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Anthropogenic food subsidies reshape the migratory behaviour of a long-distance migrant



J. Marcelino^{a,*}, A.M.A. Franco^b, M. Acácio^{b,c}, A. Soriano-Redondo^{d,e,f,g,h}, F. Moreira^{f,g,h,i}, I. Catry^{f,g,h,i}

^a Centre for Applied Ecology "Prof. Baeta Neves" (CEABN-InBIO), School of Agriculture, University of Lisbon, Tapada da Ajuda, Lisboa 1349-017, Portugal

^b School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

^c School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel

^d Helsinki Lab of Interdisciplinary Conservation Science (HELICS), Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland

^e Helsinki Institute of Sustainability Science (HELSUS), University of Helsinki, Helsinki, Finland

^f CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal

^g CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, 1349-017 Lisboa, Portugal

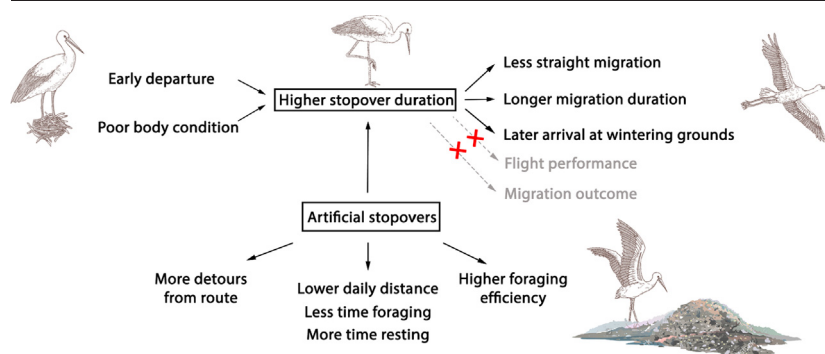
^h BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal

ⁱ REN Biodiversity Chair, CIBIO/InBIO-UP, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-601 Vairão, Portugal

HIGHLIGHTS

- White storks spend one-third of their migration time in natural and artificial stopovers.
- Stopover strategy influences migration duration and arrival date.
- Stopping at artificial sites reduces foraging time and increases foraging efficiency.
- Landfills and waste sites are attractive stopovers but delay arrival timings.
- Closure of landfill sites following EU directives may impact waste-reliant migrants.

GRAPHICAL ABSTRACT



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ABSTRACT

Bird migratory journeys are often long and hostile, requiring high energetic expenditure, and thus forcing birds to pause between migratory flights. Stopover sites allow migrants to replenish fuel reserves and rest, being crucial for the success of migration. Worldwide, the increasing accumulation of waste on landfills and rubbish dumps has been described to provide superabundant food resources for many bird species not only during the breeding and wintering seasons but also during migration, being used as stopover sites.

Using GPS-tracking data of juvenile white storks (*Ciconia ciconia*) during their first migration from the Iberia Peninsula to the sub-Saharan wintering grounds, we uncover the effects of stopping *en route* on individual migratory performance. Particularly, we examine the benefits of stopping at artificial sites (landfills and rubbish dumps) when compared to natural stopover sites (wetlands, agricultural or desert areas) and explore the influence of anthropogenic food resources on storks' migratory strategies.

Overall, white storks spent up to one-third of the migration in stopovers. We found that birds that stopped for longer periods made more detours, increasing migration duration by half a day for each stopover day. Stopping more often did not reflect on increasing in-flight energetic efficiency nor the likelihood of completing the migration.

Juvenile storks used artificial sites in 80 % of the stopover days, spending 45 % less time and 10 % less energy foraging than when using natural stopovers. While stopping in landfills did not translate into differences in migratory

* Corresponding author.

E-mail address: joanamarcelino@gmail.com (J. Marcelino).

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performance, individuals in poor body condition possibly rely on these sites to improve body weight before proceeding, enabling them to successfully complete migration.

Artificial stopover sites are attractive and likely increase the number and duration of stops for white storks. Even though the consequences of arriving late at the wintering grounds are unknown, it can lead to cascading consequences, influencing individual fitness and population dynamics.

1. Introduction

Migration is a costly endeavour regarding time, energy and survival (Flack et al., 2016; Klaassen et al., 2014; Somveille et al., 2018; Soriano-Redondo et al., 2020a, 2020b), hence individuals need to balance the need for flying to reach their destination and the need to stop to refuel and rest. Indeed, during migration, most bird species alternate between periods of active migration and periods of rest and refuelling, commonly named stopovers. To increase survival, individuals adopt the best migratory strategy to ensure that the benefits of migration outweigh its risks (Zhao et al., 2017). To this end, stopovers play a crucial role, as birds use this time to recover and refuel, for social interactions and to wait for suitable weather conditions for migration (Linscott and Senner, 2021; Miller et al., 2016).

In general, birds can adopt two different types of migratory strategy depending on their size and flight mode (Zhao et al., 2017): while small birds use flapping flight and choose to minimise migration duration (time-minimizers; Cochran et al., 2008; Karlsson et al., 2012), large birds usually use thermal soaring, taking advantage of thermal updrafts and maximising flight speed and efficiency (energy-minimizers; Hedenstrom, 1993). Even so, several species of soaring birds need to refuel along the way, especially when crossing ecological barriers that require additional energetic investment (Arizaga et al., 2018; García-Macía et al., 2022; Monti et al., 2018).

Stopover selection is not random: individuals select areas of high food availability, allowing migrants to restore depleted body reserves and accumulate fat deposits to proceed with their journeys (Moore, 2018), and ensuring migration success (e.g. Xu et al., 2019). However, stopover duration can also exponentiate predation likelihood (Lank et al., 2003) and delay arrival at the wintering sites (Blount et al., 2021), jeopardizing chances of encountering the best habitat quality and food availability (Newton, 2008).

Changes in habitat quality, often driven by human activities, can modify the accessibility to foraging resources at stopover sites. In some cases, anthropogenic habitat alterations lead to the degradation and loss of stopover sites, contributing to populational declines (Baker et al., 2004; Bayly et al., 2018; Newton, 2006). However, in other cases, species can benefit from changes in the abundance of foraging resources as a result of human activities. Landfills and dumps (i.e., artificial stopovers) provide rapid and high food availability during migration and indeed, previous studies have shown that several migratory species use these sites not only during breeding or wintering (Birdlife International, 2015; Gilbert et al., 2016; Soriano-Redondo et al., 2021), but also during migration (Arizaga et al., 2018; Birdlife International, 2015; Shephard et al., 2015). These artificial stopovers gather thousands of birds in the migration season and are particularly important when changes in climate limit access to natural foraging sites (Birdlife International, 2015). However, the extent to which artificial stopover sites influence migratory decisions, determine the migratory strategy and the migratory success is yet unknown, despite being crucial to understanding how bird species may adapt to further anthropogenic changes.

Here, we investigate the stopover ecology of the white stork (*Ciconia ciconia*) migrating through the western European flyway and, more specifically, how the use of *en route* artificial stopovers (landfills and rubbish dumps) affects their migratory strategy and performance. White storks are long-distance, social migrants, where juveniles travel with adults in mixed flocks. Until the 1980s, in Iberia, white storks were fully migratory, wintering in Sub-Saharan Africa. However, their migratory behaviour is changing and the majority of adult storks now remain in Iberia during the winter, likely due to increased year-round food availability in landfill

sites and increasingly warmer winters (Catry et al., 2017; Gordo, 2007). Yet, even though adults are predominantly residents, a large proportion of first-year juveniles still migrate to the Sahel.

In this study, we investigate the stopover ecology of juvenile white storks on their first migratory journey, travelling from the Iberian Peninsula to the Sahel. To that end, we (1) investigate the influence of stopover duration on migratory performance – by analysing the effect of stopover duration on tortuosity of the migration route, migration duration, arrival dates, flight energy expenditure and the likelihood of completing migration; and (2) identify the determinants of stopover duration – by analysing the effects of departure date and body condition at fledgling on stopover duration. Finally, (3) we assess the time and energy costs of using natural vs artificial stopovers and determine if favouring one resource type over the other impacts the migratory strategy of first-year white storks.

We hypothesise that storks' stopover strategy will influence their migratory performance, with birds that stop for longer periods having longer migrations and arriving later at the wintering areas but at a lower energetic cost. Moreover, we predict that stopover duration will be influenced by migration timing and body condition, as early birds and the ones in better body condition are expected to spend less time in stopovers (Anderson et al., 2019; Newton, 2008), reducing overall migration time and increasing the likelihood of surviving their first migration (Newton, 2008). Finally, as artificial stopovers provide predictable and abundant food resources, we predict that birds stopping in these areas will have higher foraging success than those using natural stopovers more often, decreasing stopover duration. Overall, these results can improve our knowledge of migration strategies, help identify the impacts of anthropogenic land use changes on bird migration and assist in developing comprehensive conservation management plans for migratory bird species. Specifically, this work can assist in the establishment of guidelines for migratory bird conservation in the waste management sector.

2. Methods

2.1. Data collection

We used GPS/GPRS loggers to track the autumn migration of 93 first-year juvenile white storks tagged in the Iberian Peninsula (retrieved from 22 colonies in the south of Portugal, see locations in SM1) between 2016 and 2020. After excluding 12 individuals wintering in north Morocco, and thus with different metrics of the ones wintering in the Sahel, the final dataset included 81 individuals. We retrieved pre-fledging juveniles (60 to 65 days old) from their nests for tag deployment and returned them afterwards (Gilbert et al., 2016). Flyway 50 GPS/GSM backpack loggers (Movetech Telemetry) were attached using a Teflon harness (Gilbert et al., 2016; Soriano-Redondo et al., 2020a, 2020b), and morphometric measurements (weight, g; wing length, cm) were taken for each individual during tag deployment. Loggers were programmed to take a GPS position and tri-axial acceleration bursts (9 consecutive GPS positions at 1 Hz) every 20 min. From each acceleration burst, it was possible to compute Overall Dynamic Body Acceleration (ODBA, g) and bird behaviour. ODBA can be used as a proxy for energy expenditure (Gleiss et al., 2011) and was calculated by subtracting each acceleration point from a running mean of 4 s for each axis and summing the resulting values for all three axes (Soriano-Redondo et al., 2021). To determine bird behaviour, we trained random forest machine-learning algorithms to identify four different behaviours (foraging, resting, soaring and flapping flight) from

manually classified acceleration bursts (see Soriano-Redondo et al., 2021 for more details).

2.2. Stopover identification

We classified each migration day as active migration day (a day spent migrating) or stopover day (a day spent stopping over). White storks migrating from the Iberian Peninsula to the Sahel mostly move in a southward direction, and the direction of movement is more random during stopovers, thus, daily southern or northern displacement was classified according to their daily displacement (distance travelled between consecutive night roosts). The performance of this binary classification was assessed using the receiver operating characteristics curve (ROC; Fawcett, 2006). ROC optimal threshold was 36.9 km (specificity = 0.84, sensitivity = 0.64, AUC = 0.769, SM2), and thus, stopover and migratory days were defined as days when birds moved less or >37 km, respectively. ROC curves, threshold and the Area Under the Curve (AUC) were computed using functions “roc”, “coords” and “auc”, respectively, from package “pROC” (Robin et al., 2011), in R (R Core Team, 2020).

Stopover sites were identified from the centroids of 75 % kernel ($h = 0.05$) of stopover day locations of all individuals pooled together, as we wanted to identify the utilization distribution of common stopover areas. Smaller stopover sites (used by few individuals and thus not detected in the kernel) were added manually. We computed the centroid for each kernel (stopover site) and all stopover days were attributed to a respective stopover site based on proximity to the stopover site centroid. Stopover sites were classified as artificial or natural by manually inspecting satellite images (e.g., SM3). Artificial stopover sites included landfills, rubbish dumps or waste disposal sites near urban areas, while natural stopover sites included habitats such as wetlands, agricultural or desert areas. Stopover sites were then ranked on a scale of importance first according to the number of individuals stopping over at each site, and secondly, when tied, to their stopping duration (in days). Therefore, a higher-ranking stopover site would be a site where more individuals stopped for a longer period.

2.3. Influence of stopover strategy on migratory performance

White storks cross three ecological barriers while migrating to the sub-Saharan wintering grounds: the Strait of Gibraltar, the Atlas Mountains, and the Sahara Desert. The crossing of the Atlas Mountains marks the start of the crossing of the Sahara Desert, during which there are very few artificial stopovers. Thus, we divided migration into two legs (before and after crossing the Atlas Mountains) and computed, for each leg, descriptive metrics of storks' migratory performance that could be influenced by stopover duration.

We calculated migration duration (in days), tortuosity of the migratory route, standardized arrival date (in days), mean flight energy expenditure (ODBA, in g) and the likelihood of completing migration as metrics of storks' migratory performance.

Migration duration was computed as the difference between the start (departure) and end (arrival at the wintering site) of migration. Departure date was defined as the first of three consecutive days a stork moved >60 km between roosts, outside the breeding area (calculated as the 90 % kernel of June GPS locations), while the arrival date was defined as the first three days a stork moved <60 km inside the wintering area (Soriano-Redondo et al., 2020a, 2020b, see SM4 for more details). Standardized arrival date was computed as the difference in days to the mean population arrival date.

The route tortuosity index was used as a measure of tortuosity of the migratory route, quantifying the detours from the optimal route. To define the optimal route, we computed the centreline of the minimum concave hull polygon for 14 birds that completed migration without using stopovers. As there is considerable variation on the route adopted when crossing the Sahara, depending on the area storks select for wintering (Fig. 1), we have only considered the route up to crossing the Atlas Mountains.

Therefore, the route tortuosity index was determined for each bird as the sum of daily displacement (dd) in the first leg, divided by the length of the centreline (820 km, Eq. (1), SM5).

$$\text{Route tortuosity index} = \frac{dd \text{ leg1}}{820 \text{ km}} \quad (1)$$

Flight energy expenditure was computed as the mean ODBA of all accelerometer bursts classified as flight fixes, in which higher ODBA values translate into higher energy expenditure and lower values, into the opposite.

We implemented general linear models (GLMs), using overall stopover duration (defined as the number of stopover days before crossing the Atlas) as the explanatory variable and the metrics of migratory performance (route tortuosity index, migration duration, standardized arrival date and flight energy expenditure – mean value for each individual) as response variables to investigate how stopping *en route* influenced the migratory performance. We compared the metrics of migratory performance between stopping and non-stopping birds, using logistic GLMs and then selected individuals that completed the migration and stopped along the route ($n = 41$), removing non-stopping individuals to avoid zero-related confounding effects.

The likelihood of completing migration, i.e., surviving until the arrival to the wintering grounds, was computed using the extended Cox proportional hazards model for time-dependent variables (Therneau and Grambsch, 2000), using stopover duration as a predictor. Mortality was identified through analysis of GPS and ACC data, and the date of death was defined as the first motionless day. Mortality was confirmed in the field whenever possible. Due to the lack of GSM network, it is difficult to confirm bird mortality in the Sahara Desert. This area is a hotspot of mortality of migratory birds (Klaassen et al., 2014; Strandberg et al., 2010), including white storks (Cheng et al., 2019). Individuals who disappeared in the Sahara Desert without transmitting data afterwards were treated as mortalities, as they were not sighted again in Portugal in the following years and are most probably fatalities. Individuals alive at the end of migration or that disappeared outside the Sahara area were censored (Therneau and Grambsch, 2000). For this analysis, we used all the tagged individuals except for three birds that were removed due to logger failure ($n = 78$). The model was fitted using the “coxph” function of the “survival” package. The proportional hazards assumption was met.

2.4. Determinants of stopover strategy

To investigate the drivers of stopover duration, we analysed the relationship between stopover duration and two predictors: body condition and departure date.

Body condition was calculated as the standardized residuals from a linear model of the relationship between weight (g) and wing length (mm). As these measurements were taken on the day of the deployment, in which different juveniles could have been of different ages, small variations in the body condition index could be due to age. Thus, individuals were divided into three categories: “poor”, “normal”, and “good”, according to the quantiles (25 %, 50 %, 25 %) of the population sample, as the standardized residuals seem to follow a normal distribution (see SM6). There were no significant differences in the stopover duration between individuals with “good” and “normal” body condition, thus these categories were joined in a unique category (see SM6 for details), as individuals in poorer body condition might struggle to complete their migration, when compared with individuals in normal and good body condition. The body condition was then analysed as a two-category variable named “poor” and “normal-good”.

Departure date was standardized based on the difference in the number of days to the mean population departure date. We used a GLM with body condition and standardized departure date as predictors of the stopover duration, for all individuals that completed migration up to the Sahara Desert, including non-stopping birds ($n = 65$).

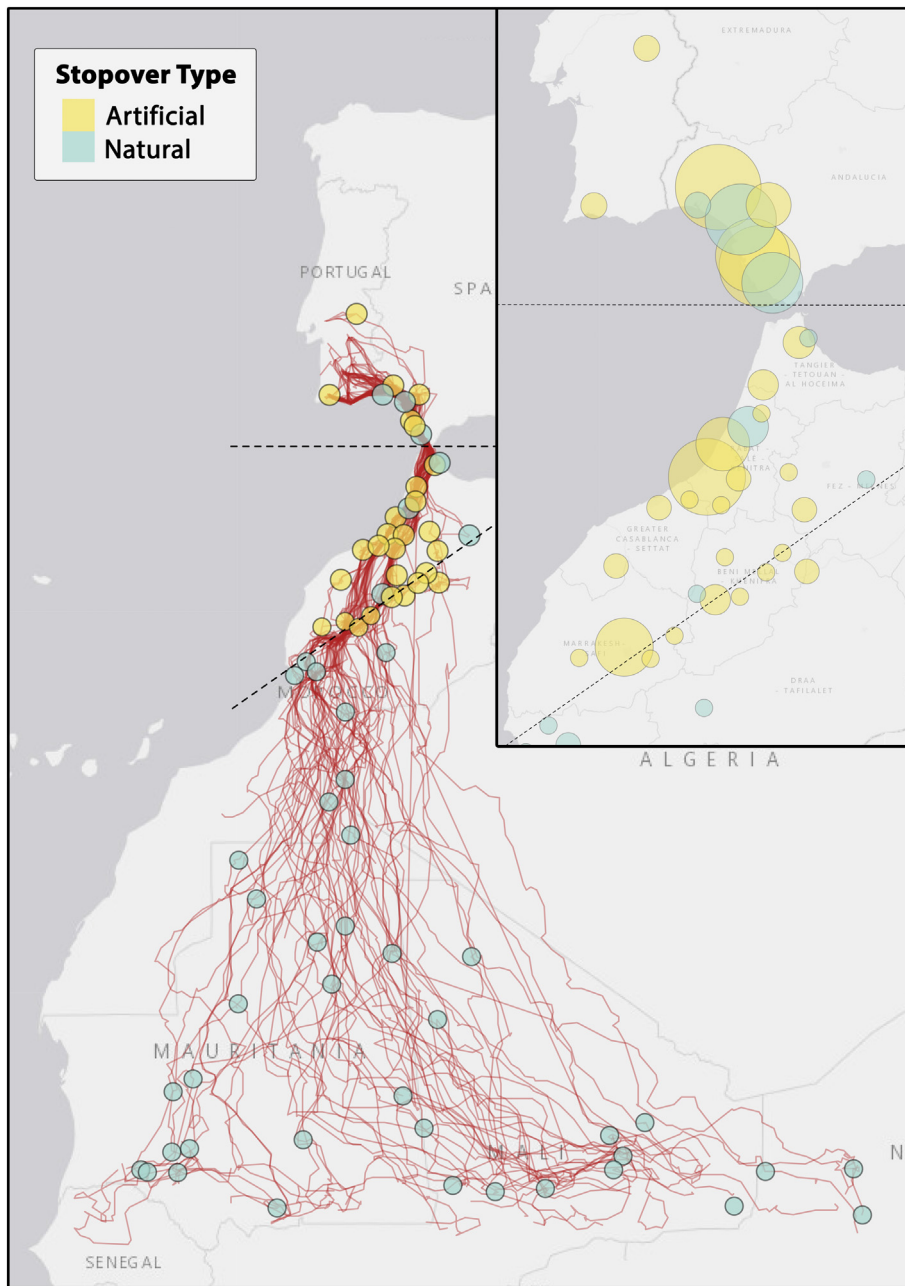


Fig. 1. Autumn migration routes and stopover sites of first-year white storks tracked from the Iberian Peninsula to the Sahelian wintering grounds. Tracks in red; yellow and blue circles represent artificial ($n = 28$) and natural stopover sites ($n = 46$), respectively. The zoomed map represents the stopover importance in legs 1 and 2. Larger circles represent the most important stopovers (ranked according to the number of individuals stopping over and their stopping duration), while smaller ones represent less important stopovers. Black dashed lines represent leg divisions. Leg 1 represents the area from Portugal up to the Atlas Mountains (defined by the equation $y = 0.58x + 36.12$), and leg 2 from the Atlas Mountains up to the south of the Sahara Desert.

2.5. Use of artificial and natural stopover sites

To investigate the advantages of stopping in artificial and natural stopover sites, we tested the differences between the two stopover types in the following metrics: daily relative foraging time (%), daily relative resting time (%), mean foraging ODBA (g, a proxy for foraging efficiency, Soriano-Redondo et al., 2021), daily distance travelled (km), and stopover detour distance (km). Daily relative foraging time was computed by dividing the number of bursts classified as foraging by the total number of bursts in a day. Relative resting time was computed by dividing the number of bursts classified as foraging by the total number of bursts. Mean forage ODBA was calculated as the daily mean ODBA for the foraging bursts: lower mean foraging ODBA values

indicate lower energy expenditure while foraging and, thus, higher foraging efficiency. Daily distance travelled was defined as the summed distance between consecutive locations for each stopover day (Soriano-Redondo et al., 2021). Stopover detour distance was defined as the Euclidean distance from the stopover to the nearest point of the optimal route.

Relative foraging time, relative resting time, mean foraging ODBA and distance travelled were compared between stopover types using generalized linear mixed models (GLMMs). The individual ID was used as a random variable to control for individual variability. We found no autocorrelation of order 1 (Durbin-Watson Test = [1.93–2.12], Phi Correlation ≈ 0). Stopover detour distance was compared between stopover types using GLMs.

To account for the fact that the same stork can stop in both artificial and natural stopovers during migration and to further investigate if there is a fitness benefit for individuals exploiting food waste resources (over individuals that exploit mostly natural resources), we defined a resource selection rate for each individual (Eq. (2)). Values equal to 1 represent a similar use of artificial and natural stopover sites, and values above or below 1 represent a higher use of artificial or natural stopover sites, respectively.

$$\text{Resource selection rate} = \log \left[\frac{n_{\text{artificial stopover days}} + 1}{n_{\text{natural stopover days}} + 1} \right] \quad (2)$$

We used the previously defined metrics of migratory performance (migration duration, route tortuosity index, standardized arrival date, and mean flight energy expenditure) to explore the association between resource selection rate and migratory performance using GLMMs, selecting individuals that completed the migration and stopped ($n = 41$).

3. Results

Between 2016 and 2020, we tracked the autumn migration of 81 first-year juvenile white storks travelling to the Sahel. The tracking dataset included 102,169 fixes (mean fixes/(day * stork) = 45.8, SD = 6.5). Juvenile storks departed from Iberia between the 6th July and the 8th September (median date = 31st August; median absolute deviation, MAD = 21 days) and arrived at the Sahelian wintering areas (Senegal to Niger, Fig. 1) between the 16th July and the 14th October (median date = 31st July, MAD = 19). Not all individuals arrived at the wintering grounds: 23 disappeared and 9 died during migration. Overall, juvenile storks took 31 days (SD = 17.4, Table 1) to complete their migration ($n = 49$), travelling on average 3202.1 km (SD = 460) with a mean daily displacement of 125.9 km (SD = 52.3).

Although some juveniles ($n = 14$) travelled continuously before reaching the wintering sites, most ($n = 67$) stopped, alternating between migratory and stopover days. Overall, they spent up to one-third of the migration in stopover sites ($n = 81$, mean = 13 days, SD = 16, Table 1). Storks spent 30.8 % of the days in stopovers before crossing the Sahel, (mean_{Sleg1} = 12.3, SD = 15.4 days, median_{Sleg1} = 6, Table 1), and 10 % after crossing the Atlas Mountains (mean_{Sleg2} = 1, SD = 2.1 days, median_{Sleg2} = 1, Table 1). Non-stopping birds completed the entire migration on average on 14.5 days (SD = 6.5), travelling 2510.2 km (SD = 1268.2).

On average, storks used 3 stopover sites (SD = 1.9, Table 1) during their migration, yet most individuals spent longer periods in few stopover sites. The most important stopover sites were located in Iberia and northern Morocco before crossing the Sahara Desert (Fig. 1). Of the 74 stopover sites identified, the ten most important (used by more individuals and for longer periods; 7 artificial and 3 natural) were used on average by 11 individuals (SD = 7) for 80 days (SD = 58).

Table 1

Summary table of autumn migration parameters of 81 first-year white storks. Mean values (\pm standard deviation) were calculated for the whole migration and for each migratory leg: leg 1 represents the area from Portugal up to the Atlas Mountains, and leg 2 from the Atlas Mountains up to the south of the Sahara Desert. Means and standard deviations for stopping and non-stopping individuals are also provided.

	Overall	Leg 1 (before crossing the Atlas Mountains)	Leg 2 (after crossing the Atlas Mountains)	Stopping individuals	Non-stopping individuals
Number of starting individuals (N)	81	81	65	67	14
Mean migration duration (days)	27 \pm 18.1	19 \pm 17	10.1 \pm 56	30 \pm 18	14.5 \pm 7
Mean migration distance (km)	3202.1 \pm 460	967 \pm 250	1817 \pm 804	2456 \pm 1136	2510 \pm 1268
Mean no. of stopover days	13 \pm 16	12.3 \pm 15.4	1.3 \pm 2.1	16 \pm 16.2	0
Mean no. of migration days	14 \pm 5.8	7 \pm 1.9	9 \pm 3.8	14 \pm 5.6	14.5 \pm 7
Mean no. of stopover sites used	3 \pm 1.9	2 \pm 1.7	0.8 \pm 0.9	3 \pm 1.6	0
Mean no. of days in artificial stopovers	10.8 \pm 14.6	10.5 \pm 14.2	0.4 \pm 1.9	13.1 \pm 15.1	0
Mean no. of days in natural stopovers	2.6 \pm 4.7	1.9 \pm 4.3	0.9 \pm 1.2	3.1 \pm 4.7	0
Mean daily displacement (km)	125.9 \pm 52.3	86.4 \pm 53.8	188.3 \pm 46.5	97.2 \pm 47.9	184.7 \pm 35.8
Mean time spent migrating (%)	64.4	57.2	89.7	56.9	100
Mean time spent in stopovers (%)	35.6	42.8	10.3	43.1	0

3.1. Influence of stopover strategy on migratory performance

When compared with individuals that stopped, non-stopping birds had a shorter migration duration ($\beta = -0.14 \pm 0.05, p = 0.002, SM7$), arriving earlier ($\beta = -0.04 \pm 0.02, p = 0.02, SM7$) and spending less energy in flight ($\beta = -19.22 \pm 9.5, p = 0.04, SM7$). Migratory performance of first-year juvenile storks was significantly influenced by differences in stopover duration. Individuals stopping for longer periods had less direct routes ($\beta = 0.004 \pm 0.002, p = 0.039, Fig. 2a$), longer migration duration ($\beta = 1.05 \pm 0.04, p < 0.0001, Fig. 2b$) and arrived later to their Sub-Saharan wintering grounds ($\beta = 0.49 \pm 0.13, p < 0.001, Fig. 2c$). Although flight energy expenditure decreased with travelled distance (see SM8 in the supplementary material), it was not affected by stopover duration ($p = 0.15, Fig. 2d$). Moreover, stopover strategy did not influence the likelihood of completing migration ($n_{\text{total}} = 78, n_{\text{events}} = 29, p = 0.28, SM9$). The number of stopover sites used by young storks influenced their migratory performance, individuals that used more stopovers made more detours and took longer to complete the migration (SM10).

3.2. Determinants of stopover strategy

Juvenile white storks that departed earlier ($\beta = -0.46 \pm 0.10, p < 0.0001, Fig. 3a$) or in poorer body condition ($\beta = -12.5 \pm 4.62, p < 0.01, Fig. 3b$) stopped for longer periods. Early departers also stopped more often (in more stopover sites, SM10).

3.3. Use of artificial and natural stopover sites

We identified 28 artificial and 46 natural stopover sites (Fig. 1). Artificial stopover sites were primarily located north of the Atlas Mountains (82 %) and included large landfill sites in Iberia and northern Morocco but also rubbish dumps and waste sites associated with smaller urban areas and human presence. Natural stopovers were mostly found south of the Atlas Mountains (87 %), a deserts, low-populated area and consequently with low availability of anthropogenic food subsidies.

Artificial stopover areas were farther from the optimal route than natural stopovers ($\beta = -25.02 \pm 8.8, p < 0.001, Fig. 4e$), and storks stayed for more extended periods in artificial stopovers (Table 1). When exploiting artificial stopover sites, juvenile storks spent overall 45 % less time foraging ($\beta = 0.09 \pm 0.02, p < 0.0001, Fig. 4a$) and spent 10 % less energy ($\beta = 0.009 \pm 0.004, p = 0.034, Fig. 4b$) than when foraging on natural prey. Moreover, storks using artificial stopover sites moved less during stopover days compared to birds stopping in natural sites ($\beta = 3.5 \pm 1, p < 0.001, Fig. 4d$) and rested more time when on artificial stopover sites ($\beta = -0.08 \pm 0.02, p < 0.001, Fig. 4c$).

Despite the differences found between stopover sites, stopping in artificial sites did not improve the migratory performance of juvenile storks. Individuals using more artificial than natural stopover sites took longer to complete migration ($\beta = 4.3 \pm 1.76, p = 0.02, Fig. 5b$) arriving slightly

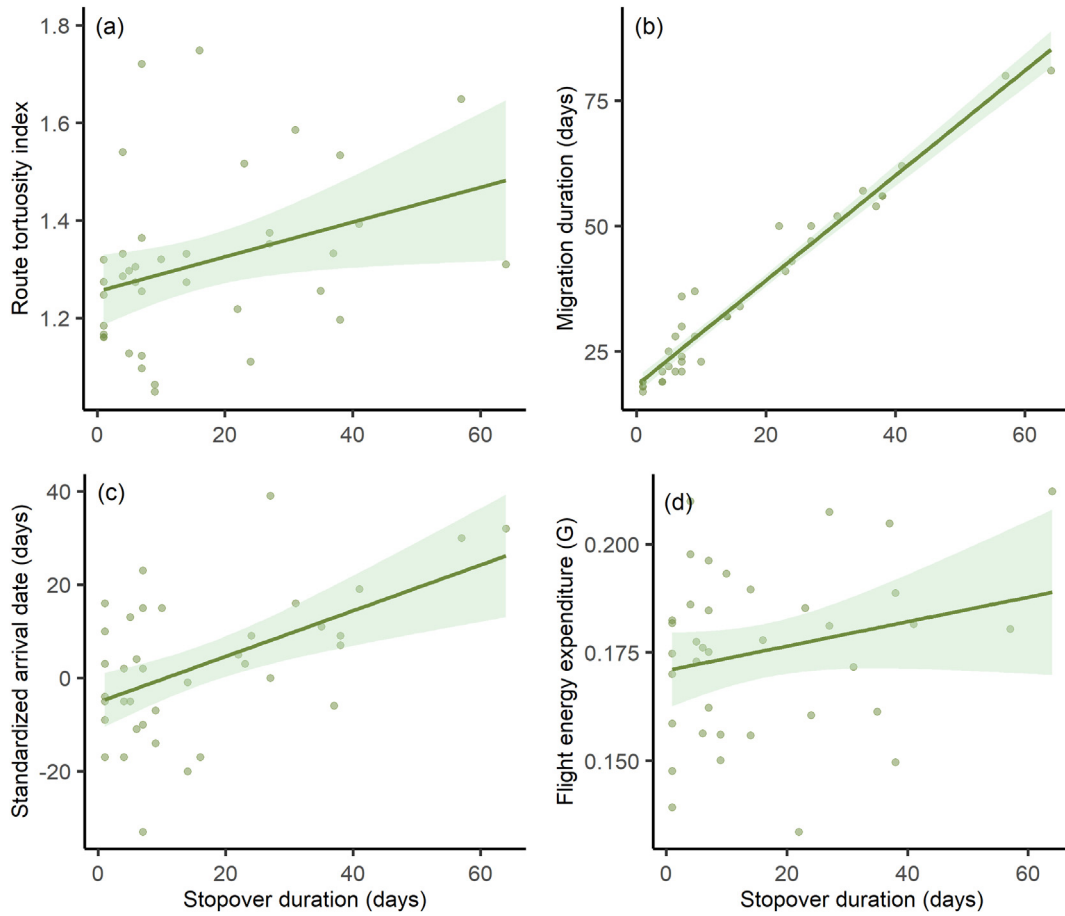


Fig. 2. Influence of stopover strategy on the migratory performance of first-year white storks: (a) route tortuosity index ($p = 0.039$), (b) migration duration ($p < 0.0001$), (c) standardized arrival date ($p < 0.001$) and (d) flight energy expenditure ($p = 0.15$). The shaded area represents 95 % confidence intervals.

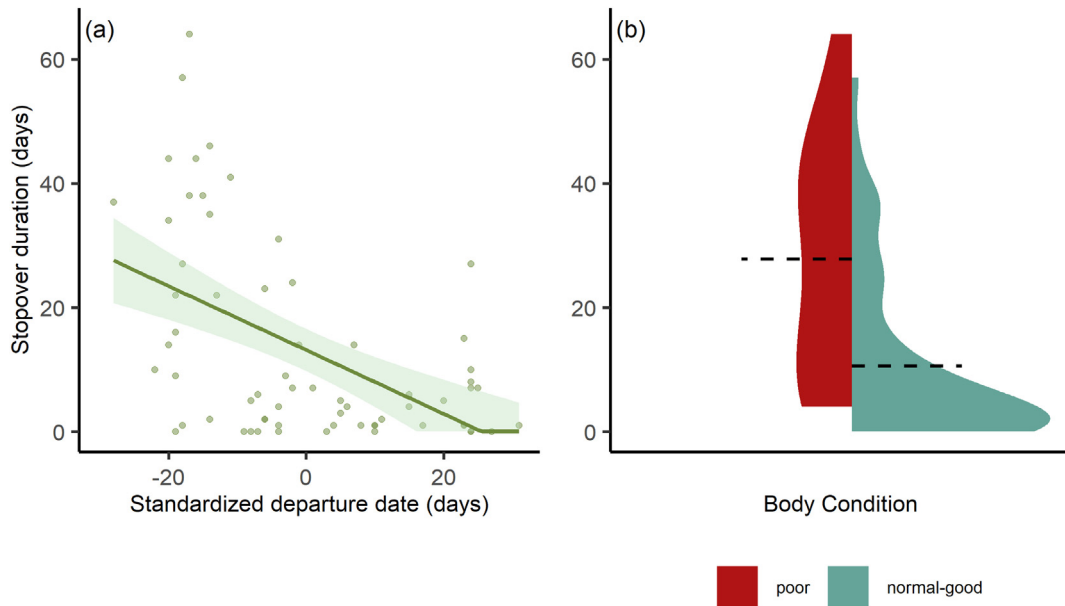


Fig. 3. Determinants of stopover strategy in first-year white storks during autumn migration: (a) mean departure date ($p < 0.0001$) and (b) body condition at fledging ($p < 0.01$). On the left, each dot represents an individual ($n = 65$), and the shaded area represents 95 % confidence intervals. On the right, dashed lines represent the mean values of body condition, and red and green shades represent the density distribution of stopover duration for “poor” ($n = 10$) and “normal-good” ($n = 55$) body conditions, respectively.

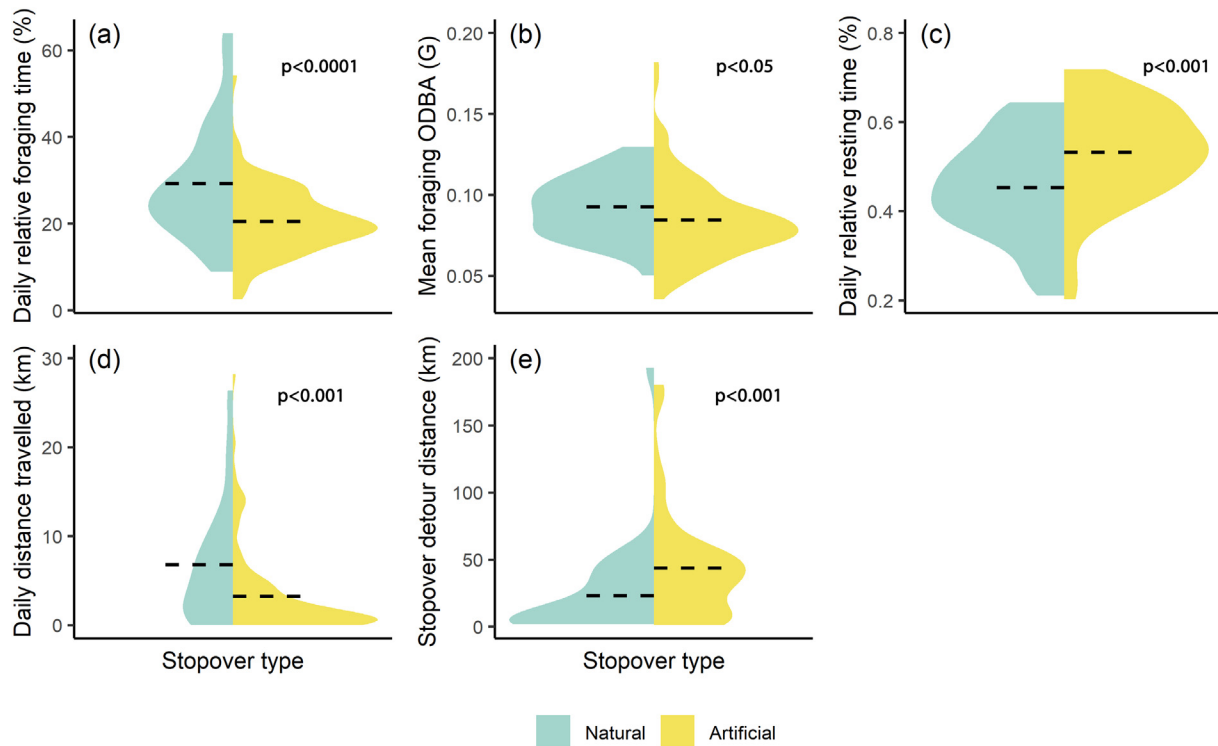


Fig. 4. Comparison of natural and artificial stopovers used by first-year white storks during autumn migration on (a) daily relative foraging time ($p < 0.0001$), (b) mean foraging ODBA ($p = 0.034$), (c) daily relative resting time ($p < 0.001$), (d) daily distance travelled (summed distance between consecutive locations for each stopover day, $p < 0.001$) and (e) stopover detour distance (distance from the nearest stopover to the optimal route, $p < 0.001$). Dashed lines represent the mean value for each stopover type. Green and yellow areas represent the density distribution of each variable for natural and artificial stopovers, respectively.

later (but not significantly: $\beta = 2.9 \pm 1.51$, $p = 0.06$, Fig. 5c) at their wintering destinations. There were no differences in flight performance ($\beta = 0.002 \pm 0.002$, $p = 0.32$, Fig. 5d) nor travelling detours from the optimal route ($\beta = 0.03 \pm 0.02$, $p = 0.15$, Fig. 5a).

4. Discussion

In this study, we identified stopover use drivers and their impacts on white stork migratory strategies, with a particular focus on artificial stopover sites. We found that first-year juveniles stop for one-third of the time during the autumn migration – mostly at artificial stopovers – but stopping more did not seem to improve performance nor the likelihood of completing the migration. Moreover, although stopping in artificial stopovers proved to be advantageous compared to natural stopovers, as storks require less energy during foraging, using landfills and rubbish dumps did not improve their migratory performance.

White storks, as many other soaring birds, use thermal and orographic uplifts to save energy in-flight, being able to progress fast and travel with low-fat reserves without stopping. Indeed, white storks have no apparent pre-migratory fattening (Michard-Picamelot et al., 2002), and likely adopt a flight and forage strategy, foraging during dusk and dawn before and after the daily migratory movements (Newton, 2008). In the eastern flyway, Rotics et al. (2016) found that 71 % of the GPS-tracked white storks did not stop during migration, and only 16 % stopped for more than one day during a ~4000 km long migration. In contrast, we found that for the western flyway, only 17 % of the individuals migrated without stopping and 78 % stopped for >1 day, for a much shorter overall travelled distance (~3000 km). Our results show that 83 % of the tracked juveniles stopped during 48 % of the migration period, suggesting they adopt an energy-minimizer strategy during autumn migration.

Stopping during migration influenced the overall duration and straightness of migration, as well as the arrival timing in the wintering grounds. Longer stops lead juveniles to adopt less straight routes, increased the

duration of the migration (non-stopping birds saved on average 15 days compared to juveniles that stopped) and delayed the arrival at the wintering grounds. While prolonged stopovers likely increase the predation risk during migration (Lank et al., 2003) and late arrival to the wintering areas in the Sahel, after the end of the rainy season, may result in a mismatch with peak food availability (Zwarts et al., 2016, see SM11), it would be expected that stopping more often or for longer periods would bring some benefits. Nevertheless, we showed that, for white storks, performing longer stopovers did not reflect on increasing in-flight energetic efficiency nor the likelihood of completing migration.

4.1. Why do storks stop then?

We found that white stork fledglings in worse body condition, and those departing earlier, stopped more. Lighter individuals probably take advantage of stopovers to balance fat storage during migration, consequently enhancing survival probability. Indeed, previous studies have shown that individuals in better body condition perform shorter stopovers (Kaiser, 1999) and are associated with enhanced first-year survival (Naef-Daenzer et al., 2001; Nisbet et al., 2016; Rotics et al., 2021). Early departers are less time-constrained and can stop to rest and forage more often, not jeopardizing migration completion and arrival to the wintering grounds.

While we did not find any obvious advantages for stopping more often or for longer periods, this behaviour could be explained by social cues, characteristic of species that travel in mixed flocks (Chernetsov et al., 2004; Rotics et al., 2016; Siekiera et al., 2021) and in which young individuals follow the more experienced ones. Juvenile storks likely rely on social interactions with older individuals when selecting their routes and deciding when to stop, rather than on their energetic efficiency or body condition. This could explain why juveniles stop more often in Morocco, where many migrating adults spend the winter (Acácio et al., 2022; Flack et al., 2016).

Finally, late departers seem to stop less often possibly as a response to progressively deteriorating weather conditions in autumn (Acácio et al.,

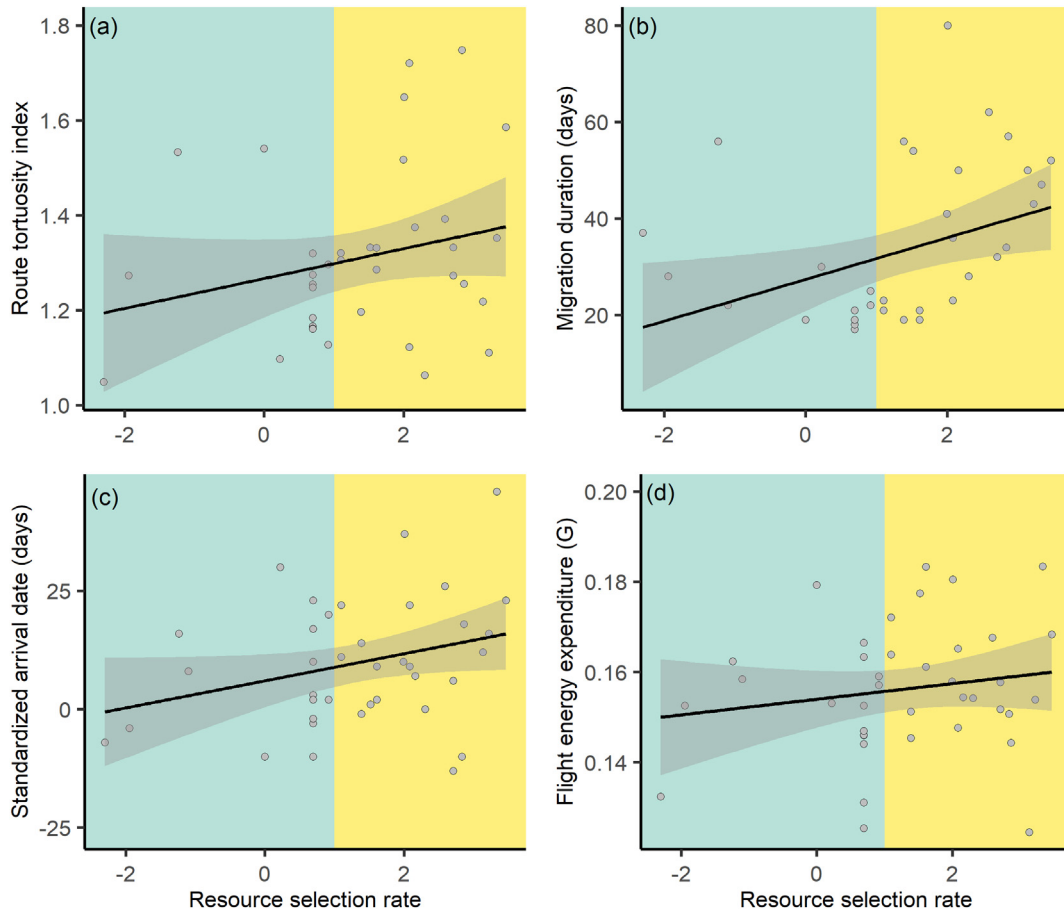


Fig. 5. Influence of natural and artificial stopover use (resource selection rate) on the migratory performance of first-year white storks: (a) route tortuosity index ($p = 0.15$), (b) migration duration ($p = 0.02$), (c) standardized arrival date ($p = 0.06$), and (d) flight energy expenditure ($p = 0.32$). Each dot represents an individual, and the shaded area represents the 95 % confidence intervals. Resource selection rate equal to 1 represents equal use of artificial and natural stopover sites – the green side represents more natural than artificial stopover use, and the yellow side, the opposite.

2022) and synchronize the timing of arrival with the birds departing earlier. Departing earlier allows birds to find better wind and thermal conditions when migrating, reducing energetic flight costs (Acácio et al., 2022; Mallon et al., 2021) and consequently widening their probability of survival.

4.2. Importance of artificial stopover sites during migration

While previous studies have shown fitness advantages and high use of landfills and dumps as feeding areas for many species at breeding and wintering sites (Arnold et al., 2021; Birdlife International, 2015; Gilbert et al., 2016), increasing evidence shows its importance during migration (Arizaga et al., 2018; Bárbara et al., 2017; Birdlife International, 2015; Kruszyk and Ciach, 2010), when these anthropogenic habitats can concentrate flocks of tens of thousands of foraging individuals. Yet, the extent to which artificial stopovers influence migratory decisions (e.g., patterns of movement, timings, energy spent) and impact migratory success remained largely unknown, but crucial to understanding shifts in population dynamics. Our results show that, in artificial stopover sites, juvenile white storks spent 45 % less time and 10 % less energy foraging than storks using natural stopovers. Furthermore, in natural stopovers, storks need to travel twice the distance on a daily basis, spending more energy and therefore being more prone to fatigue and predation (Yosef et al., 2011). Previous studies show that foraging in landfills entails detrimental effects for birds such as poisoning (Tongue et al., 2019), infections or debris consumption (Birdlife International, 2015), although the extension of these impacts is poorly known. Notwithstanding, previous findings also show that foraging on landfill waste is an energy-saving strategy for white storks during the

breeding and wintering seasons (Soriano-Redondo et al., 2021), having the potential to improve survival and fitness (Flack et al., 2016; Tortosa et al., 2002). Nonetheless, the high use of this resources during migration did not increase the likelihood of completing migration nor did reduce overall migration duration.

Previous studies suggested that the worldwide increase in waste production in the last decades likely reshaped the migratory behaviour of birds that take advantage of landfills (Ciach and Kruszyk, 2010; Pineda-Pampliega et al., 2021) such as black kites (*Milvus migrans*), Egyptian vultures (*Neophron percnopterus*), herons and several gull species (Arizaga et al., 2018). Although there is no information, to our knowledge, on the historical stopover use by white storks, this hypothesis is supported by the behaviour of white storks using the eastern European flyway. While in the east, the use of landfills is negligible (Bialas et al., 2021; Van den Bossche et al., 2002), in the western flyway storks stop for longer periods and have an intensive use of artificial stopovers. Here, we suggest that landfills reshaped migration for this species, particularly through the increase in migratory distances and timings.

Future changes in landfill waste policies can impact white stork migratory behaviour. While waste production estimates predict that by 2050 the waste generated is expected to exceed 3.4 billion tonnes (comparatively to the present 2 billion tonnes, (Kaza et al., 2018)), according to European Union regulations (Directive 2018/850/UE), landfill waste will need to be reduced to 10 % of current levels by 2035, with unknown consequences for resident European white storks. On the other hand, it is expected that waste production will become more abundant in northern Africa, which will probably lead to further storks wintering there and to higher rates of artificial stopover use, with unforeseen consequences for this species.

CRediT authorship contribution statement

J. Marcelino: Methodology, Software, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **A.M.A. Franco:** Resources, Writing – review & editing, Funding acquisition. **M. Acácio:** Conceptualization, Methodology, Investigation, Writing – review & editing. **A. Soriano-Redondo:** Methodology, Writing – review & editing, Supervision. **F. Moreira:** Writing – review & editing, Supervision, Funding acquisition. **I. Catry:** Conceptualization, Methodology, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Data availability

The data that has been used is confidential.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.159992>.

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