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Importance of artificial stopover sites through avian migration flyways: a landfill-based assessment with the White Stork *Ciconia ciconia*

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Open landfills seem to be playing an increasing role as target feeding areas for several species, not only in their breeding areas or during the winter, but also during the migration period. Evaluating the extent to which landfill sites are used by migrants is crucial to understanding their role in driving stopover decisions during migration, and in the potential health risks linked to feeding on refuse. The aim of this study was to evaluate the role of two open landfills located just before (France) and after (Spain) the East-Atlantic flyway enters Iberia through the western Pyrenees as potentially important stopover sites for the White Stork populations moving along this route. Overall, we detected that these sites were used by storks that had been ringed from many western European breeding populations, mainly during the migration period, but also in winter. The mean distance between the stork breeding/ringing origin and the landfill sites increased from summer to winter, suggesting that storks breeding further away pass through Iberia later in the season, reflecting population-specific timing of migration. During the autumn migration period (August–September), the first encountered landfill in France was estimated to be used by *c.* 1200 storks, and the other in Spain by 4000 storks. Our study hence contributes to a better understanding of the current and potentially hazardous role played by landfill sites in White Stork ecology, which is essential in order to provide management recommendations, and to evaluate the consequences of proposed open landfill closures in Europe.

Keywords: conservation biology, East-Atlantic flyway, migratory phenology and behaviour, Pyrenees, refuse tips.

During long-distance migration, most birds need to stopover to refuel so they can successfully undertake subsequent flight bouts. Sometimes, migrants depend on very specific target stopover locations for that purpose, and hence these sites are crucial for the success of migration, even of entire populations (Newton 2008). This can be the case for stopover sites close to bottlenecks which concentrate high numbers of migrants. Soaring birds, including storks or raptors, largely rely on thermal updrafts for assisted flight and normally avoid large fuel accumulations, as they have a relatively small energy consumption during migration (Alerstam 1993). However, even these species still need some refuelling along their migration routes, especially when crossing hazardous geographical obstacles such as seas, mountains or deserts, which might require additional energy investment (Yosef *et al.* 2002, Thorup *et al.* 2003, Strandberg *et al.* 2010).

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The East-Atlantic flyway is one of the main bird migration routes of the world. During spring and autumn, millions of birds use this route annually, connecting their breeding sites in Europe and their wintering areas in Iberia or western Africa (Newton 2008). This flyway enters Iberia through the western edge of the Pyrenees, where the proximity of the Bay of Biscay produces a funnel effect allowing the concentration of large numbers of migrants (Galarza & Tellería 2003). Soaring birds such as storks and raptors pass through this region during migration (Martín *et al.* 2016). The flyway continues to the south until the Strait of Gibraltar, which connects southern Iberia with northern Africa and is the chief bottleneck along this route for soaring migratory species (Martín *et al.* 2016, Miller *et al.* 2016). Iberia is, therefore, of critical importance for the conservation of all these populations, and the availability of suitable stopovers encountered along the peninsula can be crucial not only for the success of migration across this region, but also for the sea crossing between Iberia and Africa and subsequently the Sahara desert (Arizaga *et al.* 2011, Andueza *et al.* 2014).

Open landfill sites and dumps seem to be playing an increasingly important role as target artificial feeding areas for several species, not only in their breeding areas or during the winter (Belant *et al.* 1998, Tortosa *et al.* 2002, Duhem *et al.* 2008, Jordi *et al.* 2014, Gilbert *et al.* 2016), but also during the migration period (Berthold *et al.* 2002, 2004, Ciach & Kruszyk 2010, Kruszyk & Ciach 2010). Compared with natural food sources, landfills provide abundant as well as highly spatio-temporal predictable food. Nowadays, they represent one of the major worldwide sources of anthropogenic food subsidies, and opportunistic species can benefit from them by improving individual fitness (e.g. survival, reproduction) and increasing their populations (Oro *et al.* 2013). There are, however, some important associated risks to the use of landfill sites, which include potential contaminants, pathogens or poisoning, that may have a direct negative impact on population dynamics (de la Casa-Resino *et al.* 2014, Amano *et al.* 2016). Moreover, considering the new EU policies towards the closure of open landfills in the coming years, there is a need to study how different species make use of them all year round to better understand the potential impacts of landfill closure on their fitness, behaviour and population trends. For instance, the use of these artificial sites as target stopover places during migration and, therefore, their importance for some migratory bird populations is still poorly known and its magnitude remains far from being fully evaluated.

The European White Stork *Ciconia ciconia* (hereafter, White Stork) is a Holarctic species breeding from northwestern Africa through many countries of Europe to western Asia. During the winter, most of the White Stork breeding populations migrate to southern latitudes in Africa or southern Asia (Cramp 1977). Western European populations migrate through Iberia to overwinter either in Iberia or in tropical Africa (Cramp 1977). When approaching Iberia in autumn, storks tend to pass the Pyrenees on its western or eastern edge (Tellería *et al.* 1996). White Storks frequently feed on refuse tips if available, and indeed are one of the main avian species using this type of resource in Europe (Tortosa *et al.* 2002, Hilgartner *et al.* 2014, Gilbert *et al.* 2016). Overall, the species has benefited from using this anthropogenic food resource, both during the breeding season (by increasing productivity in nests located close to landfills; Tortosa *et al.* 2002) and during the winter (by apparently being one of the chief factors contributing to reducing migration distances, and even a complete suppression of migration (Flack *et al.* 2016, Gilbert *et al.* 2016, Catry *et al.* 2017)). Furthermore, the use of landfills during the migration period also seems to be high (Shephard *et al.* 2015), although there is still an important lack of knowledge regarding the population origin of those individuals and their use of landfills along their routes of migration.

Spain supports a breeding population of *c.* 33 000 pairs of White Stork (Molina & Del Moral 2005). In winter, the population has been estimated to reach about 30 000 individuals (Molina & Del Moral 2005). Overall, both the breeding and the wintering populations doubled over the period 1994–2004 (Molina & Del Moral 2005). During the autumn and spring migrations, counts at chief bottleneck areas in Spain, such as Lindus or Gibraltar, estimate passages of up to 500 000 individuals (Panuccio *et al.* 2017), mostly coming from the west of Europe (Tellería *et al.* 1996). Excluding Iberia, the White Stork population in western Europe (France, Netherlands, Switzerland, Belgium and Germany) reaches *c.* 7250 pairs (Tucker & Heath 2004, Issa & Muller 2015). Many of these birds pass over Iberia en route to their wintering areas in Africa and, as more recently seen, in Spain (Molina & Del Moral 2005, Panuccio *et al.* 2017).

The aim of this study was to evaluate the role of two open landfills located just before and after the East-Atlantic flyway enters Iberia through the western Pyrenees as potential important stopover sites for the White Stork populations moving along this route. In particular, we aimed (1) to determine the breeding/natal region of origin of migrants passing through this route and using landfill sites to stay/refuel; and (2) to evaluate the relevance of these landfill sites for the European White Stork populations entering Iberia through the East-Atlantic flyway. If important at a continental scale level, the monitored landfills would be used by birds coming from a broad breeding/natal region of origin, and would also host large numbers of storks, especially during the migration period. If the landfills are used as true stopover sites, White Storks should spend enough time to profit from the anthropic food resources available for refuelling. According to Warnock (2010), a true stopover site is a place where birds remain for a long period in order to refuel consistently. Thus, by assessing stopover duration, we test the degree of use of the study sites.

METHODS

Study sites

This study was carried out at two of the main open landfills located along the East-Atlantic flyway just after entering Iberia in northern Spain: Culebrete (42.0644°N, 1.7357°W), municipality of Tudela, Navarra; and before crossing the western Pyrenees in southern France: Zaluaga (43.3878°N, 1.5694°W), municipality of St. Pée sur Nivelle Aquitaine. The distance between these two sites was 150 km. The decision to consider these two sites was based on the fact that they are the two most important landfills within the region in terms of number of visiting storks, and these are the only two sites for which we have sufficient and consistent data collected over a relatively long period. The size of the stork population near these two sites (within a radius of 20 km around each landfill site) comprised < 620 pairs (Culebrete *c.* 600 pairs, Zaluaga < 20 pairs; J. Arizaga unpubl. data).

The landfill of Culebrete is located in the Ebro river basin surrounded by a Mediterranean agricultural mosaic mostly composed of cereal fields as well as an increasing number of irrigated crops such as rice. Culebrete receives an annual mean of 30 290 ± 1028 (sd) tonnes of refuse (range 29 352–32 008 tonnes between 2009 and 2015; source: Mancomunidad de la Ribera). The landfill of Zaluaga is situated in an Atlantic agro-forest mosaic mostly composed of meadows, maize crops and oak patches. Zaluaga received an annual mean of 41 832 ± 11 230 tonnes of refuse (range 18 080–49 642 tonnes between 2009 and 2015; source: Syndicat Mixte Bizi Garbi).

Data collection

From 2009 to 2016 (Zaluaga 2009–2016; Culebrete 2012–2016), we visited the two study sites to look for ringed White Storks and read their rings. Visits were done so as to guarantee a visit every 15 days, although in some cases this was not possible due to bad weather or logistic constraints (most of the work was done by volunteers). Only at Culebrete, and for the months of August–September 2014–2015 (coinciding with the peak of autumn migration period), a higher sampling effort (with a visit every 5 days) was carried out to estimate stopover duration. Visits were done during either the morning or the afternoon, spanning at least 1 h. In all cases the observer was situated at a fixed point (normally inside a vehicle) allowing the identification of ringed storks using a 20–60× spotting telescope or digital photo camera. Overall, we read 967 unique colour rings of known origin (Table 1). Of these, 425 were read only at Culebrete, 499 only at Zaluaga and 43 at both sites.

Table 1. Number of unique colour rings read at each landfill site (Culebrete, Zaluaga) with known region of origin.

Origin	Culebrete	Zaluaga	Total
FRA	362	437	799 (79.1%)
NDL	53	41	94 (9.3%)
DEU	42	40	82 (8.1%)
ESP	11	7	18 (1.8%)
BEL	0	15	15 (1.5%)
CHE	0	2	2 (0.2%)
Total	468	542	1010

Country abbreviations: BEL, Belgium; CHE, Switzerland; DEU, Germany; ESP, Spain; FRA, France; NDL, The Netherlands.

In parallel, non-systematic direct counts at each site were undertaken on a (minimum) monthly basis whenever possible. The counts were done during the morning or the afternoon, depending on logistic constraints. At each site, observers were situated at vantage points from which the whole area used by the storks could be seen, therefore allowing all birds to be counted whilst minimizing the likelihood of double counts. Overall, 58 counts were made at Culebrete (2014–2016) and 118 at Zaluaga (2009–2016; Table S1).

Statistical analyses

We used Cormack-Jolly-Seber (CJS) models to estimate local apparent survival at Culebrete in August–September 2014 and 2015, when visits were conducted on a 5-day period basis. This higher sampling effort allowed us to achieve a sample size sufficiently high to run CJS models. This was not possible for other months and years at either site.

CJS models permit the assessment of survival (ϕ) and recapture (i.e. re-sighting) probability (P) separately. For migrants in a stopover site, we assume that real survival from one day to the next is virtually 1, and thus apparent local survival (ϕ) is equal to staying probability at that stopover site (Schaub *et al.* 2001), and we use this term hereafter. Original sampling dates were combined into 12 intervals of 5 days (interval 1 = 1–5 August; 12 = 25–29 September). Each individual bird was considered only once per interval and year. For this analysis, we had an overall sample size of 902 storks (in this case we selected all reads, including those for which we did not get information about breeding/natal origin, as the origin region was not relevant for this analysis). From these birds, 48 (5.3%) were detected in both 2014 and 2015. Reads from each year were considered independently, i.e. as if they belonged to different individuals. Therefore, when building the models, the estimation of ϕ from the last week of 2014 and the first week of 2015 was fixed to zero. To test for the fit of the data to CJS assumptions we used the U-CARE software (Choquet *et al.* 2009). The global goodness-of-fit test was significant ($P < 0.001$), as well was the specific test to detect transients ($P < 0.001$). Overall, we tested alternative models, assuming: (1) constant ϕ (staying probability is constant from one time interval to the next and for the entire season); (2) a linear effect of time on ϕ, i.e. ϕ(time.linear) (staying probability changes linearly through the season, for example by decreasing towards the end of the migration season); (3) presence of transients, i.e. ϕ_1 and ϕ_2; ϕ_1 represents ϕ estimation from the 5-day period when the bird was seen for the first time and ϕ_2 represents staying probability for the next time intervals (a proportion of the storks may stay in the landfill for less than 5 days, whereas other birds would stay for a longer period, with constant values for the two parameters over the entire season); (4) a linear effect of time on both ϕ_1 and ϕ_2, i.e. ϕ_1(time.linear), ϕ_2(time.linear); or, alternatively, (5) only on ϕ_1 or ϕ_2, i.e. ϕ_1(time.linear), ϕ_2; ϕ_1, ϕ_2(time.linear). Models assuming time effect as factor on ϕ, i.e. ϕ(time.factor), were not run due to sample size constraints. By definition, transients are birds in which ϕ from the first capture event to the next time unit equals zero. In this work, a transient is an individual that stayed less than 5 days at a landfill. Models assuming the presence of transients consider that a sizable number of storks may stay at Culebrete for less than 5 days, thus supporting a relevant population turnover during the migration season. In models estimating ϕ_1 and ϕ_2, the proportion of transients can be calculated as $1 - (\phi_1/\phi_2)$. Regarding P, we considered constant P-values for all models because the reading effort was approximately the same throughout the time period and also due to sample size constraints. We used Akaike's information criterion corrected for small sample size (AICc) to rank the fit of models to data and for model selection (Burnham & Anderson 1998). Models with a ΔAICc < 2 were selected as the best candidates, and those with a difference in ΔAICc > 2 were discarded. CJS models were run in the program MARK (White & Burnham 1999).

We used generalized linear mixed models (GLMMs) to test for the effect of month on population counts at each landfill site. To do that, we used counts (number of storks in a given month and year and landfill) as the response variable for each landfill, with month and year as fixed and random factors, respectively. Models were built using a log-linear link function with a Poisson error distribution. Then, we used the proportion of transients as assessed from CJS models and the following equation to estimate total population sizes passing through the two study landfill sites during the autumn migration period (August–September):

$$N = N_{\mathrm{mean}} + [(n-1) \times (N_{\mathrm{mean}} \times T)]$$

where N is the estimated total population size, N_{mean} is the mean population size estimation for the time unit considered (e.g. August or September), n is the number of 5-day intervals included within the time unit considered in N_{mean}, and T is the proportion of transients. Note that T was calculated for Culebrete, but used for population size estimation at both landfills, so estimates for Zaluaga should be considered with caution. GLMMs were run with R software (R Core Team 2014).

Finally, to estimate the proportion of first-year birds of the total population passing through our study sites, we considered data from July (first month after breeding with a relevant sample size at both sites; see Results for details) to December. In this analysis, each bird was considered once per month and year, and we calculated the proportion of first-year birds as compared with all ringed birds with their hatching year known.

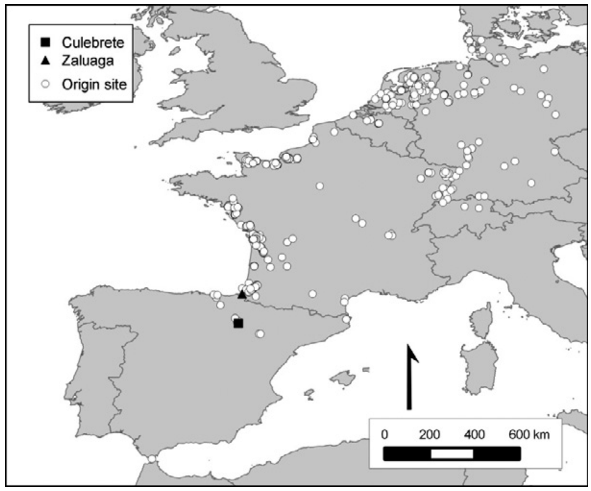

Figure 1. Location of the two study dumps (Culebrete and Zaluaga, dark square and triangle, respectively) and sites of origin (i.e. ringing, open dots) of colour-ringed White Storks. Data were compiled from 2009 to 2016.

RESULTS

Region of origin and timing of passage

White Storks using and passing through both landfills were ringed in six countries (Fig. 1): France (accounting for 79.1% of sightings), followed by The Netherlands, Germany, Spain, Belgium and Switzerland (Table 1). There was a slight but significant difference in the proportion of each region of origin between the two landfills ($\chi^2 = 21.20$, df = 5, $P < 0.001$), mainly due to the slightly higher proportion of storks from France at Zaluaga than at Culebrete (for details see Fig. S1; Fig. 1).

The majority of the rings were read only once (68.4% at Culebrete, 63.6% at Zaluaga; Fig. 2). At the other extreme, there was a bird seen 16 times at Culebrete and another up to 30 times at Zaluaga. Regarding the timing of passage, most rings were read during the autumn migration period, with a peak in August (Zaluaga) and September (Culebrete; Fig. 3). By contrast, few rings were read from March to June (1.3% at Culebrete and 3.1% at Zaluaga).

The mean distance between ringing sites and each landfill varied seasonally. There was a significant interaction between both factors (Fig. 4; ANOVA: landfill, $F = 44.82$, $P < 0.001$; months, $F = 44.49$, $P < 0.001$; landfill × months, $F = 2.06$, $P = 0.045$). Therefore at each landfill site there was a differential timing of passage in relation to ringing site. Overall, mean distance increased from summer (July–August) to winter (November–February), with the longest distances at each landfill registered in winter (Fig. 4).

The mean (±se) time elapsed between ringing date and first sighting varied between the two studied landfills (U-test: $U = 102\,553.5$, $P < 0.001$). Overall, the storks seen at Zaluaga tended to be on average 1 year younger than those at Culebrete (mean ± se: Zaluaga: 997.2 ± 45.1 days; Culebrete: 1349.5 ± 54.5). The minimum and maximum values were both obtained for the Zaluaga landfill; a stork ringed in France in July 2011 was seen 7 days later, and a stork ringed in June 1993 was seen 6279 days later (i.e. > 17 years).

For those birds seen at both landfills ($n = 43$), almost half (42%) were seen only once at each, with all the storks first seen at Zaluaga. The mean (±sd) number of days elapsed between these two-first observations was 1009.6 ± 595.8 days (range 6–2191 days). Only four of those storks (i.e. < 10%) were seen at both landfills in the same year. The mean time (±sd) elapsed between these observations within a year was 15.3 ± 15.3 days (range 6–38 days), all in September, except one bird that was seen at Zaluaga in September but at Culebrete in October.

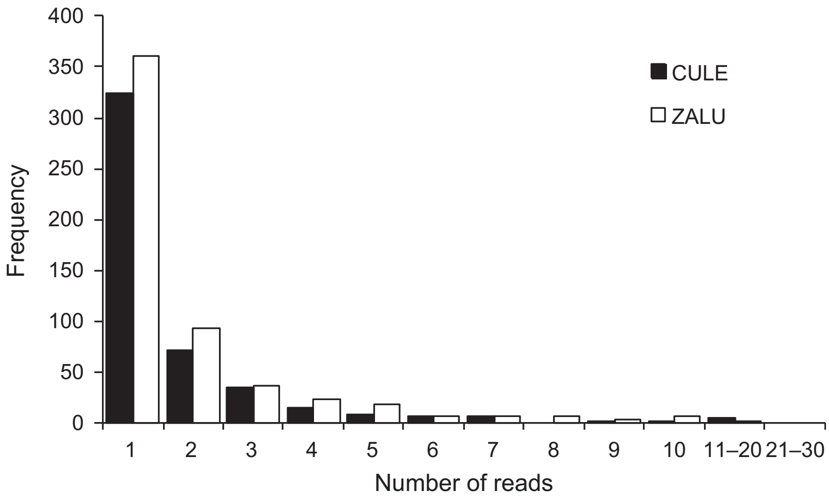

Figure 2. Number of occasions (frequency) in which individual rings were read at each of the two study sites (CULE, Culebrete; ZALU, Zaluaga).

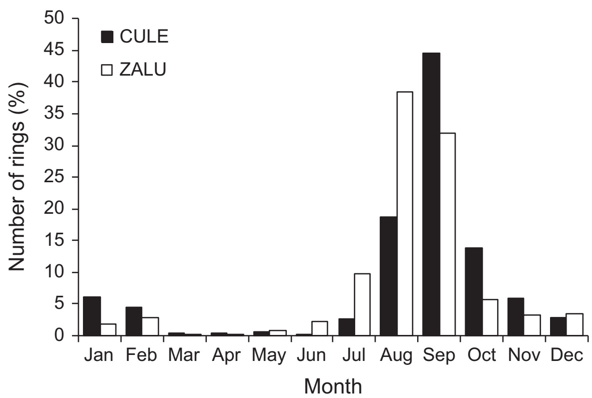

Figure 3. Yearly distribution of the number of rings read (%) in the two study landfill sites (CULE, Culebrete; ZALU, Zaluaga); each ring has been considered only once per month.

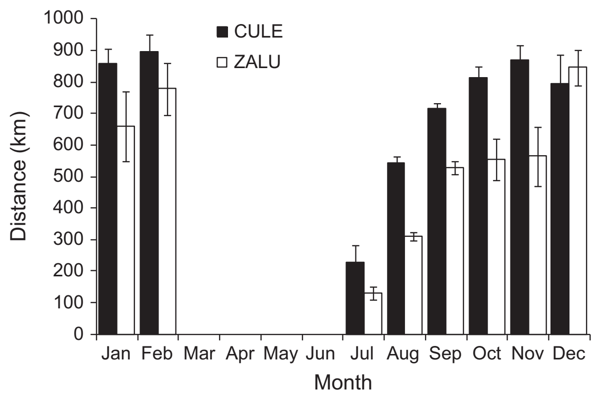

Figure 4. Mean (±se) distance between regions of origin (i.e. ringing sites) and each landfill site (CULE, Culebrete; ZALU, Zaluaga), in relation to the month when the rings were read. Data from March to June have been removed owing to their small sample sizes (n < 10 reads per month).

Staying probability

Models supporting transients fitted the data better than models ignoring them (Table 2). The first ranked model considered a decreasing linear effect of time on ϕ_1 with constant ϕ_2 values (Fig. 5). The second model, which fitted the data equally well, also assumed a decreasing linear effect of time on ϕ_1, but an increasing linear effect of time on ϕ_2 (Fig. 5). According to the first model, the proportion of transients ranged from 32.7% (interval 2 to interval 3) to 67.8% at the end of the season. In both models, however, ϕ-values were associated with very high error estimations. The third model assumed constant ϕ_1 and ϕ_2 (mean ± se: 0.31 ± 0.05 and 0.66 ± 0.05, respectively). For this third model, the estimated proportion of transients was 53.0% (95% confidence interval (CI) 44.5–60.4%). The P-estimation in these first three models was 0.27 ± 0.05.

Population size estimates

The observed population size at Culebrete varied between months (month effect: $F_{10,47}$ = 413.63, P < 0.001; year as a random factor: Z = 0.99, P = 0.32; for the B-parameter estimates see Table S2). Overall, the population at Culebrete

Table 2. Ranking of the Cormack-Jolly-Seber models used to test the probability of staying at one of the study landfill sites (Culebrete) during the autumn migration period (August–September).

Models	AICc	ΔAICc	AICc weight	np	Deviance
1. ϕ_1(time.linear), ϕ_2	68 857.08	0.00	0.39	4	67 818.51
2. ϕ_1(time.linear), ϕ_2(time.linear)	68 857.23	0.15	0.37	4	67 818.67
3. ϕ_1, ϕ_2	68 858.81	1.73	0.17	3	67 822.26
4. ϕ_1, ϕ_2(time.linear)	68 860.42	3.34	0.07	4	67 821.85
5. ϕ	68 870.31	13.23	0.00	2	67 835.77
6. ϕ(time.linear)	68 870.88	13.80	0.00	3	67 834.33

AICc, Akaike information criterion corrected for small sample size; ΔAICc, difference in AICc values in relation to the top model; np, number of parameters; ϕ_1, apparent survival (i.e. staying probability) from the first 5-day period when a ringed stork was seen to the next period; ϕ_2, staying probability in subsequent periods.

decreased from January to March, when the lowest annual values were detected (fewer than 100 individuals). From April, the number of storks tended to increase, reaching a peak in September (with mean counts of *c.* 800 storks per day). The number of storks then sharply decreased in October, before starting to increase again until January (Fig. 6, Table S2). Considering a mean population size of 338 storks in August and 782 in September (Fig. 6), and assuming a constant proportion of transients of 0.53 (95% CI 0.45–0.60), the estimated total population size passing through Culebrete during August–September (migration period) was 4088 (95% CI 3640–4480) storks.

At Zaluaga, the censused population of storks also varied between months (month effect: $F_{11,106} = 424.50$, $P < 0.001$; year as a random factor: $Z = 1.83$, $P = 0.068$; Table S2). Here, the population remained statistically constant from December to February (with a mean of *c.* 15 individuals), then decreased in March and stayed at low numbers until May (with daily mean values < five birds). In June, the population was observed to increase again until August, when it reached a

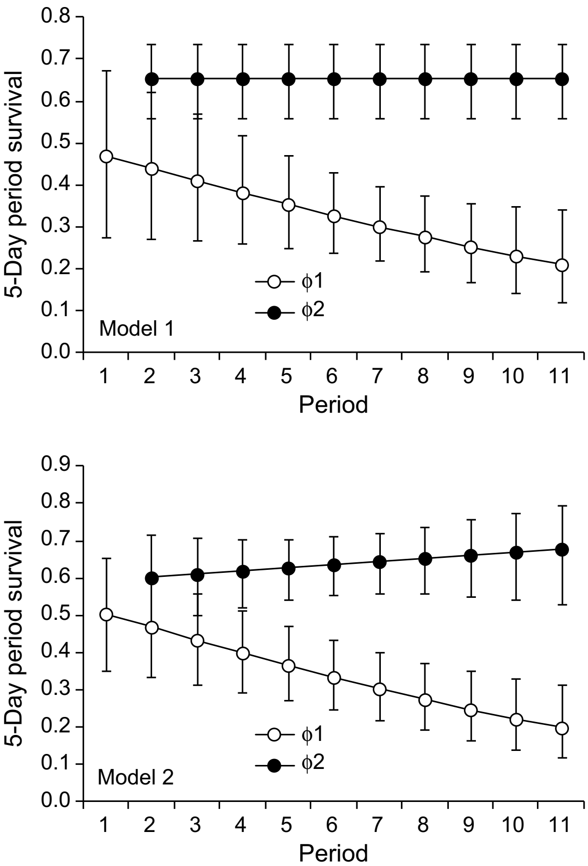

Figure 5. The 5-day period staying probability rates for White Storks seen at the Culebrete landfill during the autumn migration period (August–September) of 2014 and 2015, according to models 1 and 2 from Figure S1. Values for period 1 refer to staying probability for the interval between periods 1 and 2, and so on. Parameters: ϕ_1, staying probability from the first period when a ringed stork was seen to the next period; ϕ_2, staying probability in subsequent periods.

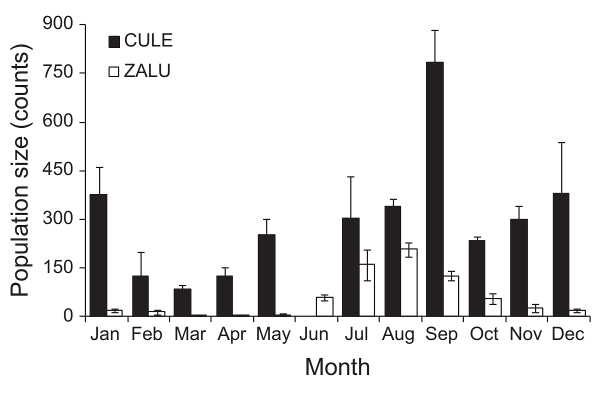

Figure 6. Mean (±se) daily number of White Storks found during the whole year at each landfill site (CULE, Culebrete; ZALU, Zaluaga) according to visual censuses (Table 2). There were no data for Culebrete in June.

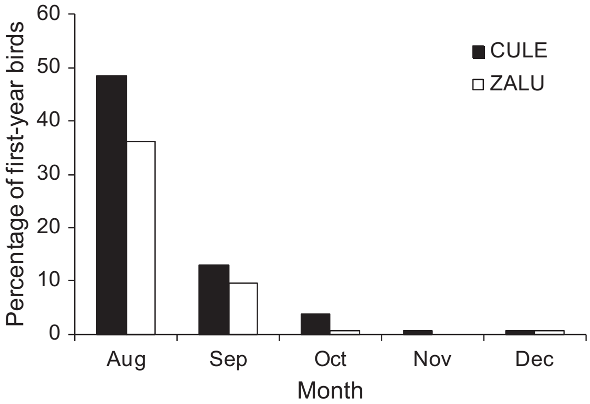

Figure 7. Percentage (%) of first-year White Storks stopping-over at the two study sites (CULE, Culebrete; ZALU, Zaluaga).

peak of mean counts of *c.* 200 storks per day. Afterwards, the number of storks decreased continuously until December (Table S2; Fig. 6). Considering a mean population size of 206 storks in August and 125 in September (Fig. 6), and assuming the same proportion of transients as at Culebrete (0.53), the total population size estimated at Zaluaga during August–September was 1208 (95% CI 1076–1324) storks.

Population age structure

The proportion of first-year birds tended to decrease from August to December at both landfills (Fig. 7). Indeed, this proportion was very low (< 1%) in November and December, as well as in October at Zaluaga, whereas in August it was *c.* 50% at Culebrete and 36% at Zaluaga.

DISCUSSION

White Storks passing over two landfills in the East-Atlantic flyway through the western Pyrenees came from a broad area that included most of the species' western European breeding range, from northern Iberia and France to Germany. Our results supported recent studies showing that storks from southern Iberia rarely move northwards in their post-natal dispersal or migratory movements (Cuadrado *et al.* 2016). Most ringed birds using the study sites belonged to the breeding population in France, especially from the northern and western populations, which began to establish in these areas during the 1980s and nowadays contain around half of the French White Stork population (Barbraud *et al.* 1999, Rojas *et al.* 2016). The (potential) connectivity between the western French and the northern Iberian breeding populations via dispersal events (i.e. birds born in one population and recruited as breeders in the other) is, however, largely unknown (but see Barbraud *et al.* 1999). Similar to ring-recovery data obtained at the Strait of Gibraltar, we found no storks coming from more easterly European regions such as Poland, Russia, Hungary or Ukraine. This is not surprising, as breeding White Storks from these regions usually migrate through the East-European flyway to reach their African winter quarters via the Bosporus, although a few individuals are known to pass through Gibraltar (Martín *et al.* 2016). These birds would most probably enter Iberia through the eastern edge of the Pyrenees and would then have a parallel migration route along the Mediterranean coast, as shown for other migrant bird species (Arizaga *et al.* 2012, Andueza *et al.* 2013).

Most ringed birds were found at the end of the summer during the autumn migration period, mostly in August–September. This result is in accord with the annual pattern of abundance for the species in Iberia, which peaks in the region during the migration period (Tellería *et al.* 1996). By contrast, the number of rings detected from March to June was very low, fitting with the annual patterns of abundance based on our censuses, and reflecting a relatively low use of the landfills during spring and the first part of the summer (Gilbert *et al.* 2016). This suggests that local breeding birds may still visit the landfills during the chick rearing period (J. Arizaga pers. obs.), but probably only those from colonies nearby to avoid long-distance foraging trips when chick-provisioning. Nevertheless, the number of ringed storks at Culebrete in May was remarkably low (n = 3) compared with the mean number of storks assessed by visual censuses (*c.* 250). Considering that those ringed birds were from abroad (French and German origin), and that none of the 288 chicks colour-marked from 2012 to 2016 in a number of colonies around Culebrete were seen at the landfill (Resano-Mayor *et al.* 2016), our results suggest that a large proportion of un-ringed storks foraging at Culebrete in May are immature birds from other breeding areas. When comparing the current dynamics of our study sites with the activity at a roosting site of storks that foraged at a landfill in Central Spain (Blanco 1996), we find some differences. For instance, in Central Spain the landfill was mostly used in early August, followed by a sharp decline, with low and stable numbers during autumn and winter (Blanco 1996). The spatial distribution of storks, however, showed annual variations (Gordo *et al.* 2013).

The increasing mean ringing site distance from summer to winter at our study sites suggests that storks breeding further away arrive or pass through Iberia later within the season, with some of them staying during the winter. This reflects population-specific timing of migration, a phenomenon well known among several European species (Arizaga & Barba 2011, Maggini *et al.* 2013), and the White Stork in particular (Cramp 1977). Local storks, many of them juveniles, feed on both landfills from June to August before they depart for their southern wintering quarters (Resano-Mayor *et al.* 2016). From August onwards, coinciding with the peak of autumn migration, foreign storks were apparently more abundant than local ones. During this period, birds from widely differing breeding/natal origins made use of the landfills. The higher mean distance of origin of the storks visiting our landfill sites during the winter (November–February) suggests a predominance of northern-origin overwintering storks, although the presence of local adult birds may have been underestimated due to the lack of long-term ringing studies (Resano-Mayor *et al.* 2016). An increasing number of storks visiting their nests during the winter have been reported in Navarra, suggesting that some of these wintering birds belong to the local breeding population. Unravelling the use of landfills by both local and non-local individuals during the winter, and how much this has contributed to the change in migratory patterns, is of particular interest (Catry *et al.* 2017). Overwintering at higher latitudes could benefit storks by allowing them to be closer to their breeding zones. In fact, the last Spanish White Stork census in winter provided an estimation of 31 200 individuals, including storks from the whole range from Iberia to central Europe (Molina & Del Moral 2005). However, the role that open-air landfills play in such observed changes in migration behaviour, and the underlying possible conservation concerns, remains as an open question (Flack *et al.* 2016, Gilbert *et al.* 2016).

Cormack-Jolly-Seber models supported the presence of transients during the migration period. In particular, we obtained a mean estimation of 53% of transients from one 5-day period to the next for the Culebrete landfill. Thus, at least in this site around half of the population was renewed on an almost weekly basis. This also suggests a relatively long stopover period for a large number of birds, as the other half of the population remained at Culebrete at least 5 days after arrival. Previous data on stopover duration of satellite tracked storks showed that the majority of stopovers were during the autumn migration period and took a mean of 9.5 days (range 5–19; Shephard *et al.* 2015). Most of those tracked birds entered Iberia through our landfills and, therefore, it is likely that some stopped over in our study sites. In fact, results from Shephard *et al.* (2015) match with our estimates of transients, with some birds staying less than a week, but others for longer. This also accords with our results showing that four storks were seen at both landfills in the same year (always first in the northern landfill, i.e. Zaluaga), for which the mean time elapsed between observations at one landfill and the other was *c.* 15 days (range 6–38). The relatively long stopover duration of a sizable fraction of the population may suggest intense foraging (Warnock 2010), although we have no data with which to estimate to what extent storks at landfills (especially those with long stays) had a net energy gain.

The percentage of storks stopping-over at our study sites may be well below the estimation of storks passing through Gibraltar, with mean annual counts of *c.* 56 000 birds, but above the mean of 354 storks passing through Lindus, a mountain pass in the western Pyrenees, located just between the two study sites (Martín *et al.* 2016). With around 4000 storks estimated to stopover at Culebrete, and considering that the estimated mean proportion of first-year birds was 18% for the months of August–September, a population of almost 3280 immature–adult birds stopping-over at Culebrete can be roughly estimated. Excluding the population of resident adult birds, estimated to be *c.* 600 pairs (Resano-Mayor *et al.* 2016) from this total gives rise to an estimate of *c.* 2080 non-local storks stopping-over at Culebrete. Considering that the western European migrant population (Iberia excluded) is assessed to be *c.* 7250 adult breeding pairs (Tucker & Heath 2004, Issa & Muller 2015), we estimate that 14% of this population may stopover at this landfill site. This estimation fits with one of the Ramsar criteria used to consider a wetland (here, a site) as relevant internationally, as it is above 1% of the size of the origin population. For Zaluaga, this value would be *c.* 4%, which still satisfies this criterion. Here, it is not our aim to highlight that these landfill sites should be protected for their role as stopover sites for White Storks (or other species using these feeding sources), but to emphasize that two artificial foraging sites, which can entail potential health risks (Amano *et al.* 2016), probably influencing the migration phenology (Catry *et al.* 2017) and/or population dynamics and spatial distribution (Oro *et al.* 2013), are currently being used by a large fraction of birds along their migration routes. This means that management actions at these sites would very probably have an influence on the fitness, behaviour and dynamics of those populations most dependent on these kinds of subsidies, and hence are worthy of further study. It should be noted, however, that when properly designed and managed, landfill sites can offer good conditions to many bird species.

The proportion of first-year birds tended to decrease very quickly after summer (August), with most birds found in winter being adults. All European White Storks used to overwinter in Africa; however, currently, an increasing number winter in southern Europe (e.g. Molina & Del Moral 2005, Catry *et al.* 2017), a phenomenon also reported for the East-European population (Kania 2006). It is also documented that adults tend to overwinter in areas further north, and that the proportion of first-year birds going to Africa is higher compared with older birds. Our results support previous findings indicating that storks overwintering in southern Europe, especially in northern latitudes of Iberia, are mostly adults (Resano-Mayor *et al.* 2016).

Overall, it can be concluded that the studied landfills were used by a large proportion of the White Stork population breeding in western Europe, especially during the autumn migration period. Culebrete, in the Ebro river basin, is of particular interest, with almost 4000 storks stopping-over during the autumn migration months (August–September). Considering the potential, but unclear, effects of these artificial stopover sites on aspects such as stopover decisions during migration and the health risks linked to feeding on refuse food, our study raises important conservation concerns, especially considering the new European policies towards banning all open-air landfills. Moreover, together with storks, these two landfills are also used by other migratory birds, including Black Kites *Milvus migrans*, Red Kites *Milvus milvus*, Egyptian Vultures *Neophron percnopterus*, herons and several gull species, as well as other resident local species of concern, including immature Spanish Imperial Eagles *Aquila adalberti* and Griffon Vultures *Gyps fulvus* (J. Arizaga, pers. obs.). Therefore, the management of these and other landfills (including associated activities such as poisoning or illegal waste dumping) can have a strong impact on the entire bird assemblage by exposing them to a potential permanent risk. That is why a better understanding of the role played by landfills in White Stork ecology in particular, and many other opportunistic birds in general, is essential in order to provide management recommendations, as well as to evaluate the consequences of the proposed open landfill closures in Europe.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Number of visual counts conducted at each landfill site (Culebrete, Zaluaga) per month and period (years).

Table S2. *B*-parameter estimates of numbers of White Storks found at the Culebrete and Zaluaga study sites.

Figure S1. Seasonal distribution (percentage) of the color-rings read per month at each landfill (each individual bird considered only once in a month) according to bird origin (Table 1).