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The challenges of the first migration: movement and behaviour of juvenile vs. adult white storks with insights regarding juvenile mortality

Shay Rotics[1]*, Michael Kaatz[2], Yehezkel S. Resheff[1,3], Sondra Feldman Turjeman[1], Damaris Zurell[4], Nir Sapir[5], Ute Eggers[6], Andrea Flack[7,8], Wolfgang Fiedler[7,8], Florian Jeltsch[6,9,10], Martin Wikelski[7,8] and Ran Nathan[1]

[1]Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel; [2]Vogelschutzwarte Storchenhof Loburg e.V., Chausseestr. 18, D-39279 Loburg, Germany; [3]Edmond and Lily Safra Center for Brain Sciences, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel; [4]Dynamic Macroecology, Department Landscape Dynamics, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland; [5]Department of Evolutionary and Environmental Biology, The University of Haifa, 3498838 Haifa, Israel; [6]Plant Ecology and Conservation Biology, Institute for Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, 14469 Potsdam, Germany; [7]Department of Migration and Immuno-Ecology, Max-Planck-Institute for Ornithology, D-78315 Radolfzell, Germany; [8]Department of Biology, University of Konstanz, D-78468 Konstanz, Germany; [9]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), D-14195 Berlin, Germany; and [10]ZALF, Leibniz-Centre for Agricultural Landscape Research, Eberswalder Str. 84, D-15374 Müncheberg, Germany

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Summary

1. Migration conveys an immense challenge, especially for juvenile birds coping with enduring and risky journeys shortly after fledging. Accordingly, juveniles exhibit considerably lower survival rates compared to adults, particularly during migration. Juvenile white storks (*Ciconia ciconia*), which are known to rely on adults during their first fall migration presumably for navigational purposes, also display much lower annual survival than adults.

2. Using detailed GPS and body acceleration data, we examined the patterns and potential causes of age-related differences in fall migration properties of white storks by comparing first-year juveniles and adults. We compared juvenile and adult parameters of movement, behaviour and energy expenditure (estimated from overall dynamic body acceleration) and placed this in the context of the juveniles' lower survival rate.

3. Juveniles used flapping flight vs. soaring flight 23% more than adults and were estimated to expend 14% more energy during flight. Juveniles did not compensate for their higher flight costs by increased refuelling or resting during migration. When juveniles and adults migrated together in the same flock, the juvenile flew mostly behind the adult and was left behind when they separated. Juveniles showed greater improvement in flight efficiency throughout migration compared to adults which appears crucial because juveniles exhibiting higher flight costs suffered increased mortality.

4. Our findings demonstrate the conflict between the juveniles' inferior flight skills and their urge to keep up with mixed adult–juvenile flocks. We suggest that increased flight costs are an important proximate cause of juvenile mortality in white storks and likely in other soaring migrants and that natural selection is operating on juvenile variation in flight efficiency.

Key-words: flight, flight efficiency, juvenile mortality, migration, white stork

Introduction

Long-distance migration presents significant challenges to the individual with consequences for population

*Correspondence author. E-mail: shay.rotics@mail.huji.ac.il

dynamics. In many migrating bird species, juveniles in their first year exhibit considerably lower annual survival rates compared to adults (Schaub & Pradel 2004; Menu, Gauthier & Reed 2005; Strandberg *et al.* 2010; Sergio *et al.* 2011; Guillemain *et al.* 2013). The migration period is considered a critical phase of annual survival (Newton 2006) with increased mortality during migration compared to stationary periods (Owen & Black 1989; Sillett & Holmes 2002; Strandberg *et al.* 2010; Klaassen *et al.* 2014; Lok, Overdijk & Piersma 2015) and juveniles in particular suffer higher mortality during the strenuous journeys (Owen & Black 1989; Menu, Gauthier & Reed 2005; Strandberg *et al.* 2010; Sergio *et al.* 2014). With the advance of biologging techniques, we are now able to collect and process data in unprecedented amount and detail which raises the opportunity to study survival as a consequence of the individual behaviour. Here, we demonstrate that investigating age-related differences in movement and behaviour during migration helps elucidate potential causes for juvenile mortality in migrating birds.

Previous bird studies showed that migrating juveniles have lower navigation capacity (Perdeck 1967; Thorup *et al.* 2007; Mueller *et al.* 2013), higher sensitivity to adverse weather (Owen & Black 1989; Thorup *et al.* 2003; Sergio *et al.* 2014), shorter wings and higher wing-loading (Perez-Tris & Telleria 2001; de la Hera, Pulido & Visser 2014) and competitive foraging inferiority (Heise & Moore 2003; Skorka & Wojcik 2008; Beron *et al.* 2011). In line with that, juveniles spend more time than adults at stopovers (Hake, Kjellen & Alerstam 2003; Mellone *et al.* 2013; Peron & Gremillet 2013; McKinnon *et al.* 2014). In some species, migration route and scheduling differed with age, generally converging over time with adults exhibiting a more efficient journey (Hake, Kjellen & Alerstam 2003; Mueller *et al.* 2013; Sergio *et al.* 2014). However, for a general understanding of age-related migratory differences, their underlying mechanisms and implications for survival, more biologging studies that enable researchers to compare whole migration tracks are needed. This is especially true for species that migrate in mixed flocks of juveniles and adults, such as geese and storks (Schuz 1950; Chernetsov, Berthold & Querner 2004; Menu, Gauthier & Reed 2005), for which age-related differences in navigational skills or routes are irrelevant.

In this study, we examined the patterns and potential causes of age-related (first-year juveniles vs. adults) differences in movement, behaviour and energy expenditure of migrating white storks. We used a multifaceted approach and unprecedented data of high temporal resolution and placed this comparative analysis in the context of juvenile stork annual survival which is considerably lower than that of adults (33% vs. 83%, respectively; based on ringing data from an area that contains our study site, Schaub, Kania & Koppen 2005). White storks migrate over 6000 km from Eurasia to Africa, mostly by soaring in thermal uplifts and gliding to the next thermal (Leshem & YomTov 1996; Berthold *et al.* 2001). Using advanced GPS-tracking technology, we recorded the storks' locations and body acceleration (ACC) to deduce behaviour and calculated overall dynamic body acceleration (ODBA) to estimate energy expenditure (Halsey *et al.* 2008; Nathan *et al.* 2012). We used these data to compare movement metrics, stopovers, behaviour during flight and on the ground (foraging and preening) between juveniles and adults while accounting for key environmental factors such as wind and thermal uplift. In addition, we focused on cases when tagged juveniles and adults flew together in the same flock to assess the position of juveniles relative to that of adults. We hypothesized that juvenile storks, being less experienced in flight and foraging, would exhibit less efficient flight (higher flapping/gliding ratio and consequently higher flight energy expenditure), forage less effectively (spend more time foraging and exhibit lower pecking success rate) and thus spend more time at stopover sites. Under the working hypothesis that adult storks outperform juveniles in terms of survivorship during migration, we further examined the role of age-related differences to explain juvenile mortality. Here, we focused on white storks flying along the eastern flyway, from Germany through the Middle East to Africa (Fig. 1) during the fall migration (August to September).

Materials and methods

BIRD TAGGING

From 2011 to 2013, we fitted solar-charged GPS/ACC transmitters (e-obs GmbH, Munich, Germany) to 62 adult and 64

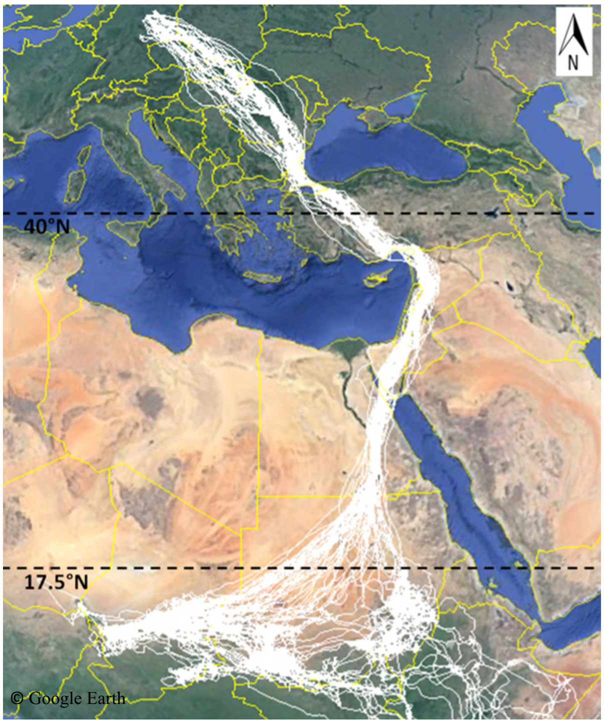

Fig. 1. Fall migration tracks of white storks ($n = 59$). Latitudes of relevance for the data analysis are marked (see 'Materials and methods').

juvenile white storks in Germany (see Appendix S1, Supporting Information, for trapping methods). We worked at three study sites: in the vicinity of Beuster (52·939° N, 11·787° E), Loburg (52·118° N, 12·087° E) and the Drömling Nature Park (52·489° N, 11·022° E). The transmitters were attached in a backpack design with a harness made of nylon string threaded through a Teflon sleeve (weight of the harness: 12 g). We used different transmitter types for adults and juveniles (see Appendix S1) that weighed 43 and 54 g, respectively, and had minor shape differences (Fig. S3). The body mass of adults and juveniles (2 weeks before fledging) did not differ and was 3·38 ± 0·35 kg (mean ± SD). Thus, the maximal total weight of transmitter plus harness was ca. 2% of the storks' weight, which is below the recommend threshold for wildlife tracking (Kenward 2001). We believe that the extra 11 gram load carried by the juveniles, which is equivalent to 0·3% of their body mass, had negligible effects on age-related flight differences described later in the manuscript, as it was much below natural variances in individuals' weight (see Appendix S1 for further explanations). After the transmitter was attached, the birds were immediately released (*c.* 30 minutes after capture). Field observations revealed that the transmitters remained in the same position for years after tagging, and we did not observe cases in which they impeded the bird's foraging or flight behaviour.

DATA SAMPLING

The transmitters recorded GPS locations (50% of the points are within 3·6 m from the true location) and ground speed between 2·00 and 20·00 GMT and tri-axial ACC between 3:00 and 19:00 GMT (for more technical details, see Nathan *et al.* 2012). GPS location and speed were recorded every 5 min when solar recharge was high (ca. 95% of the time), and otherwise every 20 min. ACC was recorded every 5 min for 3·8 s at 10·54 Hz for each of the three perpendicular axes, totalling 120 data points from each ACC sample. Data were stored onboard the transmitter and were downloaded via a UHF radio link from *c.* 300 m (see Appendix S1 for details). The transmitters of the juveniles had an additional Global System for Mobile Communications (GSM) unit that sent two short text messages (SMS) per day (limited to areas of cellular coverage) with five GPS locations of 1-h intervals in each SMS. This yielded low-resolution data compared to the high-resolution data downloaded by UHF. The SMS enabled us to locate the juveniles for UHF data download, detect mortality and retrieve the transmitters of deceased juveniles (see Appendix S1).

ESTIMATING ENERGY EXPENDITURE AND BEHAVIOURAL MODES FROM ACC DATA

The basic body acceleration data (in millivolts) were transformed to acceleration (ms^{-2}) units using tag-specific calibration values obtained prior to tag deployment. For each ACC sample, we calculated the ODBA value, a valid estimator for energy expenditure (Halsey *et al.* 2008; Nathan *et al.* 2012), by subtracting each data point from a running average of 1-s on the relevant axis (10 data points), and summing the resulting absolute values across axes (see Nathan *et al.* 2012).

We used a supervised machine-learning algorithm (radial-basis-function kernel support vector machine) to classify the ACC records to behavioural modes (Nathan *et al.* 2012). The model was trained on 3815 ground-truthed ACC records of known behaviours and classified seven behavioural modes: active flight (flapping), passive flight (soaring or gliding), walking, pecking, standing, sitting and preening, with an overall accuracy of 92% (see Appendix S1 for details). Our classifier is available for use in an open-access web application (see Resheff *et al.* 2014).

INCORPORATING ATMOSPHERIC DATA

For each GPS point, wind and thermal uplift velocity (see Bohrer *et al.* 2012) were interpolated through the Env-DATA track annotation tool of MoveBank (Dodge *et al.* 2013; see Appendix S1). Tail and cross winds (absolute values of cross wind) were then calculated by projecting the wind on the instantaneous heading direction of the bird (acquired by the transmitter), as recommended by Safi *et al.* (2013).

THE DATA SET

We compared fall migration data obtained from juvenile (age < 1 year, $n = 42$) and adult (age > 2 years, $n = 40$) white storks which completed their migration from Germany to Africa along the eastern migration flyway (over the Middle East). Details on the remaining individuals ($n = 24$) are displayed in Table S1. Within the juveniles, 19 tracks were complete high-resolution tracks, and 23 were comprised of both high and low-resolution SMS-based data, depending on whether a UHF data download took place (see Appendix S1). Most comparisons were based on high-resolution data of 19 juveniles and 40 adults during 80 migration journeys (18 adults were tracked for more than one migration; see Table S2 for the number of individuals tracked per year). We distinguished between 'flight days' and 'stopover days'. Flight days were defined as having a daily displacement of more than 100 km to exclude days of stopover or minor net progression which are substantially different in terms of stork behaviour. All analyses, unless specified otherwise, were conducted on the flight days' data. The first day of migration was defined as the first flight day southwards (100–260°) from the breeding grounds, and the last day was when the bird crossed 17·5°N, since farther south the migration tracks split to different overwintering grounds (Fig. 1). Stopover days were defined as days with daily displacement of <30 km between 50° N and 17·5° N. For comparison, the average daily displacement of flight days was 273 ± 96 km.

BEHAVIOURAL AND MOVEMENT PARAMETERS

We separated flight records (>5 m s^{-1}) from ground records (<2 m s^{-1}) using the ground speed recorded by the transmitters. Based on the ACC classification, the following behavioural parameters were analysed (i) flapping ratio: flapping flight records/total flight records and (ii) relative foraging time: walking and pecking records/total on-ground records. We referred to walking as part of the foraging activity because storks catch prey while walking (Carrascal, Alonso & Alonso 1990; Bochenski & Jerzak 2006, our observation data showed that 76% of the pecking was during walking), and because storks typically fly rather than walk to cover short distances (S. Rotics, field observations). (iii) Pecking ratio: pecking records/walking and pecking records. (iv) Relative preening time: preening records/total on-ground records. Additionally, pecking success rate: successful pecking/total pecking was obtained for non-tagged juvenile and adults by conducting field observations (5 min each) during the migration (from Poland to Turkey). A successful peck was determined by succeeding swallowing beak movements.

Flight speed was defined as the instantaneous ground speed recorded during flight. Migration duration was defined as the number of flight days between the first and last days of migration. Flight height above ground was calculated by subtracting ground elevation (obtained from ASTER DEM data set, Dodge *et al.* 2013) and geoid height (the elevation difference between ellipsoid and geoid earth models obtained by Matlab function 'geoidheight') from the ellipsoid height recorded by the transmitter. Daily flight start was defined as the time of the first four consecutive flight records with a minimum displacement of 700 m between each. Similarly, end of daily flight was defined by the time of the last of four such records. Daily flight duration was defined as the time between daily flight start and end times omitting the time on the ground.

We compared migration onset between offspring and parents in nests where both carried transmitters and migrated in the eastern flyway. We had 12 such nests. For each, the average migration onset of offspring was compared to their parent. In one nest with two nestlings, both parents were tagged and we randomly matched offspring–parent pairs (based on the order of transmitters' serial numbers).

FLIGHT ODBA DYNAMICS THROUGHOUT THE MIGRATION

We examined whether juveniles' flight efficiency improved throughout the migration compared to adults. For this purpose, we calculated the slope of the linear regression of flight ODBA (daily average) against the accumulated travel distance (from the breeding ground) for each individual (Fig. S1) and compared juveniles and adults.

JOINT MIGRATION: JUVENILES AND ADULTS IN THE SAME FLOCK

We specifically focused on cases where a tagged juvenile and a tagged adult were migrating within the same flock (hereafter juvenile–adult pair). Joint migration flight days were defined when a juvenile and an adult were <0·5 km apart before 10·30 GMT, after 16·00 GMT and for more than 75% of the day, indicating a continuous spatial association of the individuals in this migration day [actual juvenile–adults average distance within these days was only 25 m (SD = 22)]. We extracted continuous joint flight days for 16 mutually exclusive juvenile–adult pairs (See Appendix S1), four of which were offspring and parent. Under the assumption that during their joint flight days, they were flying in the same flock, we aimed to investigate whether juveniles fly in the back of the mixed flocks by examining the flight order (who is ahead) between the tagged juvenile and adult. We compared juvenile–adult pairs of GPS fixes of <20 s difference and corrected for the time difference by linear interpolation. We determined who was ahead by comparing the distance to an arbitrary position, two kilometres ahead in the flight azimuth of the pair. We then calculated the number of records that the juvenile was ahead/total records, and the average distance between the adult and the juvenile (a negative value if the juvenile was ahead). We also examined which individual was left behind on the day the pair separated.

JUVENILE MORTALITY: 'SUCCESSFUL' VS. 'UNSUCCESSFUL' INDIVIDUALS

After comparing juveniles and adult storks, we further examined whether the resulting differences can be related to juvenile mortality by comparing 'successful' vs. 'unsuccessful' juveniles. 'Unsuccessful' juveniles were defined as those who died during migration ($n = 4$), or during the first month of overwintering ($n = 3$, with bird mortality occurring during September and October). 'Successful' juveniles ($n = 25$) accomplished their migration and survived beyond October. In order to compare tracks of equal lengths, while maximizing sample size, we based the comparison of 'successful' vs. 'unsuccessful' juveniles on high-resolution data of only the first third of fall migration (from breeding grounds to latitude 40°N), as opposed to all other analyses (Fig. 1, see Appendix S1 for explanations).

STATISTICAL ANALYSIS

The same family ID was assigned to all juveniles from the same nest as well as their parents (see Appendix S1 trapping methods), to account for their relation. We compared movement and behaviour variables (Figs 1 and 2, Table 1) by comparing averages per individual per migration journey between juveniles and adult storks using LMMs (fit by REML) and GLMMs (gamma distribution, log link function, unless specified otherwise). All mixed models in this manuscript were applied with the following random factors:

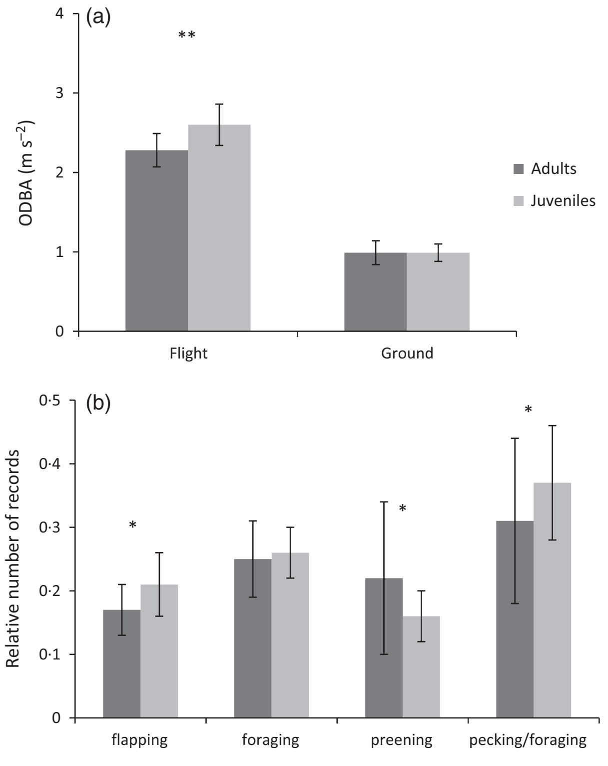

Fig. 2. Adults (n = 40) vs. juveniles (n = 19) comparisons of individuals' means (±SD) of: (a) ODBA (proxy for energy expenditure) during flight and on the ground. (b) Behavioural parameters of flapping ratio, relative foraging time, relative preening time and pecking/foraging ratio. $**P < 0{\cdot}001$, $*P < 0{\cdot}05$. See Table S3 for statistical details of the displayed comparisons.

Table 1. Summary of comparisons of adult (n = 40) vs. juvenile (n = 19) movement parameters during flight days in the fall migration

Parameter	Adults (mean ± SE)	Juveniles (mean ± SE)	$F_{1,78}$	P value
Daily displacement (km)	294·76 ± 4·02	271·39 ± 5·34	14·21*	<0·001
Flight speed (m s^{-1})	13·93 ± 0·09	13·21 ± 0·13	24·1	<0·001
Migration duration (flight days)	13·37 ± 0·22	14·84 ± 0·29	12·08*	0·001
Daily flight duration (h)	8·27 ± 0·05	8·14 ± 0·07	2·23	0·14
Daily flight start (GMT time)	7:00 ± 1·94.	7:03 ± 2·78	1·75	0·19
Straightness index	1·11 ± 0·00	1·11 ± 0·00	0·02*	0·88
Flight altitude above ground (m)	741 ± 9·26	738 ± 17·12	0·03	0·87

Parameter averages per migration journey (n = 80) were compared using LMM or GLMM (gamma distribution), using the later denoted by "*". For all models, fixed factor: age, random factors: individual, year and family ID.

Table 2. The effects of age and environmental factors on movement and flight variables of white storks during the fall migration (averages per stork, per migration journey, n = 80). Each row presents the estimated coefficients (β) of a linear mixed model with the factors listed in the table (d.f. = 1,75) plus three random factors: individual, year and family ID. Flapping ratio and daily displacement were transformed (box-cox) to normal distribution

Dependent variable	Age	Thermal uplift	Tailwind	Crosswind	Marginal R^2
Flight speed (m s^{-1})	−0·35**	−0·51	0·77**	−0·03	0·82
Daily displacement (km)	−10·24*	48·2	36·54**	−8·86	0·71
Flight ODBA (m s^{-2})	0·43**	−2·02**	0·07	0·08	0·46
Flapping ratio	0·35**	−2·85**	−0·03	0·18	0·26

*0·01 < $P \leq$ 0·05; **$P \leq$ 0·001.

individual, year and family ID. The exception is only the comparison of successful vs. unsuccessful juveniles in which *individual* was not included as random factor (juvenile data did not include more than one migration). We further examined age effects on movement and flight parameters while accounting for atmospheric effects using LMMs (Table 2) with predictors: age, thermal uplift, tail and cross wind (and the three random factors defined above). Goodness-of-fit of these LMMs was evaluated with marginal R^2 based on Nakagawa & Schielzeth (2013) using R 3.2.2 statistical software (R Core Team 2015) with lme4 package (Bates *et al.* 2015). We examined flight ODBA dynamics throughout the migration and tested the interaction between age class and accumulated travel distance on daily flight ODBA (Fig. 3) using a generalized linear mixed model (GLMM, gamma distribution, log link function) with predictors: age*travel distance, age, travel distance, thermal uplift, tail and cross wind, the same random factors as above, and with weights to account for individual differences in number of flight days. We applied the mixed models using Matlab statistics toolbox (R2013b; The MathWorks, Inc., Natick, MA, USA) and SPSS (version 21; IBM Corp, Armonk, NY, USA). The statistical analyses were tested with a critical α of 0·05, and their results are reported by their mean ± standard error, unless specified otherwise.

Results

Most analyses were based on 5-min resolution data from 19 juveniles and 40 adults consisting of a total of 279 875 data records from 1311 flight days during 80 migration journeys.

ENERGY EXPENDITURE AND BEHAVIOUR

Juvenile storks had significantly higher flight ODBA and flapping ratio than adults (Fig. 2) implying that their flight is energetically more costly. ODBA on the ground and the proportion of time spent foraging did not differ between the age classes (Fig. 2). However, while foraging, juveniles displayed higher pecking ratio (Fig. 2b) which could have opposing explanations: (i) juveniles' better prey detection or (ii) juveniles' lower success in prey capture. The latter explanation is supported by our field observation findings of juveniles' lower pecking success rates (0·38 ± 0·068, n = 13) compared to adults (0·57 ± 0·071, n = 11, $t_{\text{one-tail}}$ = 1·87, d.f. = 22, P = 0·038). Additionally, we examined the preening activity and found that juveniles spent less time preening their feathers compared to adults (Fig. 2b).

MOVEMENT

Juvenile storks progressed slightly but significantly slower than adults during the fall migration: their daily displacement distance was shorter, average flight speed was lower, and number of flight days was higher (Table 1). No differences in daily flight duration or daily flight start time were found between juveniles and adults (Table 1). Also mean daily straightness index (daily distance/daily displacement) and mean daily flight altitude did not differ between the age classes (Table 1). In nests where both offspring and their parents carried transmitters, the juveniles started migrating 6 days earlier than their parents (paired t-test, t = 2·554, d.f. = 12, P = 0·026). Stopover days were infrequent during fall migration: 71% of the individuals did not stop for a day at all, and 13% stopped for only 1 day, with no differences between juveniles and adults (Wilcoxon rank test, z = 0·29, n = 90, P = 0·77).

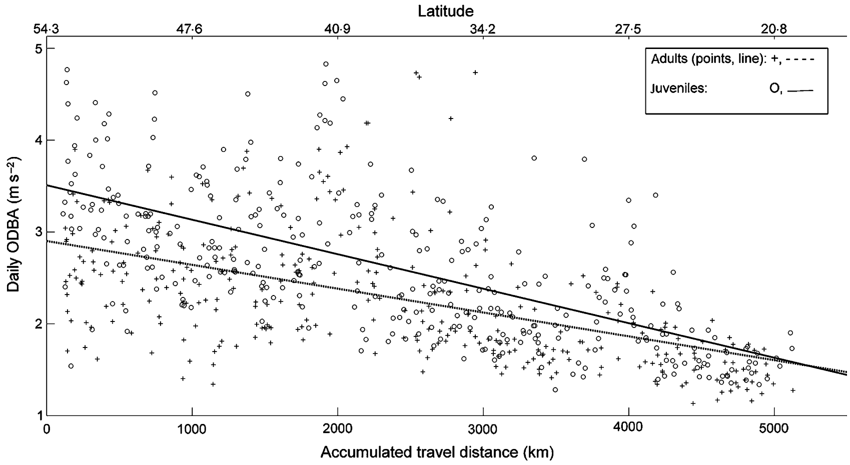

Fig. 3. Changes throughout the migration in daily averages of flight ODBA. The lower axis displays the accumulated migration distance (from breeding ground) and the corresponding latitudes are on the upper axis. Each point represents the daily average of flight ODBA. The regression line of the juveniles (generated by averaging the individual regressions, Fig. S1) has a significantly steeper slope than that of the adults. ODBA, overall dynamic body acceleration.

ACCOUNTING FOR ATMOSPHERIC EFFECTS

In accordance with the above results, juveniles migrated slower and exhibited higher flight ODBA and flapping ratio also after accounting for the significant effects of thermal uplift and wind (Table 2). Regardless of age, tail wind expedited the migration progress, whereas increased thermal uplift reduced migration effort (Table 2).

FLIGHT ODBA DYNAMICS THROUGHOUT THE MIGRATION

For each individual, we regressed daily averages of flight ODBA against accumulated travel distance (Fig. S1) and found that the juvenile regression slopes were significantly more negative compared to adults (mean slope: $-3{\cdot}76e^{-04} \pm 0{\cdot}28e^{-04}$ vs. $-2{\cdot}60e^{-04} \pm 0{\cdot}15e^{-04}$, respectively, $t = 3{\cdot}92$, d.f. = 57, $P < 0{\cdot}001$, Fig. 3). Thus, juvenile flight ODBA decreased throughout the migration at a higher rate compared to adults, such that towards the end of the migration, at latitude 18° N (Sudan), there was no difference in flight ODBA between the age classes (1·51 ± 0·07 vs. 1·49 ± 0·02, respectively; t-test with unequal variance, $t = 0{\cdot}34$, d.f. = 21·75, $P = 0{\cdot}74$). There was a positive relationship between accumulated travel distance and the thermal uplift velocity ($y = 0{\cdot}00015x + 1{\cdot}18$, $R^2 = 0{\cdot}46$, $P < 0{\cdot}001$, Fig. S2), with thermals becoming stronger as migration progressed south. This likely explains the decrease in flight ODBA throughout the migration in both age classes. Using GLMM (d.f. = 6, 1274), we found a significant interaction between accumulated migration distance and age class on daily flight ODBA ($F = 9{\cdot}7$, $P = 0{\cdot}002$, Fig. 3), even after accounting for the significant negative effects of thermal uplift ($F = 63{\cdot}2$, $P < 0{\cdot}001$), travel distance ($F = 286{\cdot}0$, $P < 0{\cdot}001$) and age ($F = 49{\cdot}0$, $P < 0{\cdot}001$), and the positive effects of wind (tailwind: $F = 6{\cdot}4$, $P = 0{\cdot}012$, crosswind: $F = 63{\cdot}3$, $P < 0{\cdot}001$). This analysis showed that the steeper decrease of juvenile flight ODBA throughout the migration was not derived solely from the effects of atmospheric conditions but genuinely resulted from age-related changes in flight performance throughout the migration.

JOINT MIGRATION: JUVENILES AND ADULTS IN THE SAME FLOCK

Focusing on cases where a tagged juvenile and a tagged adult migrated together in the same flock, we found that juveniles flew on average 21 ± 7 m behind the adults, which was significantly different from zero (one sample t-test, $t = 3{\cdot}03$, d.f. = 15, $P = 0{\cdot}008$). Correspondingly, juveniles flew behind the adults 63% ± 2% of the time, which was significantly different from 50% (one sample t-test, $t = 26{\cdot}3$, d.f. = 15, $P < 0{\cdot}001$). Within all pairs, while flying together, the juvenile exhibited higher flight ODBA than the adult (paired t-test, $t = 9{\cdot}3$. d.f. = 15, $P < 0{\cdot}001$) in line with our previous, more general, findings (Fig. 2a). The adult–juvenile pairs flew an average of 5·12 ± 0·6 days together before they separated. In 13 out of 14 recorded separation events, the juveniles were the ones who were left behind and progressed 61.5 ± 17·02 km less than adults (paired t-test, $t = 3{\cdot}37$, d.f. = 13, $P = 0{\cdot}003$) on the day of separation.

JUVENILE MORTALITY: 'SUCCESSFUL' VS. 'UNSUCCESSFUL' INDIVIDUALS

Juvenile survival is lower compared to adults (Schaub & Pradel 2004; S. Rotics, unpublished data). Since flight ODBA was the most prominent parameter differentiating between the age classes, we examined its relation to juvenile survival; we first verified that flight ODBA was a consistent trait of the individual, as indicated by its significant repeatability (Appendix S1) and then compared

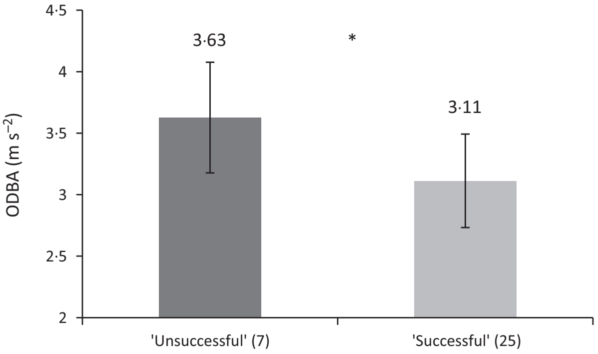

Fig. 4. Comparing flight ODBA (mean ± SD) between 'successful' vs. 'unsuccessful' juveniles based on tracking data from departure until 40° N (Turkey). Differences between the groups were statistically significant (GLMM, $F_{1,30} = 8{\cdot}23$, $^{*}P = 0{\cdot}007$). ODBA, overall dynamic body acceleration.

flight ODBA between 'successful' and 'unsuccessful' juveniles (see 'Materials and methods') during the first third of migration (prior to 'unsuccessful' juveniles mortality). We found that 'unsuccessful' juveniles showed significantly higher values of flight ODBA, that is spent more energy while flying, compared to 'successful' juveniles (Fig. 4). Further comparisons revealed no difference between these groups in thermal uplift conditions experienced *en route* (LMM, $F_{1,30} = 2{\cdot}83$, $P = 0{\cdot}1$) and in migration onset time (GLMM, $F_{1,30} = 0{\cdot}06$, $P = 0{\cdot}82$), nor in pre-migration flight experience, as deduced from the number of days ('unsuccessful': 17·9 ± 3·1, 'successful': 18·5 ± 1·5, LMM, $F_{1,30} = 0{\cdot}22$, $P = 0{\cdot}64$) and the total flight hours ('unsuccessful': 9·8 ± 2·43, 'successful': 11·23 ± 1·39, GLMM, $F_{1,28} = 2{\cdot}98$, $P = 0{\cdot}1$) from fledging time to migration onset. The ultimate mortality causes of the 'unsuccessful' juveniles were as follows: fatigue or illness (deduced from intact carcass, $n = 2$), hunting ($n = 2$) and three other cases in which we could only determine that the birds were neither hunted nor electrocuted (electrocution is a very common cause for stork mortality Schaub & Pradel 2004).

Discussion

The most prominent difference that was found between juvenile and adult storks during the fall migration was the higher energy expenditure of juveniles during flight, deduced from ODBA measurements. Nevertheless, juveniles did not spend more time at stopovers nor did they fly fewer hours per day, probably because of a strong motivation to keep up with the mixed adult–juvenile flocks (Chernetsov, Berthold & Querner 2004). These two conflicting factors acting on juvenile storks during their first migration are further discussed below, and the first evidence for the effects of flight costs on juvenile survival is provided.

As soaring-gliding migrants, white storks rely mostly on passive flight using thermal uplifts, which minimizes flight energetic costs (Leshem & YomTov 1996; Berthold *et al.* 2001). Juvenile storks expended 14% more energy during flight than adults due to more frequent use of costly flapping flight (based on ODBA data). These differences held true also after accounting for the significant effects of thermal uplift on flight effort and wind on flight speed. With only 12 h of pre-migration flight experience compared to the 8-h flight days during migration, lower flight experience of juveniles likely accounted for their less efficient flight. Additionally, while staging, juveniles spent less time than adults arranging their feathers which is expected to result in lower integrity of flight feather vanes (Gill 1995), also potentially contributing to the higher flight cost of juveniles. Juvenile passerines have shorter and rounder wings compared to adults (Perez-Tris & Telleria 2001; de la Hera, Pulido & Visser 2014) which enhance aerodynamic manoeuvrability but reduce flight efficiently. Yet, to our knowledge, there is no evidence of this in larger, soaring birds, and we could not examine this here. If age-related differences in wing-loading do exist in storks, this could potentially also contribute to the observed flight differences. However, the improvement in juvenile flight efficiency throughout migration (further discussed later) suggests it was not a major mechanism in our case. Less efficient juvenile flight was also recently reported for other avian migrants (Duerr *et al.* 2015; Mitchell *et al.* 2015); however, in contrast to our study, these differences were indirectly inferred from the bird tracks and the atmospheric conditions they experienced, rather than from body acceleration measurements.

Age-related differences in flight skills may be a prevalent feature in other birds and can explain observed differences in migratory behaviour of adults and juveniles. Previous studies showed patterns of longer stopovers taken by juveniles in soaring migrants (Hake, Kjellen & Alerstam 2003; Mellone *et al.* 2013; Peron & Gremillet 2013) and suggested explanations dealt mostly with differences in fat storage and hunting skills. We postulate age-related differences in flight cost as a potential cause for juveniles' longer stopovers, an explanation that has been neglected thus far. We further suggest that flight efficiency should be considered in addition to foraging and navigation skills for understanding age-related differences in migratory birds.

Juvenile storks did not compensate for higher flight costs by increased foraging activity outside the flight hours. Rather, our results imply lower rates of juvenile success in catching prey, as reported for other inexperienced avian predators (Heise & Moore 2003; Skorka & Wojcik 2008). Therefore, a migration flight day was more strenuous for a juvenile stork due to higher flight costs and an apparently lower energy intake. Furthermore, juvenile storks did not spend more time at stopovers than adults, unlike juveniles of other migrating species (Hake, Kjellen & Alerstam 2003; Peron & Gremillet 2013; Sergio *et al.* 2014), as all storks rarely stopped during the fall migration (except for the night roost). We postulate that the lack of increased stopover time for juvenile storks is derived from the impact of the flock.

Traditionally, white storks are obligatory social migrants where juvenile and adults migrate together in mixed flocks during the fall migration (Schuz 1950; Mayr 1952; Chernetsov, Berthold & Querner 2004). This is also supported, in our study, by the highly similar daily flight initiation times, flight durations, travel straightness indices and flight altitudes of both age classes and by the multiple adult–juvenile joint migration events. In manipulation experiments where juvenile storks migrated without adults, nearly all individuals did not reach their wintering grounds and showed poor navigational skills (Chernetsov, Berthold & Querner 2004). Similarly, three juvenile storks from our study that were observed alone in the fields in Europe, likely after failing to keep up with the flocks, did not migrate that year. Given their lower navigation capacity, juveniles likely have a strong motivation to keep up with the mixed flock, which precludes them from having longer stopovers compared to adults.

To our knowledge, this study is the first to elucidate a trade-off for juveniles between the advantages of social migration with experienced individuals (Mueller *et al.* 2013) and the physiological drawbacks of strenuous, nonstop migration with underdeveloped flight skills. Benefits gained by juveniles from migrating with experienced individuals include enhanced navigation (Thorup *et al.* 2007; Mueller *et al.* 2013), a critical factor for survival (Oppel *et al.* 2015), higher vigilance (Aviles & Bednekoff 2007) and better resource detection by adults (Maransky & Bildstein 2001; Yoda *et al.* 2011), although the latter may also entail costs of food competition. Geese and cranes even migrate in family groups, which could theoretically benefit juvenile storks as well, though presumably at the expense of fitness costs for the parents due to the extended nurturing period. Nevertheless, in many species, juveniles may carry out their first migration without adults (Marks & Redmond 1994; Newton 2008), and in such cases, they apparently benefit from longer stopovers (Hake, Kjellen & Alerstam 2003; Mellone *et al.* 2013). The presence of both strategies suggests that each has its adaptive benefits under specific circumstances. From an evolutionary perspective, it would be interesting to examine the relationship between endogenous vs. social navigation capabilities (Mueller *et al.* 2013) and the species' post-breeding migration strategy (mixed vs. separated age classes).

The above-mentioned trade-off was also supported in cases where a tagged juvenile and adult were recorded flying together in the same flock. The juvenile usually flew behind the adult at an average distance of 21 m and exhibited higher flight cost (ODBA), and at separation events, it was the juvenile which was nearly always left behind. We suggest that this illustrates the struggle of juveniles to keep up with adults in the flock in spite of their inferior flight skills, which results in juveniles increased flight effort. The juvenile–adult separation events, that occurred after an average of five joint flight days out of 15 flight days of migration, indicate that the juveniles did not keep up with the same flock for the whole migration journey but probably dropped back between following flocks. This sheds light on two of our results (i) It entirely suits our findings of a slightly slower migration of juveniles, which could not be explained if a juvenile and an adult were travelling together throughout the entire journey. (ii) It clarifies the adaptive value of earlier migration onset for juvenile storks compared to their parents. In a more general context, the average onset of juvenile fall migration in birds can be earlier, later or the same as that of adults (Newton 2008). It was suggested that adults migrate earlier in species that occupy territories in the wintering grounds (Hake, Kjellen & Alerstam 2003) and that moulting patterns affect migration onset order (Carlisle, Kaltenecker & Swanson 2005; Newton 2008). Our findings suggest that in species in which juveniles depend on adult guidance during migration it might be advantageous for juveniles to leave with early-departing flocks.

The energetic cost of flight did not remain constant throughout the migratory journey. Rather, it decreased for both juveniles and adults, which we primarily relate to an increase in thermal uplift, facilitating the soaring-gliding conditions, as migration progressed south to warmer latitudes. However, this decrease was steeper for juveniles, such that by the end of the journey, flight energy expenditure of juveniles and adults did not differ significantly. The steeper decrease in flight ODBA of the juveniles could not be explained by thermals or wind conditions; thus, we suggest that the juveniles learned to fly more efficiently and therefore improved their flight energy expenditure throughout the migration. More specifically, we believe this resulted from improved utilization of thermals, as was found in the griffon vultures *Gyps fulvus* (Roi Harel, unpublished data). Accordingly, atmospheric assistance was less effectively utilized by juveniles than adults in other species (Duerr *et al.* 2015; Mitchell *et al.* 2015), and soaring migrant black kites *Milvus migrans* showed improvement with age in their ability to cope with wind drift and to exploit tail winds (Sergio *et al.* 2014). Additionally, a developmental maturation throughout migration of body attributes, such as flight muscles (Bishop *et al.* 1996) may account for the juvenile improvement in flight and our findings cannot separate between a potential physiological mechanism and learning.

Flight efficiency improvement was apparently crucial as high flight energy costs were linked to juvenile mortality during their first migration. Juveniles that died during or just after the migration exhibited higher levels of flight energy expenditure compared to surviving juveniles. These non-surviving juveniles neither experienced less favourable weather conditions nor suffered from less pre-migration experience. We presume that being more exhausted by flight mediated their mortality during the migration or affected their subsequent mortality rates as a detrimental carry-over effect during the early wintering period. The fact that the ultimate mortality causes of the 'unsuccessful' juveniles included fatigue, hunting and possibly predation rather than electrocution (which is likely more coincidental) makes this presumption sensible. Bird mortality during migration is a large-scale phenomenon with implications on population regulation and presumably on evolutionary processes. Higher travel costs may well be one of the major factors mechanistically explaining the lower survival rates of juvenile storks (Schaub & Pradel 2004) and other soaring juveniles particularly during migration (Strandberg *et al.* 2010; Sergio *et al.* 2011). Sergio *et al.* (2014) found that young black kites that improved in coping with environmental conditions attained higher survival and breeding rates, and suggested that selection operated on improvement of migratory performance. Our results fit this notion and further pinpoint that natural selection was acting on the variance in juvenile storks' flight efficiency.

CONCLUSIONS

A thorough inspection of multifaceted migration properties, based on a very large data set, highlights the higher flight energy expenditure of juvenile white storks compared to adults. We argue that a fundamental conflict between the relatively poor flight skills of juvenile storks and their urge to fly with the adults in mixed-age flocks make the migration journey more strenuous for juveniles. Consequently, increased flight costs of juvenile storks were linked to lower survival. We hypothesize that high flight costs are a major, proximate cause of juvenile mortality in white stork and in other soaring migrants.

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Data accessibility

The GPS-ACC data are available in Movebank Data Repository (movebank.org) with doi:10.5441/001/1.hn1bd23k (Rotics *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. More details on the field work, transmitters and data analysis.

Table S1. Summary of tagged individuals.

Table S2. Number of tracks and individuals with high-resolution data of the whole migration per year.

Table S3. Summary of comparisons of adult ($n = 40$) vs. juvenile ($n = 19$) behavioral parameters during flight days in the fall migration.

Table S4. Confusion matrix for classifying the general behaviors (stage 1 of the classifier).

Table S5. Confusion matrix for classifying between walking and pecking (stage 2 of the classifier).

Table S6. Confusion matrix for classifying between standing and preening (stage 3 of the classifier).

Fig. S1. Changes in flight ODBA throughout the migration.

Fig. S2. Changes throughout the migration in thermal uplift velocity.

Fig. S3. Different transmitter types: on the left: GSM tag used for juveniles, on the right: UHF tag used for adults.