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Early-life behaviour predicts first-year survival in a long-distance avian migrant

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Early-life conditions have critical, long-lasting effects on the fate of individuals, yet early-life activity has rarely been linked to subsequent survival of animals in the wild. Using high-resolution GPS and body-acceleration data of 93 juvenile white storks (*Ciconia ciconia*), we examined the links between behaviour during both pre-fledging and post-fledging (fledging-to-migration) periods and subsequent first-year survival. Juvenile daily activity (based on overall dynamic body acceleration) showed repeatable between-individual variation, the juveniles' pre- and post-fledging activity levels were correlated and both were positively associated with subsequent survival. Daily activity increased gradually throughout the post-fledging period, and the relationship between post-fledging activity and survival was stronger in individuals who increased their daily activity level faster (an interaction effect). We suggest that high activity profiles signified individuals with increased pre-migratory experience, higher individual quality and perhaps more proactive personality, which could underlie their superior survival rates. The duration of individuals' fledging-to-migration periods had a hump-shaped relationship with survival: higher survival was associated with intermediate rather than short or long durations. Short durations reflect lower pre-migratory experience, whereas very long ones were associated with slower increases in daily activity level which possibly reflects slow behavioural development. In accordance with previous studies, heavier nestlings and those that hatched and migrated earlier had increased survival. Using extensive tracking data, our study exposed new links between early-life attributes and survival, suggesting that early activity profiles in migrating birds can explain variation in first-year survival.

1. Introduction

High juvenile mortality is a ubiquitous phenomenon across animal species, normally driven by natural selection and influencing population dynamics. It is difficult to detect why certain juveniles survive better than others, particularly among same-cohort juveniles that experience similar environmental conditions [1,2]. Nevertheless, investigating this variation in juvenile survival is imperative to understand the ecology of key life-history traits. The early-life period plays a significant role in affecting future survival by triggering long-lasting effects on individual morphology, skills and personality (the latter is also called temperament or behavioural type [3–5]). Correspondingly, it was shown that environmental conditions, parental care and juvenile attributes early in life bear fitness consequences far beyond the rearing period [3,6,7]. For example, in pheasant (*Phasianus colchicus*) chicks, the mere installation of elevated perches in rearing aviaries improved roosting behaviour, spatial memory and survival measured a year later, after release to the wild [5].

Previous bird studies have linked various nestling attributes to future survival probability [6,8–10], primarily highlighting the advantages of hatching early or having high body weight [7,11,12]. However, early-life behaviour, particularly during the pre- and post-fledging periods, has hardly been investigated as a predictor of subsequent survival, even though it probably encapsulates intrinsic (physical condition, personality) and extrinsic (environmental) early-life attributes and thereby may manifest variation in juvenile quality. Moreover, early-life activity is related to skill acquisition [5,13], which may be of particular urgency in migrating birds that face strong selection shortly after fledging, during their first migration journey [14–16]. Thus, migratory birds provide an excellent case study to investigate how early-life behaviours are linked with subsequent survival.

Here, we used high-resolution tracking to quantify individual differences in early-life behaviour in white storks (*Ciconia ciconia*) and to investigate their linkage to subsequent first-year survival. The white stork is a long-distance, Palaearctic migrant which typically breeds in Europe and overwinters in Africa. Mature stork nestlings were equipped with advanced GPS body-acceleration transmitters in Germany, and the acceleration measurements were translated to an activity proxy [17,18] and basic behavioural modes [15]. We focused on the pre-fledging period (the 10 days that preceded fledging), and the post-fledging period from fledging-to-migration onset (mean duration ± s.d.: 15.4 ± 8.7 days), wherein the juveniles become independent. For each period, we examined: (i) the individual average activity level and (ii) the individual activity-slope which indicates how quickly individuals increase their activity throughout the period, possibly reflecting the rate of behavioural development. Additionally, we examined the post-fledging (fledging-to-migration) period duration as an index for pre-migratory experience (e.g. in flight and foraging). By extracting these early-life parameters from the tracking data, we aimed to identify meaningful individual characteristics that would illuminate subsequent survival differences.

We hypothesized that early-life behaviour may reflect individual quality or acquired experience and could therefore explain subsequent survival. We predicted that individual average activity level, activity-slope and post-fledging duration would all have positive associations with first-year survival. First, activity was previously found to be positively correlated with physical condition [19], skill acquisition [13] and survival [20]. Moreover, being more active can be a consistent individual trait on the proactive-reactive personality axis [21,22], where more proactive temperament (being more bold, active and aggressive [22]) has been suggested to enhance juvenile survival in another white stork population [6]. Second, it has been shown that movement and activity increase gradually during the post-fledging period [23,24], presumably reflecting behavioural and locomotive development. Thus, a higher activity-slope may indicate faster behavioural development and possibly mark individuals of higher quality that are expected to have higher survival rates. Third, individuals with longer post-fledging periods are expected to acquire more experience prior to their first migration and, consequently, are more likely to survive this highly risky journey. Acknowledging that the above parameters might interact, we also examined their correlations and interactions. Lastly, we also tested the effects of nestling body weight, hatching and migration dates, sibling number and sex which were found to be pertinent survival predictors in previous studies [7,11,12,25].

2. Methods

(a) Tracking data

From 2011 to 2014, we fitted 93 solar-charged GPS transmitters (83 manufactured by e-obs GmbH, Munich, Germany, and 10 by Microwave Telemetry, Inc., MD, USA) to white stork nestlings in 50 nests, located in farmland areas scattered across different locations in the vicinities of Loburg, Beuster and Dromling in the state of Saxony-Anhalt, Germany (see [15] for more details). Prior to tagging, every three weeks, nestlings were observed from the ground and in some cases also using a drone, and based on these observations, we estimated their age. When they were roughly five to six weeks old, which is approximately two weeks before fledging, we went up to the nests using a cherry picker to fit the transmitters to the nestlings. The transmitters were fitted in a back-pack design and their maximal weight including the harness was 66 g, roughly 2% of the average nestling's weight (see [15] for more details). Microwave tags transmitted 2–4 GPS coordinates per day via satellite and e-obs tags transmitted 5–10 GPS fixes per day by SMS via cellular communication. The e-obs tags also recorded high-resolution GPS and body-acceleration data every 5 min from 2.00 to 20. 00 GMT, where the acceleration sampling rate was amplified to every 15 s during the time from tagging until *ca* one week after fledging. The tri-axial acceleration detection range is ±4.5 g (gravity; 9.81 m s^{-2}) with sensitivity of 0.0022 g, allowing for detection of even slight body movements. Each acceleration sample consisted of 3.8 s of recording at 10.54 Hz for each of the three perpendicular axes, totalling 120 acceleration measurements per acceleration sample. These high-resolution GPS-acceleration data could only be obtained via radio-link download at a maximal distance of about 300 m from the animal [15]. Consequently, we had two types of data: low-resolution GPS data (from satellite/SMS transmission) and high-resolution GPS-acceleration data from radio-link download. The latter could not be obtained for all birds for the entire tracking time since approaching the bird for data download was not always feasible. We had high-resolution data for 62 individuals during the pre-fledging period and for 63 during the post-fledging period (among them, we had data from 56 individuals for both periods).

(b) Early-life predictors of survival

Bird mortality was determined based on the GPS tracking data and its transmission patterns (see electronic supplementary material). We tested three sets of early-life parameters for their effects on first-year survival: activity parameters during the (i) pre-fledging and (ii) post-fledging periods, and (iii) attributes related to timing (including the post-fledging duration) and body condition.

(i) Pre-fledging activity

(i) Average activity level was estimated from the daily average of overall dynamic body acceleration (ODBA) [17] during the 10 days period prior to fledging time. ODBA reflects the extent of body movements and is considered a valid measure of

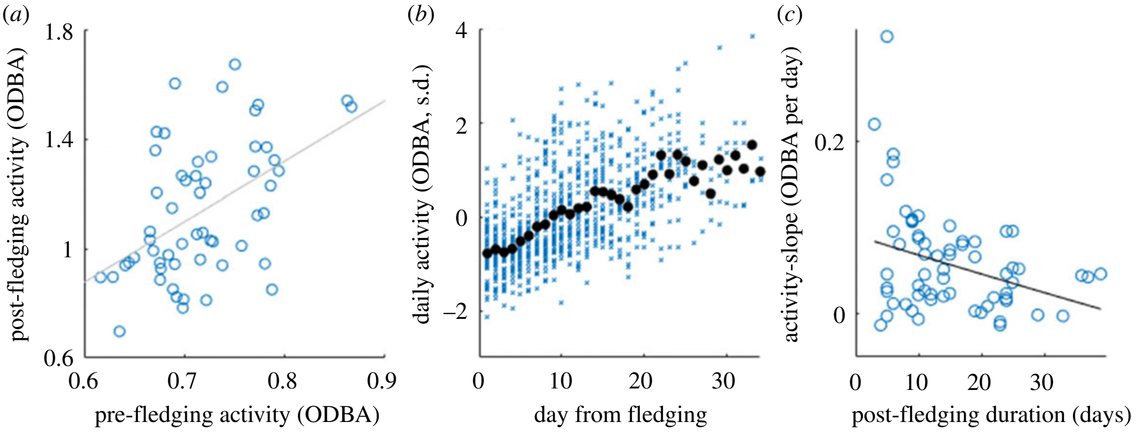

Figure 1. Associations between (*a*) post-fledging (fledging-to-migration) activity and pre-fledging activity, (*b*) daily activity and days since fledging and (*c*) activity-slope and post-fledging duration. (*a*) Individual pre-fledging activity was correlated to its activity during post-fledging period ($r = 0.49$, $p < 0.001$). (*b*) Each blue cross marks daily activity (mean ODBA) of an individual, transformed to a *z*-score using the individual's mean and s.d. (to display standardized rate of activity change between individuals with different activity levels). Black points denote daily means across individuals. There are fewer blue crosses per day with increasing day from fledging as fewer individuals had long post-fledging periods. (*c*) Negative association of activity-slope and number of post-fledging days ($p = 0.02$; statistical details are in electronic supplementary material, table S2). (Online version in colour.)

activity-related energy expenditure [17] and activity level [18,26]. For each body-acceleration sample, ODBA was calculated by subtracting each acceleration measurement from a running average of 1 s on each axis and summing the resulting absolute values across all axes. We also examined the activity-slope throughout the pre-fledging days, but it was not significantly different from zero (see Results) and thus was not included in the survival analyses (see below).

(ii) Post-fledging activity

(i) Average activity level was based on daily ODBA (as above) during the post-fledging period. (ii) Activity-slope denotes the slope coefficient of the increase in daily activity (mean ODBA) throughout the first 16 post-fledging days (afterwards, daily activity stabilized, figure 1*b*) calculated with a robust linear regression. (iii) Relative time foraging and flying is the proportion of daytime spent foraging or flying. Based on field observations on tagged storks, we collected 3815 ground-truthed body-acceleration records of known behaviours; these were used to train a supervised machine learning algorithm that classified seven main behavioural modes with 92% overall accuracy (behavioural modes: flapping, soaring/gliding, walking, pecking, standing, sitting and preening; see [15] for details). We then divided the number of records with foraging or flight behaviour (walking, pecking or flying) by the total number of records.

(iii) Early-life timing and body condition attributes

(i) Hatching date was estimated based on the bill length (see [27] for details). The bill length, as well as the weight and tarsus length (mentioned below), were measured once, when the nestlings were handled for transmitter fitting. (ii) Fall migration onset day is the first day with more than 100 km displacement southwards (azimuth 100–260°); after this day, the storks typically migrated continuously [15]. Hatching and migration dates were analysed as serial day of year numbered from 1 January. (iii) Post-fledging duration is the number of days from fledging-to-migration onset, where fledging date was defined as the first of two consecutive days in which the juvenile spent more than 5% of the tracking time (approx. 1 h) outside the nest (greater than 50 m). (iv) Relative body weight is weight in relation to size, evaluated using the residual of a linear regression of body weight as a function of tarsus length ($\text{weight} = -0.96\ \text{kg} + 0.19 \times \text{tarsus-length}$, $F_{1,92} = 64.32$, $R^2 = 0.41$, $p < 0.001$). (v) Estimated hatching order takes the bill length as an ordinal variable between nestlings (1 assigned to the longest), which presumably reflect hatching order [27]. (vi) Number of fledglings (siblings) in the nest during transmitter fitting was noted. (vii) Sex was based on molecular sex determination method (electronic supplementary material). The low-resolution data were sufficient for obtaining these early-life attributes of the juveniles ($n = 83$).

(b) Survival analysis

We used the Cox proportional hazard (CPH) models to link first-year survival with the above early-life attributes (using the 'coxme' R package; [28]). CPH models estimate predictors' effects on the time span until mortality by modelling the hazard ratio, also called mortality odds. A positive regression coefficient (β) of a predictor means that mortality odds increase with this predictor and vice versa; the hazard ratio ($\exp^{\beta}$) describes the change in mortality odds (in relation to the baseline conditions) in response to a one unit increase in the predictor value.

The dependent variable in our survival analysis was the number of days the individual survived during its first year, starting from migration onset. Individuals that did not die during the first year ($n = 18$) were included in the survival analysis as censored individuals, and individuals with transmitters that malfunctioned (microwave satellite tags that stopped transmitting, $n = 3$) were also included as censored with the tag failure time. Individuals that died or whose tag failed prior to migration onset ($n = 3$, $n = 1$, respectively) were omitted from the analyses. Six individuals that stayed to overwinter in Europe were also excluded as they faced very different conditions and behaved differently during their first year of life compared to the majority that migrated to Africa [29]. Finally, nine individuals that had less than 10 pre-fledging days of data as they fledged shortly after tagging were not included in the pre-fledging activity versus survival analysis (see below).

Three survival analyses were conducted separately on the post-fledging duration, post-fledging activity and pre-fledging activity parameters. This was necessary because each of them relied on different data resolutions which were available for a different subset of individuals, because separating the analyses mitigates the problem of over-fitting [30], and because post-fledging duration and post-fledging activity were correlated as well as post- and pre-fledging activity (see Results). Following the above-mentioned predictor sets, we first analysed the effects on survival of the early-life timing and body condition attributes ($n = 83$), then of the post-fledging activity parameters ($n = 63$), and lastly of the pre-fledging activity ($n = 62$). The predictors migration onset and relative body weight, which were found significant among the early-life timing and body condition attributes in the first analysis, were added to the models of the later analyses of the activity-related parameters (see electronic supplementary material, table S1 for details on all predictors per analysis). Second-order effects (quadratic terms) were tested for all non-categorical predictors. Following preliminary data exploration, we also tested the interaction between post-fledging activity parameters (activity level and relative time foraging and flying) and activity-slope, and predictors that took part in this interaction were standardized (to s.d. from the mean) to reduce multicollinearity and enhance interpretability [31,32]. For each survival analysis, we report the results of the best model (lowest AICc score) after comparing all predictor subset combinations, with the restriction that correlated predicators ($|r| > 0.5$) were not included in the same subset (see electronic supplementary material, table S1, for details). Model selection was applied using the 'dredge' function in R package MuMIn [33], and selection details per analysis are provided in electronic supplementary material, tables. Proportional hazard assumption was verified with scaled Schoenfeld residuals (using the 'cox.zph' function in the R package 'survival' [34]). We reported pseudo-R^2 for integral CPH models based on Cox & Snell [35] using the number of uncensored observations [36].

(c) Additional statistical notes

Correlations between parameters were examined by calculating Pearson's r and evaluating its significance using a random permutation test with 2000 iterations, to accommodate variables that are not distributed normally. In all CPH and generalized linear mixed models (GLMMs; see below), *brood ID* and *year* were included as random factors, unless specified otherwise. The linear increase in daily activity was assessed with an LMM, for which marginal R^2 was calculated based on Nakagawa & Schielzeth [37] using the R package MuMIn [33].

To understand individual variation in both pre- and post-fledging activity, we tested for between-individual consistency (repeatability) in daily activity (details below) and investigated the relationships of activity with relative body weight and with metrics of parental care (parents' provisional effort and the relative time fledglings were escorted by parents outside the nest, see electronic supplementary material). Repeatability in daily activity between individuals was tested by calculating repeatability (intra-class correlation) of individual daily activity using the 'rptR' package [38], where the grouping factor was the *individual ID* (in an LMM model that included the fixed factors: day number from fledging and daily temperature, and random factors: individual ID and year). Similarly, consistency in activity within broods was tested by calculating the repeatability of average activity between brood mates (grouping factor: *brood ID* in an LMM model that included the fixed factor: post-fledging duration and random factors: brood ID and year). Mean ± s.e. are reported unless specified otherwise. Data were processed and analysed using MATLAB (R2016a; The MathWorks, Inc., Natick, MA, USA) and R [39].

3. Results

(a) Pre- and post-fledging activity

We found repeatable between-individual variation in daily activity (daily mean ODBA) both during the pre-fledging and the post-fledging periods (repeatability = 0.43 and 0.30, respectively, $p < 0.001$). In addition, the individual pre-fledging activity and post-fledging activity were positively correlated (figure 1*a*; $r = 0.49$, $n = 56$, $p < 0.001$). Post-fledging activity (mean ODBA) was positively correlated with the relative time spent foraging and with distance travelled during post-fledging, as well as with post-fledging duration (electronic supplementary material, figure S1), but not with post-fledging activity-slope ($r = 0.19$, $n = 63$, $p = 0.13$, see below).

The origins of individual differences in activity were not clear: activity, both during pre-fledging and post-fledging periods, was not linked to relative body weight as a nestling or to the study year (GLMM with gamma distribution and log link; $p > 0.30$). Moreover, for 41 juveniles in our study, we also obtained GPS-acceleration data of at least one parent, but no relationship was found between parental provisioning effort and offspring pre-/post-fledging activity, nor between the proportion of time the fledgling was escorted by its parents while outside the nest and its post-fledging activity (electronic supplementary material). However, juvenile activity was consistent among brood mates (repeatability among brood mates in pre-fledging activity = 0.36, in post-fledging activity = 0.62; $p \leq 0.01$).

There was no significant increase in daily activity throughout the 10 pre-fledging days ($\beta = 0.002 \pm 0.001$, $t_{611} = 1.76$, $p = 0.08$; LMM with random factors: individual and brood ID). Contrarily, daily activity increased throughout the post-fledging period (figure 1*b*; $\beta = 0.04 \pm 0.001$, $t_{949} = 30.42$, $p < 0.001$, marginal $R^2 = 0.47$; LMM with random factors as above), and the slope of this increase, termed activity-slope, was negatively associated with post-fledging duration (together with hatching day, electronic supplementary material, table S2); thus, individuals with high activity-slope migrated after fewer post-fledging days (figure 1*c*). Additionally, activity-slope was positively associated with fledging date (fledging 1 day later increased activity-slope by 3% of its s.d.; $\beta = 0.0019 \pm 0.0006$, $t_{61} = 2.88$, $p = 0.005$; GLMM with gamma distribution and log link function).

(b) Pre-fledging activity effects on survival

Using CPH models, early-life activity parameters were linked to first-year survival. After accounting for the individual relative body weight and migration onset date, higher pre-fledging activity was associated with reduced mortality odds (figure 2*a* and table 1).

(c) Post-fledging activity effects on survival

After accounting for relative body weight and migration onset date, higher post-fledging activity was also linked to reduced mortality odds, and this relationship was stronger in fledglings with higher activity-slope (an interaction effect; figure 2*b*; electronic supplementary material, tables S3 and S4). This post-fledging activity × activity-slope interaction effect on survival was found to be robust when: (i) examined separately in the first 2 months after migration onset and in the rest of the year (electronic supplementary material, table S5), and (ii) when rainy days, wherein storks are less active (S.R. 2013, personal observation; electronic supplementary material, figure S3), were excluded while extracting the activity parameters (electronic supplementary material, text, table S5). Overall, activity-slope did not affect mortality odds (table 1). However, examination of the reverse direction of the post-fledging activity × activity-slope interaction indicated that an increase in activity-slope slightly reduced mortality

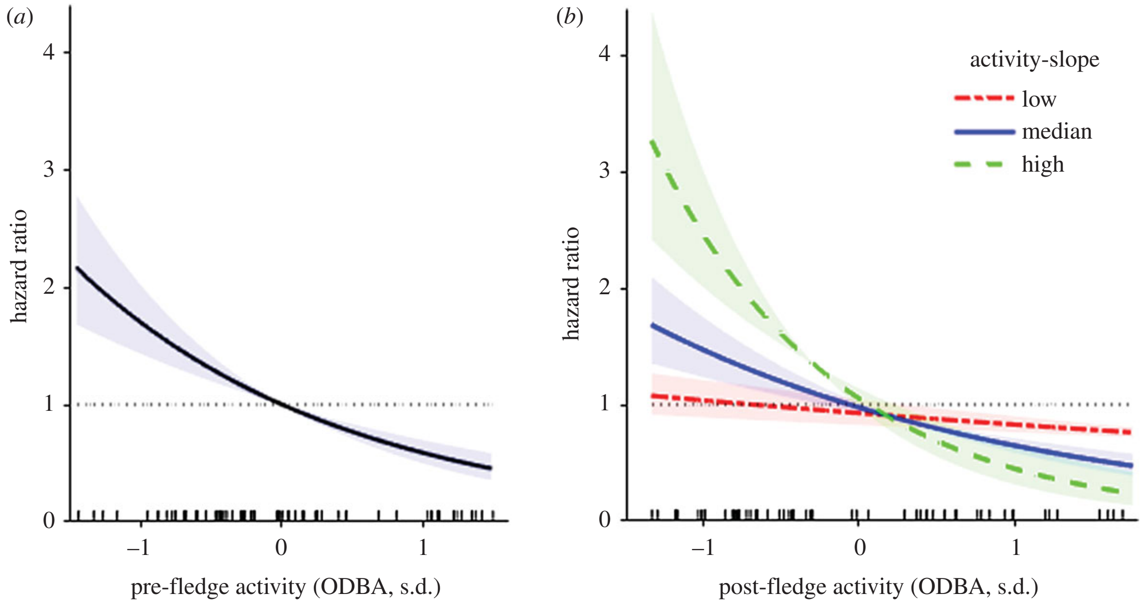

Figure 2. Activity association with first-year mortality odds. (*a*) The effect of pre-fledging activity (ODBA, overall dynamic body acceleration) on mortality odds based on a CPH model (table 1). The hazard ratio is the mortality odds in relation to the average individual. Shading denotes the s.e. and inner *x*-axis ticks mark the data distribution. s.d., standard deviation. (*b*) The interaction effect of post-fledging activity × activity-slope on mortality odds based on a CPH model ($p = 0.003$, see electronic supplementary material, table S3 for details). Low and high activity-slope values represent the 0.25 and 0.75 quantiles, respectively. (Online version in colour.)

Table 1. Pre-fledging activity effects on first year mortality. Results of a CPH model ($n = 62$, Cox and Snell pseudo-$R^2 = 0.32$). Brood ID and year were included in the model as random factors. Parameters' quadratic effects were not significant and thus not included in the model (see electronic supplementary material, tables S1 and S7 for details). HR, hazard ratio; ODBA, overall dynamic body acceleration; s.d., standard deviation; relative body weight, standardize again tarsus length (see Methods).

parameter	β	s.e.	HR	Z	p-value
pre-fledging activity (ODBA, s.d.)	−0.53	0.17	0.59	−3.05	0.002
migration onset (day of year)	0.05	0.02	1.05	2.11	0.035
relative body weight (s.d.)	−0.31	0.16	0.74	−1.88	0.060

odds in highly active individuals, but elevated mortality odds in individuals with low activity levels (figure 2*b*; electronic supplementary material, figure S2). Thus, fledglings with low post-fledging activity and a high activity-slope had the highest mortality odds (figure 2*b*). These fledglings were also characterized by shorter post-fledging durations (individuals with below median post-fledging activity and above median activity-slope [$n = 10$]: 8.6 ± 1.0 days, all others [$n = 53$]: 16.5 ± 1.2, *t*-test, $t_{61} = 4.98$, $p < 0.001$) which may contribute for their increased mortality (see below).

(d) Early-life timing and body condition attributes effects on survival

Post-fledging duration was positively correlated with the total time foraging and flying (derived from body-acceleration data) during this period ($r = 0.93$, $n = 63$, $p < 0.001$), suggesting it approximates pre-migratory experience. We found that post-fledging duration, migration onset date and relative body weight had significant effects on first-year survival (electronic supplementary material, tables S6 and S7). Post-fledging duration had a nonlinear, hump-shaped relationship with mortality odds such that intermediate durations were associated with the lowest mortality rates (figure 3). Earlier migration onset date reduced mortality odds (CPH; $\beta = 0.07 \pm 0.02$, $p = 0.002$; electronic supplementary material, table S6 and figure S4). Migration onset and hatching dates were positively correlated ($r = 0.78$, $n = 83$, $p < 0.001$) and similarly earlier hatching also reduced mortality odds, but the effect was weaker (electronic supplementary material, table S6). Higher relative body weight as a nestling reduced mortality odds ($\beta = -0.38 \pm 0.15$, $p = 0.01$; electronic supplementary material, table S6); this effect was significant here but not in the analysis presented in table 1, probably since here the analysis is based on a larger sample size ($n = 83$ versus 62, see Methods). Sex, fledgling number and estimated hatching order had no significant effects on juvenile survival.

4. Discussion

We found that both early-life activity and post-fledging (fledging-to-migration) duration were significantly associated with first-year survival, but some of these relationships were more complex than predicted. Pre- and post-fledging activity were correlated, and each was positively associated with increased first-year survival. The positive association of post-fledging activity with survival was stronger in individuals with higher activity-slopes (an interaction effect), suggesting that fledglings with both high activity and high activity-slope had the best survival odds. Post-fledging duration had a hump-shaped relationship with subsequent survival,

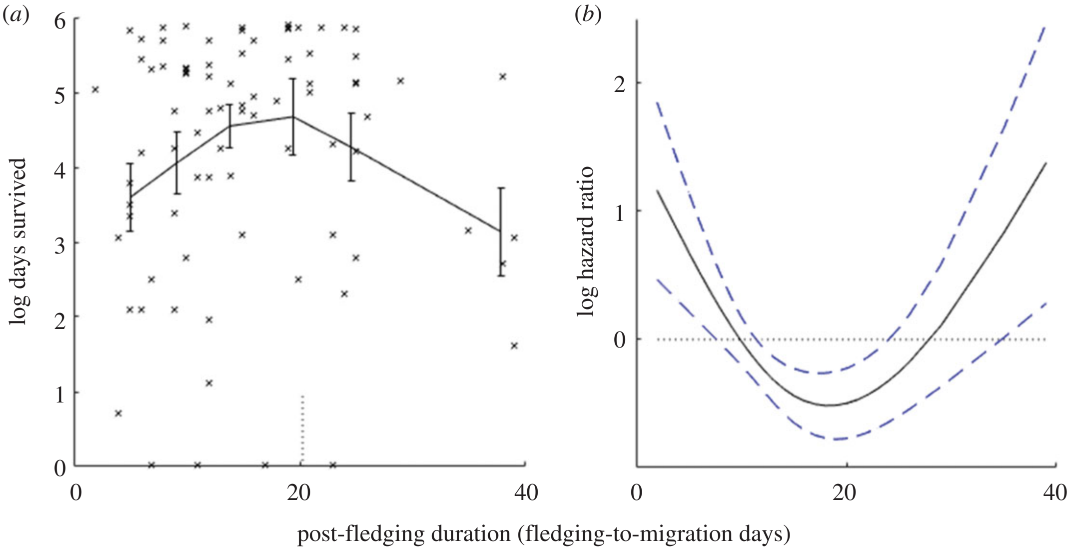

Figure 3. Association of post-fledging (fledging-to-migration) duration with first-year survival. (*a*) Number of days the individual survived in relation to its post-fledging duration. Each *x* denotes an individual, and error bars display the mean survival (±s.e.) per discrete 5-day segment of post-fledging duration (the last three segments were joined due to data scarcity). (*b*) The effect of post-fledging duration on mortality odds based on a CPH model ($p = 0.001$; electronic supplementary material, table S6). Dashed lines denote the 95% CI. The hazard ratio reflects relative mortality odds; thus, lower values denote higher survival. *Comment*: in plot (*a*), there is a decrease in survival above the 75% quantile of post-fledging duration (marked with an elongated, dashed tick on the *x*-axis) and those upper quartile individuals also had lower activity-slope values (0.04 ± 0.01) than the others (0.08 ± 0.01, *t*-test, $t_{62} = 3.43$, $p = 0.001$). (Online version in colour.)

where intermediate levels were linked with enhanced survival. Our tracking data exposed consistent individual differences in early-life activity profiles, which might reflect quality differences among individuals that could affect survival later in life.

The mortality events of the juvenile storks occurred after the focal pre-/post-fledging period, mostly during migration and wintering. Since the juveniles did not migrate and overwinter together, they experienced different conditions that probably had crucial effects on their survival, in line with the reported effects of wintering ground productivity on juvenile stork survival [40]. Further investigating these links is a promising direction for understanding proximate and ultimate mortality causes. Nevertheless, the early-life attributes could still explain a considerable part of the variation in survival (pseudo-$R^2 = 0.32$–0.41, table 1; electronic supplementary material, tables S3 and S6), emphasizing their importance.

(a) Early-life activity and survival

Post-fledging activity was positively correlated with relative foraging time and with distance travelled during the post-fledging period, indicating that more active juveniles acquired more pre-migratory experience which could contribute to their enhanced survival. Additionally, increased activity during the post-fledging period, particularly foraging activity, may reflect enhanced skill acquisition. In line with this, in juvenile macaques (*Assamese macaques*), more active individuals exhibited better locomotive skill acquisition [13], and the degree of improvement in diving and flight skills in young penguins (*Aptenodytes patagonicus*) and storks respectively, has been previously linked with increased survival [15,41]. It is important to note that spending more time foraging has been previously linked to less efficient foraging in adult birds [42]. However, early in life during the post-fledging days, juvenile storks are just learning to catch prey, their foraging skills are probably under-developed, and they are still partly fed by their parents [43]. We thus believe that in our case, fledglings' differences in relative foraging time are more likely to reflect differences in their inclinations (or abilities) to engage in foraging behaviour, than contrasts in foraging efficiency.

The post-fledging activity × activity-slope interaction effect on survival was consistently significant during both the first two months after migration onset and the rest of the year (electronic supplementary material, table S5); this long-term impact implies a deeper origin of the activity effect than sheer pre-migratory experience, which would be expected to dissipate with time. Additionally, activity levels were consistent (repeatable) between individuals over different days and periods (pre- and post-fledging periods) and showed repeatability between brood mates which may indicate a heritable genetic basis. Acknowledging that activity differences can arise from both intrinsic and extrinsic factors (further discussed below), we cautiously suggest that activity levels reflect individual quality and subsequent survival prospects of juvenile storks.

Perhaps higher early-life activity reflected better physiological or muscular competence that mediated the enhanced subsequent survival. Yet, we are not aware of previous bird studies relating nestling/fledgling activity with enhanced physiological traits, and somewhat contrarily, higher nestling activity was linked with manipulated reductions in food supply [44] and with elevated corticosterone levels that commonly reflect stress [45,46].

Alternatively, being a more active individual might be linked with having a more 'proactive' character, given the personality literature terminology in which proactive temperament characterizes individuals that are more active, bold, aggressive and fast-explorers [22], traits which are typically correlated [22,47,48]. Proactivity has been recently associated with higher survival in juvenile birds [49–51], but this relationship varies across species, environmental conditions and population density [49,52,53]. In fact, proactivity was linked to enhanced survival in another population of juvenile white storks [6]: measurements of stress-induced corticosterone levels (SICL) in stork nestlings in Spain were negatively correlated with subsequent survival [6]. Low SICL is typically coupled with a more proactive character [54,55], and therefore the authors [6] suggested that proactivity mediated the SICL effect that they found by improving the juvenile storks survival. Our results neatly support their hypothesis by complementarily linking higher early-life activity, portrayed by bio-telemetry data, with enhanced subsequent survival in juvenile storks. Nevertheless, the activity measured here inherently reflects the joint contribution of both intrinsic and extrinsic factors and thus, our referrals to animal personalities are made with caution and should be taken as potential hypotheses. Assessing animal personality from movement data collected from free-ranging animals is a challenging, emerging paradigm that has been recently promoted and demonstrated by linking the fields of animal personality and movement ecology [56–58]. We believe that our findings emphasize both the need for and potential merit in future studies integrating these fields towards a better understanding of behaviour and survival in the wild.

We could not uncover the direct source of between-individual differences in activity level. Relative body weight, which commonly correlates with habitat quality and body condition [19], was not associated with activity, possibly because juvenile activity may come at the expense of weight gain [13] or perhaps because of noise in our relative body weight index, measured just once per individual. We did not find an effect of parental provisioning effort on offspring pre/post-fledging activity, nor an effect of the extent of parental escort outside the nest on post-fledging activity (though our data might not be sensitive enough to identify such relationships; electronic supplementary material). Also, there were no inter-annual differences in activity level. With no other clear explanation emerging from our analyses, and since activity was consistent within broods, we surmise that the observed differences in activity were mainly dictated by intrinsic, potentially genetically based traits as was previously shown in other birds [22].

Focusing on the reverse direction of the post-fledging activity × activity-slope interaction (figure 2*b*; electronic supplementary material, figure S2) showed that for highly active fledglings, higher activity-slope slightly enhanced survival, but for individuals with low activity levels, higher activity-slope was unexpectedly linked to reduced survival. Examining the fledglings that underlie this surprising result (with low post-fledging activity and high activity-slope) revealed a possible role of short post-fledging duration, in line with the negative correlation between post-fledging duration and activity-slope (figure 1*c*). This implies that these individuals left too quickly for migration and displayed lower survival, presumably due to insufficient pre-migratory experience and possibly also owing to negative effects of shorter post-fledging parental care, as was shown in barn swallows *Hirundo rustica* [59]. It is likely that activity-slope during post-fledging does not purely indicate individual behavioural development, as we assumed, but rather reflected variation in the level of urgency to migrate acting on the fledglings. In accordance, late fledging was linked to higher activity-slope. Thus, higher activity-slope, marking higher pre-migration urgency and coupled with shorter post-fledging duration, could be detrimental, particularly for less active individuals who gain less experience and/or are of lower quality.

(b) Early-life timing and body condition effects on survival

Post-fledging duration reflected pre-migratory experience; however, in partial contrast to our original hypothesis, post-fledging duration had a hump-shaped relationship with survival, such that intermediate rather than maximal durations were associated with higher survival (figure 3). Short post-fledging duration was probably disadvantageous due to gaining less experience prior to facing the risky migration, as noted above. Unusually long post-fledging duration was, unexpectedly, disadvantageous as well, possibly due to its association with low activity-slope. Fledgling that stayed for very long post-fledging periods also had significantly lower activity-slopes, possibly representing delayed behavioural development which might signify lower individual quality. Thus, intermediate post-fledging duration, associated with higher survival, featured a group of individuals that gained sufficient experience prior to migration and did not display delayed development in daily activity. It is important to note, however, that migration departure time of a juvenile stork is not solely an individual decision as storks are obligatory social migrants and juveniles normally only initiate migration by joining passing or forming flocks (M.K. 2013, field observations).

As far as we know, there are no comparable studies that have related post-fledging duration and survival. Early hatching, on the other hand, is widely known to enhance survival [12,60], and we postulate that having more time to obtain pre-migratory experience is one of the understated reasons for this. Given the indicated importance of the post-fledging period, it would be interesting to investigate if adverse weather conditions during this period (such as heavy rains), hamper fledglings' preparation for migration and have detrimental carry-over effects on subsequent survival. Furthermore, our findings can have important implications for avian species that double brood (have a second brood during the breeding season). Shorter fledging-to-migration periods for second broods due to the onset of fall could reduce their first-year survival and make them less valuable to parents. There is a considerable variation in the occurrence of double brooding between and within species, which has been partly related to time limitation differences [61–63], and our findings support this explanation by demonstrating the detrimental effects of insufficient post-fledging time.

Finally, earlier hatching and migrating dates (which were correlated) as well as higher relative body weight (standardized against tarsus length) were associated with enhanced first-year survival, in agreement with many previous studies (e.g. [7,12]). Survival in these previous studies was mostly estimated from mark–recapture data that cannot distinguish mortality from emigration [64], which is problematic, particularly for young, dispersing birds. Our study showed compatible findings in storks based on a tracking dataset in which the fate for most individuals was known, which strengthens the reliability and generality of these reported relationships.

5. Conclusion

Overall, our results highlight the importance of the short pre- and post-fledging periods in determining subsequent survival of juvenile birds in the wild. They also suggest that (i) variation in juvenile quality is already manifested by early-life behaviour, (ii) that this variation can be identified in the wild using bio-telemetry data, and (iii) can serve to predict future survival prospects. Our study shows the unique merits of using tracking data to relate early-life development and behaviour to the fate of an individual, which can advance our knowledge of avian life histories, and may be relevant to conservation reintroduction schemes by emphasizing the importance and predictive value of early-life activity.

Ethics. No bird was injured during the trapping and tagging procedure. The research was carried out with approvals from (i) the National Administrative Office of Sachsen-Anhalt, Germany, Division of Nature Conservation, 407.3.3/255.13-2248/2, (ii) the State Office for Environment, Health and Consumer Protection of Brandenburg, Germany, V3-2347-8-2012.

Data accessibility. The data supporting the analyses are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rn8pk0p83 [65].

Authors contributions. S.R., R.N., F.J., M.W. and N.S. conceived the idea. S.R. and M.K. carried out the fieldwork with the help of S.T., U.E., M.W. and D.Z. Y.S.R. built the computational tool to classify body-acceleration data to behaviours. S.R. wrote the first draft of the manuscript and all authors substantially contributed to the revisions.

Competing interests. We declare we have no competing interests.

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