© 2019. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2019) 222, jeb183517. doi:10.1242/jeb.183517

RESEARCH ARTICLE

Wing morphology, flight type and migration distance predict accumulated fuel load in birds

Orsolya Vincze[1,2,*], **Csongor I. Vágási**[1,2], **Péter László Pap**[1,2], **Colin Palmer**[3] and **Anders Pape Møller**[4]

ABSTRACT

Birds often accumulate large fat and protein reserves to fuel long-distance flights. While it is well known that species that fly the longest accumulate the largest amounts of fuel, considerable cross-species variation in fuel load is seen after controlling for overall migration distance. It remains unclear whether this variation can be explained by aerodynamic attributes of different species, despite obvious ecological and conservation implications. Here, we collected data on wing morphology, flight type, migration distance and fuel load from 213 European bird species and explored three questions: (1) does maximum fuel load relate to migration distance across species?; (2) does wing morphology, as described by wing aspect ratio and wing loading, influence maximum fuel load?; and (3) does flight type influence maximum fuel load? Our results indicate that maximum fuel load increases with migration across species, but residual variance is high. The latter variance is explained by aspect ratio and flight type, while wing loading and body mass explain little variance. Birds with slender wings accumulate less fuel than species with low wing aspect ratio when covering a similar migration distance. Continuously flapping species accumulate the largest amounts of fuel, followed by flapping and soaring species and flapping and gliding species, while the smallest fuel loads were observed in birds with passerine-type flight. These results highlight complex eco-evolutionary adaptations to migratory behaviour, pointing toward the importance of energy minimisation.

KEY WORDS: Aspect ratio, Fat reserves, Flight range, Flapping, Gliding, Soaring, Wing loading

INTRODUCTION

Millions of birds migrate each year, flying over vast distances of up to tens of thousands of kilometres to exploit seasonally variable resources (Berthold, 2001; Dingle, 2014; Somveille et al., 2015). The longest migratory flights recorded so far in birds include the approximately 11,000 km long, non-stop trans-Pacific commute of the bar-tailed godwit (*Limosa lapponica baueri*) (Gill et al., 2009) and the more than 90,000 km travelled annually by Arctic terns (*Sterna paradisaea*) from the Arctic to the Antarctic and back (Egevang et al., 2010; Fijn et al., 2013). During such strenuous flights, strong natural selection operates on the physiology, morphology and behaviour of migrants (Newton, 2007). The intensity of selection during migration is manifested by the high mortality rates experienced during this period, which are often higher than during any other part of the annual cycle (Guillemain et al., 2010; Owen and Black, 1989).

In order to deal with the exceptionally high energetic demands of sustained, high-intensity migratory flight, birds accumulate fuel prior to departure as well as at stopover sites en route to their wintering and/or breeding grounds (Bairlein, 2003; Lindström, 1991). This behaviour is called pre-migratory fattening, as birds consume food in excess (hyperphagia) and gain weight quickly. Daily gain in fat mass as a percentage of lean body mass averages 4–5% in different bird species (Lindström, 1991). Some individuals are capable of doubling their body mass within a short period of 1–3 weeks prior to departure (Biebach, 1996; Hedenström and Alerstam, 1992; Newton, 2007; Odum and Connell, 1956). Fuel reserves are especially important and reach maximum levels when birds embark on long spells of non-stop flight, usually over ecological barriers such as seas and deserts that are devoid of feeding opportunities (Bairlein, 2003; Berthold, 2001; Odum and Connell, 1956).

The migratory fuel of birds comprises mostly lipids (Jenni and Jenni-Eiermann, 1998). Lipids provide seven-to-nine times more energy per unit mass than alternative oxidative fuel sources, including proteins and carbohydrates; thus, lipids are both rich in energy and economic in terms of transport costs (McWilliams et al., 2004; Newton, 2007). In addition, as fat is deposited subcutaneously, it augments thermoregulation and buoyancy, and imparts mechanical protection (Lind et al., 1999; McWilliams et al., 2004; Witter and Cuthill, 1993). Birds were traditionally considered exceptional among vertebrates in their ability to fuel high-intensity, sustained muscle work with fatty acids that are transported from extra-muscular adipose tissues directly to working muscles by the circulatory system (Jenni-Eiermann et al., 2002; McWilliams et al., 2004). Migratory bats show similar convergent adaptations, as fat might provide the exclusive fuel to muscles during endurance flights (McGuire and Guglielmo, 2009). To achieve this, lipids in birds, as well as in volant mammals, need to be mobilised, transported and oxidised at much higher rates than the highest rates ever measured in non-volant mammals (Jenni-Eiermann et al., 2002). A switch to lipid-based metabolism was probably associated with the evolution of flight, which implies the need for reduced weight of stored fuel and the demand for continuous energy production to support muscles during endurance flights.

Besides these benefits, there is a wide variety of disadvantages to fuel accumulation. First, fuel accumulation is itself costly because of altered behavioural patterns that increase predation risk (Metcalfe and Furness, 1984). Second, an increase in body mass leads to higher metabolic rates, while an increase in wing loading results in elevated costs of lift, more energy consumed per unit distance

---

[1]Evolutionary Ecology Group, Hungarian Department of Biology and Ecology, Babeş-Bolyai University, RO-400006 Cluj-Napoca, Romania. [2]Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, H-4032 Debrecen, Hungary. [3]School of Earth Sciences, University of Bristol, Bristol BS8 1RL, UK. [4]Ecologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, F-91405 Orsay Cedex, France.

*Author for correspondence (orsolya.vincze@vocs.unideb.hu)

O.V., 0000-0001-5789-2124; C.I.V., 0000-0002-8736-2391; P.L.P., 0000-0002-3659-7684

Received 25 April 2018; Accepted 8 November 2018

travelled, decreased manoeuvrability, lower angle of ascent and higher risk of injury and predation (Hedenström, 1992, 2010; Pennycuick, 1975, 2008; Witter and Cuthill, 1993). Third, fuel deposited subcutaneously increases the projected frontal area, which has aerodynamic implications including increased body drag, decreased lift-to-drag ratio and elevated power required for flight (Hedenström and Alerstam, 1997, 1992; Hedenström, 2010; Pennycuick, 1975). As a consequence, increasing fuel load has diminishing returns and the size of the fuel load depends on a number of anatomical attributes. For instance, with increasing lean body mass for a given wing area, the power margin (i.e. the difference between the maximum power producible by flight muscles and the power required for flight) decreases (Hedenström and Alerstam, 1997). As a consequence, larger birds are more constrained by their narrower power margin and hence are expected to have smaller fuel loads relative to their lean body mass than smaller species (Hedenström and Alerstam, 1997, 1992). Similarly, aerodynamic attributes define costs and benefits of fuel transportation and might define the size of optimal fuel stores.

Migratory birds exhibit a range of morphological, physiological and behavioural adaptations to optimise their flight (e.g. Berthold, 2001; Dingle, 2014; Hedenström, 2008; Norberg, 1990; Pennycuick, 1998; Rayner, 1988, 1990; Vágási et al., 2016; Vincze, 2016). Two optimisation strategies are paramount, maximising time or energy efficiency (Lindström and Alerstam, 1992). High wing loading (i.e. weight per unit wing area) enables fast flight speed and helps minimise the time of migration, while high wing aspect ratio (i.e. squared wingspan divided by wing area, an index reflecting wing shape with larger values indicating a long and slender wing) and low wing loading ensure low energy expenditure by reducing flight power, but increasing the time of travel (Norberg, 1990). Wing morphology in particular is strongly related to flight type; high wing aspect ratio and low wing loading are often associated with soaring, while high wing loading is correlated with flapping flight (Ricklefs, 1996). Of all types, flapping flight is energetically the most demanding, while soaring, gliding and alternate flapping–gliding require lower power output (Ricklefs, 1996). It was shown that wing aspect ratio increases and wing loading decreases with increasing migration distance in birds (Vágási et al., 2016), indicating that long-distance migration co-evolves with wing traits to ensure energy-efficient flight. Although wing design and flight type determine the power required for flight, how these factors relate to energy storage prior to migration remains poorly understood.

Fuel store size must be carefully planned to safeguard premature energy depletion during migratory flight, as well as to reduce the costs associated with surplus weight. Empirical data on how morphological, behavioural and physiological factors explain interspecific differences in fuel accumulation are limited, however, probably because of the difficulties inherent in measuring fuel load, especially in a comparable manner across species with diverse fuel-accumulation strategies (Krementz and Pendleton, 1990). Filling this gap in our knowledge of the fuelling capacity of migratory birds has broad implications from both ecological and evolutionary perspectives (Bairlein and Hüppop, 2004).

In this study, we quantified fuel stores across species using data from the literature and checked the validity of these data using individual body condition indices and fat scores collected in the field during migration. Using species-specific fuel store data, we investigated how fuel load relates to phylogeny, migration distance, wing morphology and flight type. We predicted the use of larger relative fuel stores in species that: (1) travel longer distances during migration, irrespective of phylogeny; (2) have smaller body masses (i.e. wider power margin); (3) have wing architecture that is less economic in terms of energetic demand (i.e. low wing aspect ratio and high wing loading); and (4) utilise continuous flapping flight, in contrast to species with intermittent flight (flapping and soaring, flapping and gliding, and passerine-type flight; sensu Bruderer et al., 2010).

MATERIALS AND METHODS

Wing architecture and flight type

We photographed stretched wings of numerous European bird species that we captured in the wild or collected as fresh carcasses. We measured wing architecture from the photographs using ImageJ (http://rsbweb.nih.gov/ij/; see Vágási et al., 2016, for details). We described wing architecture as wing loading (kg m^{-2}) and wing aspect ratio (dimensionless). Wing loading was calculated by dividing average body mass (kg, see source below) by wing area (m^2), while wing aspect ratio was estimated as squared wingspan divided by wing area (both m^2). Wing parameters were measured excluding body area between the wings, but these measurements are strongly positively correlated with wing morphology measurements that include body area (R^2>0.99 for both wing aspect ratio and wing area in 152 species; Vágási et al., 2016). Species were assigned to one of the four flight type categories listed by Pennycuick (2008) and Bruderer et al. (2010), incorporating small modifications suggested by Pap et al. (2015): flapping and soaring, flapping and gliding, continuous flapping and passerine-type flight. Wing morphology and flight-type data are available in Table S1.

Fuel factor

In order to quantify interspecific differences in accumulated fuel load, we extracted average and maximum body mass data from the literature (see Table S1 for species-specific data and references), separately for adult males and females, and separately for each species for which we had measured wing morphology. In cases when body mass was reported for multiple subspecies or populations, we chose the ones in which distribution overlapped with the site of collection of the wing morphology photographs. In all cases, average and maximum body mass as well as data on males and females were extracted from the same literature source. Species values of average and maximum body mass were then calculated as the arithmetic mean of the values extracted for the two sexes separately. Fuel factor was calculated as the ratio of species-specific maximum body mass to average body mass. This measure thus reflects how many times larger maximum compared with average body mass is for a given species (see also Hedenström and Alerstam, 1992). Our assumption is that fuel factor reflects accumulated fuel load as a function of lean body mass.

Validation of fuel factor

Body size can vary significantly among subspecies as well as across geographic regions inhabited by a single species (Cramp, 1998). Although we made sure to extract mean and maximum body mass from the same literature source, geographic variation in body size may bias our measure of fuel factor because of possible population mixing during migration. To counter this, we tested whether maximum body condition in a given species can be reliably estimated using fuel factor derived from the literature. We used data obtained at a migratory bird ringing station in the Danube-Delta Biosphere Reserve, on the coast of the Black Sea, Romania (44°32′N, 28°52′E). At this station, migratory birds were captured, measured and ringed throughout the peak migratory season, and it operates with a fixed number of mist nets that are usually open continuously. Activity at this ringing camp was concentrated around the peak of the autumn migratory season (from 4 August 2014 to 23 October 2014); individuals captured were almost exclusively migrants, as most do not breed in the area, and very few were re-captured weeks or months following the first encounter. We extracted body mass, wing length and fat score data from the ringing database. Fat score was recorded by assessing the visible subcutaneous fat deposit in each individual and was scored on a scale of 1 to 8 following Kaiser (1993). We built separate linear regression models for each species using log body mass (dependent variable) and log wing length (explanatory variable). To exclude outliers from these regressions, we calculated Mahalanobis distances (using function *mahalanobis* as implemented in R package *stats*) and excluded data points that had distances >9 to refit the model. The regression was only considered for species with at least 10 individual measurements available following the exclusion of outliers (a total of 12,214 captures, 45 species; see Table S1 for regression results). Individual body condition indices were extracted from the above regressions as residuals, reflecting the net difference between actual and expected body mass based on body size. In some poorly sampled species, the regression was weak, or in some cases a negative association between wing length and body mass was found, and it was therefore likely to reflect an erroneous fit. Consequently, the condition index was only considered further for species in which the association was at least close to significant ($P<0.1$, a total of 11,036 captures of 26 species).

Using individual body condition indices, we first tested whether the latter is correlated with individual fat scores using single-predictor linear regression models for each species separately. Second, to validate interspecific fuel factor data, we calculated species-specific maximum condition indices and analysed how fuel factor correlates with the latter across species. Maximum condition was calculated as the 95th percentile of individual condition data for each species, reflecting the high end of body condition or fuel accumulation of a given species during the autumn migratory period. We used the 95th percentile because extreme values, such as minima and maxima, are often unreliable and originate from measurement or data-handling errors. For this validation, we used a weighted linear regression between fuel factor (dependent variable) and maximum condition (predictor variable), with weights represented by the log number of captured individuals in the ringing database.

Estimating migration distance

Distribution maps of the breeding and wintering ranges of western Palaearctic bird species (shape files) were retrieved from http://www.birdlife.org/datazone/info/spcdownload (BirdLife International and NatureServe, 2014). Geometric centroids of the spatial polygons for breeding (i.e. breeding and resident) and wintering (i.e. wintering and resident) ranges were then calculated from these maps using the gCentroid function of the R package rgeos (https://rdrr.io/cran/rgeos/), while migration distance was calculated as the geographic distance between the two centroids using a custom-written function in R (Vágási et al., 2016; Vincze, 2016; Vincze et al., 2015).

Comparative analyses

We conducted all analyses using phylogenetic generalised least squares (PGLS) models, implemented in the R packages nlme (https://CRAN.R-project.org/package=nlme) and ape (Paradis et al., 2004). We used fuel factor as a dependent variable with migration distance, mean body mass, wing aspect ratio, wing loading and flight type as explanatory variables. Body mass was $\log_{10}$-transformed prior to the analyses. All models were weighted by the log sample size of individuals measured for each species. To control for similarity among taxa due to common phylogenetic descent, we downloaded 1000 phylogenetic trees from birdtree.org (Jetz et al., 2012), using the backbone tree of Hackett et al. (2008). The rooted consensus phylogenetic tree used in analyses was obtained using *sumtrees* software (Sukumaran and Holder, 2010), and models were fitted using maximum likelihood. We estimated phylogenetic dependence using Pagel's λ, set to take the most appropriate value in each model, as evaluated by likelihood ratio statistics. Model predictions and associated standard errors used for graphical presentation were extracted from PGLS models using the *predictSE.gls* function in the R package *AICcmodavg* (https://cran.r-project.org/package=AICcmodavg), while contrasts were extracted using the *emmeans* function from R package *emmeans* (https://CRAN.R-project.org/package=emmeans). We constructed models using all possible combinations of the five explanatory variables, and used second-order Akaike's information criterion corrected for small sample size (AICc) to compare them. We evaluated the importance of all candidate models using relative Akaike weights (ωi), and those of the predictors by the sums of their ωi across all models that contain the given predictor ($\Sigma\omega i$). ωi and $\Sigma\omega i$ were computed for the whole model set; values close to 1 indicate high importance, while those close to 0 indicate low importance in explaining variance in the dependent variable. All analyses were conducted in R version 3.3.2 (http://www.R-project.org/) and all data are available in Table S1.

Given that wing aspect ratio and flight style are both key characteristics of bird flight, we ran a model to test how these two parameters are related. We built a PGLS model using wing aspect ratio as a dependent variable and flight style as the only independent variable. We controlled for phylogenetic inertia in a similar fashion to the models described above.

RESULTS

Fuel factor validation

Individual condition was strongly positively correlated with individual fat scores in most species tested based on the ringing database ($P<0.05$ in 22 out of 26 species; see Fig. S1 for graphical presentations of the associations). This indicated that individual condition calculated as the residuals of a log–log linear regression between body mass and wing length reliably reflects body fat content within species. Fuel factor and maximum condition were strongly positively correlated across species (linear regression, $n=26$, $\beta=2.29$, s.e.=0.36, $t=6.36$, $R^2=0.64$, $P<0.0001$; Fig. 1). Therefore, we conclude that fuel factor is a suitable cross-species measure for the maximum size of fuel stored during the migratory season.

Correlates of fuel factor

In our sample of 213 European bird species, wing aspect ratio ranged between 3.51 (*Poecile montanus*) and 9.54 (*Calonectris diomedea*) (mean±s.e.m. 5.49±0.09), while wing loading ranged between 1.09 kg m^{-2} (*Phylloscopus collybita*) and 23.44 kg m^{-2} (*Gavia arctica*) (mean±s.e.m. 4.36±0.27 kg m^{-2}). Fuel factor ranged from 1.06 (*Picus viridis*) to 1.80 (*Sylvia borin*) (mean±s.e.m. 1.26±0.01), while average body mass varied between 5.6 g (*Regulus ignicapilla*) and 10,735 g (*Cygnus olor*) (mean±s.e.m. 554.11±94.91 g). Migration distance varied from 0 km (residents) to 9856 km (*Arenaria interpres*) (mean±s.e.m. 3145.01±179.96 km).

The AICc-based comparison of all possible PGLS models explaining variation in fuel factor indicated that a single best-fitting model exists with an ωi value of 0.98 (see the entire model set and

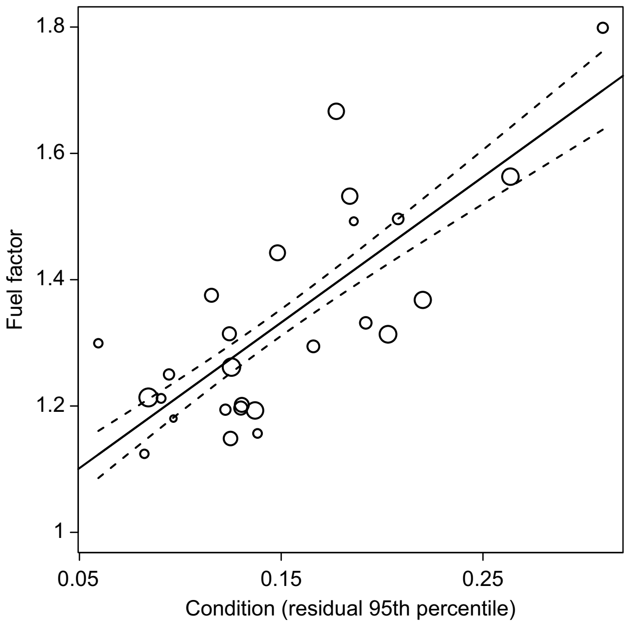

Fig. 1. Association between maximum condition (i.e. 95th percentile of condition indices) and fuel factor in 26 species of birds. Slope and associated standard errors (continuous and dashed lines, respectively) were obtained from a weighted linear regression between these two variables. Point sizes are proportional to the log number of individuals measured for each species at the bird ringing station from the Danube-Delta Biosphere Reserve.

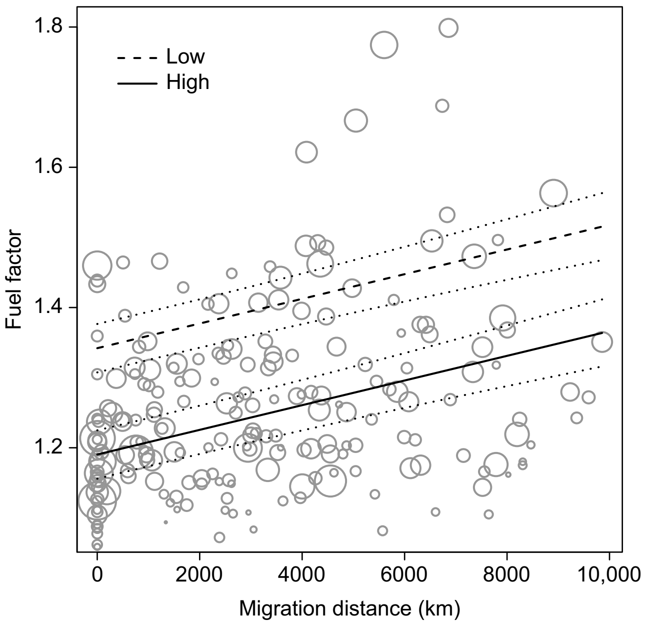

Fig. 2. Association between fuel factor and migration distance across 213 European bird species. Slopes are drawn for the lowest and highest wing aspect ratios in our database (3.51 and 9.54, respectively). Slopes (continuous and dashed line for high and low aspect ratio, respectively) and associated standard errors (dotted lines) were obtained from the model presented in Table 1. Point sizes are proportional to the log number of individuals for which the fuel factor estimate was based.

associated AICc values in Table S2). This model contained migration distance, wing aspect ratio and flight type as explanatory variables (Table 1). The second best-fitting model had ΔAICc=7.46, indicating a significantly lower fit. Summing Akaike weights for each parameter indicated that migration distance and flight style have the highest importance (Σωi=1), followed by wing aspect ratio (Σωi=0.98), while body mass (Σωi=0.02) and wing loading (Σωi=0.00) had little explanatory power.

As predicted, fuel factor increased with increasing length of the migratory journey (Table 1, Fig. 2). Nonetheless, significant variation remained unexplained across this regression slope (Fig. 2). Some of this residual variance was explained by wing aspect ratio, indicating that species with higher wing aspect ratio (i.e. slender wings) accumulated less fuel than species characterized by a low wing aspect ratio (i.e. rounder wings; Table 1, Fig. 2). Finally, the effect of flight type was also significant, indicating different fuel factors in species with different flight styles even after accounting for wing architecture and migration distance. Our results indicate that continuously flapping species accumulated the highest fuel stores, followed by flapping and soaring species, and flapping and gliding species, while the smallest fuel factors were observed in species with passerine-type flight (Table 1, Fig. 3). Note, however, that the difference was only significant between continuous flapping and passerine-type flight styles (t=5.70, P<0.0001), between flapping and soaring and passerine-type flight styles (t=6.33, P<0.0001), as well as between continuous flapping and flapping and gliding flight types (t=2.96, P=0.0180; Fig. 3). Although the association between wing aspect ratio and flight type is strong, the effects of these variables were consistent across models, and the results were not affected by collinearity (variance inflation factor was <4 in all models).

Table 1. Results of the best-fitting PGLS model as indicated by the lowest AICc values across all possible model scenarios (see Table S2), explaining variation in fuel loading in 213 European bird species

	β	s.e.	t	P
Intercept	1.44	0.05	28.00	<0.0001
Migration distance	0.02	0.00	8.43	<0.0001
Wing aspect ratio	−0.03	0.01	4.11	0.0001
Flight type				
Flapping and soaring	−0.02	0.02	0.99	0.3254
Flapping and gliding	−0.07	0.02	2.96	0.0035
Passerine type	−0.11	0.02	5.70	<0.0001

The effect of the three flight types indicating the difference from the continuous flapping flight group. PGLS, phylogenetic generalised least squares.

The results of the model testing the effect of flight style on wing aspect ratio indicated a significant effect (n=213, F=6.47, P=0.0003; Fig. 4). A *post hoc* test revealed that birds having a passerine-type flight have the lowest wing aspect ratio (i.e. broader and rounder wings), and this was significantly lower than that in birds having a flapping and soaring (t=3.33, P=0.0056) or flapping and gliding flight type (t=3.64, P=0.0020). No other flight style category pairs differed significantly in wing aspect ratio according to these results (Fig. 4).

DISCUSSION

Our study highlights a number of key traits that are related to the cross-species variation in migratory fuelling strategy of birds. First, we show that, as expected, accumulated fuel stores in birds significantly increase with the geographic distance covered during their migratory flight. This association holds even after controlling for phylogeny, but there is large variation among species in fuelling strategy once migration distance is controlled for. Second, species with high wing aspect ratio accumulate less fuel prior to migratory departure than species with low wing aspect ratio. Third, flight type further influences fuel stores irrespective of wing morphology and

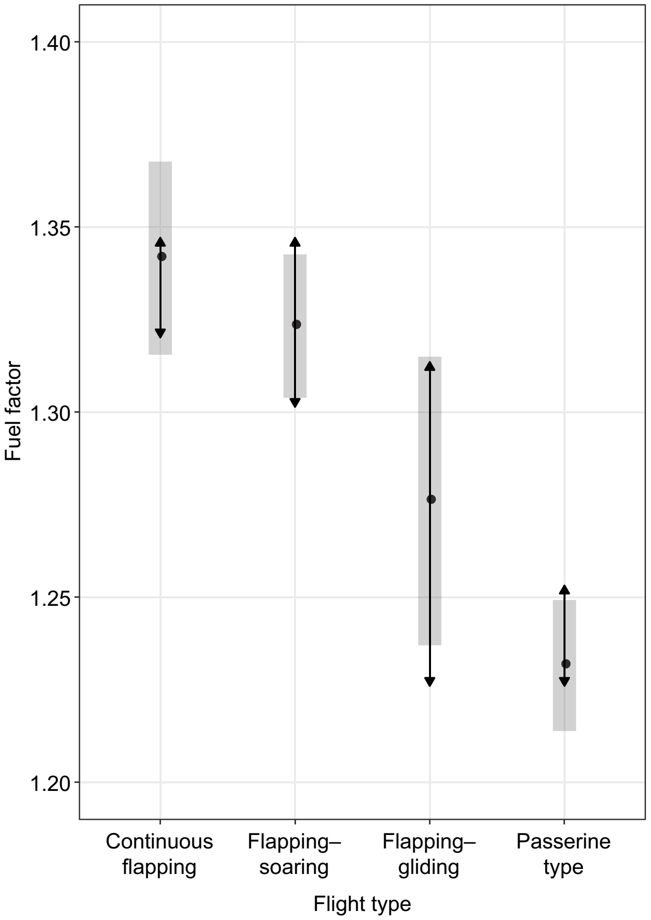

Fig. 3. Fuel factor as a function of flight type in 213 European bird species. Dots represent estimated marginal means, grey bars are confidence intervals and arrows show the difference between the groups. Significant group differences are indicated by a lack of overlap between the arrows.

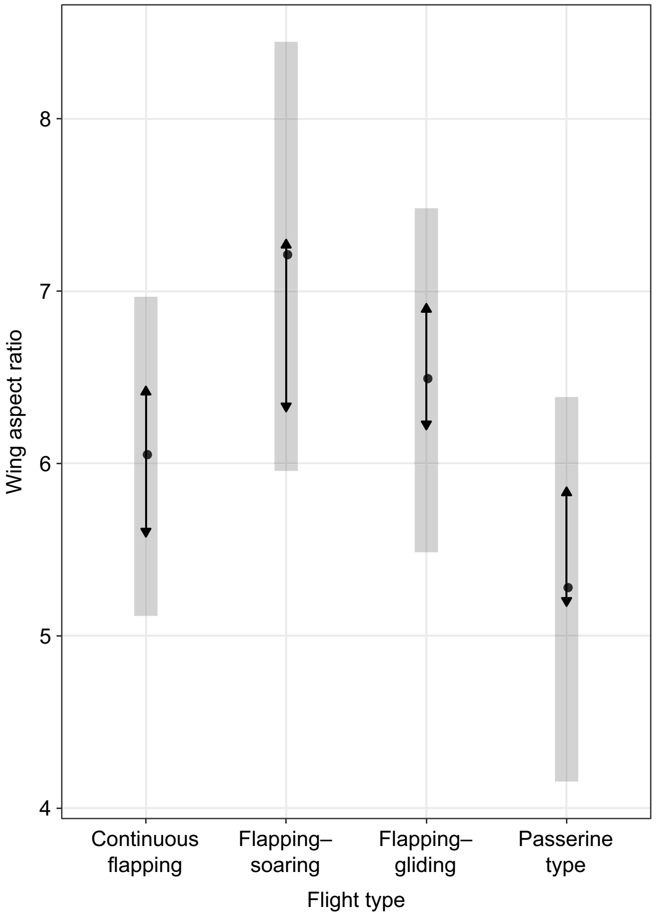

Fig. 4. Difference in wing aspect ratio among flight style categories across 213 species of birds. Dots represent estimated marginal means, grey bars are confidence intervals and arrows show the difference between the groups. Significant group differences are indicated by a lack of overlap between the arrows.

migration distance, implying that fuel stores are fine tuned in accordance with wing-beat frequency. Fourth, wing loading and body mass probably have little influence on the amount of fuel stored for migration.

Migration is one of the most energy-demanding behaviours in birds, with long-distance non-stop flights often assumed to be close to the edge of physiological endurance (Hedenström, 2010; Weber, 2009). Because of the energetic expense of avian flight and the frequent lack of refuelling sites en route, pre-migratory fuelling is an important determinant of flight range (Hedenström, 2010; Hedenström and Alerstam, 1992). The obvious positive association between fuel load and migration distance has previously been demonstrated at the species level. For instance, the size of the fuel reserves in three populations of redbilled queleas (*Quelea quelea*) differs in accordance with the distance each of these travels during their migration (Ward and Jones, 2010). A similar pattern of fuel storage was found across different barn swallow (*Hirundo rustica*) populations, where pre-migratory fat stores increased with the length of the ecological barrier to be crossed upon departure (Rubolini et al., 2002). Although here we quantified overall migration distance, and not the longest flight section, our results still reinforce the prediction that species optimise their fuel stores in proportion to the energy required for their migratory flight. Nonetheless, the considerable residual variance in fuel load highlights that additional factors influence fuelling strategy. Among these, the frequency and length of stopovers is certainly a key component that influences fuelling decisions (Rubolini et al., 2002).

Among the wing morphological characters tested here, wing aspect ratio is the most strongly correlated with flight energy efficiency in birds. Long and narrow wings (i.e. high wing aspect ratio), especially when combined with low wing loading, ensure energy efficient flight (Bowlin and Wikelski, 2008; Sapir et al., 2010; Vágási et al., 2016; Weber, 2009). Given that the induced drag is proportional to the inverse square of the wingspan, higher aspect ratio reduces the induced drag, at similar wing loading and flight speed. Accordingly, the cost of flight per unit distance is lower in species with a high wing aspect ratio, as maximal accumulated fuel load decreased with increasing wing aspect ratio across birds, indicating lower amounts of stored energy required when the expected cost of flight per unit distance is lower. The role of energy efficiency in determining fuel load can also be concluded from the significant effect of flight type on fuel factor, even after accounting for wing morphology.

The different energetic needs of various flight types appear to be supported by data (Norberg, 1990). Continuous flapping flight mostly occurs in birds with relatively high wing loading (Bruderer et al., 2010), which requires a large energy expenditure (Agostini et al., 2015; Pennycuick, 2008). It is therefore straightforward why continuously flapping species are forced to accumulate the largest amounts of fuel per unit length of migration distance in comparison to species belonging to the other three flight-type categories. In support of this, the longest non-stop flight ever recorded for birds was accomplished by a continuous flapping species, the bar-tailed godwit (*Limosa lapponica*) (Gill et al., 2009). Surprisingly though, species with flapping and soaring flight accumulated only slightly lower amounts of fuel than continuously flapping species and hence the two groups did not differ statistically. Soaring is often referred to as one the most energy-efficient ways of locomotion, requiring slightly more energy than sitting still, but this only applies if thermal currents are available (Hedenström, 1993). During migration, soaring birds often cross areas where thermal currents are weak, such as large water surfaces, and they need to switch to powered flight for prolonged periods (Agostini et al., 2015; Pennycuick, 2008). The generous fuel store observed in soaring species could therefore serve as a safety margin, offering a source of energy during prolonged powered flight under unfavourable conditions, such as storms or weak thermals (Pennycuick, 2008). An alternative strategy often observed in soaring migrants is to take large detours and avoid flying over large open water surfaces, with the aim of avoiding powered flight (Agostini et al., 2015). This strategy also depends on body mass, as a larger body mass entails larger energetic costs of powered flight, and consequently heavier soaring species are most reluctant to fly over open sea (Agostini et al., 2015; Panuccio et al., 2013).

The flapping and gliding flight style observed in birds such as swifts, falcons or bee-eaters is theoretically also energetically cheaper than continuous flapping flight (Sapir et al., 2010). Detailed data on migrating bee-eaters equipped with ratio transmitters indicates that they use flapping and gliding flight intermittently, with flapping flight depending on wind conditions (Sapir et al., 2010). Consequently, intermittent use of these two flight styles could help save energy, as gliding phases in these species are not dependent on thermal currents like in soaring birds, and could therefore explain the lower fuel factor of flapping and gliding species compared with continuous flapping or soaring species. Passerine-type flight is an extreme form of intermittent flight mostly confined to species with a relatively low wing aspect ratio (Bruderer et al., 2010; Sachs, 2015). This flight style involves short phases of high-frequency flapping interrupted by short glides (Bruderer et al., 2010). During the gliding phase the wings fold against the body and no mechanical power is required. Therefore, some models suggest there are energetic advantages to passerine-type flight when compared with continuous flapping (Sachs, 2015); however, this advantage is still disputed (Pennycuick, 2008). Our results corroborate the energetic advantage of passerine-type flight over continuous flapping, as we show that species in the former group accumulate the smallest fuel stores per unit distance of migration among the four flight types tested, after accounting for wing morphology. Although passerine-type fliers usually have small body sizes and consequently broad power margins (Norberg, 1996), they store the smallest amounts of fuel, which might indicate little energetic constraint in these species. Overall, our results on the effect of flight type on fuel factor are intriguing and the explanations we provided above are speculative; therefore, further research is needed to investigate the metabolic needs of various flight types during migration and how flight type relates to utilisation of stopover sites.

Our results on the effect of wing aspect ratio and flight style on fuel factor support the assumption that maximum fuel load in birds evolved to meet the energetic requirements of the flight apparatus and birds aim to avoid carrying extra load that is unlikely to be burnt. This suggestion is also supported by the fact that birds often maintain stable reserve levels that are well below the maximum that could possibly be attained (Biebach, 1996; Blem, 1990; Witter and Cuthill, 1993). This optimisation of fuel load is driven by the increased flight cost imposed by the weight of the reserves by means of elevated wing loading and associated elevated costs of locomotion (Hedenström, 2010; Witter and Cuthill, 1993). Large fuel reserves also impose elevated metabolic expenditure, increased risk of injury or predation, impaired foraging and take-off ability or impaired flight performance (Biebach, 1996; Witter and Cuthill, 1993). The fact that most organs suffer a significant reduction in size prior to or during migration to reduce the cost of transportation also highlights the costs of extra weight (Battley et al., 2000).

Species with large wing loading may require more energy to cover a given distance than species with lower body mass per unit wing area (Schmidt-Wellenburg et al., 2008), because wing loading is positively related to flight velocity (Norberg, 1990). Nonetheless, fuelling capabilities are also more limited in species with higher wing loading because of their lower power margin. Our results indicate that wing loading has very little predictive power for fuel factor and are in accordance with earlier studies demonstrating no association between wing loading and migration distance among species (Vágási et al., 2016; Winkler and Leisler, 2008).

In conclusion, our results indicate that fuel stores are optimised as a function of overall distance to be covered during the migratory flight as well of the energetics of species-specific locomotion. Species with slender wings and therefore more energy-efficient locomotion accumulate smaller fuel stores, pointing towards the importance of minimisation of the amount of stored fuel in accordance with the expected energy expenditure of the migratory flight. The optimal fuel store should safeguard against premature energy depletion, but also avoid costs associated with carrying surplus weight that is unlikely to be used and is associated with physiological and environmental threats. Our results are also important from a conservation point of view. Habitat fragmentation, degradation or disappearance of stopover sites interferes with fuelling and re-fuelling during migration. Our results suggest that birds may possess little safety margin concerning their stored energy and the integrity of stopover sites is paramount for a successful migratory journey. Future studies should collect more detailed information about the longest flight spans, the number and position of stopover sites and body condition indices of numerous species at stopover sites for a better understanding of fuelling strategies of birds. Detailed data on fuelling strategy and the conditions of stopover sites together might also help to explain large-scale declines in migrant birds (Both et al., 2010).

Acknowledgements

We thank the members of the 'Milvus Group' Bird and Nature Protection Association for providing data from the 2014 Chituc Ringing Camp, Romania. We thank Gareth Dyke for his linguistic corrections on an earlier version of the manuscript. This study forms part of the PhD thesis (2017) of O.V. at the University of Debrecen, Hungary.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: O.V., C.I.V., P.L.P., A.P.M.; Methodology: O.V., C.I.V., P.L.P., A.P.M.; Validation: O.V.; Formal analysis: O.V.; Data curation: O.V., C.I.V.; Writing - original draft: O.V., C.I.V., P.L.P., C.P., A.P.M.; Supervision: P.L.P., A.P.M.

Funding

O.V. was supported by the Hungarian Ministry of Human Resources, National Talent Program (Oktatási és Kulturális Minisztérium; NTP-EFÖ-P-15-0043), the Hungarian Eötvös Scholarship (MÁEÖ2016_15/76740) awarded by the Tempus Public Foundation; C.I.V. was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences (HAS) and a post-doctoral grant from the Hungarian Research, Development and Innovation Office (PD 121166); and P.L.P. was supported by the János Bolyai Research Scholarship of the HAS. This research was supported by an Exploratory Research Grant of the Romanian Ministry of Research and Innovation (PN-III-P4-ID-PCE-2016-0404).

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.183517.supplemental

References

Agostini, N., Panuccio, M. and Pasquaretta, C. (2015). Morphology, flight performance, and water crossing tendencies of Afro-Palearctic raptors during migration. *Curr. Zool.* **61**, 951-958.

Bairlein, F. (2003). Nutritional strategies in migratory birds. In *Avian Migration* (ed. P. Berthold, E. Gwinner and E. Sonnenschein), pp. 321-332. Berlin, Heidelberg: Springer Berlin Heidelberg.

Bairlein, F. and Hüppop, O. (2004). *Migratory Fuelling and Global Climate Change*, pp. 33-47. Academic Press.

Battley, P. F., Piersma, T., Dietz, M. W., Tang, S., Dekinga, A. and Hulsman, K. (2000). Empirical evidence for differential organ reductions during trans-oceanic bird flight. *Proc. R. Soc. B Biol. Sci.* **267**, 191-195.

Berthold, P. (2001). *Bird Migration: A General Survey*. Oxford University Press.

Biebach, H. (1996). Energetics of winter and migratory fattening. In *Avian Energetics and Nutritional Ecology* (ed. C. Carey), pp. 280-323. Boston, MA: Springer US.

BirdLife International and NatureServe (2014). *Bird Species Distribution Maps of the World*. UK: BirdLife International, Cambridge and Arlington, USA: NatureServe.

Blem, C. R. (1990). Avian energy storage. *Curr. Ornithol.* **7**, 59-113.

Both, C., Van Turnhout, C. A. M., Bijlsma, R. G., Siepel, H., Van Strien, A. J. and Foppen, R. P. B. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc. R. Soc. B Biol. Sci.* **277**, 1259-1266.

Bowlin, M. S. and Wikelski, M. (2008). Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. *PLoS ONE* **3**, e2154.

Bruderer, B., Peter, D., Boldt, A. and Liechti, F. (2010). Wing-beat characteristics of birds recorded with tracking radar and cine camera. *Ibis* **152**, 272-291.

Cramp, S. (1998). *The Complete Birds of the Western Palearctic on CD-ROM*. Oxford: Oxford University Press.

Dingle, H. (2014). *Migration*, 2nd edn. Oxford University Press.

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W. and Silk, J. R. D. (2010). Tracking of Arctic Terns *Sterna paradisaea* reveals longest animal migration. *Proc. Natl. Acad. Sci. USA* **107**, 2078-2081.

Fijn, R. C., Hiemstra, D., Phillips, R. A. and van der Winden, J. (2013). Arctic Terns *Sterna paradisaea* from the Netherlands migrate record distances across three oceans to Wilkes Land, East Antarctica. *Ardea* **101**, 3-12.

Gill, R. E., Tibbitts, T. L., Douglas, D. C., Handel, C. M., Mulcahy, D. M., Gottschalck, J. C., Warnock, N., McCaffery, B. J., Battley, P. F. and Piersma, T. (2009). Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proc. R. Soc. B Biol. Sci.* **276**, 447-457.

Guillemain, M., Bertout, J.-M., Christensen, T. K., Pöysa, H., Väänänen, V.-M., Triplet, P., Schricke, V. and Fox, A. D. (2010). How many juvenile Teal *Anas crecca* reach the wintering grounds? Flyway-scale survival rate inferred from wing age-ratios. *J. Ornithol.* **151**, 51-60.

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., Chojnowski, J. L., Cox, W. A., Han, K.-L., Harshman, J. et al. (2008). A Phylogenomic study of birds reveals their evolutionary history. *Science* **320**, 1763-1768.

Hedenström, A. (1992). Flight performance in relation to fuel load in birds. *J. Theor. Biol.* **158**, 535-537.

Hedenström, A. (1993). Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Philos. Trans. R. Soc. B Biol. Sci.* **342**, 353-361.

Hedenström, A. (2008). Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 287-299.

Hedenström, A. (2010). Extreme endurance migration: what is the limit to non-stop flight? *PLoS Biol.* **8**, e1000362.

Hedenström, A. and Alerstam, T. (1992). Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *J. Exp. Biol.* **164**, 19-38.

Hedenström, A. and Alerstam, T. (1997). Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *J. Theor. Biol.* **189**, 227-234.

Jenni, L. and Jenni-Eiermann, S. (1998). Fuel supply and metabolic constraints in migrating birds. *J. Avian Biol.* **29**, 521-528.

Jenni-Eiermann, S., Jenni, L., Kvist, A., Lindström, Å., Piersma, T. and Visser, G. H. (2002). Fuel use and metabolic response to endurance exercise: a wind tunnel study of a long-distance migrant shorebird. *J. Exp. Biol.* **205**, 2453-2460.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. and Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature* **491**, 444-448.

Kaiser, A. (1993). A new multi-category classification of subcutaneous fat deposits of songbirds. *J. Field Ornithol.* **64**, 246-255.

Krementz, D. G. and Pendleton, G. W. (1990). Fat scoring: sources of variability. *Condor* **92**, 500.

Lind, J., Fransson, T., Jakobsson, S. and Kullberg, C. (1999). Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. *Behav. Ecol. Sociobiol.* **46**, 65-70.

Lindström, Å. (1991). Maximum fat deposition rates in migrating birds. *Ornis Scand.* **22**, 12.

Lindström, Å. and Alerstam, T. (1992). Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *Am. Nat.* **140**, 477-491.

McGuire, L. P. and Guglielmo, C. G. (2009). What can birds tell us about the migration physiology of bats? *J. Mammal.* **90**, 1290-1297.

McWilliams, S. R., Guglielmo, C., Pierce, B. and Klaassen, M. (2004). Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *J. Avian Biol.* **35**, 377-393.

Metcalfe, N. B. and Furness, R. W. (1984). Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. *Behav. Ecol. Sociobiol.* **15**, 203-206.

Newton, I. (2007). *The Migration Ecology of Birds*. Elsevier.

Norberg, U. M. (1990). *Vertebrate Flight*. Berlin, Heidelberg: Springer Berlin Heidelberg.

Norberg, U. M. (1996). Energetics of flight. In *Avian Energetics and Nutritional Ecology*, pp. 199-249. Boston, MA: Springer US.

Odum, E. P. and Connell, C. E. (1956). Lipid levels in migrating birds. *Science* **123**, 892-894.

Owen, M. and Black, J. M. (1989). Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. *J. Anim. Ecol.* **58**, 603-617.

Panuccio, M., Chiatante, G. and Tarini, D. (2013). Two different migration strategies in response to an ecological barrier: Western Marsh Harriers and juvenile European Honey Buzzards crossing the central-eastern Mediterranean in autumn. *J. Biol. Res.* **19**, 10-18.

Pap, P. L., Osváth, G., Sándor, K., Vincze, O., Bărbos, L., Marton, A., Nudds, R. L. and Vágási, C. I. (2015). Interspecific variation in the structural properties of flight feathers in birds indicates adaptation to flight requirements and habitat. *Funct. Ecol.* **29**, 746-757.

Paradis, E., Claude, J. and Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289-290.

Pennycuick, C. J. (1975). Mechanics of flight. In *Avian Biology*, Vol. 5 (ed. D. S. Farner and J. R. King), pp. 1-75. Academic Press.

Pennycuick, C. J. (1998). Computer simulation of fat and muscle burn in long-distance bird migration. *J. Theor. Biol.* **191**, 47-61.

Pennycuick, C. J. (2008). Modelling the flying bird. *Igarss* **2014**, 1-5.

Rayner, J. M. V. (1988). Form and function in avian flight. In *Current Ornithology* (ed. R. Johnston), pp. 1-66. Boston, MA: Springer US.

Rayner, J. M. V. (1990). The mechanics of flight and bird migration performance. In *Bird Migration* (ed. E. Gwinner), pp. 283-299. Berlin, Heidelberg: Springer Berlin Heidelberg.

Ricklefs, R. E. (1996). Avian energetics, ecology, and evolution. In *Avian Energetics and Nutritional Ecology* (ed. C. Carey), pp. 1-30. Boston, MA: Springer US.

Rubolini, D., Gardiazabal Pastor, A., Pilastro, A. and Spina, F. (2002). Ecological barriers shaping fuel stores in barn swallows *Hirundo rustica* following the central and western Mediterranean flyways. *J. Avian Biol.* **33**, 15-22.

Sachs, G. (2015). New model of flap-gliding flight. *J. Theor. Biol.* **377**, 110-116.

Sapir, N., Wikelski, M., McCue, M. D., Pinshow, B. and Nathan, R. (2010). Flight modes in migrating European Bee-Eaters: heart rate may indicate low metabolic rate during soaring and gliding. *PLoS ONE* **5**, e13956.

Schmidt-Wellenburg, C. A., Engel, S. and Visser, G. H. (2008). Energy expenditure during flight in relation to body mass: effects of natural increases in mass and artificial load in Rose Coloured Starlings. *J. Comp. Physiol. B* **178**, 767-777.

Somveille, M., Rodrigues, A. S. L. and Manica, A. (2015). Why do birds migrate? A macroecological perspective. *Glob. Ecol. Biogeogr.* **24**, 664-674.

Sukumaran, J. and Holder, M. T. (2010). DendroPy: a Python library for phylogenetic computing. *Bioinformatics* **26**, 1569-1571.

Vágási, C. I., Pap, P. L., Vincze, O., Osváth, G., Erritzøe, J. and Møller, A. P. (2016). Morphological adaptations to migration in birds. *Evol. Biol.* **43**, 48-59.

Vincze, O. (2016). Light enough to travel or wise enough to stay? Brain size evolution and migratory behavior in birds. *Evolution* **70**, 2123-2133.

Vincze, O., Vágási, C. I., Pap, P. L., Osváth, G. and Møller, A. P. (2015). Brain regions associated with visual cues are important for bird migration. *Biol. Lett.* **11**, 20150678.

Ward, P. and Jones, P. J. (2010). Pre-migratory fattening in three races of the Red-billed quelea *Quelea quelea* (Aves: Ploceidae), an intra-tropical migrant. *J. Zool.* **181**, 43-56.

Weber, J.-M. (2009). The physiology of long-distance migration: extending the limits of endurance metabolism. *J. Exp. Biol.* **212**, 593-597.

Winkler, H. and Leisler, B. (2008). On the ecomorphology of migrants. *Ibis* **134**, 21-28.

Witter, M. S. and Cuthill, I. C. (1993). The ecological costs of avian fat storage. *Philos. Trans. R. Soc. B Biol. Sci.* **340**, 73-92.