day). Thick black lines correspond to the across-individual slopes. The thin black line represents the line of unity.

maintenance costs (especially during the early development of the pre-fledging phase) are not equally connected to high levels of overall energy expenditure but are accompanied by lower activity levels [slope of daily f_H and activity energy (difference between mean and minimum daily f_H): -0.36 , conditional $R^2=0.24$]. Conversely, an increase of movement during the post-fledging/migration phase increased activity energy expenditure and coincided with a decrease in maintenance processes (GLMM, slope: -0.30 ; conditional $R^2=0.35$).

Our study showed that in juvenile white storks, f_H -based proxies for RMR and DEE are positively related to each other with across-individual slope >0 and <1 . This means that high maintenance or activity energy will be partially compensated in order to constrain the overall level of DEE. High values of maintenance energy during the pre-fledging phase may be connected to prevailing growth processes. Although the beak and feathers of white storks continue to grow even after they have fledged, individuals generally reach their maximum mass before their first flight, ~ 45 days after hatching (Tsachalidis et al., 2005). Thus, the decrease in maintenance energy expenditure during the pre-fledging phase may be connected to a reduction of overall body growth and development.

At the end of the nesting period, juveniles increase their movement activity as they leave their nests to fly and to forage on their own. Although activity f_H increased together with movement activity (ODBA), we still observed a general reduction of DEE over the post-fledging period. This apparent disconnect between increased energetic costs during flight and the overall decrease in DEE with maturation suggests several possibilities. A reduction of DEE may indicate that the transition to independent living includes learning to fly more efficiently and/or to forage more effectively. This development may be part of processes preparing the juveniles for migration. It has been shown in the past that many migrants can undertake these incredible, long journeys without any apparent change in behaviour prior to their departure (Portugal et al., 2011; Hawkes et al., 2017). Large birds in particular have evolved behaviours such as soaring, gliding and thermalling to reduce flight costs (Duriez et al., 2014; Flack et al., 2016; Sherub et al., 2016), requiring them to flap very little and not to increase their muscle protein content prior to migration (Pennycuik, 1975).

Our intra-specific study of a developing bird also shows that DEE can vary during different developmental or life stages. During the early pre-fledging phase, juveniles had a larger DEE although they showed little movement activity. During this time, when food

availability may be higher as a result of parental provisioning, nestling storks apparently spent more energy (higher minimum f_H , presumably higher RMR) on growth to increase their muscle and lipid stores. Once individuals fledge, they experience not only an increase in activity levels but also lower, unknown feeding rates because of immature foraging skills. It may be important to experience lower maintenance costs during this phase to compensate for the high costs of activity. We must also consider that there are additional factors, including maturation of cardiovascular functions or varying responses to elevated T_b , which may all affect these outcomes. However, as our models suggest a strong effect of the overall maturation process, our proxy for energy use appears robust.

Because of high mortality in juvenile storks (Cheng et al., 2019), we did not succeed in recording the entire annual cycle of these birds. But our study nevertheless reveals that factors determining energy management strategies can vary throughout early ontogeny depending on different constraining factors. Because important stages of an animal's life cycle, like periods of high or low energetic costs (or food availability), may drive changes in energy management patterns, we need to further explore empirically and experimentally energetic constraints in individual free-living animals.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.F., W.F.; Methodology: I.M.; Formal analysis: A.F.; Data curation: P.J.S.; Writing - original draft: A.F.; Writing - review & editing: A.F., P.J.S.; Project administration: J.R.E.T., W.F.; Funding acquisition: J.R.E.T., M.W., W.F.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.219337.supplemental>

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