Flight Strategies of Migrating Northern Bald Ibises – Analysis of GPS Data During Human-led Migration Flights

Flugstrategien migrierender Waldrappe (Geronticus Eremita) – Analyse von GPS-Daten einer menschengeführten Migration

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Abstract: In the past, studying birds in free flight has been extremely difficult, though recently developed technologies, e. g. small and light GNSS-data loggers, allow the gaining of new insights into the behaviour and flight strategies of birds. As logger weight is a limiting factor and battery size dictates the number of positional fixes, knowledge of species-specific flight strategies is still restricted. During a human led migration of fourteen juvenile Northern Bald Ibis in 2014 we could, for the first time, record a complete GNSS dataset from all flock members over a four day migration from Salzburg to Tuscany. Data was collected by the Waldrappteam, in the course of an EU-LIFE+ project. The following paper analyses this dataset. The aim of this paper is to show the different flight strategies of migratory birds and furthermore the capabilities and limitations of the used GPS-modules for the study of free-flying birds.

Keywords: Flight strategy, Northern Bald Ibis, GPS data analysis

Zusammenfassung: *Das Erforschen von Vögeln und deren Flugstrategien war in der Vergangenheit sehr schwierig. Mittlerweile ermöglichen neue Methoden und Technologien, wie kleine und leichte GNSS-Datenlogger, einen tiefen Einblick in das Flugverhalten der Vögel. Trotzdem ist das Wissen über artenspezifische Flugstrategien noch immer begrenzt. Weiterhin sind die Batterien der GNSS-Geräte aus Gewichtsgründen sehr klein, was ein langfristiges Datenlogging erschwert. Während der menschengeführten Migration des Waldrapps im Jahr 2014 gelang es nun, einen GPS Datensatz von vierzehn Jungvögeln über vier Flugtage zu sammeln. Ein Ziel dieser Arbeit ist es, die unterschiedlichen Flugstrategien von Zugvögeln am Beispiel des Waldrapps aufzuzeigen und die Stärken und Schwächen der verwendeten GPS-Datenlogger für Studien frei fliegender Vögel zu prüfen.*

Schüsselwörter: *Flugstrategien, Waldrapp, GPS Datenanalyse*

1 Introduction

The Northern Bald Ibis (NBI; *Geronticus eremita*) is a roughly 75 cm large migrating bird, with a wing span of up to 140 cm and a weight of 1000 to 1500 grams. The NBI appeared in Europe as a breeding bird until the end of the 17th century (Schenker, 1977). Population decline was mainly driven by over-hunting (Fritz & Unsöld, 2015). Nowadays, the NBI is one of the most endangered bird species in the world (IUCN Red List). Since 2002, the Austrian project *Waldrappteam* developed methods to reintroduce the NBI as a migratory species (Fritz et al., 2016). Based on this feasibility study, a European reintroduction project, co-financed by the European Union under the LIFE+ program (LIFE+12-BIO_AT_000143) has

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been running since 2014. Human foster parents raise NBI chicks from zoo breeding colonies. The young birds, imprinted on the foster parents, are trained to follow two ultralight aircrafts (microlights), with one of the foster parents as co-pilot. In late summer, a human-led migration (HLM) takes place where the foster parents, using the microlights, lead the young birds from the breeding site north of the Alps to the wintering site in southern Tuscany (Fritz & Unsöld, 2015; Fritz et al., in press). From 2004 to 2016, a total of 165 chicks from various zoo breeding colonies in Austria, Germany, Switzerland and Czech Republic were taken for the reintroduction program and ten human-led migrations were performed. During the first migration journeys, the mean daily flight distance was about 60 km. Flights took place only in the morning to avoid thermals. Over the years, the method was optimized. The daily flights now lead over distances up to 360 km and last up to 8 hours. A differentiated understanding of the NBI behaviour and improved flight technique of the pilots allows the birds to be led also during thermally active periods of the day, where the birds change from formation flight to soaring and gliding (Fritz & Unsöld, 2015).

A crucial aspect of the project is the successful combination of applied species conservation and basic research. The human-led migration offers a unique opportunity to equip the animals with electronic devices for collecting physiological and positional data from real migrating birds (Voelkl et al., in press). Accurate position data in formation flying NBIs, collected during the human-led migration, could provide the first empirical evidence that birds flying in V-formation are able to save energy (Portugal et al., 2014). Other papers, based on data collected during human-led migration flights, present the formation flight as one rare example of direct reciprocation – a form of cooperation – in animals (Voelkl et al., 2015). Another study focused on the physiology and energetics of bird migration, investigating how the metabolism changes with the length of migratory flights (Bairlein et al., 2015).

In this paper, we present outcomes of data collections from GPS devices during human-led migration flights in the course of the LIFE Northern Bald Ibis project, collected in 2014. Our focus is on the technical description and comparison of the different flight strategies used by the birds, the active formation flight and the use of upwash by soaring and gliding.

2 Methods

The approach is based on the derivation of flight strategies from recorded GPS-Data. These data are collected using GPS-Logger which were carried by 14 Birds during the whole migration. The derivation of flight strategies is particularly based on the observation of changes in various parameters like flight speed and flight altitude. A similar approach was pursued by Katzner et al. (2016) analyzing data from golden eagles. To get a complete record of GPS-Data, we equipped Northern Bald Ibis from the *Waldrappteam* with GPS-Dataloggers. As these birds are hand raised, it is easy for the foster parents to catch the birds and fix the equipment to them. In 2014, 14 chicks of Northern Bald Ibis chicks (NBI; *Geronticus eremita*) were taken from a free flying breeding colony at Zoo Rosegg in Carinthia, Austria. The chicks hatched between April 13th and April 20th were raised by two experienced members of *Waldrappteam*, Corinna Esterer and Anne-Gabriela Schmalstieg, following a detailed protocol (Fritz, 2010). On Aug 25, the human-led migration journey started from Anif near Salzburg, Austria. It led across the Alps to Carinthia and further to Italy, across the Po valley to the delta of the Po river (Valle Gaffaro), then further across the Apennine to Florence in

Tuscany and finally to the WWF nature reserve Laguna di Orbetello in southern Tuscany (Fig. 1). A total distance of 944 km was covered within eleven days with four flight stages (min 153 km, max 301 km).

On September 4th 2014, during the final flight leg of the migration, twelve birds lost contact with the microlights after 70 km of flight, probably scared off by a TV team helicopter. The microlights with the two remaining birds continued further south, while the lost birds headed back north towards the place of departure of this flight stage, located at the southern foothills of the Apennines (Fig. 1). This flight occurred in absence of the foster parents and the microlights, and constitutes a unique case where the flight path of all flock animals, flying independently of the microlights, could be recorded.

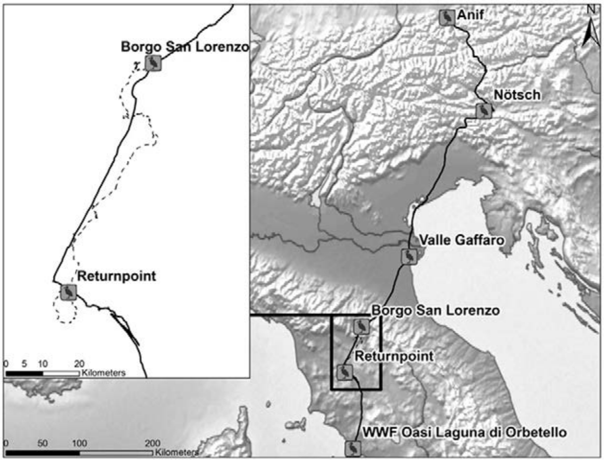


Fig. 1:
Overview of human-led migration 2014 from the Province of Salzburg to Tuscany. Solid line: human-led migration route; dotted line: return flight route to B. S. Lorenzo; Data source LIFE+ Northern Bald Ibis project; background map Natural Earth Data.

At the end of July, birds were equipped with leg-loop harnesses and dummy loggers to habituate them to the procedure of being equipped with loggers and carrying an additional mass during the migration (~3.5 % of the body mass of the smallest bird). The mass of the GPS data loggers from e-obs digital telemetry (http://www.e-obs.de/) was 23 grams. Given a mean body mass of 1.308 g for the birds, this was below the recommended 5 % limit for flying animals (Voelkl et al., 2015). During the migration journey, before the start of a flight stage, the dummy loggers on the back of the birds were replaced by the activated data logger. In addition, data loggers were also fixed on both microlights. The logger recorded GPS-Positions every second (1 Hz). In a first step of data processing, flight phases were selected from of the whole data set. The data was projected into the UTM format and stored in a GRASS GIS database. Since the GPS data loggers did not record the altitude above sea level (msl) but the altitude above the ellipsoid WGS84, this elevation data had to be corrected. For this, the Earth Gravitational Model 2008 (EGM2008) was used (Pavlis et al., 2012). In the next step, the altitude change ($\Delta h = h_t - h_{t-1}$) from the previous GPS point was calculated for every timestamp. Furthermore, the terrain height, at the corresponding GPS coordinate, was determined for each point in time. Table (1) gives an overview of the data recorded as well as the data derived therefrom.

As long-distance migrations are energetically demanding, it is assumed that mechanisms have evolved to cover the distance in an energy-efficient way. One means of achieving this is by circling in ascending air masses (Voelkl et al., 2015; Voelkl et al., in press). In order to investigate this more closely using the collected GPS data, a script has been created using the Python programming language, which captures all the circles of each data record. The script recognizes circles on the basis of three criteria: (1) the maximum duration required for a circle is 20 seconds; (2) the yaw angle difference (heading difference) of neighbouring GPS coordinates summed up during a flight section is between 200 degrees and 360 degrees; (3) in addition to criterion two, the route must cross during the defined period of 20 seconds. Circles were only detected using 2D criteria. The altitude attribute was not used.

Since the flight segments between the individual GPS positions are straight, the findings are essentially based on the calculation of the intersection point of two straight-line equations ($y = k * x + d$). The detected circles were stored together with the most important circle attributes in tabular and geometric form (line feature class).

Table 1: Recorded GPS-Logger attributes and derived attributes

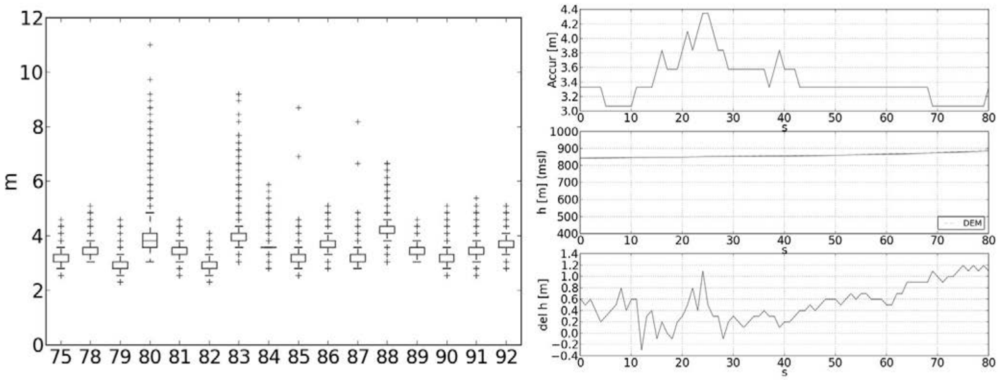
Description	**Recorded GPS-Logger Attributes**
Coordinates	x and y [decimal degree]
Altitude above the ellipsoid (WGS84)	h [m]
Horizontal flight speed (Groundspeed)	v [m/s]
Heading	[N: 0, 360 °]
Horizonal accuracy	Accuracy [m]
Timestamp	t
Description	**Derived Attributes**
Altitude corrected	h (msl) [m]
Delta h between two GPS-Points	Δh [m] ($\Delta h = h_t - h_{t-1}$)
Δh per Second and circle	Δh_{sec}
Max. and min. horizontal flight speed within a circle	v_{max}, v_{min}
Heading during v_{max}, v_{min}	$heading_{vmax}$, $heading_{vmin}$

Within a test setting we tried to estimate the horizontal and vertical accuracy of the GPS tags. The results showed that the horizontal accuracy of the GPS data is at its best within the range of about three meters (Fig. 2a). Two devices had a remarkably deviating accuracy (Fig. 2a, No 80, 83), both of them were installed on the microlight. It is possible that the paraglider blocked the satellite signal.

Regarding the vertical accuracy, the main focus was on the changing altitude during consecutive positons ($\Delta h = h_t - h_{t-1}$). It showed that the altitude change (Δh) remains relatively accurate as long as the accuracy calculated by the GPS loggers is stable. Fluctuations in the calculated accuracy score of the GPS logger are instantly mirrored by fluctuations in the parameter altitude and speed. Thus, changes in these parameters can be tested quite well during stable accuracy values. In Fig. 2b the amplitude of the oscillation of Δh (bottom graph) becomes smaller shortly after the fluctuation of the accuracy (top graph) decreases. Since in this study the focus is on the relative altitude change of the birds, slight inaccuracies regarding the absolute altitude are not essential.

In the examined flight sections, it was found that for the different individuals, the measured parameters resemble each other and change synchronously. For example, the birds often fly the same patterns in the soaring phase with similar vertical speed parameters (climbing values). Outliers usually occurred in the form of extreme Δh or v values and were filtered out if possible.

To link the GPS-Positions with wind data, we used the Movebank Track Annotation Tool (Dodge et al., 2013) with ERA-Interim-data from the European Centre for Medium-Range Weather Forecasts (http://www.ecmwf.int/; Dee et al., 2011).



(a) (b)

Fig. 2: (a) Accuracy of GPS logger at flight stage 3; Boxplot: upper and lower quartile, line: median, whiskers: 1,5 × IQR
(b) from top to bottom accuracy, altitude and Δh

3 Results

3.1 Characterization of the Flight Strategies

We compared two characteristic flight strategies which can be observed regularly during the migration flights of the NBI, the active formation flight and the use of upwash by soaring and gliding (Voelkl et al., in press). For the analysis, characteristic sequences for both flight strategies where chosen, both in the Po valley with flat underlying terrain almost at sea level. The soaring-gliding sequence was taken from the afternoon of the second flight stage, August 28th 2014 14:45 to 15:30 CET (Fig. 3b). The active flight sequence is in the morning of the third flight stage, August 30th 2014 9:00 to 9:30 CET (Fig. 3b).

During the soaring-gliding sequence in the early afternoon, the birds regularly used thermal upwash. During the 45-minute sequence, they performed six soaring phases. These soaring phases are characterised by a positive vertical speed (height increase; Fig. 4a) and a low and oscillating horizontal speed (ground speed Fig. 4a). Soaring phases often are made up of individual circles (Fig. 3a), with a mean of eleven seconds per circle. The mean vertical speed (height increase) during soaring was 1.7 m/s (min 0.75 m/s, max 1.94 m/s). The mean absolute height increase per soaring phase was 60 m (min. 22 m, max. 106 m). Soaring phases lasted for a mean of 57 seconds (min 17 s, max 96 s).

The soaring phase is followed by a gliding phase, which, in the narrow sense, is characterized by a comparatively higher horizontal speed (ground speed) and a negative vertical speed (height decrease). In the regarding sequence the mean horizontal speed (ground speed) was 17 m/s (max 26 m/s) and the mean vertical speed was –1.3 m/s (max –3.8 m/s). During such gliding phases the birds usually form a V-formation without flapping. This gliding phase turns into a phase with active flight, as described in the following paragraph. It lasts until the birds find another air column to start again with the soaring phase. Thus, the soaring-gliding flight contains three distinguishable, recurring phases - soaring, gliding and active flight.

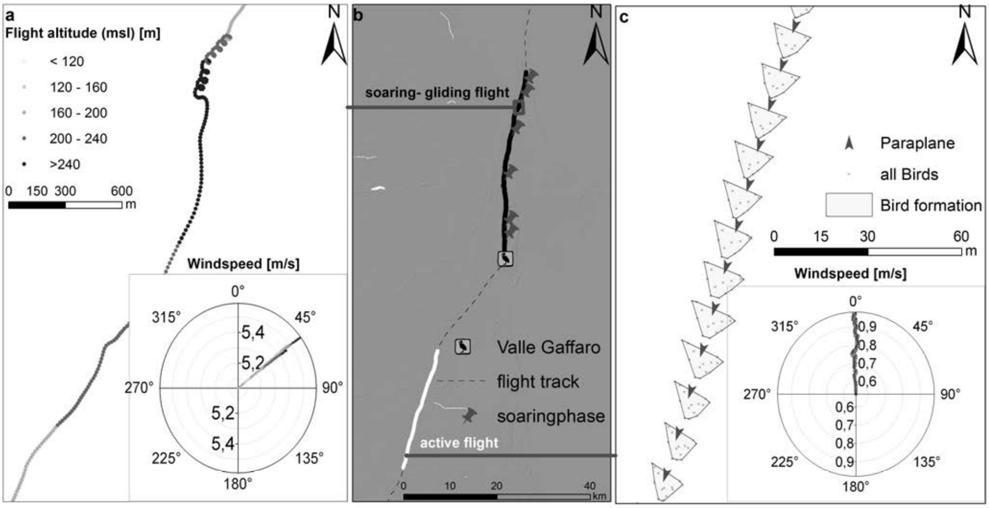


Fig. 3: Soaring-gliding phase (a); Active flight phase (b); Overview of Day 2 and 3 (c). Data source LIFE+ Northern Bald Ibis project; DEM: EU-DEM: Produced using Copernicus data and information funded by the European Union – EU-DEM layers.

During a characteristic active flight phase, the birds continuously head towards the destination, in our case SSW (Fig. 3b, c). In the regarding sequence, the mean horizontal speed (ground speed) was 14.7 m/s (Fig. 4b). The birds showed very low fluctuation of the vertical speed, as is characteristic for the soaring-gliding flight, apart from a slight continuous increase of the flight level during the 30-minute sequence (60 m, from 220 m to 280 m msl). According to previous studies with NBI the birds fly in a typically V-shaped formation (Portugal et al., 2014; Voelkl et al., 2015). The mean wing beat frequency during active flight is 3-4 beats/sec, with intermediate short gliding phases. (Fritz et al., 2008).

3.2 Comparison of the Flight Strategies

During the active flight, the flight route (26.4 km) almost equals the straight air-line distance towards the destination (26.2 km; Table 2). During the soaring-gliding flight, in contrast, the flight route (43.1 km) is 8 % longer than the air-line distance (39.9 km). This difference is presumably partly due to the birds' need to search for thermal and, to a lesser extend, due to the circling itself.

During the soaring-gliding flight the horizontal flight speed varies within a broad range (from 4 m/s to 26 m/s; Table 2, Fig. 4a) and in a periodic way, in accordance with the three phases described above, while during active flight the speed range is much lower (12 m/s to 17 m/s, Fig. 4b). Also, the vertical flight speed (altitude profile Fig. 4a) varies during soaring-gliding, with positive values during soaring (mean +1.7 m/s) and negative values during gliding (mean –1.3 m/s; Table 2), while during the active flight (altitude profile Fig. 4b) the vertical speed is usually close to zero. According to the differences in vertical flight speed, the flight altitude range varies between 224 m during the soaring-gliding sequence and 60 m during the active flight sequence.

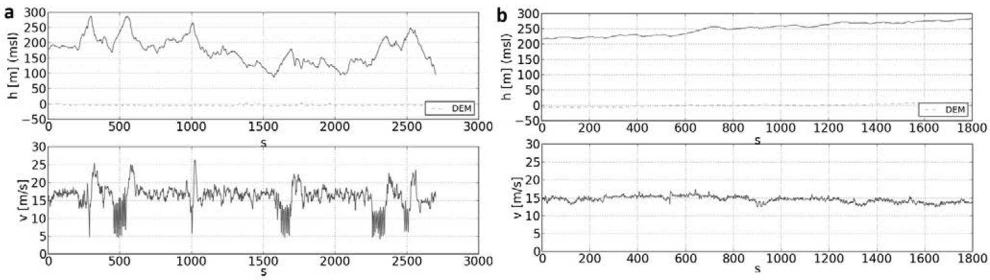


Fig. 4: Comparison of soaring-gliding flight (a) and active flight (b); upper graphs: flight altitude; lower graph: flight speed

Table 2: Comparison of the two flight strategies

Flight strategy	**Active flight**	**Soaring-gliding flight**
Flight route / air-line distance	26.4 km / 26.2 km	43.1 km / 39.9 km
Horizontal flight speed (min / max)	12 m/s / 17 m/s	4 m/s / 26 m/s
Vertical flight speed (min / max)	~ 0	–3.8 m/s / 1.94 m/s
Flight altitude range	60 m	224 m
Wind strength and direction (estimated supportive component)	0.7 m/s N (0.6 m/s)	5 m/s NE (4.8 m/s)
Mean horizontal speed along the air-line distance (corrected value)	14.67 m/s (~14 m/s)	14.55 m/s (~10 m/s)

The mean horizontal speed along the air-line distance of each sequence is quite similar, ranging between 14.67 m/s (active flight) and 14.55 m/s (soaring-gliding flight). However, it must be taken into account that the wind strength and wind direction differed during the two flight sequences (Fig. 3a, c). During the active flight sequence, the wind speed was low (mean wind 0.7 m/s N). In contrast, during the soaring-gliding sequence there was substantial wind (mean 5 m/s NE). During gliding flight and active flight the wind was supportive (tailwind) and during the soaring phase it caused a significant drift of the birds in the flight direction (Fig. 3a). The horizontal flight speed varies with the heading as well. When subtracting the estimated supportive wind component, the horizontal speed along the air-line distance during the active flight sequence (~14 m/s) was about 35 % faster compared to the soaring-gliding sequence (~10 m/s).

4 Discussion

On the basis of the previous dataset analysis, different flight strategies can be clearly revealed by the sampled data. The soaring flights, for instance, can be distinguished from the active and gliding flights by higher positive Δh as well as lower and oscillating horizontal flight speed. This result was also detected in research on the Golden Eagle by Katzner et al. (2016).

The reason why the birds lost flight altitude during the gliding phase at the second flight stage so quickly is not clear. During the gliding phases at the fourth flight stage, the birds also had a negative vertical speed and a higher groundspeed like during the active flight, but not in such an extent as during the second flight stage. One likely reason is that they wanted to catch up to the microlight because of an increasing gap after a more inefficient soaring phase by the microlight.

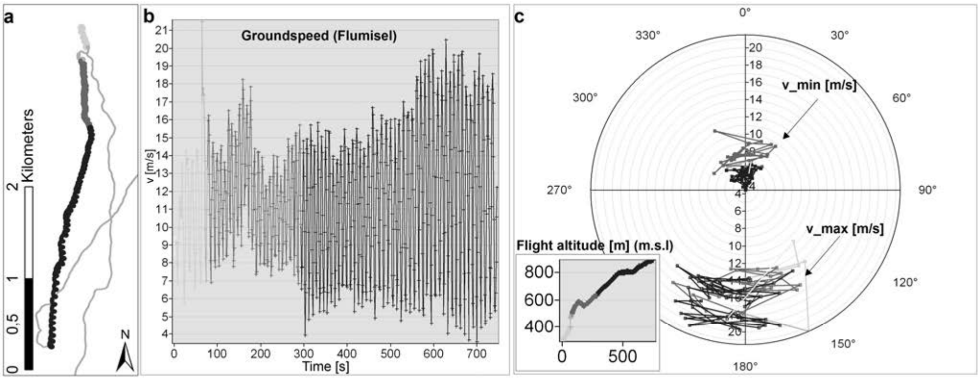


Fig. 5: A soaring phase (78 circles) of the single bird "Flumisel" at day 4; (a) flight route with an extended soaring phase; (b) oscillating ground speed during the soaring phase (colour gradation: flight altitude); (c) v_{max} and v_{min} within a circle differs with heading; Legend and flight profile. Data source: LIFE+ Northern Bald Ibis project.

The horizontal flight speed (ground speed) is a combination of the effects of different wind components with the actual flight speed. According to the dataset, the birds achieved a horizontal flight speed of about 14 m/s during the active flight. In earlier studies (Fritz et al., 2008) the horizontal flight speed was 12.5 m/s. It is difficult to estimate to what extent wind speed and direction influences the horizontal flight speed of the active flight. Also, the bird's lack of experience to fly in V-formation at the beginning of the migration could be a reason for the lower flight speed in 2008. The drift of the soaring phases (Fig. 5a; Fig. 3a) and different headings at v_{max} and v_{min} within the circles (Fig. 5c) are a clear indication of wind. Accurate wind data are often difficult to obtain. Also, the wind component varies with alternating flight level, which is of particular relevance during soaring. This can be seen in the changing wind drift during soaring, the oscillating speed depending on the heading and amplitude of this oscillation (Fig. 5a, b). The use of weather models, as done by Safi et al. (2013), may provide clues about horizontal and vertical winds.

Including data of a weather model from the European Centre for Medium-Range Weather Forecasts (http://www.ecmwf.int/) allows an explanation for the unexpectedly small difference in the mean flight speed during the soaring-gliding phase on the second flight day and the active flight phase on the third day. However, the wind data has a spatial resolution of 0.75 degrees and a temporal resolution of 6 hours (Dee et al., 2011), leading to uncertainties concerning wind speed and direction. Moreover, in a small mountainous environment like the Apennines, local winds on a small scale can differ substantially from modelled wind. Getting detailed wind information in combination with GPS datalogging will require further studies. Measuring head and tailwind directly on the microlight might be a feasible solution.

Parameters like the climbing and gliding rate vary strongly due to the atmospheric conditions. This can be seen during the fourth stage, when the birds flew alone and higher climbing rates were achieved (above Florence at 12:20 ECT mean 2.4 m/s max 3 m/s min 1.5 m/s). Furthermore the flight altitude above ground was apparently higher than in the former stages (up to 800 m near Florence). The difficult wind condition on that day makes it hard to interpret the fourth flight day so the data can only be used for comparison. Also, regarding the fact that the flight back to Borgo San Lorenzo took six times longer than the flight to the refuelling stop, it can be assumed that this flight was energy inefficient. Typical flight strategies can therefore not be explained with this part of the dataset.

Initial tests of the GPS loggers suggested accuracies for absolute spatial positions in the horizontal plane of ±3 m. These findings are in accordance with the often proclaimed accuracy of uncorrected GPS data of ±2.5 m. With such an accuracy it seems questionable whether estimates regarding fine-scale positional changes, as required for studying bird formation flight, can be made. However, as our discussion of time-changing parameters has shown, the GPS loggers provided data of sufficient accuracy and precision over substantial proportions of the flight. For example, in some examined flight sections it could be determined that the recorded parameters, like the change in altitude, change in the speed with the direction of flight and the altitude, are very similar for all examined birds. When the birds were flying in the circular series, they had closely matching climb rates at corresponding positions. In the case of strongly fluctuating accuracies, outliers usually appear in the form of extreme Δh or v values. Such outliers (compare Fig. 5b between 50 and 100 seconds) were filtered if possible. Studies of detailed proximity relations, will require GPS-Logger with a higher sample rate and accuracy.

In summary, the use of lightweight GNSS technology allows a series of new insights into flight behaviour and flight patterns of migrating birds. With the development of lightweight dataloggers a new era of bird-migration research has begun. So far, most research projects applying GNSS technology have focused on long-term data collection over periods of weeks to several months or years. The purpose of those studies was to gain new insights into large-scale movement patterns, though these long data logging periods come at the expense of temporal resolution (with positional fixes at hourly or daily rates, only). Here, we have investigated and demonstrated the potential of using GNSS technology for studying fine-scale movement behaviour of birds by recording positional data at a temporal resolution of 1 second or even higher. Taking such an approach allows us to investigate details of flight manoeuvres and flight strategies of free flying, migrating birds.

Literature

Bairlein, F., Fritz, J., Scope, A., Schwendenwein, I., Stanclova, G., van Dijk, G., Meijer, H. A. J., Verhulst, S., & Dittami, J., (2015). Energy Expenditure and Metabolic Changes of Free-Flying Migrating Northern bald ibis. *PLoS ONE, 10*(9). e0134433. doi:10.1371/journal.pone.0134433.

Dee, D. P., Uppala, S. M., Simmons, A. J., Berrisford, P., Poli, P., Kobayashi, S., Andrae, U., Balmaseda, M. A., Balsamo, G., Bauer, P., Bechtold, P., Beljaars, A. C. M., van de Berg, L., Bidlot, J., Bormann, N., Delsol, C., Dragani, R., Fuentes, M., Geer, A. J., Haimberger, L., Healy, S. B., Hersbach, H., Hólm, E. V., Isaksen, L., Kållberg, P., Köhler, M., Matricardi, M., McNally, A. P., Monge-Sanz, B. M., Morcrette, J.-J., Park, B.-K., Peubey, C., de Rosnay, P., Tavolato, C., Thépaut, J.-N., & Vitart, F. (2011). The ERA-Interim reanalysis: configuration and performance of the data assimilation system. *Q.J.R. Meteorol. Soc., 137*, 553–597. doi:10.1002/qj.828.

Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S. C., Kays, R., Douglas, D., Cruz, S., Han, J., Brandes, D., & Wilkelski, M. (2013). The Environmental-Data Automated Track Annotation (Env-DATA) System: Linking animal tracks with environmental data. *Movement Ecology*, *1*(3). doi:10.1186/2051-3933-1-3.

Fritz, J. (2010). On the experimental introduction of migratory Northern Bald Ibis colonies. In: C. Böhm, & C. G. R. Bowden (Eds.), *Proceedings of the International Advisory Group for the Northern Bald Ibis (IAGNBI) meeting Palmyra, Syria 2009* (pp. 62–68). Sandy, Beds: Royal Society for the Protection of Birds.

Fritz, J., Dietl, J., Kotrschal, K., Bairlein, F., & Dittami, J. (2008). Flugstilanalysen bei ziehenden Waldrappen. *Vogelwarte, 46,* 350–351 (Proceedings der DOG Tagung 2008 Bremen).

Fritz, J., Hoffmann, W., & Unsöld, M. (2016). Back into European ecosystems: the LIFE+ northern bald ibis reintroduction project in central Europe. In: C. Böhm, & C. G. R. Bowden (Eds.), *Proceedings of 4th International Advisory Group for the Northern Bald Ibis (IAGNBI) meeting Seekirchen, Austria, August 2016*, (pp. 47–56). Sandy, Beds: Royal Society for the Protection of Birds.

Fritz, J., Kramer, R., Hoffmann, W., & Unsöld, M. (in press). Project LIFE+ Reason for Hope: The reintroduction of the Northern bald ibis Geronticus eremita in central Europe. *International Zoo Yearbook 2017*.

Fritz, J., & Unsöld, M. (2015). Internationaler Artenschutz im Kontext der IUCN Reintroduction Guidelines: Argumente zur Wiederansiedlung des Waldrapps Geronticus eremita in Europa. *Vogelwarte, 53*, 157–168.

Katzner, T. E., Turk, P. J., Duerr, A. E., Miller, T. A., Lanzone, M. J., Cooper, J. L., Brandes, D., Tremblay, J. A., & Lemaitre, J. (2015). Use of multiple modes of flight subsidy by a soaring terrestrial bird, the golden eagle Aquila chrysaetos, when on migration. *Journal of The Royal Society Interface, 12*. doi:10.1098/rsif.2015.0530.

Pavlis, N. K., Holmes, S. A., Kenyon, S. C., & Factor, J. K. (2012). The development and evaluation of the Earth Gravitational Model 2008 (EGM2008). *J. Geophys. Res, 117*. doi:10.1029/2011JB008916.

Portugal, S. J., Hubel, T. Y., Fritz, J., Heese, F., Trobe, D., Voelkl, B., Hailes, S., Wilson, A. M., & Usherwood, J. R. (2014). Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature, 505*, 399–402. doi: 10.1038/nature12939.

Safi, K., Kranstauber, B., Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., Cruz, S., Proano, C., Takekawa, J. Y., Newman, S. H., Waldenström, J., Bengtsson, D., Kays, R., Wikelski, M., & Bohrer, G. (2013). Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight. *Movement Ecology 1*(4). doi:10.1186/2051-3933-1-4.

Schenker, A. (1977). Das ehemalige Verbreitungsgebiet des Waldrapps Geronticus eremita in Europa. *Orn. Beob., 74*, 13–30.

Voelkl, B., & Fritz J. (in press). Relation between travel strategy and social organization of migrating birds with special consideration of formation flight in the northern bald ibis. *Philosophical Transactions of the Royal Society B.*

Voelkl, B, Portugal, S. J., Unsöld M., Usherwood J. R., Wilson A. M., & Fritz, J. (2015). Matching times of leading and following suggest cooperation through direct reciprocity during V-formation flight in ibis. *Proceedings of the National Academy of Sciences 112*(7), 2115–2120. doi:10.1073/pnas.1413589112.