



Soaring and intermittent flap-gliding during migratory flights of Northern Bald Ibis

Helena Wehner¹ · Johannes Fritz¹ · Bernhard Voelkl^{1,2}

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Abstract

Migratory journeys represent an energetic challenge for many long-distance migrants. The choice of flight times, migration route, altitude, travelling speed, wingbeat patterns, soaring as well as formation flight can all affect the energy expenditure for the journey. We monitored the flight patterns of two Northern Bald Ibises (*Geronticus eremita*) equipped with data loggers while crossing the Alps during a human-led migration from southern Germany to Tuscany. We observed that the birds used an intermittent flapping pattern, where phases of active flapping flight were regularly interrupted by short gliding phases. As a result of intermittent flight, the effective wing beat frequency was 13–20% lower than the observed wing beat frequency of 4.0 s^{-1} . When local conditions allowed, the birds gained altitude through circling in thermal updrafts. During those circling bouts, gliding on the outstretched wing was predominant, though active wing flapping was still observed. Overall, the two birds spent 19 and 22% of the time soaring on the outstretched wing, accruing during that time 26 and 28% of the altitude gain required for the crossing of a major mountain range. This shows that, apart from formation flight, northern bald ibis use at least two more strategies—thermal soaring and intermittent flap-gliding—for improving energy economy during migratory flights.

Keywords Intermittent flight · Soaring · Circling · Energy · Flight costs · Orographic lift

Zusammenfassung

Thermikgleiten und intermittierender Flügelschlag bei Zugflügen des Waldrapps

Migrationsflüge stellen für viele Langstreckenzieher eine energetische Herausforderung dar. Die Wahl von Flugzeiten, Zugroute, Flughöhe, Reisegeschwindigkeit, Flügelschlagmuster, Segelflug und Formationsflug können den Energieaufwand für die Migration beeinflussen. Während einer menschengeführten Migration von Süddeutschland in die Toskana haben wir die Flugmuster von zwei, mit Datenloggern ausgestatteten Waldrapen (*Geronticus eremita*) bei der Überquerung der Alpen analysiert. Die Vögel verwendeten ein intermittierendes Schlagmuster, bei dem Phasen von aktivem Schlagflug regelmäßig durch kurze Gleitphasen mit gestreckten Flügeln unterbrochen wurden. Infolge des intermittierenden Fluges war die effektive Flügelschlagfrequenz 13–20 Prozent niedriger, als die beobachtete Flügelschlagfrequenz von $4,0 \text{ s}^{-1}$. Wenn es die topographischen und mikroklimatischen Bedingungen zuließen, gewannen die Vögel durch Kreisen in thermischen Aufwinden an Höhe. Während dieser Kreiselsequenzen war Gleiten mit ausgestreckten Flügeln vorherrschend, obwohl auch aktives Flügelschlagen beobachtet wurde. Insgesamt verbrachten die beiden Vögel 19 bzw. 22 Prozent der Zeit gleitend und erreichten in dieser Zeit 26 bzw. 28 Prozent des Höhengewinns, der für die Überquerung eines großen Gebirgszuges

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✉ Bernhard Voelkl
bernhard.voelkl@vetsuisse.unibe.ch

¹ Waldrappteam Conservation & Research, Schulgasse 28,
6162 Mutters, Austria

² Animal Welfare Division, University of Bern,
Laenggassstrasse 120, CH-3012 Bern, Switzerland

erforderlich war. Dies zeigt, dass der Waldrapp neben dem Formationsflug mindestens zwei weitere Strategien – thermisches Kreisen und intermittierenden Gleitflug – zur Verbesserung der Energiebilanz während des Zugs einsetzt.

Introduction

Almost 20% of all bird species are long-distance migrants, undertaking seasonal migrations of up to several thousand kilometres (Alerstam 1990). These journeys are energetically demanding and presumably as a consequence mortality during migration is higher than during other times of the year (Bairlein 1992; Menu et al. 2005; Owen and Black 1991; Sillett and Holmes 2002). Birds have thus evolved various strategies to reduce energy requirements for migration. These include choice of flight times, migration route, altitude, and travelling speed, as well as specific flight patterns (Newton 2010).

In active flapping flight, the flight muscles actively produce the power required for both producing forward thrust and counteracting gravity. This flight mode is energetically demanding (Nudds and Bryant 2000; Pennycuick 1989; Tucker 1968) and the metabolic rate of birds during flapping flight is several times higher than their resting metabolic rate (Butler and Woakes 1990; Duriez et al. 2014; Newton 2010; Norberg 1996). Flight patterns where the birds replace active flapping flight by short or long phases of gliding can reduce the overall energy requirement for locomotion (Tobalske 2007).

Many species use intermittent flight, where phases of flapping are interrupted by non-flapping phases. Intermittent flight presumably saves energy because periods of muscle inactivity and isometric contractions during non-flapping phases are likely to allow savings of metabolic power output relative to isotonic contractions during flapping (Goldspink 1981). During the non-flapping phases, the wings of the birds can either be flexed and pressed to the body—in this case of flap-bounding, the bird is losing altitude during the non-flapping phase, leading to a characteristic undulating pattern—or the wings can be stretched out and the bird is losing no or only little altitude during the non-flapping phases of this flap-gliding flight pattern (Pennycuick 2008; Tobalske 2016). Flap-bounding is only observed in small species with less than 300 g body mass, where it helps to reduce profile drag (Bruderer et al., 2010; Bruderer and Boldt 2001). Some species, like the House Martin (*Delichon urbicum*) use both bounding and gliding bouts (Tobalske 2001). Apart from body mass, the propensity for flap-bounding flight seems to be affected by the wing shape. Birds with low aspect ratio like Zebra Finches (*Taeniopygia guttata*) use exclusively flap-bounding, while birds with higher aspect ratios are more prone to flap-gliding (Pennycuick 2008; Tobalske 2001).

Soaring is a special form of gliding, where energy is harvested from the environment (Ellington 1991; Pennycuick 2008). During thermal soaring, birds make use of columns

of warm air rising up vertically. If the speed of the rising air is faster than the sink rate of the bird, it can gain altitude entirely by gliding on the outstretched wings. As those columns are often rather limited in their horizontal dimension, birds have to fly in tight spirals to stay within the thermal, leading to the typical circling behaviour (Voelkl and Fritz 2017). The metabolic rate for this type of locomotion is estimated to be only 1.5 to 2 times the basal metabolic rate and close to the resting metabolic rate (Newton 2010; Sapir et al. 2010). During slope soaring, birds use winds deflected upwards by landscape structures like mountain slopes and cliffs (Bishop et al. 2015; Bohrer et al. 2012; Katzner et al. 2015; Lanzone et al. 2012; Shamoun-Baranes et al. 2003), though this type of soaring has so far received far less attention from the research community.

The Northern Bald Ibis (*Geronticus eremita*) is a migratory bird with an average body mass of 1300 g and a wingspan of about 130 cm. In historic populations, migrations over 3000 km from Syria to wintering grounds in Ethiopia have been observed (Serra et al. 2015). The species is listed as endangered, with only one wild population remaining at the Atlantic coast in Morocco, which changed to a sedentary lifestyle (Bowden et al. 2008; Boehm et al. 2020). Information about natural migration patterns is limited, though observations indicate that juvenile birds travel together during their first autumn migration, following adult individuals (Fritz et al. 2017, 2019). During migratory flights, the birds make use of flight in echelon or U-shaped formations (Portugal et al. 2014; Voelkl et al. 2015) but also of extensive soaring (Sperger et al. 2017; Voelkl and Fritz 2017).

In this study, we took a closer look at the flight patterns of the birds while crossing the Alps on their first south-bound migration. Specifically, we wanted to know whether they use thermal updrafts as well as orographic lift along alpine mountain ridges. Additionally, as we have previously observed that the ibises frequently glide on the outstretched wing even during steady-level flight, we aimed to investigate how frequent and how long those gliding phases are and when they occur.

Methods

Subjects

Study subjects were two juvenile Northern Bald Ibises (*Geronticus eremita*), Bernado (BE, male, hatched 18.04.2018 in Rosegg, 225) and Akuma (AK, male, hatched 16.04.2018 in Rosegg, 217). The birds were hand raised by two foster parents in a flock of 31 birds as part of the European

LIFE+ reintroduction project Reason for Hope (LIFE+12-BIO_AT_000143). All birds were habituated to two ultra-light planes and trained to follow those planes. A detailed description of the reintroduction scheme and the human-led migration is given by Fritz and colleagues (Fritz et al. 2017, 2019; Fritz 2021). From August 15, to August 28, 2018, the flock of 31 birds was guided by the ultra-light planes from the designated breeding area in Überlingen near Lake Constance (47.7931N, 9.1402E) to the wintering site at the WWF Oasi Laguna di Orbetello (42.4765N, 11.2092E). This human-led migration was split up into 5 stages of 99 to 249 km (117–316 min flight time). During the 2nd stage on August 19, 2018 over a distance of 120 km from Andelsbuch (47.4084N, 9.8899E, 615 m a.s.l.) to Nauders (46.8496N, 10.5060E, 1459 m a.s.l.), henceforth flight 1, and the 3rd stage on August 21, 2018 over a distance of 189 km from Nauders to Thiene (45.6766N, 11.4960E, 96 m a.s.l.), henceforth flight 2, custom built data loggers were fitted with leg-loop harnesses to the lower back of the two focus birds flying with the flock.

Data logger

The data loggers were built by one of the authors (BV) and based on the Feather 32u4 microprocessor board from Adafruit Inc. with an 8 MHz ATmega32u4 processor and an Adafruit IMU breakout board with a Bosch thermometer and pressure sensor BMP180 with a resolution of 1 Pa for pressure and 0.1 °C for temperature, an ST 3D accelerometer and 3D magnetometer LSM303D and an ST three-axis digital gyroscope L3GD20. The linear acceleration range was set to ± 2 g, the magnetic measurement range was set to ± 1.3 Gauss and the measurement range of the gyroscope was set to 0–250 degree per second. Temperature was recorded with 8 bit resolution, all other channels had 16 bit resolution. Data were stored on an 8 GB microSD card. Sensor readings were sampled at a rate of 19 Hz. Fluctuations in sampling rates were usually within the range of ± 2 ms. The housing was made of balsa wood and light carbon composite with an aerodynamic drop-like shape (Fig. 1). Twelve holes in the housing ensured air circulation and tests showed that the sensors within the housing responded to pressure changes within 0.5 s and to temperature changes within 2 s. The housing was painted white to minimize the effect of thermal radiation on the temperature readings. The total mass of the logger including housing and battery was 25 g.

Data analysis

To distinguish between times of active flapping flight and times of gliding, we used a simple decision rule, defining gliding as a continuous time frame of at least 0.25 s (5 consecutive sample points, which is slightly longer than



Fig. 1 A Northern Bald Ibis fitted with a data logger

the phase length of one typical wing beat, 0.22–0.23 s) with absolute vertical acceleration (after band-pass filtering) of less than 0.153 g. Time phases of flapping are defined as phases where birds are not gliding; thus by definition bouts of flapping and gliding always alternated and the combined flapping and gliding bouts account for 100% of the flight time. For each flapping and gliding bout, we calculated the difference in altitude (gain or loss) by subtracting the altitude of the first sample point of a bout from the altitude of the last sample point of the respective bout. Summary statistics for total altitude changes are based on the summed altitude differences of gliding and flapping bouts.

We define the wing beat frequency through the local maximum of the power spectrum of the Fourier transform of the (unfiltered) vertical acceleration. Bruderer et al. (2001) defined the 'effective wing-beat frequency' as the mean number of wingbeats per second (including non-flapping—i.e. gliding—phases). Following this definition, we calculated effective wing-beat frequencies for different phases of the flight (circling, straight flight, etc.) by dividing the product of the flapping time and flapping frequency by the combined flight time of flapping and gliding bouts for the respective phase.

To identify circling events, likely indicating thermal soaring, we used an algorithm (Supplementary material) to search for sequences with directional change of at least 720 degree in one direction (two full circles) within a 30 s interval and a positive altitude difference between start and end of the time window (altitude gain). Sequences flagged by this algorithm had to fulfil two additional criteria for defining a sequence as a circling bout: (i) a clear deviation from zero of the gyroscope's z-axis (yaw) reading as well as (ii) a visually detectable sinusoidal signal in the flight direction. Start and stop times of circling bouts were identified based

on the deviation of the yaw reading from zero. Visualizations of all circling bouts are given in supplementary Figure S4.

Information about the underlying landscape was based on GPS coordinates logged by one of the ultra-light planes accompanying the birds. Landcover maps and digital elevation models (DEM) covering the flight paths were downloaded from the Copernicus Land Monitoring Service (CORINE Land Monitoring Service, 2016). For extracting landscape information, calculation of slope and aspect out of the DEM and mapping, QGIS, a free and open-source geographic information system, was used (QGIS Development Team 2018). Data were analysed using the statistical software *R* v.4.0 (R Core Team 2014) and Wolfram *Mathematica* v 11.0 (see supplementary information for code).

Ethical note

Bird care, keeping, training and release followed well established standards in accordance with the legal framework and under the supervision of Waldrappteam Conservation & Research experts. The weight of the GPS devices was about 25 g, well below the recommended maximum value of 3% of the birds' body weight of about 1300 g (Fritz et al. 2020). The loggers were fixed on the lower back of the birds via a Teflon tubes leg-loop harness. This position is known to cause the least drag and minimize additional disadvantages and risks for the carrier (Fritz et al. 2020).

All translocation and management measures have been implemented in the framework of the European LIFE+ reintroduction LIFE+12-BIO_AT_000143. National approvals were provided by the County of Salzburg (21302-02/239/352-2012), Carinthia (11-JAG-s/75-2004),

Baden-Württemberg (11-7.3.3_Waldrapp), Bavaria (55.1-8646.NAT_03-10-1) and Italy (0027720-09/04/2013).

Results

During flight 1, we identified 7 (BE) and 8 (AK) circling bouts. Bird BE spent 754 s circling (9% of the flight time) and 7600 s (91%) flying straight (i.e. non-circling). Bird AK spent 853 s (10.2%) circling and 7474 s (89.8%) flying straight. The total altitude gain during this flight was 3056 m for BE and 3171 m for AK and the birds accrued 29% (BE) and 30% (AK) of the total altitude gain during circling. During flight 2, the birds BE and AK circled 10 times for 1013 s (7.5%) and 923 s (6.8%), achieving both 30% of their total altitude gain of respectively 2788 m and 2952 m during circling. Tables 1 and 2 give a more detailed break-up of the activity during those flights.

Plotting the vertical acceleration against time shows a distinctive pattern of strong positive and negative acceleration, indicating wing flapping (Fig. 2a). The spectrogram for the entire flight (Fig. 2b) clearly shows a dominant frequency around 4 Hz. The power spectrum of the Fourier transform shows local maxima for the two flights between 3.9 and 4.1 Hz (Table 3). Verifying the wing beat frequencies by manually counting peaks in the acceleration data stream for bouts of 30 s of continuous flapping (10 bouts per flight and bird), we obtained very similar estimates for the wing beat frequencies (supplementary material: ManualFrequencyValidation.pdf). A comparison of the frequency decomposition of the first and last 30 min of a flight suggests a small shift in the wing beat frequency with birds flapping slightly slower at the end of the flight (Fig. 2c, Table 3). Calculating the

Table 1 Summary statistics of flight characteristics during straight flight

Measure	BE flight 1	BE flight 2	AK flight 1	AK flight 2
Time spent flapping (s)	6516	10,341	6232	10,065
Median duration (quartiles) of flapping bouts (s)	3.6 (1.6, 8.3)	3.3 (1.9, 5.6)	3.6 (1.8, 6.7)	3.2 (2.0, 5.2)
Duration of longest flapping bout (s)	340	350	178	199
Time spent gliding (s)	1091	2203	1215	2579
Number of gliding bouts (#)	725	1737	1019	2129
A gliding bout every × seconds (s)	10.5	7.2	7.3	5.9
Median duration (quartiles) of gliding bouts (s)	0.7 (0.5, 1.2)	0.9 (0.6, 1.4)	0.7 (0.5, 1.2)	0.9 (0.6, 1.3)
Duration of longest gliding bout (s)	36	49	34	37
Total altitude gain (m)	2171	1942	2120	2057
Altitude gain during flapping (m)	1924	1609	1889	1679
Altitude gain during gliding (m)	247	333	231	378
Total altitude loss (m)	−2307	−4203	−2530	−4665
Altitude loss during flapping (m)	−1127	−2360	−1233	−2267
Altitude loss during gliding (m)	−1181	−1843	−1296	−2398
Numbers of gliding bouts with more than 5 m altitude gain (#)	2	2	3	7

Table 2 Summary statistics of flight characteristics during circling

Measure	BE flight 1	BE flight 2	AK flight 1	AK flight 2
Total altitude gain (m)	885	846	1051	895
Overall altitude gain accrued (%)	29	30	33	30
Average climb rate (m/s)	1.5	1.0	1.3	1.0
Maximum climb rate (m/s)	2.4	1.1	2.5	1.4
Altitude gain while flapping (m)	465	352	529	339
Altitude gain while gliding (m)	420	493	522	556
Total altitude loss (m)	−61	−68	−49	−71
Overall altitude loss (%)	2.6	1.6	1.9	1.5
Numbers of gliding bouts with more than 5 m altitude gain (#)	21	27	28	31

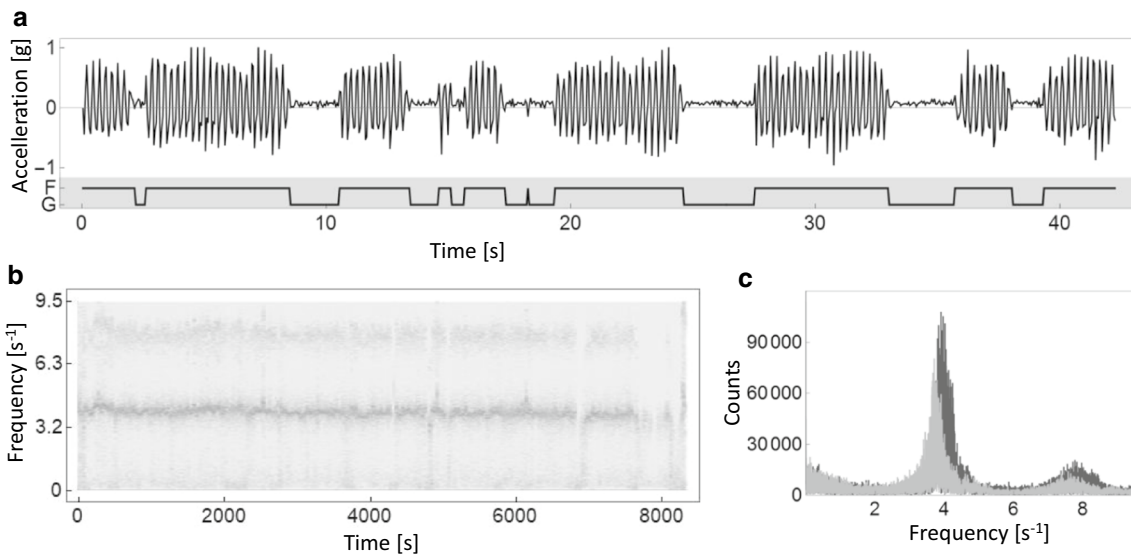


Fig. 2 Wing-beat patterns during migratory flight. **a** Vertical acceleration after band-pass filtering during steady-level flight over 42 s. We categorized flight as flapping flight (grey box, F) or gliding flight (G). **b** Spectrogram of the vertical acceleration over the entire flight

1 of bird BE; shading indicates frequency density. **c** Power spectrum based on Fast Fourier Transformation for the first 30 min (dark grey) and last 30 min (light grey) of the second stage of bird BE

Table 3 Observed and effective wing beat frequency

	BE flight 1	BE flight 2	AK flight 1	AK flight 2
Overall wing beat frequency (s^{-1})	4.0	3.9	4.1	4.0
Wing beat frequency first 30 min (s^{-1})	4.1	4.1	4.1	4.0
Wing beat frequency last 30 min (s^{-1})	3.9	3.9	4.0	3.9
Wing beat frequency during circling (s^{-1})	4.3	4.2	4.4	4.2
Effective wing beat frequency during straight flight (s^{-1})	3.5	3.2	3.4	3.2
Reduction of effective frequency during straight flight (%)	13	18	17	20
Effective wing beat frequency during circling (s^{-1})	2.2	1.8	2.2	1.4
Reduction of effective frequency during circling (%)	45	54	46	65

Estimates of wing beat frequencies are based on the maxima in the power spectrum. The reduction of the effective wing beat frequency is also expressed in percent of the overall wing beat frequency. 'Straight flight' comprise all flight times where the birds were not circling

local maximum of the power spectrum for each consecutive minute of a flight, disregarding bouts of thermal soaring and landing at the end of the flight, allowed us fitting a linear regression model with wing beat frequency at the power maximum (i.e. wing beat frequency) as response variable and time (minute), bird and flight as fixed factors. Over the flights, the wing beat frequency decreased by 1.5×10^{-3} Hz per minute flight time ($C.I_{95}$: 1.3×10^{-3} , 1.7×10^{-3} , Supplementary table S3), probably hinting at fatigue towards the end of the flight.

Wing flapping is interrupted from time to time by gliding phases with only little vertical acceleration where the birds are gliding on outstretched wings (Fig. 2a). These phases vary in length (median duration: 0.5 s, interquartile range: 0.6–1.4 s) and they occur at irregular intervals, though on average every 5.9–10.5 s (Table 1). Gliding sequences were observed both during circling and during straight flight, though they were much more frequent and longer during circling (compare Table 1, Table 2). Those short phases of gliding in intermittent flight have the effect that the effective wing beat frequency, as the average number of wingbeats per second, is lower than the wing beat frequency during active flapping flight (Table 3).

Circling bouts lasted from 38 to 285 s and climb rate and altitude gain differed markedly between bouts. In one instance, we observed a climb rate of 2.45 ms^{-1} , leading to an altitude gain of 187 m, while in another case, a climb rate of only 0.04 ms^{-1} led to an altitude gain of only 3 m after 4 full circles (see Suppl. Tab. 1 for details for all bouts). We also observed substantial differences in the proportion of time the birds were gliding during those circling bouts (range: 3–99%, median: 62%). These substantial differences are hinting at differences in the strength of the thermal updraft—an interpretation that is further supported by variation of the temperature rise within the thermal, which varied between 0.09 and $1.11 \text{ }^\circ\text{C}$ per circling bout. A post hoc analysis of the relation between temperature differential and soaring performance in terms of altitude gain, climb rate and proportion of circling did, however, not show clear effects (supplementary table S4).

Circling and straight flight differ markedly in the altitude change during gliding bouts (Fig. 3). With increasing length of gliding bouts, birds gained altitude when circling but—with a few exceptions—lost altitude when gliding during straight flight. We see this as indication that circling birds made use of updrafts that were faster than the sink speed of the gliding bird, whereas during straight flight birds do—in most cases—not encounter strong updrafts and lose altitude while gliding. Supplementary figure S2b gives an example of a circling bout where the bird gained 170 m altitude within 193 s equalling a climb rate of 0.88 ms^{-1} . During this circling bout, the air temperature increased by $0.9 \text{ }^\circ\text{C}$ but dropped again by $0.7 \text{ }^\circ\text{C}$

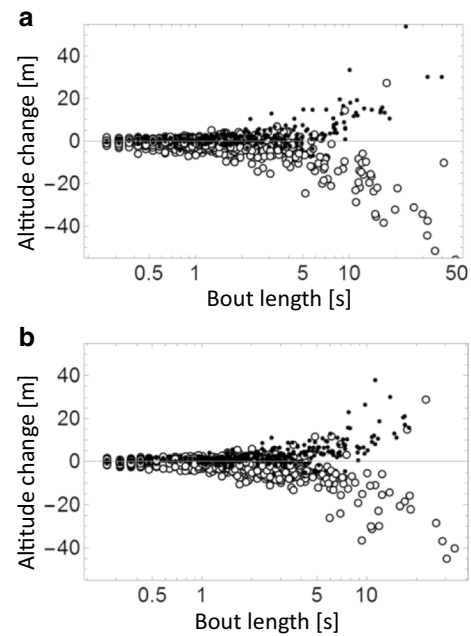


Fig. 3 Altitude gain and loss during circling and straight flight. Altitude difference (m) in course of a gliding bout is plotted against duration (s) of the gliding bouts of birds BE (a) and AK (b). Full points: gliding bouts during circling, open points: gliding bouts during straight flight. Combined data for flights 1 and 2

as soon as the bird continued in straight flight, indicating that the birds were circling within a column of warmer air.

We took a closer look at those few gliding phases during straight flight where altitude was gained (Fig. 3). In these cases, the temperature curve shows no indication for thermal updrafts, since no higher temperatures were recorded, yet altitude gain during prolonged gliding phases suggests the existence of upwards directed air movements. In some instances, the elevation profile at the position where those gliding events occurred, indicated a ridge along which orographic uplift likely occurred (Suppl. Figs. 3 and 4).

Sorting both flapping and gliding bouts by vertical velocity, an interesting pattern emerges (Fig. 4). The effective wing beat frequency was closest to actual wing beat frequency during steady-level flight (bouts with climb or sink rate of less than 0.5 ms^{-1}), while during descending bouts (sink rate $> 0.5 \text{ ms}^{-1}$) the effective wing beat frequency was clearly lower—indicating that birds increase the proportion of gliding time during descend. However, we can also see a decrease in the effective wing-beat frequency during ascends (climb rate $> 0.5 \text{ ms}^{-1}$) despite the birds' need to work against gravity, indicating that the birds ascended by utilising thermals or orographic uplifts that allowed them to increase the proportion of gliding (from 17 to 56%) on the expense of energetically demanding flapping.

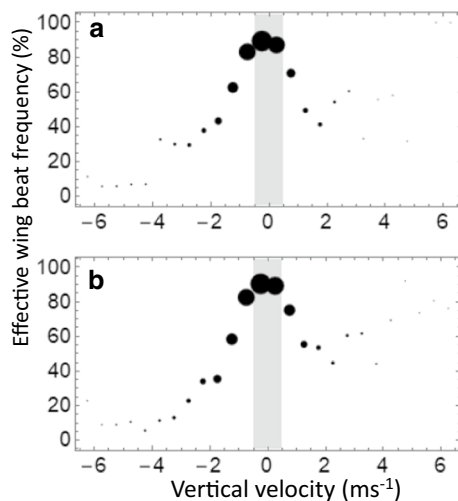


Fig. 4 Effective wing beat frequency for steady-level flight, ascend and descend. The effective wing-beat frequency in percent of the typical wing beat frequency is plotted against vertical velocity (ms^{-1}) in increments of 0.5 ms^{-1} for birds BE (a) and AK (b). The area of the bubbles is proportional to summed time of all bouts with the respective vertical velocity. Negative velocity: descend, positive velocity: ascend, grey-shaded area: approximate steady-level flight

Discussion

During migration, birds use behavioural strategies to minimize flight costs. Timing and the choice of the travel route can have a substantial impact on the overall duration and energy requirement for a journey (Newton 2010). Flight style during migratory legs is a further factor determining energy expenditure. Previously, authors have deplored that precise data about flight performance of free-flying birds, particularly during migration, are scarce and difficult to obtain (Bruderer et al. 2010; Pennycuik 2001). For a long time, video observations and radar measurements were the only options to identify flapping patterns of free-flying birds. More recently, the development of lightweight bio-logging devices, fitted directly to animals, opened up new avenues for research (Fehlmann and King 2016). Here, we provide continuous high-resolution data of flight patterns of two Northern Bald Ibises crossing a major mountain range—the Alps—during their southbound migration. These data show that the birds use an intermittent flight pattern of flap-gliding, as well as thermal soaring and—in a few instances—also ridge soaring.

Pennycuik (1990) suggested that body mass and wing morphology together with environmental parameters (specifically air density) define a 'natural' wing-beat frequency from which a bird cannot stray too far. This suggestion was based on anatomical properties of the flight muscle, as muscle fibre types have their characteristic force–velocity relationships with a narrow range of peak work and power

for a given contractile velocity (Hill 1950; Tobalske 2001). This proposition seems to be corroborated by observations that many passerines vary their vertical speed mainly by varying the duration of flapping and non-flapping phases (Bruderer et al. 2010). Intermittent flight is, thus, a possible solution for fine-tuning the required power output for a respective flight manoeuvre, while simultaneously not departing from the optimal wing flapping frequency (Tobalske 1995; Tobalske et al. 1999; Tobalske and Dial 1994). Alongside a narrow range for an optimal flapping frequency, Rayner (1985) proposed that birds have clearly distinct 'gaits' for different types of flight (e.g. ascending, steady-level flight, etc.), which differ in their upstroke kinematics and the produced vortex patterns. However, Tobalske et al. (1997) observed continuous variation in the flapping patterns of the medium-sized Magpies (*Pica pica*). Such continuous variation was also confirmed for small passerines (Hedenström et al. 2006; Spedding et al. 2003).

In Northern Bald Ibises, we observed a wing-beat frequency that decreased slightly from around 4.1 s^{-1} at the start to 3.9 s^{-1} at the end of the flight. Even during thermal circling, the reduced requirement for mechanic power output did not lead to a clear change in the wing-beat frequency once the birds were flapping, but to fewer and shorter flapping bouts. These observations are principle in line with the idea of a 'fixed gear', where modulation in power requirement is primarily achieved by 'switching the engine on and off' instead of changing the flapping frequency. Our acceleration data do not allow an in-depth analysis of wing stroke patterns, though we note that the observed wingbeat invariance during steady-level flight and circling might instigate interesting question for future research.

Intermittent flapping flight with short gliding phases is a typical flight mode for Bee-eaters (*Merops sp.*; Sapir et al. 2010), swifts and swallows and many raptors (Alerstam et al. 2007). In raptors, gliding is often associated with a reduction in cruising speed (Pennycuik 2001). Calculating the expected cruising speed for the Northern Bald Ibises, given a body mass of 1300 g and a scaling relationship between cruising speed (U) and body mass (m) of $U = 16 \times (m)^{0.13}$, with scaling parameters based on (Alerstam et al. 2007), we get an expected cruising speed of 16.6 ms^{-1} . This is, however, substantially faster than the observed travel speed of 11.6 ms^{-1} (Voelkl et al. 2015). During migration, Northern Bald Ibises, thus, fly slower than expected based on their body mass and also slower than other bird species of comparable body mass like, e.g. the Brent Goose (*Branta barnicla*) with a body mass of 1300 g and a cruising speed of 17.7 ms^{-1} (Alerstam et al. 2007). We suggest, that the difference between expected and observed cruising speed in Northern Bald Ibises is partly explicable by their intermittent flight style.

Power curves for birds typically have a U-shaped form, suggesting an optimal travel speed, where energy requirement per distance is minimal (Norberg 1990; Tobalske 2007). The location of this minimum (i.e. the optimal speed) depends amongst several other parameters on the wing span and the body mass of the bird. These parameters have also an intraspecific variation and thus, the optimal travel speed may slightly differ between individuals. Yet, if birds of a flock travel together, they have to adjust their individual flight speeds to the overall speed of the flock to stay together. Adjusting the flight speed can be achieved through changes in the strength of the wing beats, the wing beat frequency, or—alternatively—the effective wingbeat frequency. The latter method might be advantageous because deviating too much from the optimal wing beat frequency and wing beat amplitude might incur additional power costs. As such, intermittent flight, where individuals can vary the frequency and length of the gliding phases, might be a good mechanism for fine-tuning travel speed for group travel without incurring additional costs through deviating from the optimal wing beat frequency and amplitude.

A soaring-gliding migration mode results in a considerably slower horizontal speed compared to continuous flapping flight (Hedenström 1993), because of the time of circling without horizontal motion and because soaring is restricted to specific locations and certain time windows, when thermal up-winds are produced by the sun heating the ground. As a consequence, soaring-gliding is mainly observed in large species, such as raptors, pelicans and storks, for which it is much more energetically expensive to use flapping flight (Pennycuick 1975, 2008).

The Northern Bald Ibis is an opportunistic soarer—covering large distances in active flapping flight but soaring in thermals when encountered en route (Sperger et al. 2017; Voelkl and Fritz 2017). Our data show that a substantial part of the altitude gain required to cross a major mountain range was accrued while circling in thermals. During circling, birds showed occasional bouts of wing flapping, though the effective wing beat frequency during circling was substantially lower than during straight steady-level flight. We found, however, no indication that the birds were using ‘thermal streets’ (several thermals aligned in a row by wind direction, Pennycuick 1998). The pilots accompanying the birds on their migration reported substantially higher climb rates during other stages of the migration (particularly over the Po valley and the Apennines), suggesting that the local conditions during the crossing of the Alps might not have been specifically favourable for thermal soaring and that the altitude gain accrued through soaring might have been substantially higher at other parts of the migration path where no data are available.

We also observed a few instances, where birds gained altitude during extended gliding phases in straight flight.

The landscape profile at the locations where this happened suggests that those instances were examples of ridge soaring, where birds profited from upwards deflected winds (orographic lift). Yet, these instances were rare, and the altitude gained in this way was rather insignificant. Ridge soaring seems to be more common in soaring specialists like the Golden Eagle (*Aquila chrysaetos*) or the Turkey Vulture (*Cathartes aura*; Dennhardt et al. 2015; Lanzone et al. 2012).

The attachment of bio-logging devices to birds during migration flights enables data collections that are otherwise not possible. However, the logger itself is known to affect the aerodynamic properties of the bird by increasing drag and, hence, potentially influencing the flight pattern of logged birds (Pennycuick et al. 2012; Fritz et al. 2020). To minimize these effects, we designed a housing with an aerodynamically advantageous drop-like shape (Fig. 1). In addition, the crew of the accompanying microlight aircrafts closely observed the flight behaviour of the logged birds in comparison with the other individuals in the flock and found no indications of impairment by the devices. Thus, there is no indication that the fitted loggers had substantially affected the birds' flight ability.

The effect of the accompanying microlight airplanes on the flight behaviour of the birds has already been discussed previously (Voelkl et al. 2015). While the birds are generally following the ultra-light plane, they keep an average distance of 38 ± 17 m, mainly at a lateral position or below the planes (Voelkl and Fritz 2017; Suppl. Fig. S5). Therefore, the birds are hardly affected by turbulences or up-wash caused by the planes. Nonetheless, travel time, direction, altitude, and speed are to a certain degree imposed on the birds by the pilot and this may have affected to some degree the proportions of gliding and flapping times. The pilots tried to mimic the flight habits of the birds as closely as possible based on knowledge about the migration patterns of the species (Bairlein et al. 2015; Voelkl et al. 2015; Voelkl and Fritz 2017; Sperger et al. 2017) as well as and the pilots' years of experience in migrating with these birds. The pilots constantly monitored the birds, adjusted their flight speed and altitude based on the response of the birds and started circling whenever the birds did. Analysis of tracking data from wild migrating individuals indicates that the human-led migration largely matches the pattern of wild migrating Northern Bald Ibises with respect to leg length (average 225 km), duration (mean 270 min., max. 480 min.), flight speed (average: 42 km/h) and altitude (up to 2.200 m a.s.l.) and flight/rest ratio.

The overall route across the Alps as well as duration and time of day of the flights is determined by the pilots. These choices might have influenced the likelihood of encountering thermal updrafts. Thus, while the reported values of altitude gain accrued through circling indicate that it is feasible for the

birds to substantially reduce energy expenditure with the help of this strategy, those values are not necessarily indicative of the typical extent to which free-flying birds make use of this flight style. Anecdotal observations during other legs of the migration suggest that birds can also reach substantially higher climb rates than reported during these two stages. We also note that during one instance (circling about 1 during flight 1), the pilot actively tried to instigate soaring under presumably sub-optimal soaring conditions to build up altitude for traversing a mountain pass.

Conclusion

Energy requirements are a limiting factor for the length of migratory flights. Birds have developed various behavioural strategies to reduce the energy requirement for locomotion during migration. Large birds with large wing area and low wing loading use thermal up-drafts for gaining altitude, travelling in a soaring-gliding fashion. Intermittent flight, where phases of active flapping flight are interrupted by short gliding phases, can help to reduce mechanical power output at slow to moderate speeds (Rayner 1977, 1985; Ward-Smith 1984). Finally, several large- and intermediate-sized birds travel in groups in ordered V-shaped or echelon formations which, presumably, offer aerodynamic advantages. In previous work, we could show how Northern Bald Ibis on their first south-bound migration make use of formation flight (Portugal et al. 2014; Voelkl et al. 2015; Voelkl and Fritz 2017) and here we show that Northern Bald Ibis additionally make use of intermittent flight and thermal soaring as further means to reduce energy expenditure.

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