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Article

Dynamic body acceleration increases by 20% during flight ontogeny of greylag geese *Anser anser*

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Despite our knowledge of the biophysical and behavioural changes during flight ontogeny in juvenile birds, little is known about the changes in the mechanical aspects of energy expenditure during early flight development, particularly in migratory species. Here, we investigate in a unique experimental setup how energy expended during flights changes over time beginning with early ontogeny. We calculate overall dynamic body acceleration (ODBA) as a proxy for energy expenditure in a group of hand raised greylag geese *Anser anser* trained to fly behind a microlight aircraft. We propose two potential hypotheses; energy expenditure either increases with increasing physiological suitability (the 'physical development hypothesis'), or decreases as a result of behavioural improvements mitigating flight costs (the 'behavioural development hypothesis'). There was a significant temporal increase of flight duration and ODBA over time, supporting the 'physical development hypothesis'. This suggests that early on in flight ontogeny behavioural development leading to flight efficiency plays a weaker role in shaping ODBA changes than the increased physical ability to expend energy in flight. We discuss these findings and the implications of flight development on the life history of migratory species.

Keywords: biologging, flight, life history, movement ecology, ontogeny

Introduction

Konstanzer Online-Publikations-System (KOPS)

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The study of the development of flight in birds has been notably concerned with the biophysical and behavioural changes experienced by juveniles in an attempt to draw parallels with the evolution of flight (Dial et al. 2006, Heers et al. 2011, 2014, Heers and Dial 2012, Heers 2016). Studies on ground-dwelling birds have found relationships between changes in wing and flight feather morphology and flapping behaviour during flight ontogeny – younger birds exploit the drag produced by their flexible, symmetrical and open feather structure to contribute to weight support whereas older birds change their flapping behaviour to generate greater lift with their stiffer wings and more asymmetrical flight feathers (Heers et al. 2011). However, fewer investigations have been carried out on the ontogeny of flight in more volant, migratory species. As a result, we know little



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about the changes in the energetic cost of flying over the first weeks of flight experienced in young birds.

Here we analyse how energy expenditure during flight changes during ontogeny in a group of hand-raised greylag geese *Anser anser* trained to fly behind a microlight aircraft. Greylag geese are altricial-flying social birds, living in extended family units and regularly flying moderately long distances, sometimes up to 10 km, between feeding and roosting sites. Goslings reach flying ability within the 10th week of life, shortly before concluding outermost primary growth (Bauer and Von Blotzheim 1968, Kear 2005). As a result, flight development has consequences on social cohesion and movement ecology, more so in migratory populations in preparation for longer autumn migratory displacements (Yésou 1991, Andersson et al. 2007).

Ontogenetic changes in flight behaviour are known for fledged brown boobies *Sula leucogaster* and migrating juvenile white storks *Ciconia ciconia*, who appear to change their flying behaviour to incorporate greater proportions of gliding into their flights with age, a shift linked to improved energetic efficiency (Yoda et al. 2004, Rotics et al. 2016). Geese are predominantly flapping flyers but may incorporate brief periods of gliding in their profiles (Butler and Woakes 1980, Ely et al. 1999), and it could be hypothesised that young geese learn how to behaviourally increase their flying efficiency with experience, for instance by optimising flight formation in groups (Weimerskirch et al. 2001), reducing their energy expenditure with time – the ‘behavioural development hypothesis’. Concurrently, muscle development in goslings changes to reflect the predominant form of locomotion, shifting to ventricular and pectoralis growth on the onset of flight (Bishop et al. 1996). The development of the pectoralis muscle mass in barnacle geese *Branta leucopsis* appears to be better explained by endogenous, hormonal cues rather than through direct flight training. In fact, the geese only partake in very few, short flights and bouts of wing training prior to commencing their first autumn migration (Bishop et al. 1998). As a result, flying ability is hypothesized to develop primarily with age, largely irrespective of the time spent in flight during ontogeny and in parallel with developmental changes in feather structure. In this case, energy expenditure for flight could be expected to increase with age and physical ability – the ‘physical development hypothesis’.

To assess the respective importance of these two non-mutually exclusive hypotheses in early flight development, we investigated the relationship between energy expenditure and age over the first 10 weeks of flight. We use overall dynamic body acceleration (ODBA) as a proxy for energy expenditure as measured through the triaxial acceleration measurements of a moving animal (Gleiss et al. 2011, Nathan et al. 2012). Several studies on a range of wild and captive bird and mammal species have found significant, positive correlations between ODBA and other variables that reflect metabolic activity and energy expenditure, such as heart rate, respiratory frequency and doubly labelled water turnover (Wilson et al. 2006, Halsey et al. 2008, Green et al. 2009, Gleiss et al. 2011, Elliott et al. 2012, Van Walsum et al. 2019).

Methods

Seven male greylag geese – all siblings except for one (‘Calimero’), a half-sibling to all the rest – were imprinted and hand-raised from eggs collected from a wild migratory population in northern Germany. The geese were kept in an outdoor aviary and regularly engaged in physical activity (walking, swimming and later flying) outside the aviary. All were subsequently trained to follow a microlight aircraft (ATOS VRS 280) flown by their adoptive human parent (MQ) to allow for controlled flights to be carried out in the same area and at the same time of day with all geese. Regular data was successfully obtained from five individuals – ‘Calimero’ (C), ‘Gloria’ (G), ‘Maddin’ (M), ‘Nils’ (N) and ‘Paula’ (P). Gloria, Maddin and Paula hatched on 15 May 2015 while Calimero and Nils hatched on 17 May 2015.

Triaxial acceleration and GPS recording loggers (Bird battery tags MC-2, e-obs Digital Telemetry) were fitted onto the geese’s backs onto plates mounted on Teflon tape wing-loop harnesses. Acceleration data was sampled at 12 Hz and GPS location at 1 Hz. The harnesses were permanently worn by the geese, ensuring that the position of attachment of the data logger was kept constant throughout the study period and as close as possible to the animal’s centre of mass, aligned to the plane of the body. The loggers recorded activity during regular morning flight training between July and September 2015. The microlight flew at a constant cruising speed of 60 km h⁻¹ at an altitude between 20 m and 30 m above ground with a climb rate of around 4 ms⁻¹. The geese successfully reached the microlight’s altitude during flights by the end of July, using a climb rate of around 0.5 ms⁻¹ as estimated by the pilot of the aircraft with the aid of the air navigation panel. The duration of the flights was primarily and deliberately dictated by the birds, which could land and abort the flight at will. When only a portion of the flock landed, the pilot continued to fly with the remaining goose or geese. Flights were carried out in the morning to take advantage of steady atmospheric conditions, and we avoided flying in days of strong wind. The experienced wind conditions ranged from 0 km h⁻¹ to occasional instances of localised wind gusts up to 30 km h⁻¹ caused by strong thermals.

The geese were weighed four times during this period (minimised to avoid handling stress). Weights varied from 2.5–3.1 kg aged 59/61 DPH (days post-hatching) up to 3.5–4.2 kg at 136/138 DPH. Similar to previous observations of young geese (Bishop et al. 1996), body weight increased almost linearly. The tag, plate and harness set-up weighed around 27 g. This is below 1% of the body mass of all birds during most of the duration of the study, at which percentage negative behavioural and life history impacts are greatly reduced (Bodey et al. 2017).

The triaxial acceleration data were transformed into ODBA as described by Gleiss et al. (2011), calculating the static component by rolling means over the total acceleration with a 3 s window (Shepard et al. 2008). Video footage of the geese in flight does not suggest that their flight orientation changes greatly during ontogeny. Under these

circumstances, there is no evidence that calculating vectorial dynamic body acceleration (VeDBA) produces a more representative measure than ODBA for the estimation of energy expenditure due to movement (Qasem et al. 2012, Wilson et al. 2019). We assume that ODBA is proportional to mass specific energy expenditure. While changes in wingstroke frequency may also influence measures of DBA the accelerometer sampling frequency was too low to effectively assess this (Spivey and Bishop 2013, Van Walsum et al. 2019).

In order to assess ODBA during flight we differentiated between take-off and cruising, as identified in the ODBA profile of each flight (Fig. 1). Take-off was taken as the span between the start of the increase of ODBA from resting due to high frequency flapping and the first instance following the peak where the decrease in ODBA meets the subsequent data plateau. Cruising was defined by the plateau in ODBA following take off and before acceleration anomalies related to landing (decreases in ODBA during gliding descent and peaks related to high flapping frequency on touch-down). The maximum ODBA value reached during take-off and the mean ODBA of cruising flight were considered in the following analyses. Ground speed, calculated from the displacement between successive GPS location data, was also selected for cruising flight and averaged over each flight.

We formulated a linear regression model (R function lm) to investigate whether age (DPH), average ground speed, and cruising duration influenced changes in mean cruising ODBA. In order to assess the presence of significant inter-individual differences, we included the interaction between age (DPH) and individual. The significance of the explanatory terms was tested using F tests (R function anova). Cruising duration did not add interpretative value and was removed ($F=1.888$, $p=0.171$). Owing to the significance of the interaction term ($F=5.031$, $df=4$, $p<0.001$), we ran

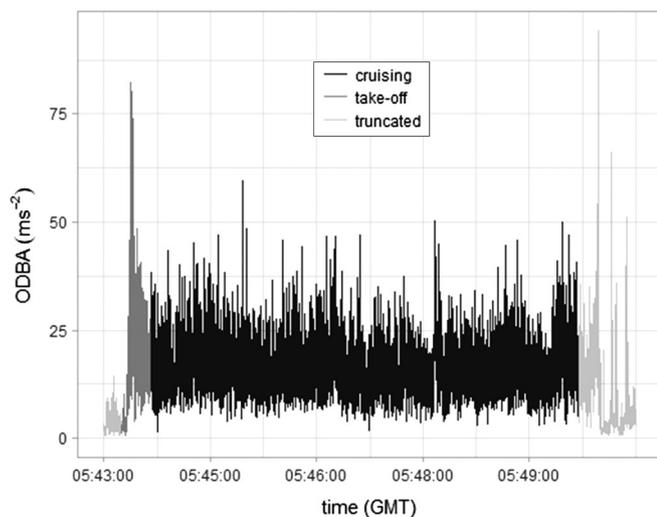


Figure 1. An example of ODBA, calculated at 12Hz, during an entire flight, showing the cut-off points used to classify take-off and cruising portions of flights.

separate linear regression models for each goose including age (DPH) and ground speed as explanatory variables.

Similarly, we created a linear regression model explaining maximum take-off ODBA with the interaction between age (DPH) and individual as a fixed effect. The interaction term was not significant ($F=1.758$, $df=4$, $p=0.140$), and keeping individual as an explanatory variable added no value to the model ($F=1.333$, $df=4$, $p=0.259$), therefore the final model explaining maximum take-off ODBA contained only age (DPH) as an explanatory variable.

The duration of flights varied greatly (cruising range = 13–473 s, mean \pm SD = 146 ± 119 s) and shorter flights were more variable in mean cruising ODBA. To investigate links between developmental changes in ODBA and the duration of flights, we isolated the first four sequential 50 s segments of cruising flights and calculated the mean ODBA for each. We ran Pearson's correlations between mean cruising ODBA for each segment and age (DPH). To determine whether there were changes in ODBA across the flight progression we compared the segments against each other using an analysis of variance test (R function anova) after the removal of two outliers.

All analyses were carried out using the R statistical package (<www.r-project.org>).

Results

Data from 61 group flights on 25 dates conducted between 60 and 130 DPH were obtained, resulting in 183 individual flights by the five geese. The first of these tracked flights were carried out very soon after the geese's first flight at the age of 56/58 DPH. Cruising flight duration increased significantly during the period of study until around 100 DPH ($t=18.238$, $p<0.001$, $R^2=0.67$), ranging from around 20 s to just over 7 min (Fig. 2). Following this date, the geese were observed to be less likely to take-off during flight training and conducted much shorter flights (mean \pm SD = 63 ± 34 s). The duration of cruising does not significantly contribute to the prediction of the mean cruising ODBA over the entire flight (χ^2 ($df=1$) = 1.757, $p=0.185$).

Average cruising ground speed varied between 11.3 ms^{-1} and 15.8 ms^{-1} and changed in a similar way to flight duration, increasing until around 85 DPH after which it decreased again, coinciding with the geese's reduced flight activity (Fig. 2).

Age explains the increase in the maximum ODBA during take-off (Est = 0.166, SE = 0.063, $t=2.634$, $p=0.009$). However, the significance of age and ground speed in explaining changes in mean cruising ODBA differed between individual geese (Table 1). The relationship between ODBA and age is stronger when analysing the first four 50 s segments of cruising flight separately (Fig. 3, Table 2), over which ODBA increases up to around 20% over the course of the study. In addition, it appears that ODBA gradually decreases throughout the duration of flight ($F=32.695$, $df=3$, $p\text{-value}<0.001$).

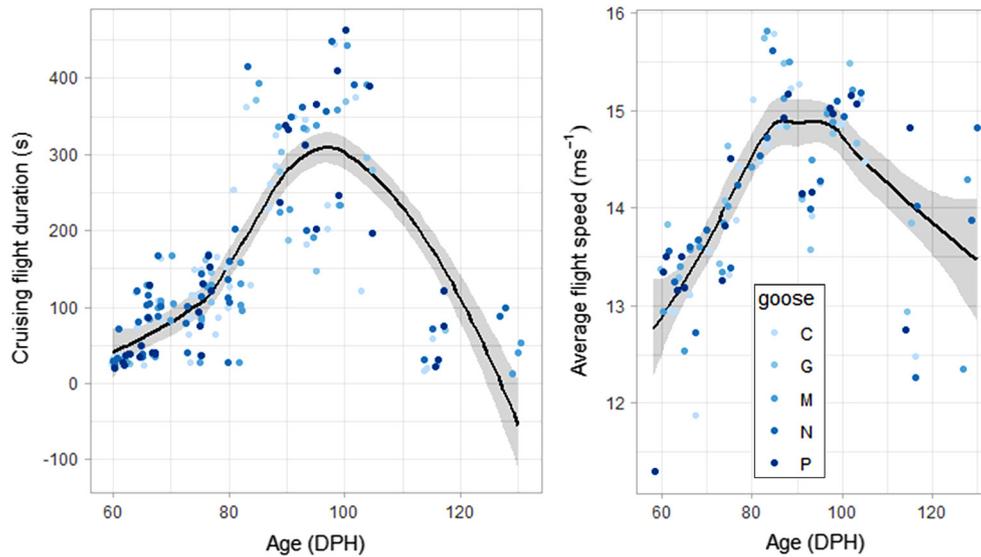


Figure 2. The duration of cruising flight (left) and average speed (right) gradually increases during flight development with age (days post-hatching) but then decreases again after 100 DPH possibly as a result of energetically demanding body moult. Shaded area around LOESS lines corresponds to the 95% confidence interval.

Discussion

This is among the first studies assessing changes in dynamic body acceleration during early flight development in a volant bird. Hand raised geese show no significant alteration to their wild counterparts in terms of life-history, but are generally less physiologically and behaviourally reactive to stressors (Hemetsberger et al. 2010), and no intrinsic developmental or physiological differences should be expected between wild and captive populations (Bishop et al. 1998). As a result, we can assume that our results on wild sourced, hand-raised greylag geese can be extrapolated to natural populations.

In all cases where there was a significant temporal trend in ODBA, it increased with time. This suggests that early on in flight ontogeny behavioural development leading to flight efficiency plays a weaker role in shaping ODBA changes than the increased ability to expend energy in flight due to physical and aerodynamic development. While our limited data quantifying changes in physical development may limit our ability to properly test the effect behavioural adaptations during this period have on flight energetics, the geese's increasing flight endurance and speed with age, as has also been observed in the

brown booby (Yoda et al. 2004), further supports the 'physical development hypothesis'. Observations on the aerodynamics of wings from both precocial-flying chukars *Alectoris chukar* and altricial-flying mallards *Anas platyrhynchos* found that developmental changes in feather microstructure contributing to feather stiffness, asymmetry, overlap and transmissivity strongly improve wing performance (lift and drag) (Heers et al. 2011, Dial et al. 2012). In addition to this, the improvement of wing stiffness and impermeability in mallards during ontogeny also contributes to the generation of greater aerodynamic force (Dial et al. 2012). Our results are in accordance with these observations of increased flight force with age. The fact that the goslings were still growing their flight feathers when they started flying as well as experiencing muscle growth during the period of study, as suggested by the apparent linearity of body weight increase, may explain the stronger role of the 'physical development hypothesis' in our results (Bishop et al. 1996). Indeed, given that ODBA reflects mass-specific energy expenditure, the total energy expenditure also increased as a result of the increase in body mass over this period. While increased energy expenditure is not the objective of the bird, the physical development that

Table 1. Statistical results from linear regression models relating mean cruising ODBA with age (DPH) and average cruising ground speed for each goose. Linear regression slope estimates are presented with their standard error. Significant terms are in italics.

Goose ID	Factors explaining mean cruising ODBA						R ²	df
	Age (DPH)			Ground speed (ms ⁻¹)				
	Est (\pm SE)	t	p	Est (\pm SE)	t	p		
Calimero	<i>0.051 (\pm0.01)</i>	6.303	<i><0.001</i>	-0.399 (\pm 0.12)	-3.259	<i>0.002</i>	0.47	44
Gloria	<i>0.035 (\pm0.01)</i>	3.259	<i>0.004</i>	-0.412 (\pm 0.21)	-1.956	0.064	0.35	21
Maddin	0.005 (\pm 0.01)	0.888	0.38	0.141 (\pm 0.12)	1.187	0.243	0.1	36
Nils	0.011 (\pm 0.01)	1.38	0.176	-0.445 (\pm 0.19)	-2.288	<i>0.028</i>	0.14	35
Paula	0.005 (\pm 0.01)	0.6	0.553	0.109 (\pm 0.16)	1.956	0.666	0.05	32

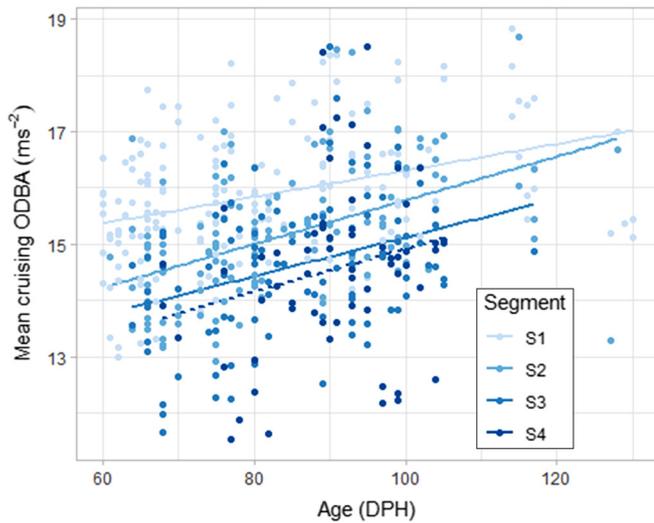


Figure 3. The relationship between age (days post-hatching) and mean ODBA (ms^{-2}) over each of the first four successive 50 s segments of cruising flight (S1–S4), combining data for all individuals together. Solid lines represent significant trends.

allows for the increased work done is necessary for the birds to successfully follow the microlight in our experiment, and adult geese in their natural environment. We could expect that behavioural effects become more important in energy expenditure at a later stage once the birds' physiology is already adapted for flight. Evidence to suggest this lies in the energy expenditure of adults and juveniles in mixed flocks of migrating white storks, where juveniles were found to decrease their energy expenditure in flight to equal that of adults by the end of migration (Rotics et al. 2016).

The consistent reduction in energy expenditure as approximated by ODBA over the first four successive 50 s segments of cruising flight in greylag geese likely reflects the progression of flight after take-off, specifically the transition from climbing flight, which requires high power output to arrive at the higher cruising altitudes, into less energy-demanding phases of flight at a constant altitude (Hedenström and Ålerstam 1992, 1994). This would also explain the high variability in mean ODBA of earlier flights as the geese were still struggling to gain height. This reduction in ODBA over flight duration probably masks the trend of the overall increase in cruising ODBA with age in the mixed model. Another potential reason for the decrease of flight energy over time is that during the flight the geese adjust their positions to take advantage of energy saving formation flight and the upwash created by

Table 2. Statistical results of Pearson correlations relating mean ODBA over each of the first four 50 s cruising segments to age (DPH).

Segment	t	df	r	p
S1	5.224	181	0.362	<0.001
S2	6.312	130	0.484	<0.001
S3	3.628	98	0.344	<0.001
S4	1.883	61	0.234	0.065

the microlight (Hummel 1995, Butler et al. 2003, Portugal 2016).

Our results highlight the substantial inter-individual differences in performance, particularly as it compares body acceleration between related individuals. One reason could be that, under the pressure of flying together as a flock, birds of different ability must exert different degrees of effort. Differences that remain unexplained in controlled environments, by body mass or by measurement error can potentially be explained by animal personality – the consistent difference in behaviour between individuals over time and/or a variety of scenarios (Réale et al. 2007, Careau et al. 2008). The role of personality as a major driver of population ecology and its assessment in both wild and captive populations has already been developed and applied over various taxa, including birds (Réale et al. 2000, Chapman et al. 2011, Wolf and Weissing 2012, Carter et al. 2013). Our personal observations of the geese suggest the existence of persistent personality types in our study individuals, but in the absence of objective and regular assessments of their behaviour we can only encourage future studies to consider personality in inter-individual comparisons of flight performance.

The development of flight has strong implications on the ecology of populations. The ability to fly plays an important role in survival in terms of predator escape and foraging movements. The goslings undertake a partial post-juvenile moult starting at around 89 DPH, moulting the tail, underparts and back between September and November (Bauer and Von Blotzheim 1968, Demongin 2016). This corresponds with the generally decreased activity levels recorded in the geese starting at around 100 DPH, probably due to energetic trade-offs to conserve energy for the generation of new feathers. Waterfowl such as geese differ from ground-dwelling birds in that wing development is substantially delayed in juveniles, but early hind-limb development allows young to exploit predator-poor and nutrient-rich ponds before the onset of flight (Heers et al. 2011, Dial et al. 2012). Breeding greylag geese undergo a flightless period that coincides with juvenile flightlessness as they moult their wing feathers simultaneously as part of their complete post-breeding moult starting a few weeks after hatching (Demongin 2016). In species depending on flight for foraging, flight development also dictates the extent of parental care (Yoda et al. 2004). Additionally, for birds which migrate in family groups of adults and juveniles, such as geese the flight skills of juveniles by the onset of migration has implications on their survival due to the benefits of keeping up with adults in terms of navigation, vigilance and resource detection (Menu et al. 2005, Rotics et al. 2016).

To summarise, we report that energy expenditure during flight, as approximated by ODBA, increases during early ontogeny in young greylag geese, supporting the greater importance of the 'physical development' hypothesis. It is possible that behavioural optimisation, lowering the energetic flight cost, becomes more important later in life once the birds' physiological developments are complete. Our observations add value to the discussion on the ontogeny of

aerodynamics, which is largely based on propeller and force-plate models with dried wings. The direct consequences that the progression of flight ontogeny has on species life history and extent of parental care highlight the strong adaptive control it is under.

Data availability statement

The raw acceleration data on which our study is based are available under the Movebank Data Repository (<www.movebank.org>) (<<https://doi.org/10.5441/001/1.1n4d187p>>).

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