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

Shay Rotics1, Michael Kaatz2, Sondra Turjeman1, Damaris Zurell3, Martin Wikelski4,5, Nir Sapi6, Ute Eggers7, Wolfgang Fiedler4,5, Florian Jeltsch8, Ran Nathan1

1Movement Ecology Laboratory, Department of Ecology, Evolution and Behaviour, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem, Israel; 2Vogelschutzwarte Storchenhof Loburg e.V., Loburg, Germany; 3Geography Department, Humboldt-Universität zu Berlin, Berlin, Germany; 4Department of Migration and Immuno-Ecology, Max-Planck-Institute for Ornithology, Radolfzell, Germany; 5Department of Biology, University of Konstanz, Konstanz, Germany; 6The Animal Flight Laboratory, Department of Evolutionary and Environmental Biology, University of Haifa, Haifa, Israel; 7Department of Plant Ecology and Conservation Biology, Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany and 8Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

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.

**KEYWORDS**
arrival date, bird migration, breeding success, carry-over effects, Ciconia ciconia, climate change, white stork

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; Möller, 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, & Philimore, 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; Matyjasik, 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 & Barraud, 1999), but vital clashes over nests are fairly common (pers. obs.; Wuczenski, 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.

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 & Barraud, 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.

![Figure 1](attachment://figure1.png)

**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 [Colour figure can be viewed at wileyonlinelibrary.com]
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 winter-
ing 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, ther-
mal 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 ap-
proaching 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 pre-
ferred 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 num-
ber from January 1.

Departure date was identified with a backward-forward al-
gorithm; 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
movement <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 expendi-
ture 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, ef-
teffects of migrating in different geographical regions (Chevallier et al.,
2010; Klaassen, Strandberg, Hake, & Alerstam, 2008), as for exam-
ple, 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 loca-
tion 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 tem-
perature (7:00–16:00 GMT) and daylight length (calculated in Matlab
with the sun cycle function, Pawlovicz, 2009), and the wintering be-
haviour: daily distance in stationary days, and relative time spent
foraging. The latter was the ratio of walking and pecking records di-
vided 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 breed-
ings areas 23 ± 3 days after the average arrival time of nesting birds,
and were thus excluded from the analyses except for when por-
traying 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 prop-
teurs 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 ar-
ival time was examined separately with a linear mixed model (LMM;
year and individual as random factors) and the models' likelihood and
marginal R² were compared. Marginal R² 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 ismeans() R
function (Lenth, 2016). Individual consistency in departure time
and location was examined by calculating repeatability across years (Intraclass correlation) using the rptR 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; $\beta = -0.032 \pm 0.006$, $t_{50} = -4.76$, $p < 0.001$), 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

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**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 (Colour figure can be viewed at wileyonlinelibrary.com)
fledglings number (Table 2), but because southern wintering was as-
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 nega-
tive effect of late arrival (GLMM with Poisson distribution; arrival
time: \(\beta = -0.039 \pm 0.009, t_{54} = -4.12, p < 0.001\); wintering latitude:
\(\beta = -0.023 \pm 0.008\) days, \(t_{54} = -2.87, p = 0.005\)). 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 \pm 3.43 days, nesting: 7.88 \pm 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 se-
lection (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, \(t_{88} = -1.96, p = 0.05\)). However, the dif-
ference 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, flight 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

![Figure 3](image_url)

**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 \(R^2\)’s are 0.18,
0.35 and 0.22, respectively (Colour figure can be viewed at
wileyonlinelibrary.com)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Sahel (mean ± SE)</th>
<th>Southern (mean ± SE)</th>
<th>(t_{88})</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NDVI</td>
<td>0.24 ± 0.01</td>
<td>0.47 ± 0.02</td>
<td>11.59</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Precipitation (mm/day)</td>
<td>0.007 ± 0.006</td>
<td>0.073 ± 0.080</td>
<td>13.77</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Daytime temperature (°C)</td>
<td>30.48 ± 0.19</td>
<td>26.26 ± 0.60</td>
<td>-8.67</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Daylight (hours)</td>
<td>11.47 ± 0.01</td>
<td>12.28 ± 0.10</td>
<td>11.75</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Daily distance (km)</td>
<td>69.06 ± 3.10</td>
<td>35.59 ± 3.78</td>
<td>-6.28</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Relative foraging time</td>
<td>0.21 ± 0.01</td>
<td>0.30 ± 0.01</td>
<td>5.98</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Departure day (DOY)</td>
<td>49.8 ± 1.23</td>
<td>56.8 ± 1.82</td>
<td>2.29</td>
<td>0.02</td>
</tr>
</tbody>
</table>

**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.
TABLE 2  Arrival time and wintering latitude effects on breeding success (fledglings number) based on a GLMM with Poisson error distribution and year and individual as random factors. Lower wintering latitudes mean more southern locations

<table>
<thead>
<tr>
<th>Parameter</th>
<th>β</th>
<th>SE</th>
<th>TSE</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arrival time (days)</td>
<td>-0.017</td>
<td>0.008</td>
<td>-2.14</td>
<td>0.03</td>
</tr>
<tr>
<td>Wintering latitude (°N)</td>
<td>-0.021</td>
<td>0.010</td>
<td>-2.07</td>
<td>0.04</td>
</tr>
</tbody>
</table>

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, \( t_{90} = 3.42, p < 0.001 \), and stopover duration was negatively affected by thermal uplift (GLMM with Poisson distribution; \( \beta = -1.47 \pm 0.31, t_{90} = -4.72, p < 0.001 \)). 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 (Tøttrup 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 confirmed 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 (Cherki, 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 fledging 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 fledging 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 fledging 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 (Cadaia 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; Vansteelandt 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 (Duerst 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.

ORCID

Shay Rotics http://orcid.org/0000-0002-3858-1811

Damaris Zurell http://orcid.org/0000-0002-4628-3558

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