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ORIGINAL ARTICLE

To stay or to go: an analysis of fledging timing in White Stork *Ciconia ciconia* fledglings

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Abstract

Fledging is a critical stage in the life of altricial birds, marking their transition from nest dependence to independence. This study examines the timing of nest-leaving in White Stork (*Ciconia ciconia*) fledglings, focusing on how factors such as day of the year, brood size, chick age, habitat, and temperature influence the onset of fledging. Between 2012 and 2023, 121 fledglings in southern Poland were tagged with solar-powered GPS–GSM loggers to track their departure from nests. Our findings indicate that fledging occurred, on average, at 67 days after hatching, with most fledglings leaving their nests around 6–7 h after sunrise, typically during the late morning (median: 11.00 h local time). However, diel fledging times varied widely, with some chicks leaving as early as sunrise and others as late as 23.00 h. Brood size had a significant impact on fledging behaviour: older chicks in larger broods tended to fledge later in the day, while this pattern was not evident in smaller broods. Environmental factors, such as temperature and habitat type, had no significant effect on timing of fledging. However, fledging time exhibited a non-linear relationship with date, with chicks departing later in the morning in mid-July but earlier in the day by early August, possibly due to changing day lengths and the pressures of migration. This study provides new insights into the complex factors that influence fledging in White Storks, highlighting the role of sibling competition and seasonal variations in shaping fledging behaviour.

Keywords Brood size · Chicks · *Ciconia ciconia* · Fledging behaviour · GPS tracking · Phenology · Sibling competition · Timing of fledging · White Stork · Nest-leaving

Zusammenfassung

Bleiben oder Gehen: eine Analyse des Zeitpunkts des Ausfliegens von Jungvögeln des Weißstorchs *Ciconia ciconia*

Das Flüggewerden ist eine kritische Phase im Leben von Jungvögeln, sie markiert den Übergang von der Nestabhängigkeit zur Unabhängigkeit. In dieser Studie wird der Zeitpunkt des Ausfliegens flügger Weißstörche (*Ciconia ciconia*) untersucht, wobei der Schwerpunkt darauf liegt, wie Faktoren wie das Datum, die Gelegegröße, das Alter der Küken, der Lebensraum und die Temperatur den Beginn des Ausfliegens beeinflussen. Zwischen 2012 und 2023 wurden 121 flügge Jungvögel in Südpolen mit solarbetriebenen GPS–GSM–Loggern markiert, um ihren Abflug vom Nest zu verfolgen. Unsere Ergebnisse

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zeigen, dass die Jungvögel im Durchschnitt 67 Tage nach dem Schlüpfen flügge wurden, wobei die meisten Jungvögel ihre Nester etwa sechs bis sieben Stunden nach Sonnenaufgang verließen, typischerweise am späten Vormittag (Median: 11.00 Uhr Ortszeit). Die Tageszeiten, zu denen die Küken flügge wurden, waren jedoch sehr unterschiedlich: Einige flogen bereits bei Sonnenaufgang aus, andere erst um 23.00 Uhr. Die Gelegegröße hatte einen signifikanten Einfluss auf das Ausfliegeverhalten: Ältere Küken in größeren Gelegen flogen tendenziell später am Tag aus, während es bei kleineren Gelegen kein derartiges Muster gab. Umweltfaktoren wie Temperatur und Habitattyp hatten keinen signifikanten Einfluss auf den Zeitpunkt des Ausfliegens. Der Zeitpunkt des Ausfliegens der Küken war jedoch nichtlinear vom Datum abhängig: Mitte Juli flogen die Küken vormittags aus, Anfang August hingegen früher am Tag, was möglicherweise auf die sich ändernden Tageslängen und den sich aufbauenden Druck des Wegzugs zurückzuführen ist. Diese Untersuchung bietet neue Einblicke in die komplexen Faktoren, die das Flüggewerden bei Weißstörchen beeinflussen, und betont die Rolle der Konkurrenz unter den Geschwistern sowie der jahreszeitlichen Veränderungen in der Ausprägung des Ausfliegeverhaltens.

Introduction

Ontogenetic transition to independence is a critical period in the life of animals (Clutton-Brock 1991; Elliott et al. 2017). In altricial birds, fledging represents a pivotal moment, as young birds lose the safety of the nest and direct parental care, which includes food provisioning and protection from predators (Mainwaring 2016). On the other hand, prolonged parental care is energetically costly, leading to parent–offspring conflict (Clark and Ydenberg 1990; Graves et al. 1991). Moreover, nests can harbour numerous parasites that negatively impact nestling condition (Roulin et al. 2003). In addition, food restriction, increased corticosterone levels (Corbel and Groscolas 2008) and sibling interactions may stimulate the onset of fledging (Bowers et al. 2013). Thus, the decision to fledge must be carefully timed—birds shall be sufficiently developed and in good physiological condition, which is closely linked to growth mechanisms (Ricklefs 1968; Ruaux et al. 2020). Moreover, the time of day at which birds leave the nest is also important, as different challenges may arise depending on whether they fledge in the morning or in the evening (Radersma et al. 2015; Santema et al. 2021).

Fledging, one of the most critical moments in the life cycle of altricial birds, is associated with high mortality risk (Santema et al. 2021). However, the time spent in the nest varies not only between species but also within species, and the factors driving these variations are still poorly understood (Stodola et al. 2010; Yoda et al. 2017; Moreno 2020, 2022). However, traditional research methods, such as direct nest checks, can distort findings by prompting earlier fledging (Mayer-Gross et al. 1997). Moreover, in larger species, there are additional safety concerns related to field observations (Simmons 1952), as both adult birds and fledglings can become aggressive toward humans.

Previous studies have mainly focused on small cavity-nesting species, particularly tits (Paridae), due to the technical feasibility of installing cameras and temperature loggers to monitor the fledging events (Dubiec and Mazgajski 2023). However, when studying individual fledging behaviour, more advanced techniques, such as equipping nestlings with RFID tags, are required (Santema et al. 2021). Our understanding of the mechanisms driving fledging behaviour remains limited, necessitating further research, particularly experimental studies, to better comprehend both the causes and consequences of this process (Mainwaring 2016). For instance, factors such as habitat type, predation risk, and nest conditions (e.g., number of siblings) are known to influence the timing of fledging (Mainwaring 2016; Santema et al. 2021; Jones et al. 2024), but interactions of these factors remain uncharted.

As mentioned, previous studies have largely focused on small species, where nest predation and early post-fledging predation are significant threats (Ibáñez-Álamo et al. 2015). This raises the question: how does fledging behaviour manifest in larger species, where predation pressure is almost negligible? One such species is the White Stork (*Ciconia ciconia*), an iconic farmland bird of Europe (Kronenberg et al. 2017). White Storks build large nests—reaching two meters in height, 1.5 m in diameter, and weighing on average 378 kg (Zbyryt et al. 2021). Predatory pressure on nestlings is extremely low (Profus 1991; Kosicki 2012).

With the advancement of new technologies, it is now possible to equip White Storks with GPS transmitters, which not only allow precise tracking of individual birds but also provide valuable data on their behaviour (Flack et al. 2020; Turjeman et al. 2021). The use of bio-tagging technology offers a unique opportunity to gather information about the timing of fledging, including the specific day of life, time of year, and hour of day.

The primary objectives of this study are to: (1) determine how long White Stork chicks remain in nests and reveal average age during fledging; (2) investigate whether fledging time is affected by temperature and habitat type; (3) assess how brood size influences the timing of fledging, particularly in the context of sibling competition and age; and (4) analyze the relationship between the date (day of year) and the diel time of fledging, with a focus on seasonal differences in fledging behaviour. By achieving these goals, we aim to deepen our understanding of the mechanisms driving fledging in White Storks, which could have important implications for the conservation of this charismatic species and the management of its habitats.

Methods

From 2012 to 2023, we tagged a cumulative total of 121 White Storks as follows: one in 2012, eight in 2013, eleven in 2014, 42 in 2015, 37 in 2016, four in 2017, one in 2018, five in 2019, six in 2020, four in 2021, and two in 2023. These storks were identified and tagged approximately 1–2 weeks prior to their fledging phase within their nesting sites located in the Opole Voivodeship, situated in the southern Poland.

For tracking purposes, the storks were equipped with solar GSM–GPS–ACC loggers each weighing approximately 27 g. Specifically, DUCK-3 GSM model was used until 2015, after which SAKER-H model—both manufactured by Ecotone—was employed. After 2019, the Flex 2G model from Druid Technology was used. These loggers were securely attached to storks using a backpack-style arrangement, facilitated by a teflon–nylon harness.

The transmitters were programmed to record GPS coordinates at 30-min intervals. However, during the initial years, due to certain technological constraints, primarily rapid battery depletion, the interval for GPS recordings was adjusted to 60 min. In the case of Flex 2G model, the intervals for GPS recordings depended on acceleration, being set to 20 s for movement and 5 min for immobility. All acquired data were stored within the device and then sent by a GSM tower. The temperature measurements from GPS/GSP tags were obtained only from DUCK-3 and SAKER-H models.

Ethical note

All storks were measured and tagged by JS under licenses (293/2014 to 311/2018). All procedures were conducted in line with the guidelines of the Gdańsk Bird Ringing Centre at the Museum of Zoology Polish Academy of Sciences. Given a stork weights 3000–3500 g, a logger together with a harness weighting 28 g stays well below the recommended 3% threshold, constituting 0.8–0.93% of animal's weight. In this way, any potential hindrance to storks' natural behaviour was drastically minimized.

Analysis

The timing of fledging was determined by manually analysing GPS–GSM tags. The coordinates were identified based on the densest cluster of GPS data points, with the majority of these points falling within a 30-m radius, similar to the method of roosting site localisation described in Siekiera et al. (2022). The precision of the GPS–GSM tag can vary up to 30 m, but under optimal meteorological conditions, its accuracy can be as precise as five meters, as indicated by producer's specifications.

First, we detected day of 'off-nest' points by computing daily sums of point-to-point travel distances. Our data indicated that stationary or near-stationary behaviour yielded minimal daily totals, whereas genuine flights produced conspicuously larger sums. Occasional short 'test flights', sometimes spanning only one or two fixes, did not qualify as fledging unless the bird remained off the nest. We then reviewed the data to identify consecutive out-of-nest positions—two or more in sequence—as evidence of an actual nest departure (see electronical supplementary material for more details). Single 'off-nest' points were interpreted with caution, given that vigorous nest-based activity can alter the logger's orientation and occasionally yield apparently off-nest coordinates. We recorded the fledging date and hour as the earliest verifiable off-nest time (backed by at least one subsequent off-nest fix) not followed by an immediate return. To compare events across dates, fledging times were standardized relative to local sunrise. Because logging intervals differed over the course of the study, all times were rounded to the nearest hour.

The age of tagged fledglings was estimated using beak measurement according to the equation of Kania (1988) and was expressed in days after hatching. The beak measurement was performed on the occasion of ringing (first visit to the nest), while the tagging was done on the second visit. Therefore, the age of a fledgling was obtained by summing age estimated during the first visit with difference between leaving the nest (fledge date) and ringing time (first visit by ringer). During the visits, number of chicks in nest was also noted. In nests where a second beak measurement was also taken during the tagging visit, we substituted or combined this additional measurement to refine the initial age estimate.

Buffer zones with a radius of 500 m were established around nests. Subsequently, the land cover within these buffer zones, classified using CORINE land cover data

2018, was analyzed. The areas of each land cover type were calculated and expressed in percentage terms, providing insights into the environmental characteristics near nests. We pooled the categories into higher levels and further used only meadow and grassland land cover (CLC codes 231, 321, 322).

The main analysis involved modelling the time of fledging using generalized linear mixed models (GLMMs) with a negative binomial distribution (R function *glmer.nb*). The models incorporated several fixed effects, such as age of leaving nest, number of chicks, fledging day, meadow and grassland cover, and night temperature. For day of year, we employed non-linear effects through the inclusion of quadratic terms. Variables such as age of leaving nest, fledging day, and night temperature were centred around mean. To account for random effects, we included a random intercept for year and a nested random intercept for Year:id_nest, acknowledging potential yearly variations and nest-specific differences. Interaction terms between the age at leaving the nest and the number of chicks were scrutinized to understand their possible combined impact on the diel fledging time. Model selection was conscientiously done based on likelihood ratio tests (LRT) facilitated by the *drop1* function. This function contrasts the comprehensive model against a simplified version, excluding the focal variable, and the comparison is based on the Akaike information criterion (AIC). The variance inflation factor (VIF) was calculated to assess multicollinearity among continuous predictors, and we found no issue (the highest value was 1.34).

The analysis was conducted using R software version 4.1.1 (R Development Core Team 2018) with the integration of packages, such as *lme4* (Bates et al. 2015), *ggplot2* (Wickham 2016), *emmeans* (Lenth 2020), and *ggeffects* (Lüdecke 2018). All geospatial data analyses were carried out with the assistance of QGIS software (QGIS.org 2020).

Results

Fledging day, time and age

The mean fledging day was 28th July (± 12 SD; median date 24th July; Fig. 1a). The mean diel fledging time was 7 (± 5 SD) h after sunrise, with median time 6 h after sunrise. This timing translates to an average local clock time (Central European Summer Time CEST, UTC + 2) fledging of 12.00 h and a median clock time fledging 11.00 h,

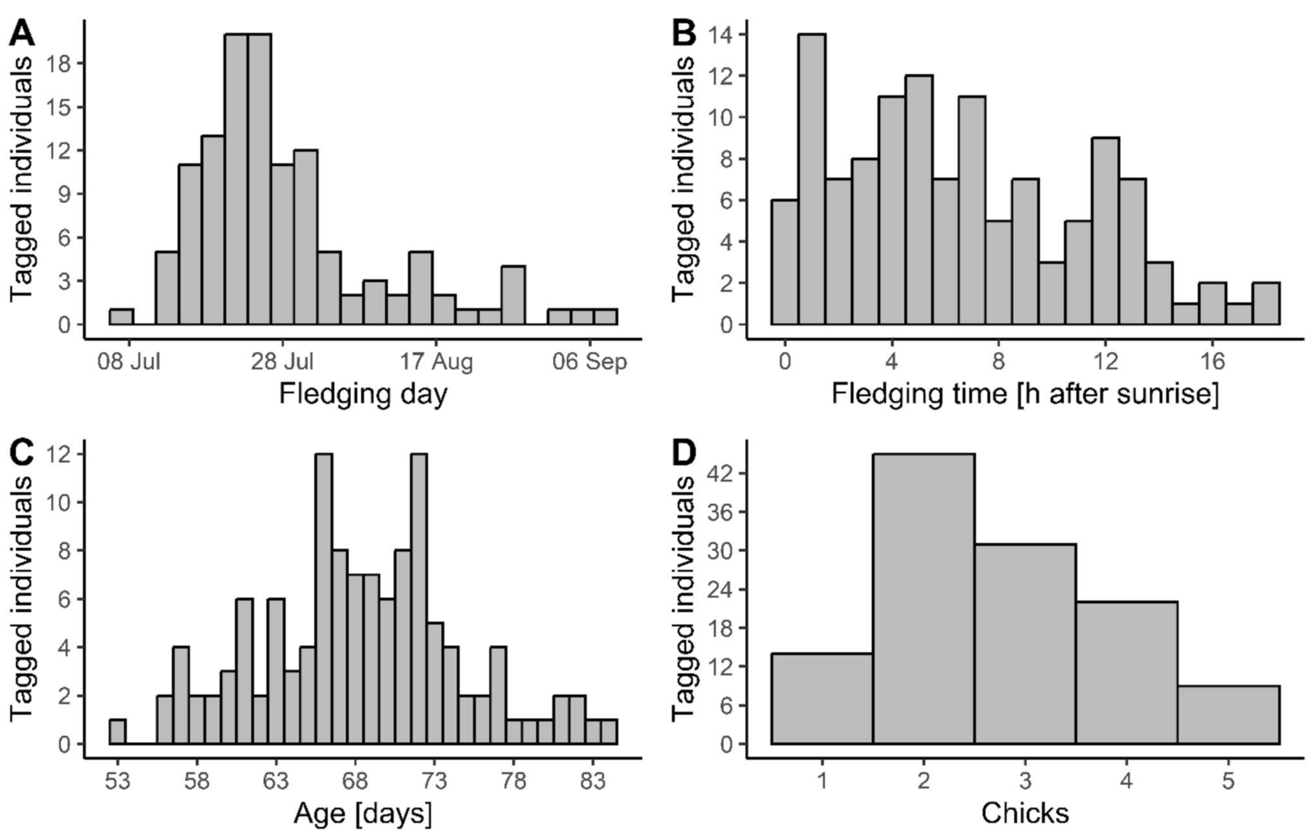

Fig. 1 Number of tagged individuals of White Stork (*Ciconia ciconia*) according to different variables. **A** Fledging day. **B** Diel fledging time. **C** Age at the time of fledging. **D** Number of offspring in brood of the tagged young

suggesting fledging typically occurs in the late-morning hours. The range of fledging time was broad, spanning 18 h post-sunrise, from as early as 0 h (at sunrise) to as late as 18 h post-sunrise, and from 05.00 h to 23.00 h local time (Fig. 1b). The mean age of chicks during the fledging was 67 days (±7 SD; median = 68; Fig. 1c). The mean number of chicks was 2.7 (±1.1 SD, median 3; Fig. 1d).

Temperature and habitat type

Because only 101 out of 121 GPS/GSM tags that we used recorded temperature, we initially focused on testing this variable. The results indicated no effect of temperature (LRT = 0.017, $df = 1$, $p = 0.896$), so this variable was excluded from further analysis, and the full data set was used. For the full data set ($n = 121$), we found that the proportion of meadow or grassland within nests' land cover buffers was not statistically significant (LRT = 0.535, $df = 1$, $p = 0.464$). Consequently, the land cover variable was excluded from further analysis.

Brood size, chick age and day of year

Detailed parameters' estimation of the resulting model is provided in Table 1. The interaction between age and number of chicks was found to be statistically significant (LRT = 5.388, $p = 0.020$), suggesting a varying effect of age on diel fledging time depending on the number of chicks (Fig. 2a). In nests with a large number of chicks, the younger individual fledge early morning (being possibly pushed out by other chicks), while older fledglings leave nest later (being not sensitive to the other birds due to their size). In the case of one or two siblings in the nest, this pattern does not hold, and there is even a tendency to fledge later if a bird is younger. In other words, there is a positive correlation between the time of leaving a nest and the bird's age, but only for individuals with numerous siblings.

Table 1 Parameters estimation of mixed-effects negative binomial regression model of White Stork (*Ciconia ciconia*) fledging time

Fixed effects	Estimate	SE	*z* value	*pr*(>|z|)
(Intercept)	1.968	0.248		
DayOfYear	− 2.957	1.032	− 2.864	**0.004**
I(DayOfYear ^2)	0.125	0.041	3.030	**0.002**
Number of chicks	− 0.085	0.083	− 1.033	0.302
Age	− 0.035	0.031	− 1.115	0.265
Number of chicks × age	0.021	0.011	1.970	**0.049**

Random effects: Year:id_nest (Intercept) = 0.081 ± 0.285 SD, Year (Intercept) = 0.074 ± 0.273 SD

Day of year parameter multiplied by 100. Significant results are marked in bold

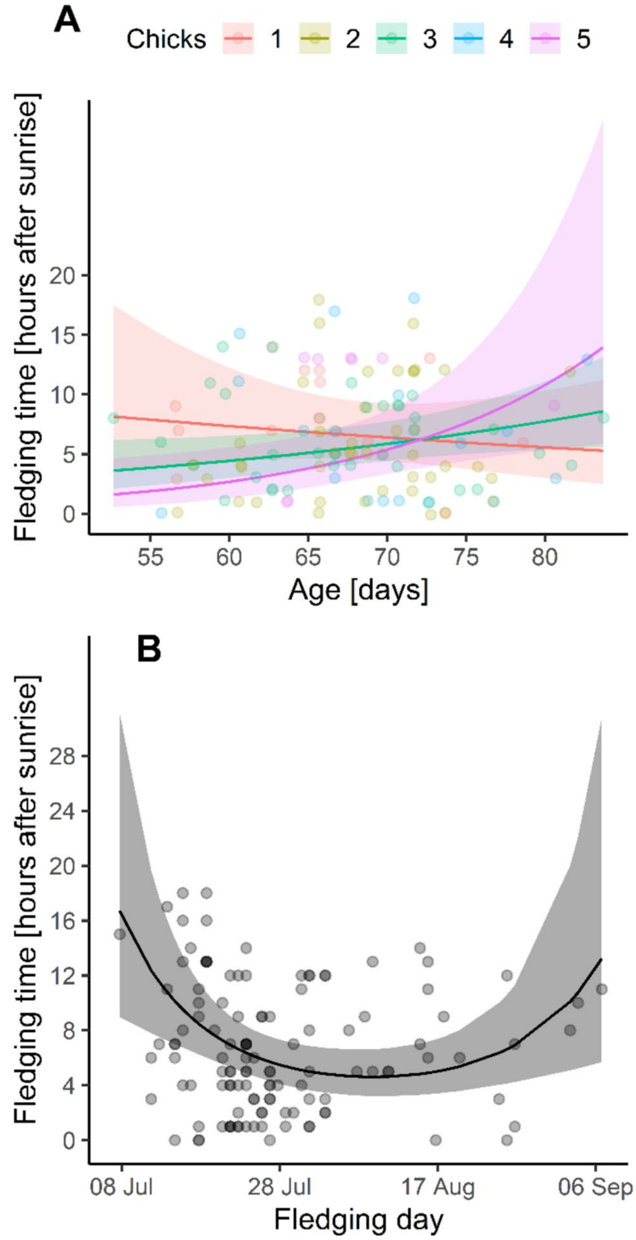

Fig. 2 Significant predictions (solid lines) of fitted model explaining the diel fledging time of White Stork. Circles represent observed data points, jittered to increase readability. Shaded area denotes 95% confidence intervals. **A** Significant interaction of individual's age and number of chicks. For clarity, we show the interaction only for broods of one, three and five chicks. **B** Significant quadratic effect of fledging day

The quadratic effect of fledging day was statistically significant (LRT = 7.720, $df = 1$, $p = 0.005$), indicating a non-linear relationship with diel fledging time (Fig. 2b). This shows that birds fledge later after sunrise around 10th July compared to early August, but by the end of August, there is again a tendency for fledging to occur later (Fig. 2b).

Discussion

The results of this study indicate that mean age of chicks during the fledging was 67 days and the average fledging date for White Stork chicks occurred at the end of July, with the average and median diel fledging time being 7 and 6 h after sunrise, respectively. This means that most chicks fledged during the late morning, around 11.00–12.00 h local time (CEST, UTC + 2). These findings align with those observed in numerous other bird species, where fledglings tend to leave the nest in the early hours after sunrise (Chiavacci et al. 2015; Ribic et al. 2021; Santema et al. 2021), likely due to increased survival chances, although the evidence for this hypothesis is still limited (Radersma et al. 2015; Jones et al. 2024). However, fledging time range in this study was wide, spanning 18 h, from sunrise until as late as 23.00 h local time. This may be related to the very low predation rates on young storks, which, although increasing in recent years due to predation by White-tailed Eagles (*Haliaeetus albicilla*; Zbyryt et al. 2022; Mirski and Komar 2023), were not recorded in the population where this study was carried out. Analysis of the possible effect of temperature on the diel fledging time did not reveal any significant impact, nor did meadow cover prove to be a significant factor.

Furthermore, a significant interaction between the time of fledging and the number of chicks in the nest was observed. This suggests that in broods with more chicks, younger ones fledged earlier, likely due to intra-brood competition, whereas older chicks left the nest later. In smaller broods (one or two chicks), this pattern was not evident, and younger chicks tended to fledge later. This could indicate a form of competition between chicks, which, although not strong in White Storks and typically moderated by parental behaviour (Djerdali et al. 2008; Romero and Redondo 2017), has previously only been linked to food availability, rather than time spent in the nest. This finding also hints at the possibility that fledging may be influenced by both direct (e.g., nudging by siblings) and indirect (e.g., reduction of feeding) pressures from parents (Touati et al. 2023).

The non-linear effect of the fledging date on the diel fledging time was found. Birds fledged later in the morning around 10th July, but earlier in the day at the beginning of August, followed by a tendency to fledge later again toward the end of August. This may be associated with changes in day length (Kosicki et al. 2004; Podlaszczuk et al. 2015), as well as social pressure from already migrating birds and the inclination to join flocks in passage (Flack et al. 2016; Siekiera et al. 2021).

In conclusion, White Stork chicks generally fledge in the late morning, and the timing of fledging is shaped by both the time of year and the number of chicks in the nest. No significant effect of temperature or habitat type was found. Particularly interesting and warranting further investigation are the mechanisms behind the non-linear effect of day of the year on diel fledging time, as well as potential shifts in fledging behaviour in response to increasing predation pressure from the white-tailed eagle.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-025-02309-w.

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Data availability Raw data underlying this study are provided in the electronic supplementary material attached to this article. The R scripts used for the statistical analyses are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare they have no conflicts of interest.

Ethical statement All storks were measured and tagged by JS under licenses (293/2014 to 311/2018). All procedures were conducted in line with the guidelines of the Gdańsk Bird Ringing Centre at the Museum of Zoology Polish Academy of Sciences. Given a stork weights 3000–3500 g, a logger together with a harness weighting 28 g stays well below the recommended 3% threshold, constituting 0.8–0.93% of animal's weight. In this way, any potential hindrance to storks' natural behaviour was drastically minimized.

Declarations of generative AI and AI-assisted technologies in the writing process During the preparation of this work the authors used ChatGPT to improve the readability and flow of the text. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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