RESEARCH ARTICLE

Early arrival at breeding grounds: Causes, costs and a trade-off with overwintering latitude

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Abstract

1. Early arrival at breeding grounds is of prime importance for migrating birds as it is known to enhance breeding success. Adults, males and higher quality individuals typically arrive earlier, and across years, early arrival has been linked to warmer spring temperatures. However, the mechanisms and potential costs of early arrival are not well understood.

2. To deepen the understanding of arrival date differences between individuals and years, we studied them in light of the preceding spring migration behaviour and atmospheric conditions *en route*.

3. GPS and body acceleration (ACC) data were obtained for 35 adult white storks (*Ciconia ciconia*) over five years (2012–2016). ACC records were translated to energy expenditure estimates (overall dynamic body acceleration; ODBA) and to behavioural modes, and GPS fixes were coupled with environmental parameters.

4. At the interindividual level (within years), early arrival was attributed primarily to departing earlier for migration and from more northern wintering sites (closer to breeding grounds), rather than to migration speed. In fact, early-departing birds flew slower, experienced weaker thermal uplifts and expended more energy during flight, but still arrived earlier, emphasizing the cost and the significance of early departure. Individuals that wintered further south arrived later at the breeding grounds but did not produce fewer fledglings, presumably due to positive carry-over effects of advantageous wintering conditions (increased precipitation, vegetation productivity and daylight time). Therefore, early arrival increased breeding success only after controlling for wintering latitude. Males arrived slightly ahead of females. Between years, late arrival was linked to colder temperatures *en route* through two different mechanisms: stronger headwinds causing slower migration and lower thermal uplifts resulting in longer stopovers.

5. This study showed that distinct migratory properties underlie arrival time variation within and between years. It highlighted (a) an overlooked cost of early arrival induced by unfavourable atmospheric conditions during migration, (b) an important fitness trade-off in storks between arrival date and wintering habitat quality and (c) mechanistic explanations for the negative temperature–arrival date correlation in soaring birds. Such understanding of arrival time can facilitate forecasting migrating species responses to climate changes.

1 | INTRODUCTION

Arrival time of migratory birds to their breeding grounds is of high importance due to its negative correlation with breeding success (Newton, 2008; Smith & Moore, 2005). Birds that arrive relatively early benefit from acquiring higher quality territories, nesting locations and mates (Gunnarsson et al., 2006; Janiszewski, Minias, & Wojciechowski, 2013; Møller, 1994; Newton, 2008; Smith & Moore, 2005). Furthermore, earlier arriving parents produce relatively early-hatching offspring (Smith & Moore, 2005; Vergara, Aguirre, & Fernandez-Cruz, 2007) which in turn attain higher postfledging survival rates (Lok, Veldhoen, Overdijk, Tinbergen, & Piersma, 2017; Monros, Belda, & Barba, 2002; Verboven & Visser, 1998). Arrival time is also of prime importance in relation to global warming, which triggers advances in spring phenology and an earlier peak in food during breeding (Menzel et al., 2006). Correspondingly, advances in arrival time were recorded in many migrating species (Gordo & Sanz, 2006; Huppop & Huppop, 2003; Usui, Butchart, & Phillimore, 2017), but bird populations that do not adjust their timing can suffer from detrimental trophic mismatch (Both, Bouwhuis, Lessells, & Visser, 2006; Saino et al., 2011). Considering the profound effects of arrival time on individual fitness and population dynamics, understanding its underlying causes of variation is of major importance in bird ecology.

In line with that, a large volume of research targeted the variation in arrival time between individuals and years. Interindividual variation was mostly studied by describing *which* individuals arrive first; these were typically the adults (Dittmann & Becker, 2003; Newton, 2008; Sergio et al., 2014), males (Cadahia et al., 2017; Ouwehand & Both, 2017) and higher quality individuals (Blums, Nichols, Hines, Lindberg, & Mednis, 2005; Dittmann & Becker, 2003; Matyjasiak, 2013). However, *which* spring migration properties underlie individual differences in arrival time was rarely studied (but see Lemke et al., 2013; Ouwehand & Both, 2017); that is, do early-arriving birds fly faster, stop less, depart earlier for migration or from closer wintering sites? Recent biotelemetry-based studies highlighted the significant role of departure date rather than migration progress (speed and stopovers) in determining arrival time (Lemke et al., 2013;

Ouwehand & Both, 2017; Sergio et al., 2014). However, other studies also pointed out the importance of speed (McKinnon, Macdonald, Gilchrist, & Love, 2016; Schmaljohann et al., 2016), and there were contradicting findings regarding the linkage between wintering site distance and arrival time (Gunnarsson et al., 2006; Kentie et al., 2017; Lok et al., 2017). Thus, current findings are ambiguous and limited to a few species, and the nature of the relationships between the migratory properties and arrival date is not clear. Furthermore, the costs of early arrival are much less acknowledged than its benefits. A few studies have pointed out the drawbacks of facing harsh environmental conditions upon arriving (too) early in the breeding grounds (Newton, 2008), but similar effects that can potentially act on early migrants *en route* were overlooked. These questions highlight the need to study the interplay between the return migration properties and arrival time to uncover basic aspects of the birds' migratory "race" to the breeding grounds.

At the interannual level, arrival time variation has been shown to correlate with several environmental factors (Gordo, 2007), where the main findings pointed out that high temperatures along the migration route and in the breeding grounds promoted earlier arrival (Cadahia et al., 2017; Gordo, Tryjanowski, Kosicki, & Fulin, 2013; Huppop & Huppop, 2003; Marra, Francis, Mulvihill, & Moore, 2005; Vaitkuviene, Dagys, Bartkeviciene, & Romanovskaja, 2015). However, there is a lack of direct evidence connecting these environmental factors with migratory journeys of individual birds, which is needed to develop a more mechanistic understanding of their effects (Gordo, 2007). This information gap originated from the difficulty to obtain high-resolution tracking data of migrating birds, though in recent years, this has become more feasible with the ongoing advances in biotelemetry technology.

We studied the spring migration of adult white storks equipped with advanced GPS–body acceleration (ACC) transmitters aiming to understand variation in arrival time between individuals and years. White storks are iconic, long-distance, migrants, which mostly breed in Eurasia and migrate to sub-Saharan Africa. They migrate during daylight using soaring-gliding flight, utilizing thermal uplifts to minimize travel costs (Leshem & YomTov, 1996; Rotics et al., 2016) along two central flyways, east and west of the Mediterranean; here, we

studied the eastern flyway (Figure 1). White stork exhibits substantial, and yet unexplained, individual variation in wintering sites along the eastern flyway (Figure 1; Berthold, Kaatz, & Querner, 2004), which may affect their subsequent arrival time to breeding grounds. Upon arrival, storks display high fidelity to former nest site and mate (Barbraud, Barbraud & Barbraud, 1999), but vital clashes over nests are fairly common (pers. obs.; Wuczynski, 2005). As in other species, earlier arrival was linked to enhanced breeding success in white storks (Fulin, Jerzak, Sparks, & Tryjanowski, 2009; Janiszewski et al., 2013; Kosicki, Sparks, & Tryjanowski, 2004).

Adult storks from a breeding population in Saxony-Anhalt, Germany, were fitted with solar transmitters that recorded high-resolution GPS and body acceleration (ACC) data. GPS fixes were coupled with environmental parameters (Dodge et al., 2013), and ACC records were used to approximate activity-related energy expenditure (by calculating ODBA; Wilson et al., 2006) and to deduce behavioural modes (Rotics et al., 2016). Overall, we used 90 spring migration tracks consisting of ca. 400,000 GPS-ACC records, from 35 adult storks across five years (2012–2016). These multifaceted data allowed us to study the causes, costs, trade-offs and implications of interindividual and interannual variation in arrival time.
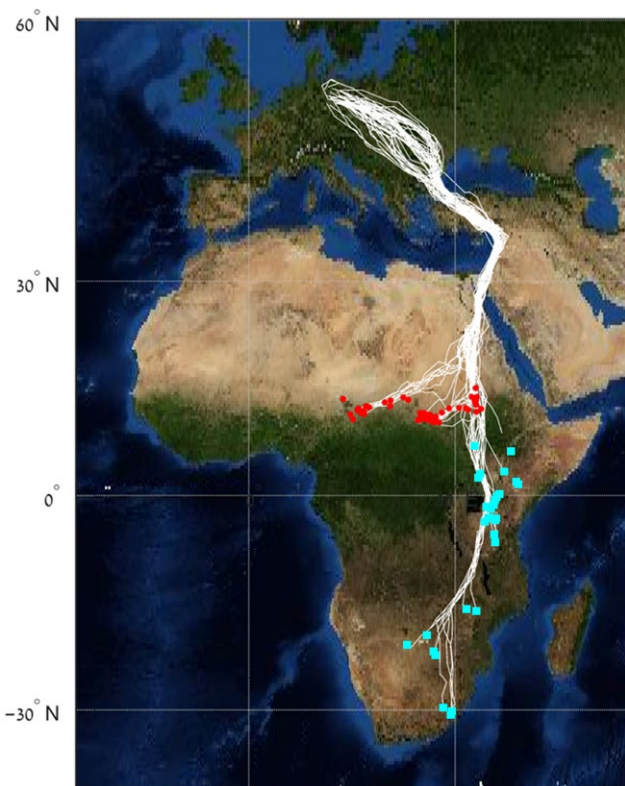

FIGURE 1 White stork spring migration tracks. Dots and squares mark spring migration departure locations (i.e. wintering site): red dots for the Sahel and pale blue squares for more southern locations. Sixty-one of the 90 departure locations were in the Sahel (overlapping red dots). A third of the tracks were randomly excluded from the figure to reduce the visual load

At the interindividual level, we first examined which of the following spring migration properties primarily characterized the early-arriving individuals: (a) migration speed (daily displacement), (b) total stopovers duration, (c) departure time and (d) departure location (latitude of last wintering site). As discussed above, there was no strong basis for informed predictions regarding the relative importance of these properties for arrival time, but several recent studies put forward the significance of departure time (Lemke et al., 2013; Ouwehand & Both, 2017; Sergio et al., 2014). We further explored the relationships between the migration properties targeting two potential migratory trade-offs: (a) Along with the well-documented breeding enhancement by early arrival, which was re-assessed here, we examined a potential cost in the form of high migratory flight effort (flight ODBA) while migrating earlier due to less favourable atmospheric conditions. (b) We investigated whether individuals that wintered further south departed earlier or migrated faster to compensate for the longer journey, or alternatively arrived later and had lower breeding success (as in spoonbills, Lok et al., 2017). In fact, some of the studied individuals wintered thousands of kilometres further south than the commonly used wintering region in the Sahel (Figure 1), and we aimed to understand the drivers and consequences of this by comparing environmental conditions and behaviour at wintering sites and subsequent breeding success. The last interindividual analyses were to examine whether protandry (male-first arrival) exists in white storks; previous studies have reported contradictory findings in this regard (Barbraud & Barbraud, 1999; Vergara et al., 2007).

In our interannual analyses, we aimed to go beyond the widely reported correlation between high-temperature and early arrival (Gordo, 2007; Usui et al., 2017), to examine the effects of atmospheric factors *en route* (wind and thermal uplift) on migratory parameters (speed, stopovers, departure time) that may underlie annual differences in arrival time.

2 | MATERIALS AND METHODS

2.1 | Study site and tracking data

We trapped 62 adult storks in the state of Saxony-Anhalt, Germany, and fitted them with solar GPS-ACC transmitters (e-obs GmbH; Munich, Germany) that weighed 55 g including harness, ca. 2% of the average stork's weight (see Rotics et al., 2016). Bird sex was determined by molecular methods (Supporting Information Appendix S1). The transmitters recorded GPS fixes every 5 min when solar conditions were good (95% of the time) or every 20 min, otherwise. Every five minutes an ACC burst of 3.8 s was recorded at 10.54 Hz for the three perpendicular axes. ODBA—a valid proxy for activity-related energy expenditure (Wilson et al., 2006)—was calculated for every ACC burst (see Rotics et al., 2016 for details). Data were stored onboard and were downloaded via a VHF radio link upon locating the stork (Rotics et al., 2016). Out of 62 tagged individuals, we used data from 35 birds. For 21 birds, data were not available

due to birds not being found in the year after tagging (n = 15), tag malfunctions (n = 5) or user-related errors (n = 1). Six individuals that migrated through the Western European flyway and wintered in Spain were excluded from the analysis as their migration and wintering were substantially different from all others that took the eastern flyway and wintered in Africa.

Nests were identified based on the tracking data and verified with field observations. The number of fledglings was monitored by ground observations and drone-based filming flights (ca. every 3 weeks). Fledgling number could not be obtained for three nesting events, which were excluded from the breeding success analysis.

2.2 | Environmental data

Each GPS fix was annotated with environmental data of wind, thermal uplift velocity, ambient temperature, precipitation and NDVI using the Env-DATA track annotation tool of MoveBank (Dodge et al., 2013; see Supporting Information Appendix S2 for details).

2.3 | Data analysis

Arrival time to the breeding area was defined as the date of approaching within 20 km of the nest. It was the same as the arrival date to the nest itself in 85% of the cases, but the former was preferred as it disregarded the time the bird spent searching for a nest after arriving in the nesting area (results were consistent across methods). Dates were analysed as day of year (DOY): serial day number from January 1.

Departure date was identified with a backward–forward algorithm; starting from a point at which the bird was undoubtedly migrating (crossing 17.5°N northward), we searched backwards until reaching a stationary phase of five consecutive days of daily displacement <50 km. From this point, we searched forward for the first three consecutive days of (a) more than 50 km displacement each day, (b) more than 150 km total displacement and (c) general northward direction (azimuth >320° and <110°). Departure day was defined as the first of these three days. The method was extensively validated by visual examination of the tracks. Accordingly, departure location was the last stationary location before departure date. It was included in analyses either by its °N latitude (negative values south of the equator) or categorized into two classes: *Sahel-* (latitude >9°N) and more *southern*-wintering locations (Figure 1).

Migration speed was the average daily displacement in progress days (>30 km displacement), whereas stopover duration was the total number of stationary days (<30 km). Migratory flight energy expenditure was deduced from the mean ODBA during flight (speed >5 m/s). Wind was examined during flight and unless specified otherwise also thermal uplift (see Supporting Information Appendix S2 for details).

There was very high variation in the stork migration tracks due to different departure (wintering) locations (Figure 1). Given our research objectives, we aimed to compare similar migration tracks among individuals to avoid the prominent, potentially masking, effects of migrating in different geographical regions (Chevallier et al., 2010; Klaassen, Strandberg, Hake, & Alerstam, 2008), as for example, a migration journey starting from South Africa and from Sudan (Figure 1). Therefore, the migration properties of speed, stopovers, flight cost and *en route* environmental conditions were examined within a spatial window between latitudes 20° and 51.5°N, in which all birds displayed similar tracks (Figure 1). Migration departure location and date were calculated irrespectively of this spatial window.

We also explored the birds' late wintering period of the two months prior to migration and compared Sahel-wintering and southern-wintering conditions: NDVI, precipitation, diurnal temperature (7:00–16:00 GMT) and daylight length (calculated in Matlab with the suncycle function, Pawlowicz, 2009), and the wintering behaviour: daily distance in stationary days, and relative time spent foraging. The latter was the ratio of walking and pecking records divided by total records, based on ACC data classified into behavioural modes with supervised machine learning (see Rotics et al., 2016 for details). We repeated this comparison for a fixed wintering period of Dec-Jan, dismissing the link to, and potential effects of, migration onset and the results were robust (not reported).

Spring migrations of individuals that did not attempt to breed in that year (i.e. did not have a nest; eight cases originating from seven birds) were extreme outliers in their phenology, reaching the breeding areas 23 ± 3 days after the average arrival time of nesting birds, and were thus excluded from the analyses except for when portraying their differences (*Non-nesting storks* section of the results). Furthermore, our basic, underlying working assumption was that the storks had a motive to arrive early for breeding propose, which cannot be ascertained in the non-nesting cases.

2.4 | Statistical notes

The spring migration departure time, departure latitude, speed and stopover length have altogether straightforward effects on arrival date when included in a single model (Supporting Information Table S1) deriving from the basic speed–time–distance kinematic relation. We were interested in determining which of these migratory properties primarily explained individual variation in arrival time within years, that is which properties mainly characterized early-arriving individuals. For this, the effect of each migratory property on arrival time was examined separately with a linear mixed model (LMM; *year* and *individual* as random factors) and the models' likelihood and marginal R^2 were compared. Marginal R^2 was calculated following Nakagawa and Schielzeth (2013) using the R package MUMIN (Barton, 2016).

Generalized linear mixed models (GLMMs) with error distribution according to the dependent variable (normal distribution was tested with Lilliefors test) and LMMs were used with *year* and *individual* as random factors in (almost) all statistical analyses. The exceptions were analyses where the annual effects were of explicit interest and thus the *year* was a fixed factor (e.g. annual differences in arrival time reported in Figure 4). To further examine differences between years, post hoc tests (Tukey) were conducted using the *lsmeans()* R function (Lenth, 2016). Individual consistency in departure time

and location was examined by calculating repeatability across years (Intraclass correlation) using the RPTR R package (Stoffel, Nakagawa, & Schielzeth, 2017). Multicollinearity was tested, verifying that all predictors in multiple regressions had a variance inflation factor (VIF) <3 (Zuur, Ieno, & Elphick, 2010).

3 | RESULTS

3.1 | Individual variation in arrival time—effect of migration departure date

Spring migration departure time and location (latitude), speed and stopover length all had statistically significant effects on arrival time when examined together (Supporting Information Table S1). Examining them separately revealed that departure time and latitude were of major importance in explaining individual variation within years, but not migration speed and stopovers duration (Figure 2). Thus, the early-arriving individuals were those that departed earlier and from more northern wintering locations, but not necessarily progressed faster. In fact, early departure date was associated with slower migration speed (Figure 3a; Supporting Information Appendix S3) and longer stopovers (GLMM with Poisson error distribution; $\beta = -0.032 \pm 0.006$, $t_{80} = -4.76$, $p < 0.001$), emphasizing that early-departing individuals arrived earlier at breeding grounds despite their slower migration progress. Correspondingly, individuals that departed earlier experienced lower thermal uplift during migration (Figure 3b) and exhibited higher flight energy expenditure (flight ODBA; Figure 3c). Additionally, earlier migrants had slightly less daytime *en route* which might be linked

to reduced thermals and slower migration (Supporting Information Appendix S3). Individual departure date was rather consistent between years (repeatability $r = 0.51 \pm 0.11$, $p < 0.001$) and arrival date (repeatability $r = 0.49 \pm 0.12$, $p < 0.001$).

3.2 | Wintering location and breeding success

Birds that wintered further south than the Sahel did not compensate for their longer migration distance by departing earlier; on the contrary, they departed later (Table 1) and arrived later at the breeding grounds (Figure 2b). Yet, their late arrival did not result in lower breeding success (see below), possibly because of better environmental conditions experienced in the southern-wintering grounds, reflected by higher NDVI and precipitation, milder temperatures (Table 1) and longer daylight time compared to the Sahel-wintering region (Table 1). Correspondingly, during stationary wintering days, southern-wintering birds moved half the amount of daily distance and spent relatively more time foraging compared to the Sahel-wintering individuals (Table 1). Individual wintering habits (Sahel vs. Southern) were moderately repeatable ($r = 0.45 \pm 0.17$, $p < 0.001$) indicating significant but not absolute consistency (six out of the 26 birds that wintered in the Sahel, also wintered south of the Sahel in other years, see Supporting Information Appendix S4 for more details). Wintering site selection was not affected by year or sex (GLMM with binomial error distribution; year: $F_{4,76} = 1.06$, $p = 0.38$; sex: $F_{1,76} = 0.004$, $p = 0.95$).

Wintering location and arrival time counteracted each other in affecting breeding success. Southern wintering and early arrival increased
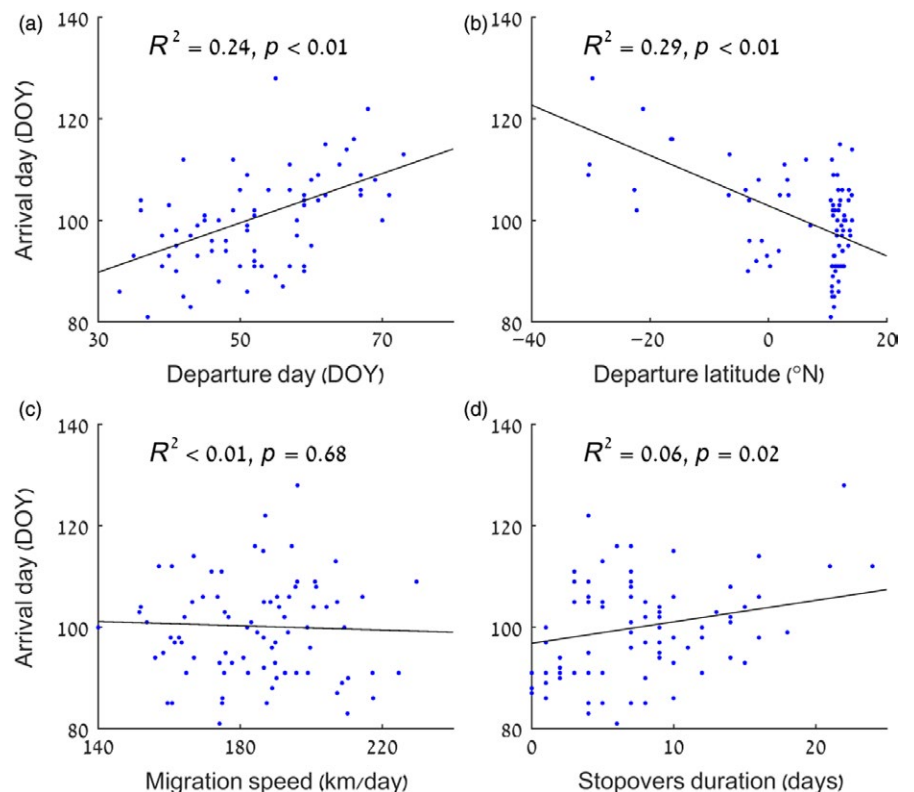

FIGURE 2 The relationships between arrival time (day of year, DOY) and spring migration properties: (a) departure time, (b) departure location, (c) migration speed and (d) stopover length based on 82 migrations from 34 individuals. Each plot's regression line and R^2—which is a marginal R^2 (Nakagawa & Schielzeth, 2013)—are based on a separate linear mixed model detailed in Supporting Information Table S2
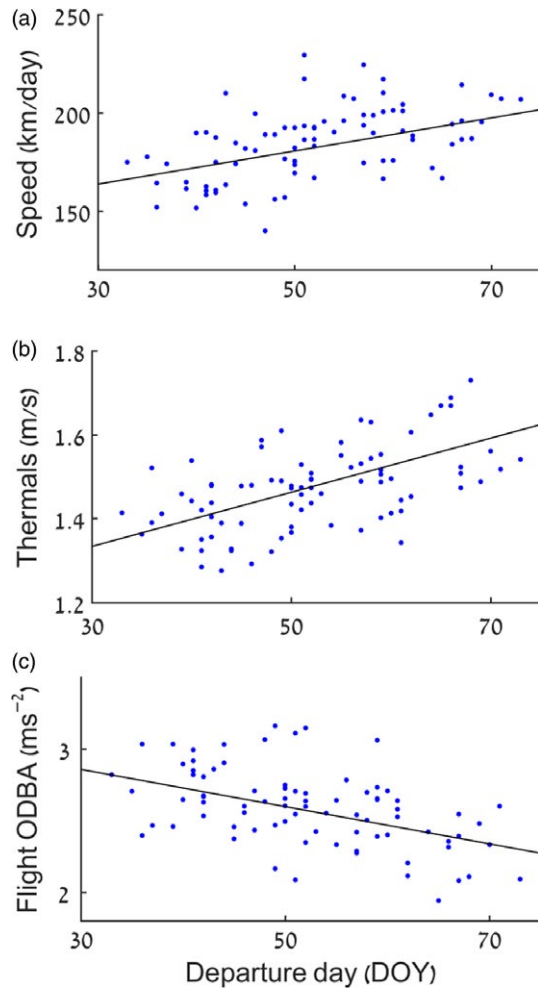
FIGURE 3 Effects of departure day on (a) migration speed (daily displacement), (b) thermal uplift experienced en route and (c) flight energy expenditure (82 tracks from 34 individuals). All effects are significant at $p < 0.001$ (LMMs; see Supporting Information Table S3 for statistical details) and their marginal R^2s are 0.18, 0.35 and 0.22, respectively

fledglings number (Table 2), but because southern wintering was associated with late arrival (Figure 2b), these factors counteracted each other when examined separately (i.e. without controlling for each other;

Supporting Information Table S5). Thus, wintering latitude affected breeding success only after controlling for arrival time and vice versa.

3.3 | Non-nesting storks

Non-nesting storks arrived later at the breeding grounds compared to nesting storks (LMM; $\beta = 23 \pm 3.3$ days, $t_{88} = 7.1$, $p < 0.001$, Supporting Information Figure S1). Thus, including the non-nesting storks in the above breeding success analysis increased the negative effect of late arrival (GLMM with Poisson distribution; arrival time: $\beta = -0.039 \pm 0.009$, $t_{84} = -4.12$, $p < 0.001$; wintering latitude: $\beta = -0.023 \pm 0.008$ days, $t_{84} = -2.87$, $p = 0.005$). Compared to nesting individuals, non-nesting birds departed later for spring migration (LMM; $\beta = 13.6 \pm 4.0$ days, $t_{88} = 3.41$, $p < 0.001$), took longer stopovers (GLMM with Poisson distribution; non-nesting: 12.25 ± 3.43 days, nesting: 7.88 ± 0.58, $t_{88} = 4.85$, $p < 0.001$) and migrated slower (LMM; $\beta = -15.44 \pm 6.17$ km/days, $t_{88} = 2.50$, $p = 0.014$), but no differences were found in wintering sites selection (Southern vs. Sahel; GLMM with binomial distribution; $\beta = 0.27 \pm 1.03$, $t_{88} = 0.26$, $p = 0.80$).

3.4 | Sex differences

Males arrived at the breeding area five days earlier than females (LMM; $\beta = -5.11 \pm 2.61$ days, $t_{80} = -1.96$, $p = 0.05$). However, the difference between sexes was not clear-cut; selecting randomly a male and a female from the same year yielded male-first arrival only in 68% of the cases (based on 10,000 random selections). Similarly, in seven cases in which arrival times of both pair-mates were available (originating from three tagged pairs across multiple years), the male arrived on average 6.5 days ahead of its female, but only in five of the cases was he the first. There were no sex-related differences in the other migration properties (departure time and location, speed, stopovers, fight ODBA; GLMMs, N.S.).

3.5 | Interannual variation

There were detectable differences in arrival time between the study years (LMM; $F_{4,52.8} = 7.7$, $p < 0.001$) with birds arriving earlier in

Parameter	Sahel (mean ± SE)	Southern (mean ± SE)	t_{80}	p
NDVI	0.24 ± 0.01	0.47 ± 0.02	11.59	<0.001
Precipitation (mm/day)	0.007 ± 0.006	7.13 ± 0.80	13.77	<0.001
Daytime temperature (°C)	30.48 ± 0.19	26.26 ± 0.60	−8.67	<0.001
Daylight (hours)	11.47 ± 0.01	12.28 ± 0.10	11.75	<0.001
Daily distance (km)	69.06 ± 3.10	35.59 ± 3.78	−6.28	<0.001
Relative foraging time	0.21 ± 0.01	0.30 ± 0.01	5.98	<0.001
Departure day (DOY)	49.8 ± 1.23	56.8 ± 1.82	2.29	0.02

TABLE 1 Comparisons of environmental conditions and behaviour during wintering between storks in the Sahel belt and in more southern-wintering sites (Figure 1). Each line details parameter differences that were examined using a LMM with wintering site (Sahel/Southern) as a fixed factor, *year* and *individual* as random factors and the parameter as the dependent variable. Daily distance and relative foraging time were calculated during stationary wintering days

Note. DOY: day of year; see Supporting Information Table S4 for random effect variances.

Parameter	β	SE	T_{76}	p
Arrival time (days)	−0.017	0.008	−2.14	0.03
Wintering latitude (°N)	−0.021	0.010	−2.07	0.04

Note. Year variance: 0.09; individual variance: <0.001.

2014 compared to *2012*, *2013* and *2015*, but not compared to *2016* (Figure 4a). Correspondingly, temperatures during migration were warmer in *2014* than in *2012*, *2013* and *2015* (Figure 4b). Two different migratory patterns underlie the relatively early arrival in *2014*: slower average migration speed in *2012* and *2015* that could be related to stronger headwinds during flight in these years (Figure 4) and longer stopovers in *2013* and *2015* that could be explained in part by lower thermal uplift conditions in 2013 (during flight and while on the ground, see Supporting Information Appendix S2; Figure 4). Correspondingly, migration speed was negatively associated with headwind velocity (LMM; $\beta = -9.59 \pm 2.80$ km/days,

FIGURE 4 Annual differences in (a) spring migration patterns and (b) environmental conditions *en route*. Underneath each migratory pattern in (a) is a potentially related environmental factor in (b). Z scores (standard deviations from the overall mean) are displayed to unify the variables on one Y-axis. *denotes significant differences **compared to year 2014** (*p* < 0.001; Tukey's post hoc test following a GLMM with *individual* as a random factor). Legend displays: year (sample size). The dashed line across the *headwind* bars in (b) marks zero wind speed (raw value), below which headwind is negative (i.e. positive tailwind)

$t_{80} = 3.42$, $p < 0.001$), and stopover duration was negatively affected by thermal uplift (GLMM with Poisson distribution; $\beta = -1.47 \pm 0.31$, $t_{80} = -4.72$, $p < 0.001$). Migration departure time and departure location did not differ between years (GLMMs; N.S). Year *2016* presented an intermediate arrival time value between year *2014* and the others (*2012*, *2013 and 2015*), not differing from any of the study years.

4 | DISCUSSION

Our study aimed to illuminate individual differences in arrival time by investigating the spring migration properties. We found that departing for spring migration early and from more northern locations underlie the early arrival of individuals within years (Figure 2); however, they came at the cost of migrating and wintering in less favourable conditions. Migration speed and stopover length mediated between-year differences in arrival time that were associated with annual variation in atmospheric conditions *en route* (Figure 4), but had smaller impacts on individual differences within years.

Storks that departed earlier for spring migration arrived earlier at the breeding grounds, despite migrating slower and taking more stopovers. This emphasizes the importance of migration departure time, in line with previous studies in migrating birds along different flyways (Lemke et al., 2013; Ouwehand & Both, 2017; Sergio et al., 2014). This relationship also explains why the prevailing effects of migration departure time and location masked the effect of migration speed on individual arrival time within years, when examined separately. A very similar association between early departure and slower migration was described in black kites (Sergio et al., 2014), and it was suggested that early-departing birds (which were generally older) mainly minimized energy expenditure and thus travelled more slowly, whereas late ones minimized migration time and travelled "in a hurry" to advance their arrival. In our case, we suggest a different explanation as earlier migrants were exposed to less favourable conditions of weaker thermal uplift *en route*, an essential transport resource for soaring birds (Hedenstrom, 1993; Sapir, Wikelski, McCue, Pinshow, & Nathan, 2010). This resulted in higher flight costs (flight ODBA), most likely due to using relatively more costly flapping vs. gliding flight (Rotics et al., 2016). Thus, migrating earlier was more strenuous in terms of flight effort which can also explain the slower migration progress. More notably, these findings present explicit migration-related costs of early arrival at breeding grounds that have not been acknowledged thus far, namely energy and time costs induced by unfavourable conditions *en route*. This adds up to harsh environmental conditions at the breeding areas themselves upon early arrival (Møller, 1994; Newton, 2008).

Early migrating birds need to be sufficiently fit to cope with these costs, and correspondingly, bird physical condition has been found to affect departure timing (Cooper, Sherry, & Marra, 2015). Our findings showed that migration departure time was a rather consistent
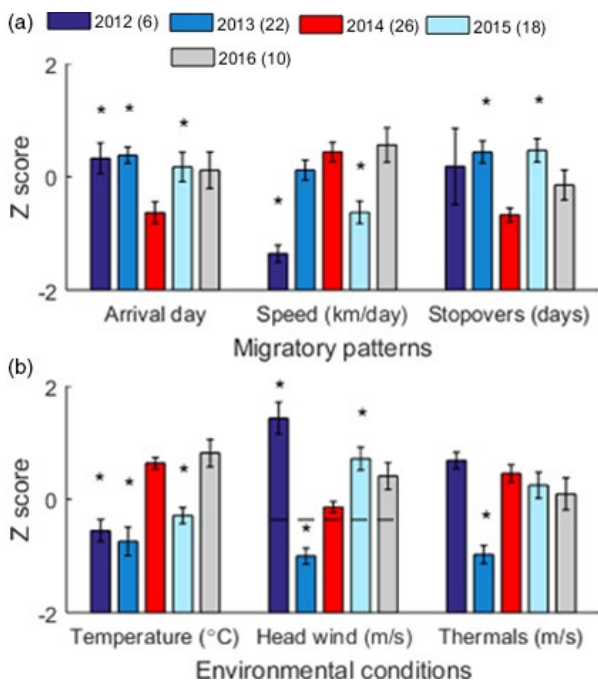
feature of the individual, in accordance with previous findings from different flyways (Tottrup et al., 2012; Yamamoto et al., 2014), likely related to sex (discussed below), age and individual quality (Dittmann & Becker, 2003; Matyjasiak, 2013; Newton, 2008; Sergio et al., 2014). Thus, presumably the fittest storks started migrating and arrived earlier at the breeding grounds. Alongside its costs, our data reconfirmed the renowned association of early arrival with enhanced breeding success, after controlling for wintering location (latitude).

Storks that wintered at more southern latitudes arrived later at the breeding grounds. Obviously, they took a longer journey, but notably, they also departed later. This hints that the departure decision was irrespective of the wintering distance, but possibly relied on an endogenous circannual clock (Gwinner, 1996) tuned with external signals leading to a delayed departure at more southern-wintering latitudes. Such potential signals could be day-length (Kumar et al., 2010) and temperature (Sokolov & Tsvey, 2016) that have different trends during spring in the different wintering sites. We propose that the variation in departure time was related to individual quality within wintering sites and to relevant environmental cues between sites. In some contrast to our findings, birds in better wintering habitats were reported to advance their departure time (Paxton & Moore, 2015), stressing that the internal and external factors regulating migration onset vary between study systems and should be further investigated.

Even though they arrived late to the breeding grounds, storks from southern-wintering sites did not suffer from lower breeding success. In fact, wintering at southern latitudes enhanced breeding success after controlling for arrival date. A probable cause was the better environmental conditions at more southern-wintering sites, involving milder temperatures and increased day-length, precipitation and NDVI. The latter was positively correlated with insect abundance (Schlaich et al., 2016), a prime food resource of white storks (Cheriak, Barbraud, Doumandji, & Bouguessa, 2014). Correspondingly, southern-wintering storks moved half the daily distance compared to Sahel-wintering ones during winter, presumably due to more abundant resources. Similarly, Montagu's Harriers (*Circus pygargus*) wintering in the Sahel exhibited a negative NDVI-daily distance correlation (Schlaich et al., 2016). Additionally, southern-wintering storks spent relatively more time foraging, probably due to reduced movement time and extended daylight time. These enhancements may explain the remarkable lengthening of migration distance exhibited by some of the individuals, wintering up to 4,500 km farther south than the central wintering region (Figure 1). Furthermore, our findings add support to the elusive evidence of carry-over effects (Lok et al., 2017; Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004), in which wintering conditions have delayed impacts later on, during breeding.

There was an apparent trade-off between arrival time and wintering latitude.

Early-arriving birds wintered and migrated under less favourable environmental conditions but enjoyed the multiple advantages of early arrival (discussed in the Introduction). Contrarily, southern-wintering birds experienced better environmental conditions during

wintering and during their delayed migration, arriving later at breeding grounds but probably less exhausted. These two factors acted in opposite directions, balancing each other in respect to breeding success, such that early arrival as well as more southern wintering enhanced fledgling number, but only after controlling for each other's effect. At the individual level, storks rather consistently used one of the two strategies. From population and evolutionary perspectives, divergent wintering strategies reflect migratory plasticity that enhances the storks ability to adjust to global changes (Gordo & Sanz, 2006) and to cope with highly variable environmental conditions, like rainfall in the Sahel (Nevoux, Barbraud, & Barbraud, 2008). More broadly, bird migration is a flexible phenomenon (Alerstam, Hedenström, & Åkesson, 2003; Newton, 2008), and many species display significant variation in migration flyways between and within populations (e.g. Barbraud, Barbraud, & Barbraud, 1999; Shamoun-Baranes, Burant, Loon, Bouten, & Camphuysen, 2017; Weimerskirch et al., 2017). Further research on the differences and trade-offs between migration strategies would advance our knowledge on the evolution and conservation of bird migration.

Even though early arrival and southern-wintering balanced each other in affecting fledgling numbers, there is still an advantage for early arrival in the form of having earlier-hatching offspring that typically have higher survival (Lok et al., 2017; Monros et al., 2002; Verboven & Visser, 1998), as was also seen in our study population (S. Rotics, unpublished data). Similarly, spoonbills (*Platalea leucorodia*) that wintered farther away arrived later at their breeding grounds and still did not raise less offspring, but had lower offspring recruitment rates (Lok et al., 2017). This could explain why most of our storks wintered in the Sahel, preferring early arrival over wintering habitat quality. There might also be survival implications for the different migratory strategies (e.g. Lok, Overdijk, Tinbergen, & Piersma, 2011; Rotics et al., 2017). Better wintering and migrating conditions may promote survival of southern-wintering individuals, or on the other hand, reduced migration risk may benefit ones that wintered closer to breeding grounds. Such implications, however, could not be evaluated here due to the nature of the data; only tracks of returning adults were available (see Methods) and disappearance could not be confidently assigned to mortality vs. large breeding-site displacement.

The above wintering-arrival time trade-off can explain the decrease in the effect of arrival date on stork breeding success in Spain (Gordo et al., 2013) and the lack of differences in fledgling number between sedentary and migratory storks in France (Massemin-Challet et al., 2006), assuming that the early-arriving/sedentary birds wintered in lower-quality habitats. However, our results contradict previous stork studies that found an effect of arrival time on breeding success without controlling for wintering location (Fulin et al., 2009; Janiszewski et al., 2013; Kosicki et al., 2004). One potential explanation is that wintering site variation was lower in these earlier studies as compared to our study population. This could arise from inherent population differences or from temporal changes—a recent trend of increase in storks wintering variation (Martín, Onrubia, de la Cruz, & Ferrer, 2016). Alternatively, much larger sample sizes in

previous studies ($n > 1{,}000$ in Fulin et al., 2009; Janiszewski et al., 2013) allowed detection of the effect of arrival time independently. Hypothetically, arrival time might have less prominent effects in the long-term monogamous white stork, since the individual does not need to find a new pair mate, but just to arrive "on time" to rejoin its former partner.

In eight cases in our study, adult storks that returned to the breeding grounds did not nest. Their arrival dates were exceptionally late as they departed for spring migration two weeks later, migrated slower and took longer stopovers, compared to nesting birds. These patterns may imply that the decision not to nest was made in advance and was then manifested by more relaxed spring migration behaviour. Alternatively, tardy migration and failure to nest might both be the outcomes of inferior physical conditions.

Male storks arrived at the breeding grounds on average five days ahead of females, similar to a large number a species in which protandry was described (Cadahia et al., 2017; Saino et al., 2010). However, the sex differences in stork arrival were not very strong ($p = 0.05$), and the divide was not absolute (sometimes the female arrived first). We believe that the sensitive tracking data allowed us to identify them here and the use of less precise nest-monitoring methods may account for the ambiguity regarding stork protandry in previous studies (Barbraud & Barbraud, 1999; Tortosa & Redondo, 1992; Vergara et al., 2007). Thus, assuming the first stork arriving at the nest is the male, as in Gordo et al. (2013), would be correct in ca. 70% of the cases according to our data.

Interannual differences in arrival time reconfirmed the association between early arrival and higher temperatures *en route* (Gordo et al., 2013; Huppop & Huppop, 2003; Marra et al., 2005; Vaitkuviene et al., 2015). Linking stork migration tracks with atmospheric factors uncovered two nonexclusive mechanisms that were responsible for this association: (1) lower temperatures were accompanied by north-to-south winds (that possibly brought cold weather along the migration range) which presented stronger headwinds for the northward-migrating storks resulting in slower migration speed. (2) Lower thermal uplift *en route* in colder years was linked with longer stopover time, probably due to elevated flight effort (Rotics et al., 2016). Thus, delayed arrival in colder years resulted from increased headwinds and/or reduced thermal uplift. Correspondingly, winds are known to affect flight speed (Shamoun-Baranes et al., 2003; Vansteelant et al., 2015) and strong thermal uplift reduces flight effort (Chevallier et al., 2010; Harel et al., 2016; Sapir et al., 2010) and stopover duration (Duerr et al., 2015; Nourani & Yamaguchi, 2017). However, as far as we know, this study is the first to link these atmospheric factors explicitly with interannual differences in arrival time.

In summary, distinct factors mediated interindividual (within year) and interannual variation in arrival time, similar to previous findings in black-tailed godwits (Gunnarsson et al., 2006). We suggest that migration departure timing and location were chiefly determined by intrinsic factors and therefore explained arrival time variation within years, whereas migration speed and stopover were more related to environmental factors, accounting for the variation between years. At the individual level, our study emphasized the importance of spring migration departure time and pointed out increased flight effort for early migrants, as well as a potential trade-off between early arrival and wintering habitat quality. Considering the significance of spring departure timing, more knowledge on the endogenous and external mechanisms that modulate bird departure decisions is required. This, together with the insights on arrival date reported here, can facilitate forecasting migrating birds' responses under climate change scenarios.

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AUTHOR'S CONTRIBUTIONS

S.R., R.N., F.J. and M.W. conceived the idea. S.R. and M.K. carried out the field work with the help of S.F., U.E., M.W. and D.Z. S.R. wrote the first draft and all authors contributed to the revisions.

DATA ACCESSIBILITY

The GPS-ACC data are available in Movebank Data Repository with doi: https://doi.org/10.5441/001.1.v8d24552 (Rotics et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.