Age mediates access to landfill food resources and foraging proficiency in a long-lived bird species

Bruno Herlander Martins [a, b, c, d, *] , Andrea Soriano-Redondo [a, b, c, e, f] ,
Aldina M. A. Franco [d] , Inês Catry [a, b, c]

[a] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Portugal
[b] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, Portugal
[c] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, Campus de Vairão, Portugal
[d] School of Environmental Sciences, University of East Anglia, Norwich, UK
[e] HELICS, Helsinki Lab of Interdisciplinary Conservation Science, Department of Geosciences and Geography, University of Helsinki, Finland
[f] HELSUS, Helsinki Institute of Sustainability Science, University of Helsinki, Finland

ARTICLE INFO

Human activities have altered the availability of resources for wildlife. Landfill sites now provide abundant and predictable anthropogenic food subsidies worldwide, sustaining increasing numbers of opportunistic species and shaping their foraging behaviour. However, although individuals may differ in their ability to use these resources, the factors influencing this variability within species are still poorly known. Using GPS data from 68 adult and 67 juvenile white storks, *Ciconia ciconia*, tracked during their premigratory periods between 2018 and 2020, we investigated whether age determines landfill attendance and the ability to compete for space and food. Additionally, using video recordings of 165 adults and 124 juveniles obtained in the 2020 premigratory period, we investigated whether age influences landfill foraging proficiency and dominance over resources. Adult storks visited landfills on 57% of the days, while juveniles only visited landfills on 29% of the days. There was strong competition for food at landfills, with adults exerting dominance over juveniles, foraging predominantly in areas with higher food availability and outcompeting juveniles in food acquisition. Juveniles had significantly lower food intake rates in the best foraging areas and showed less aggressiveness, being forced to use adjacent lower quality areas. Overall, juveniles had limited access to landfill resources, suggesting that landfill diet specialization is mediated by age-related improvements in foraging expertise and increased competitiveness developed during maturation. Thus, landfill use is shaping foraging strategies and species behaviour from an early age, with potential consequences for population dynamics.

© 2023 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Humans have greatly transformed ecosystems over recent centuries, changing the availability of foraging resources for wildlife across the world (Ellis et al., 2010; Foley et al., 2005). Food waste disposal at landfills and dumps currently provides a major source of predictable anthropogenic food subsidies (PAFS; Oro et al., 2013), which is exploited by a growing number of species (Oro et al., 2013; Plaza & Lambertucci, 2017). The superabundance of food and easy access, combined with high spatial and temporal predictability (Oro et al., 2013; Plaza & Lambertucci, 2017; Thyberg & Tonjes, 2016), are substantially reducing foraging times and energetic costs of species and shaping the foraging strategies of individuals (Patenaude-Monette et al., 2014; Soriano-Redondo et al., 2021; van Donk et al., 2019).

In recent decades, the exploitation of anthropogenic food waste has often been associated with dietary shifts in opportunistic and scavenger species (Bialas et al., 2020; Newsome et al., 2015; Oro et al., 2013; Tauler-Ametller et al., 2017). These changes are linked with positive fitness effects, such as improvement in body condition, and increased breeding performance and survival leading to population growth (Newsome et al., 2015; Oro et al., 2013; Plaza & Lambertucci, 2017; Weiser & Powell, 2010). Nevertheless, foraging in landfills can produce contrasting and detrimental effects, through increased risk of pathogen infections, poisoning or ingestion of foreign bodies, affecting the health and survival of

* Corresponding author.
E-mail address: brunohmartins@cibio.up.pt (B. H. Martins).

individuals (Plaza & Lambertucci, 2017). Additionally, the concentration of organic waste in restricted areas attracts high densities of individuals, especially birds (Blanco, 1994; Novaes & Cintra, 2013; Soriano-Redondo et al., 2021; Tauler-Ametller et al., 2017), and probably increases intraspecific and interspecific competition mediated by density-dependent processes, which may result in reduced food acquisition with detrimental consequences for individual fitness (Araújo et al., 2011).

Increased competition for food resources can have a strong effect on population dominance structure, in which dominant individuals outcompete subordinates in food acquisition, forcing them to move to alternative foraging areas (Kaufmann, 1983; Tibbetts et al., 2022). Bird dominance phenotypic attributes often include age, sex and body size (Lundberg, 1985; Richner, 1989). Older individuals are usually dominant, as young ones lack the skills to recognize or compete for profitable foraging sites, due to inexperience and physical immaturity (Marchetti & Price, 1989; Wunderle, 1991). Experience can be especially relevant in the choice of foraging grounds, where adults repeatedly and efficiently exploit the same areas from learned predictable habitat features (Votier et al., 2017; Wakefield et al., 2015). In young birds, foraging specialization is developed during individual exploratory behaviour in early life and is later refined as they grow older and gain more experience (Bolnick et al., 2003; Campioni et al., 2020; Marchetti & Price, 1989; Wunderle, 1991).

In long-lived species with slow maturation, physical development and individual learning can further delay the acquisition of adult-like foraging skills, increasing the differences in foraging proficiency between adults and naïve juveniles (Grecian et al., 2018; Mendez et al., 2017; Riotte-Lambert & Weimerskirch, 2013). Ultimately, this might prevent the specialization on some food sources and the development of foraging expertise (Diamond & Bond, 1991; Marchetti & Price, 1989; Wunderle, 1991). Age segregation in the use of the best foraging sites or resources can have significant spillover effects, lowering long-term survival and thus individual fitness, with consequences for the demography of populations (Rotics et al., 2021; Sæther et al., 2013). While exploitation of human food subsidies, such as landfill waste, has enabled the rapid population growth of generalist species, the influence of age and experience on an individual's ability to compete for space and resources remains poorly understood. This knowledge will help us understand how species adapt to new resources and changes in food availability.

The white stork, *Ciconia ciconia*, is a very adaptable and opportunistic long-lived species with slow maturation, for which early-life learning and experience play an important role in the acquisition of foraging skills (Bocheński & Jerzak, 2006; Elliott et al., 2020). In the last few decades, the breeding population in southern Europe has increased considerably, driven by their trophic plasticity and ability to exploit new anthropogenic resources, mainly those available at landfill sites (Molina & Del Moral, 2006; Rosa et al., 2005, p. 41). Thousands of storks now use landfills (Catry et al., 2017; Gilbert et al., 2016; Soriano-Redondo et al., 2021), and this time- and energy-saving strategy improves feeding efficiency when compared to foraging on natural prey (Soriano-Redondo et al., 2021).

The migratory behaviour of white storks has been changing and an increasing number of individuals no longer carry out their annual autumn migration from Europe to sub-Saharan Africa, remaining in Iberia throughout the year (Catry et al., 2017; Gilbert et al., 2016). Abundant year-round food available at landfills is one of the factors that may have contributed to the suppression of migratory behaviour and to the steep increase in the resident population (Catry et al., 2017; Tortosa et al., 2002). However, while Iberian adult white storks are predominantly resident, juveniles are still mostly migratory (Acácio, 2021; Acácio et al., 2022; Bécares et al., 2019). Therefore, understanding the use of landfill resources, by adult and juvenile storks, can help unravel the processes acting on individual movement behaviour and on development of foraging strategies, including exploitation of anthropogenic food sources.

In this study, we analysed age-related differences in landfill use by white storks. Combining GPS tracking data, monthly counts in landfills and behavioural data from video recordings at landfills, we investigated the influence of age and experience in determining (1) landfill attendance, (2) access to food resources and (3) foraging proficiency (behaviour time budgets, feeding success and agonistic interactions), during the premigratory period. We hypothesized that landfill foraging skills are progressively acquired with age; hence we expected adults to use landfills more often and show higher feeding success.

METHODS

GPS Deployment

We used GPS tracking data from 68 adult and 67 juvenile white storks tagged in southern Portugal between 2018 and 2020. Storks were tagged with 'Flyway 50' GPS/GSM loggers from Movetech Telemetry (Thetford, U.K.; four different models varying slightly in weight), 'Ornitrack-50' GPS/GSM loggers from Ornitela (Vilnius, Lithuania) and 'Bird solar tags' GPS/GSM loggers from e-obs GmbH (Grünwald, Germany). Adult birds were captured for tagging at multiple landfill sites using leg loop traps, or at their nests with a remotely activated clap net. Birds tagged at landfills were further confirmed as breeding adults by identifying their nests from the GPS data and visiting them to verify the presence of eggs and/or chicks. Juvenile birds were retrieved from their nests for tagging 50—55 days after hatching and returned afterwards. All birds were measured and ringed, and the tracking devices were deployed as backpacks with a Teflon harness and programmed to transmit locations every 20 min.

GPS Data Set Selection

This study focused on the white stork premigratory period, when both adults and juvenile birds that recently fledged gather at landfills, probably facilitating learning from conspecifics but also competition for resources (Araújo et al., 2011; Mueller et al., 2013). For all storks, only the premigratory period of the tagging year was included. That period for adult storks was set between 1 June (corresponding to the earliest fledging day for juveniles) and the day migration started or 30 September for nonmigratory birds. The premigratory period for juvenile storks was set between the fledging day (when they moved more than 50 m from their nest) and the day migration started or the last day alive for birds that did not survive to migration. Juveniles that died soon after fledging ($N = 4$) and never moved beyond the vicinity of the nest were not included. To establish the start of migration, we used the spatiotemporal displacement method described in Soriano-Redondo et al. (2020), which combines movement displacement and spatial and temporal thresholds to identify the beginning and end of migratory movements. Following this method, the departure date was defined as the first of 3 consecutive days a stork moved more than 60 km between roosts after leaving the breeding area (calculated as the 90% kernel of June GPS locations). Lastly, in order to include only ground GPS locations in the analysis that represented the use of possible foraging sites, all locations at the nests or in flight with ground speed above 1.39 m/s (Marcelino et al., 2021) were excluded.

Classification of Landfill Areas

All landfill sites in Portugal and Spain used by the tracked white storks were initially identified from the GPS data and later confirmed in the field. Furthermore, from 2018 to 2020, we carried out monthly visits, between June and September, to five landfills in southern Portugal, which were the most used landfills by the tracked storks (Évora, Ermidas do Sado, Beja, Barlavento and Sotavento; Fig. 1). In all visits, the exact location where the waste was discarded (dump site) was visually confirmed and mapped, enabling the classification of three landfill areas with a decreasing gradient of food availability. The landfill 'core area' was defined as the area within a radius of 25 m around the dump site, where piles of fresh waste were highly clumped and food availability was the highest. The area between 25 m and 50 m from the dump site was defined as the 'buffer area', where the waste was spread over a larger area and compacted by the landfill machinery, making organic matter less accessible and gradually reducing the amount of food available. The remaining landfill area, more than 50 m away from the dump site, was defined as the 'outer area', being the area with the lowest food availability.

GPS Data Analysis

Age-related differences in landfill attendance were investigated by comparing the daily and overall landfill attendance of adult ($N = 68$) and juvenile ($N = 67$) storks. For each individual, daily landfill attendance was determined as the proportion of days of the premigratory period with at least one GPS location at a landfill, and overall landfill attendance was calculated as the proportion of GPS locations obtained during the premigratory period at landfill sites.

Age-related differences in access to food resources were investigated by comparing the proportion of GPS locations of adult and juvenile storks in areas where food was available within landfills (core and buffer area attendance) during the premigratory period. This was only possible to determine for the 61 adult and 47 juvenile storks that used the five landfills where food availability areas (core, buffer and outer areas) were identified. To determine core area attendance, the GPS locations of each bird and at each landfill were first classified as 'inside the core area', where food resources were most abundant, or 'outside the core area'. The subset of locations obtained outside the core area was then considered to determine buffer area attendance, where food resources were less abundant; thus the GPS locations were classified as 'inside the buffer area' or 'inside the outer area'.

Stork Counts and Video Recording at Landfills

In 2020, monthly visits to the five landfills in southern Portugal enabled us to determine the number of adult and juvenile white storks in each area (core, buffer and outer area) of the landfills. Storks were counted three times during the visits, with intervals of approximately 30 min, to account for variability in numbers due to stork arrivals and departures. The average monthly number of storks using each landfill and each area of the landfills was calculated. At each count, the proportion of storks actively feeding was visually estimated, and the monthly average proportion of storks foraging in each landfill area was determined.

In July 2020, using a Canon Power Shot SX50 HS camera, B.H.M. recorded on video the behaviour of 165 adult storks and 124 juveniles during 3 consecutive minutes for each individual, across the different food availability areas of the five landfills. As the number of juveniles at each landfill site was always very low, especially in the core areas, only those that were observed simultaneously and confirmed as different individuals on a given visit were recorded. Hence, only a maximum of five juvenile storks were recorded in some landfill areas. In contrast, as adults were always numerous, five adult storks were randomly selected and recorded in each area per visit. Since it was not possible to reliably identify birds between different visits, to prevent pseudoreplication, recordings were performed at the five different landfills located hundreds of kilometres apart and visits to the same landfill on consecutive days were avoided. We obtained 55 videos for adult storks in each landfill area, while for juvenile storks, we obtained 17 videos in the core area, 55 in the buffer area and 52 in the outer area. For both counts and videos, birds were classified as adults (>2 years) or juveniles (first year) through direct observation of phenotypic characteristics (Van den Bossche et al., 2002). Adults
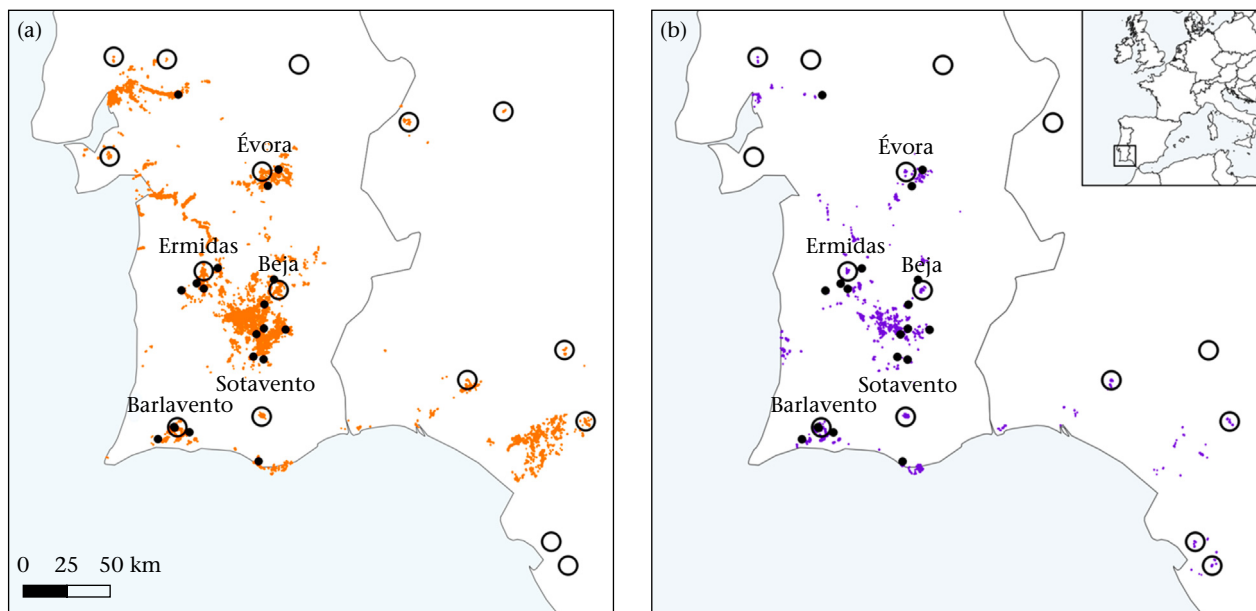

Figure 1. Total ground GPS locations of (a) adult ($N = 68$) and (b) juvenile ($N = 67$) tracked white storks during their premigratory periods between 2018 and 2020. Black circles and dots indicate landfills and nesting sites, respectively.

have a red beak, lack glossy feathers and have extensive moult, while juveniles have a dark beak, glossy feathers and no moult. It was not possible to distinguish further age classes based on phenotypic characteristics. Entry to the landfills and filming was authorized by the local authorities, which provided access to the best place for counting and filming while avoiding disturbing the birds. The visits were all completed during the morning, as this is the time when most waste is dumped at landfills.

Video Recording Analysis

Age-related differences in landfill foraging proficiency were examined by comparing information obtained through video recordings of the behaviours of 165 adult and 124 juvenile storks. All videos were analysed by B.H.M. and were used to determine behaviour time budgets, feeding success and agonistic interactions of each stork. For behaviour time budgets, the predominant behaviour in each 10 s period of the 3 min videos was identified using an ethogram (Table A1), to facilitate interpretation and guarantee consistency. All behaviours were then merged into three main categories ('foraging', 'alert' or 'inactive'; Table A1), and were used to determine the individual proportion of foraging, alert and inactive periods. For feeding success, the total number of food units ingested during the 3 min videos was estimated. To quantify food intake, all ingested items were classified into size categories using bill length as a reference and considering a food unit equivalent to one-quarter of the bill size. Thereafter, all estimated corresponding food units were counted to determine total food intake. For agonistic interactions, the overall aggressiveness during the 3 min videos was quantified. All agonistic encounters were identified and classified as 'aggressor type' or 'victim type', and used to determine the individual proportion of interactions as the aggressor.

Statistical Analysis

Data were analysed using R version 4.2.1 (R Core Team, 2022). To evaluate age-related differences in landfill attendance and understand how often tracked storks visited landfills during their premigratory periods, we fitted two generalized linear models (GLMs), with the 'glm' function. The first model included the daily landfill attendance (individual proportion of days visiting landfills during the premigratory period) and the second model included the overall landfill attendance (individual proportion of GPS locations in landfills during the premigratory period), both as binomial response variables. Both models included age (adult or juvenile) as the explanatory variable and a quasibinomial distribution due to residual overdispersion.

To evaluate age-related differences in access to food resources and understand how tracked storks were able to use the landfill areas with higher food availability during their premigratory periods, we fitted two generalized linear mixed models (GLMMs), with the 'glmer' function in the 'lme4' package (Bates et al., 2015). The first model included the landfill core area attendance (individual proportion of GPS locations in the core area) and the second model included the landfill buffer area attendance (individual proportion of GPS locations in the buffer area) as binomial responses. In both models, age (adult or juvenile) was specified as the explanatory variable, while bird ID and landfill site were set as random effects to account for variations in access to food resources by individuals that used more than one landfill.

To examine the foraging proficiency of adult and juvenile storks at landfills, we first fitted three GLMMs to specifically explore the influence of age and landfill area on time spent performing each of the main behaviours observed when using landfills. The models included the foraging time (individual proportion of foraging periods), alert time (individual proportion of alert periods) and inactive time (individual proportion of inactive periods) as binomial responses. For the three models, age (adult or juvenile), landfill area (core, buffer or outer area) and their interaction were specified as explanatory variables, while landfill site was set as a random effect. Second, we explored the influence of age and landfill area on feeding success. The GLMM model included food intake (number of food units ingested) as a Poisson response, while age (adult or juvenile), landfill area (core or buffer area) and their interaction were specified as explanatory variables, and landfill site was included as a random effect. Food intake was not examined in the outer area as it rarely took place, reflecting the low food availability in this area. Finally, we fitted one GLMM to explore the influence of age and landfill area on agonistic interactions. This model included aggressiveness (individual proportion of interactions as the aggressor) as the binomial response. Age (adult or juvenile), landfill area (core or buffer area) and their interaction were specified as explanatory variables, while landfill site was included as a random effect. There were no agonistic interactions observed in the outer area; hence this was excluded from the analysis. Whenever necessary, we performed post hoc Tukey tests to assess differences between landfill areas, using the 'emmeans' function in the 'emmeans' package (Searle et al., 1980).

Ethical Note

The white stork is not endangered or threatened and is common in Portugal, where this study was conducted. The procedure was approved by the Institute for Nature Conservation and Forests in Portugal (licence numbers: 548/2018/CAPT, 248/2019/CAPT and 365/2020/CAPT). Storks were trapped, handled and tagged by trained researchers and released at the point of capture. The tag and harness together weighed 50–90 g, representing 1.1–3.7% of the bird's body mass. Most birds were resighted in the days following tag deployment and throughout the breeding season, and no abnormal behaviour or adverse effects due to tagging were observed. Additionally, to reduce the long-term effects of the loggers, all devices were deployed with a weak-link harness design. The four Teflon straps that made up the harness were secured together with a biodegradable cotton thread, acting as the weak link that deteriorates over time until it breaks and the entire harness falls off.

RESULTS

Landfill Use During the Premigratory Period

Tracking data for 68 adult and 67 juvenile white storks tagged in southern Portugal were obtained during the premigratory period. This included 7499 adult stork tracking days (mean 111 ± 22 days per individual) and 2952 juvenile stork tracking days (mean 44 ± 22 days per individual). In total, there were 259,995 adult and 63,232 juvenile GPS locations recorded. Storks foraged mainly in areas around their nests and at landfills in southern Iberia (Fig. 1). The majority of the tracked storks visited landfills (96% of adults and 76% of juveniles), while the remaining birds (4% of adults and 14% of juveniles) only foraged in natural areas. In addition, 78% of the adult birds were residents, staying in Iberia during the full

Table 1
Parameters of GLMs explaining the influence of age (adult or juvenile) of GPS-tagged white storks in determining landfill attendance during the premigratory period

GLM response	Explanatory variable	Estimate	SE	t	P
Daily landfill attendance	Intercept	0.293	0.111	2.641	**<0.009**
	Age juvenile	−1.203	0.223	−5.405	**<0.001**
Overall landfill attendance	Intercept	−1.004	0.080	−12.540	**<0.001**
	Age juvenile	−0.361	0.196	−1.843	0.068

Data were collected from 68 adult and 67 juvenile storks. The reference level for age is 'adult'. Significant P values are shown in bold.
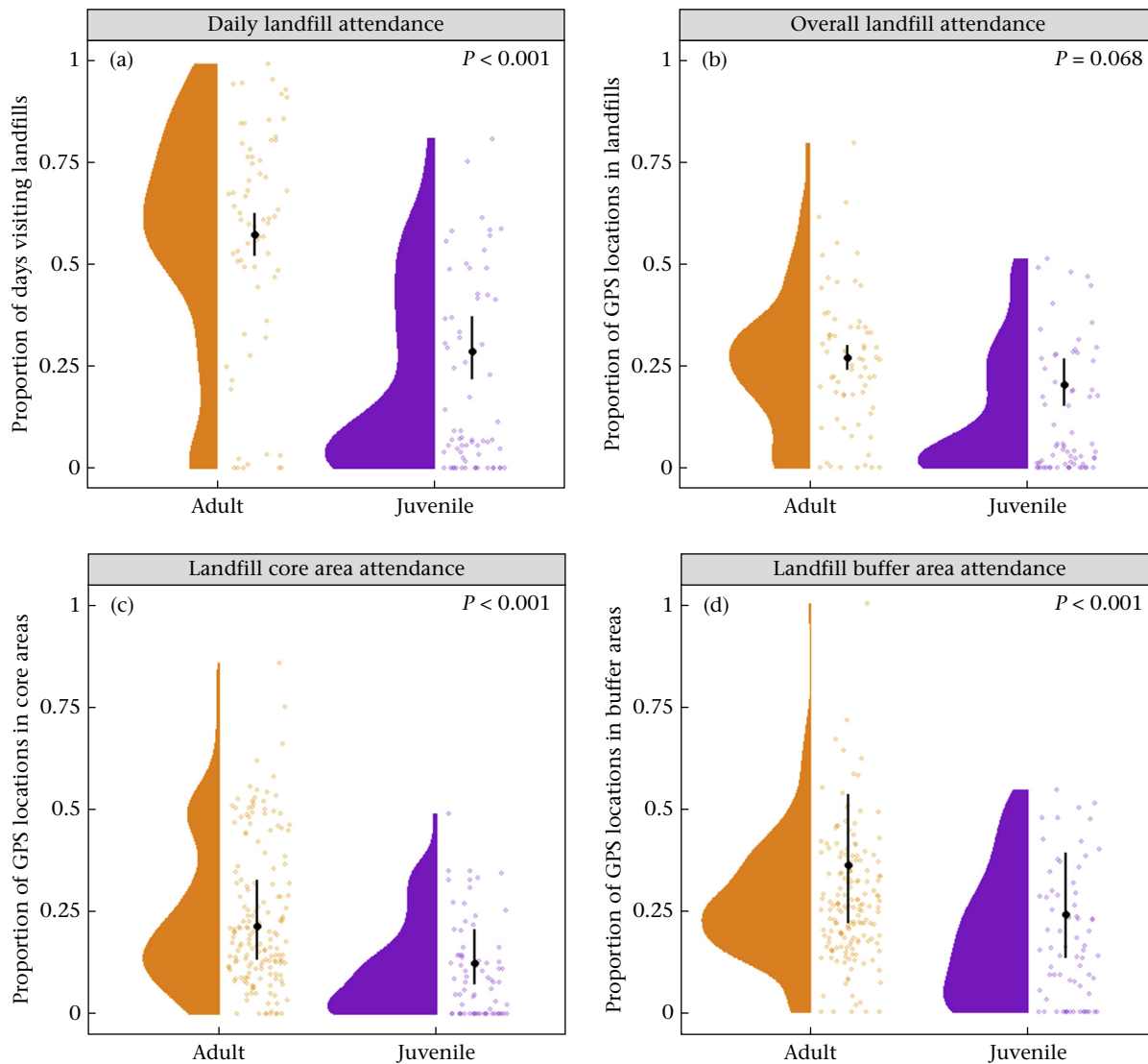
Figure 2. Predicted values and 95% confidence intervals of the estimates from the GLMs and GLMMs explaining the influence of age (adult or juvenile) of tagged white storks in determining (a) daily landfill attendance and (b) overall landfill attendance ($N = 68$ adults, $N = 67$ juveniles); and in determining (c) landfill core area attendance and (d) landfill buffer area attendance ($N = 61$ adults, $N = 47$ juveniles) during the premigratory period. Orange and purple areas represent the density distribution of attendance for adult and juvenile birds, respectively. Dots represent raw individual data.

Table 2
Parameters of the GLMMs explaining the influence of age (adult or juvenile) of GPS-tagged white storks in determining access to landfill resources during the premigratory period

GLMM response	Explanatory variable	Estimate	SE	z	P
Landfill core area attendance	Intercept	−1.292	0.295	−4.379	**<0.001**
	Age juvenile	−0.657	0.154	−4.259	**<0.001**
Landfill buffer area attendance	Intercept	−0.568	0.359	−1.584	0.113
	Age juvenile	−0.590	0.610	−4.225	**<0.001**

Data were collected from 61 adult and 47 juvenile storks. The reference level for age is 'adult'. Significant P values are shown in bold.

annual cycle, while all juveniles alive at the end of the premigratory period migrated to Africa.

Monthly counts at landfills confirmed the regular use of these sites by thousands of storks during the premigratory period (Fig. A1). Adults were always present in large numbers, yet their numbers increased steeply between June (mean 578 ± 330 individuals) and August (mean 2133 ± 1472 individuals), decreasing towards the end of the period in September (mean 1273 ± 307 individuals). Juveniles were only present between June and August in relatively small numbers (maximum count was 172 individuals), in proportions always lower than 3% of the total number of storks counted (Fig. A1).

Landfill Attendance and Access to Food Resources

Tracking data showed clear age-related differences in daily landfill attendance during the premigratory period (Table 1).

The proportion of days adult storks visited landfills was twice as high as for juveniles (predicted values $\pm$ SE: adults $= 0.57 \pm 0.11$; juveniles $= 0.29 \pm 0.19$; $P < 0.001$; Fig. 2a). However, the overall landfill attendance (proportion of GPS locations in landfills) of adult storks was not significantly higher than that of juveniles (predicted values $\pm$ SE: adults $= 0.27 \pm 0.08$; juveniles $= 0.20 \pm 0.18$; $P = 0.068$; Fig. 2b).

The distribution of storks in the three areas of the landfills (core, buffer and outer areas), representing the decreasing gradient of food availability, was also strongly associated with bird age (Table 2). The proportion of adult stork GPS locations in landfill core feeding areas was nearly twice as high as that of juveniles (predicted values $\pm$ SE: adults $= 0.22 \pm 0.29$; juveniles $= 0.12 \pm 0.31$; $P < 0.001$; Fig. 2c). In the adjacent buffer areas, the proportion of GPS locations was also considerably higher for adults (predicted values $\pm$ SE: adults $= 0.36 \pm 0.36$; juveniles $= 0.24 \pm 0.37$; $P < 0.001$; Fig. 2d).
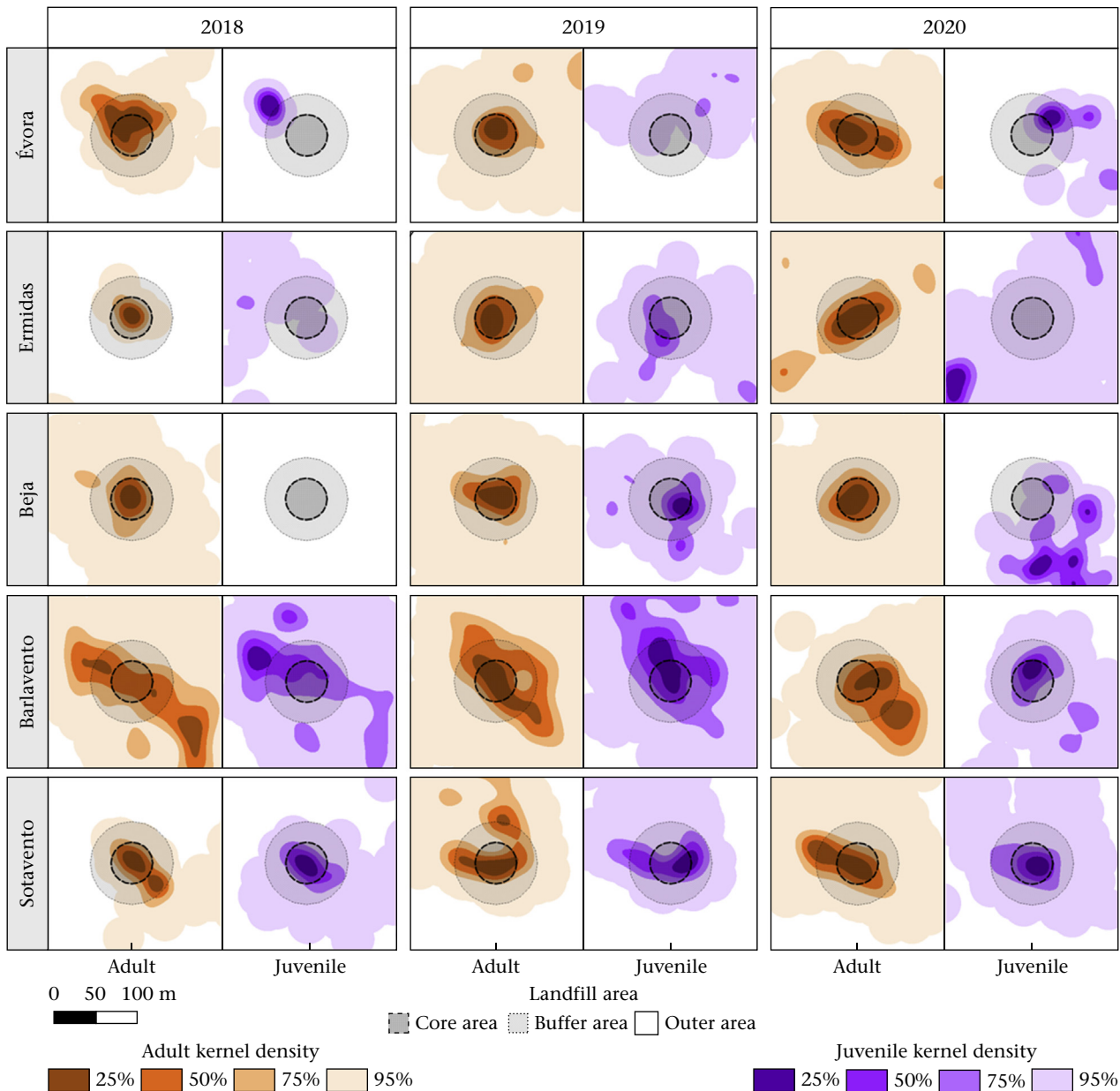

Figure 3. Kernel utilization distributions (KUD) calculated from the combined data of GPS-tracked adult ($N = 61$) and juvenile ($N = 47$) white storks that used the five landfills in southern Portugal during the 2018–2020 premigratory periods. Density of GPS locations decreases along the decreasing gradient of food availability (core > buffer > outer areas). Colours represent specific KUD contours; landfill areas are represented by black dashed circles.

Table 3
Parameters of the GLMMs explaining the influence of age (adult or juvenile) and landfill area (core, buffer or outer area) in determining foraging proficiency of white storks using landfills during the premigratory period

GLMM response	Explanatory variable	Estimate	SE	z	P
Foraging time	Intercept	0.690	0.177	3.899	**<0.001**
	Age juvenile	−1.329	0.142	−9.326	**<0.001**
	Buffer area	−1.027	0.095	−10.858	**<0.001**
	Outer area	−4.959	0.278	−17.818	**<0.001**
	Age juvenile * Buffer area	1.233	0.170	7.240	**<0.001**
	Age juvenile * Outer area	2.189	0.357	6.129	**<0.001**
Alert time	Intercept	−1.008	0.105	−9.596	**<0.001**
	Age juvenile	1.496	0.142	10.554	**<0.001**
	Buffer area	−0.356	0.107	−3.331	**<0.001**
	Outer area	−3.698	0.342	−10.798	**<0.001**
	Age juvenile * Buffer area	−0.515	0.175	−2.948	**0.003**
	Age juvenile * Outer area	0.752	0.383	1.963	**0.050**
Inactive time	Intercept	−2.555	0.194	−13.171	**<0.001**
	Age juvenile	−1.699	0.519	−3.277	**0.001**
	Buffer area	2.024	0.136	14.918	**<0.001**
	Outer area	6.302	0.244	25.880	**<0.001**
	Age juvenile * Buffer area	0.796	0.529	1.505	0.132
	Age juvenile * Outer area	−0.003	0.570	−0.005	0.996
Food intake	Intercept	2.150	0.100	21.506	**<0.001**
	Age juvenile	−1.264	0.165	−7.669	**<0.001**
	Buffer area	0.974	0.087	−11.206	**<0.001**
	Age juvenile * Buffer area	1.369	0.194	7.058	**<0.001**
Aggressiveness	Intercept	0.430	0.184	2.340	**0.019**
	Age juvenile	−1.230	0.395	−3.115	**0.002**
	Buffer area	0.132	0.277	0.476	0.634
	Age juvenile * Buffer area	−0.087	0.531	−0.164	0.870

Data were collected from 55 adult storks per landfill area and 17, 55 and 52 juveniles per landfill area. The reference level for age is 'adult' and for landfill area is 'core area'. Significant *P* values are shown in bold.

Juvenile storks were mainly restricted to the outer areas of the landfill sites (Fig. 3).

Stork counts confirmed that the core and buffer areas were dominated by adults, whereas juveniles were mostly absent from these areas and dispersed in the outer areas (Fig. A2). Storks were more aggregated in areas with higher food availability and their density decreased towards the outer areas (average density in the core, buffer and outer areas = 0.167, 0.083 and 0.001 storks/m², respectively), along the decreasing gradient of food availability.

Landfill Foraging Proficiency

Video recording analysis showed that foraging proficiency was influenced by bird age and landfill area (Table 3, Table A2). Behaviour time budgets showed that adult birds spent most time foraging in core areas and were mostly inactive in other landfill areas, while juveniles spent most of their time alert in core and buffer areas, and less time inactive than adults in outer areas. Adults spent almost twice as much time foraging in core areas as juveniles (predicted values ± SE: adults = 0.67 ± 0.18; juveniles = 0.35 ± 0.21; *P* < 0.001); in buffer areas, adults and juveniles had similar foraging levels (adults = 0.42 ± 0.18; juveniles = 0.40 ± 0.18; *P* = 0.909); and in outer areas foraging was almost nonexistent (adults = 0.01 ± 0.32; juveniles = 0.03 ± 0.25; *P* = 0.091; Fig. 4a). In contrast, the proportion of time alert was more than twice as high in juveniles as in adults, both in core (predicted values ± SE: adults = 0.26 ± 0.11; juveniles = 0.62 + 0.14; *P* < 0.001) and buffer (adult = 0.21 ± 0.11; juvenile = 0.41 ± 0.10; *P* < 0.001) areas. In outer areas, the time spent alert was low for both age classes, but significantly higher for juveniles (adults = 0.01 ± 0.34; juveniles = 0.08 ± 0.14; *P* < 0.001; Fig. 4b). Finally, the proportion of time inactive in core areas was low for both ages, but significantly higher for adults (predicted

values ± SE: adults = 0.07 ± 0.19; juveniles = 0.03 ± 0.52; *P* = 0.013); in buffer areas, it increased considerably for both ages, but remained higher for adults (adults = 0.37 ± 0.17; juveniles = 0.19 ± 0.17; *P* < 0.001); and in outer areas, almost all individuals observed were inactive but fewer juveniles were inactive than adults (adults = 0.98 ± 0.26; juveniles = 0.89 ± 0.19; *P* < 0.001; Fig. 4c). Stork counts at landfills reinforced the results of the video recordings, confirming that adult foraging birds were concentrated in the core areas while juveniles occasionally managed to forage in buffer areas (Fig. A3).

Regarding feeding success, adults showed higher food intake compared to juveniles. Adults consumed nearly four times as many food units as juveniles in core areas (predicted values ± SE: adults = 8.6 ± 0.1; juveniles = 2.4 ± 0.2; *P* < 0.001). The number of food units consumed by adults in buffer areas was significantly lower than in core areas and similar to juveniles (adults = 3.2 ± 0.1; juveniles = 3.6 ± 0.1; *P* = 0.737; Fig. 5).

Concerning agonistic interactions, adults showed substantially higher levels of aggressiveness in both areas. The greater aggressiveness, resulting from the higher proportion of interactions as aggressors, was twice as high in adults as in juveniles, both in core (predicted values ± SE: adults = 0.61 ± 0.18; juveniles = 0.31 ± 0.39; *P* = 0.010) and buffer (adult = 0.64 ± 0.26; juvenile = 0.32 ± 0.28; *P* = 0.001) areas (Fig. 6).

DISCUSSION

By combining multiple fine-scale methods, this study reveals that, in a long-lived opportunistic species, age determines landfill attendance, food access and foraging proficiency in landfill sites. In line with our predictions, adult white storks visited landfills more often than juveniles and were always present at these sites in very high numbers. They were also more likely to occur and forage in
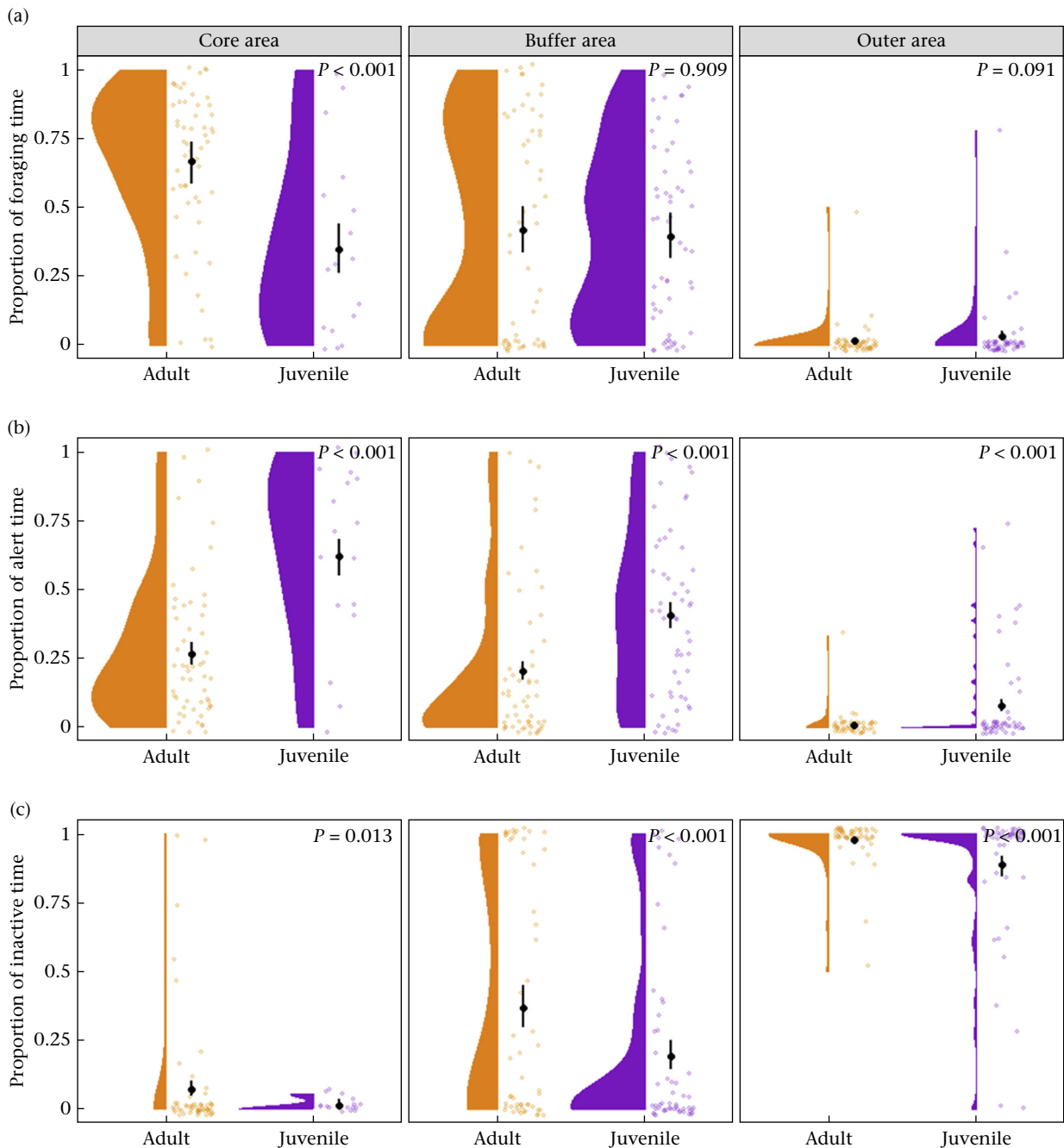
Figure 4. Predicted values and 95% confidence intervals of the estimates from the GLMMs explaining the influence of age (adult or juvenile) and landfill area (core, buffer or outer area) in determining (a) foraging, (b) alert and (c) inactive time budgets ($N = 55$ adults per landfill area; $N = 17$, 55 and 52 juveniles per landfill area) of white storks using landfills during the premigratory period. Orange and purple areas represent the density distribution of behaviour time budgets for adult and juvenile birds, respectively. Dots represent raw individual data.

core areas where resources were highly available, while juveniles were displaced to outer areas with less food availability. Additionally, adults had higher feeding success in core areas and showed higher dominance over resources. Together, these findings show that the resources available at landfills are predominantly used by adult storks, which outcompete subordinate juveniles. This supports the hypothesis that competitive abilities for foraging in landfills are probably developed as storks age.

Juvenile white storks showed similar preferences to adults in selecting foraging sites and were able to locate and attend landfills just after fledging, which is in line with what would be expected in birds using social information and behavioural cues from older birds (Franks et al., 2018; Marchetti & Price, 1989). The number of storks using landfills increased from June to August, which coincided with the end of the breeding season, after juveniles fledged and when breeding adults were no longer constrained to the nests. Stork numbers at landfills started to decrease in September, as most migratory individuals (especially juveniles) initiated their journey then (Arizaga et al., 2018; Blanco, 1996). Thus, during the premigratory period (between June and September), thousands of adult and juvenile storks congregated at landfill sites, particularly in the small core and buffer areas where the waste is dumped. This
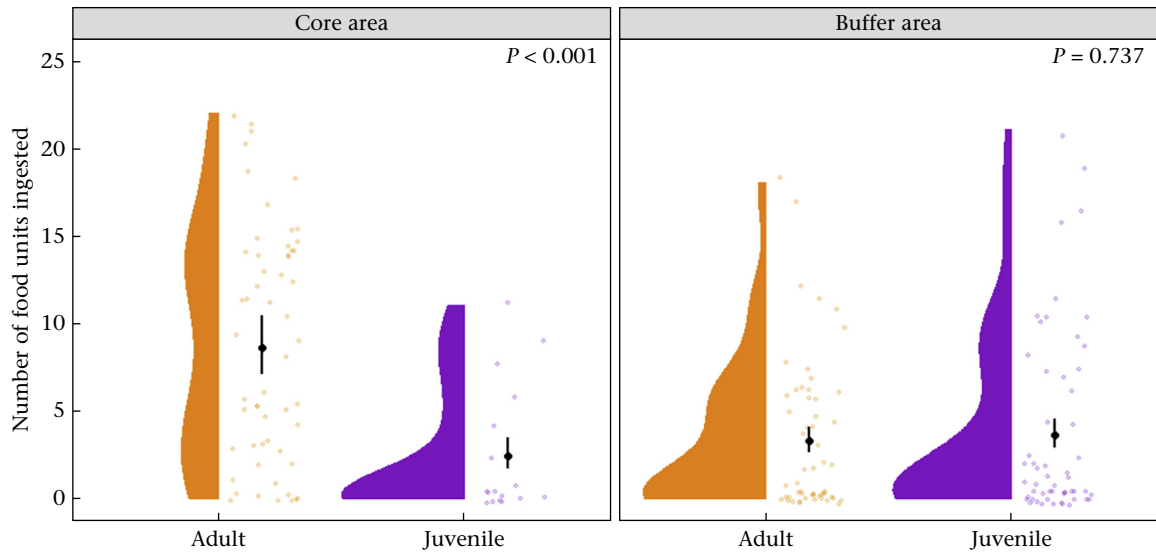
Figure 5. Predicted values and 95% confidence intervals of the estimates from the GLMMs explaining the influence of age (adult or juvenile) and landfill area (core or buffer area) in determining food intake (N = 55 adults per landfill area; N = 17 and 55 juveniles per landfill area) of white storks using landfills during the premigratory period. Orange and purple areas represent the density distribution of food intake for adult and juvenile birds, respectively. Dots represent raw individual data.

behaviour may promote changes in foraging processes, intensifying intraspecific competition for limited food resources (Real et al., 2017), and leading to the establishment of hierarchies in the population dominance structure (Kaufmann, 1983; Tibbetts et al., 2022).

We show evidence of considerable age differences in storks using landfill sites during the premigratory period. Adult storks were twice as likely as juveniles to visit landfills daily (57% and 29% of the days, respectively). However, the overall proportion of GPS locations in landfills was similar for adults and juveniles (27% versus 20%), indicating that juveniles spent more time at landfills during their landfill days. Within these sites, storks were spatially segregated by age, with adults predominantly using areas with higher food availability (core areas) and juveniles being forced to use areas with almost no food. The lower attendance at landfills by juvenile storks, although proportionately as intensive as adults,

together with their inability to access optimal landfill areas, is probably related to their lack of skills to compete with older birds, which are normally acquired through learning and foraging experience, as well as physical development (Diamond & Bond, 1991; Grecian et al., 2018; Marchetti & Price, 1989; Mendez et al., 2017; Wunderle, 1991).

Adult storks used landfills more efficiently, primarily foraging in core areas and resting and preening in the other areas. Juveniles spent most of their time alert, looking for foraging opportunities and food, and avoiding confrontations with adults. Overall, adults had significantly greater feeding success and consistently demonstrated higher aggressiveness to ensure dominance over resources, consuming nearly four times more food than juveniles in core areas. Owing to the low densities of juvenile storks and the inability to identify them individually between different landfill visits, we were unable to completely eliminate the possibility of pseudoreplication influencing
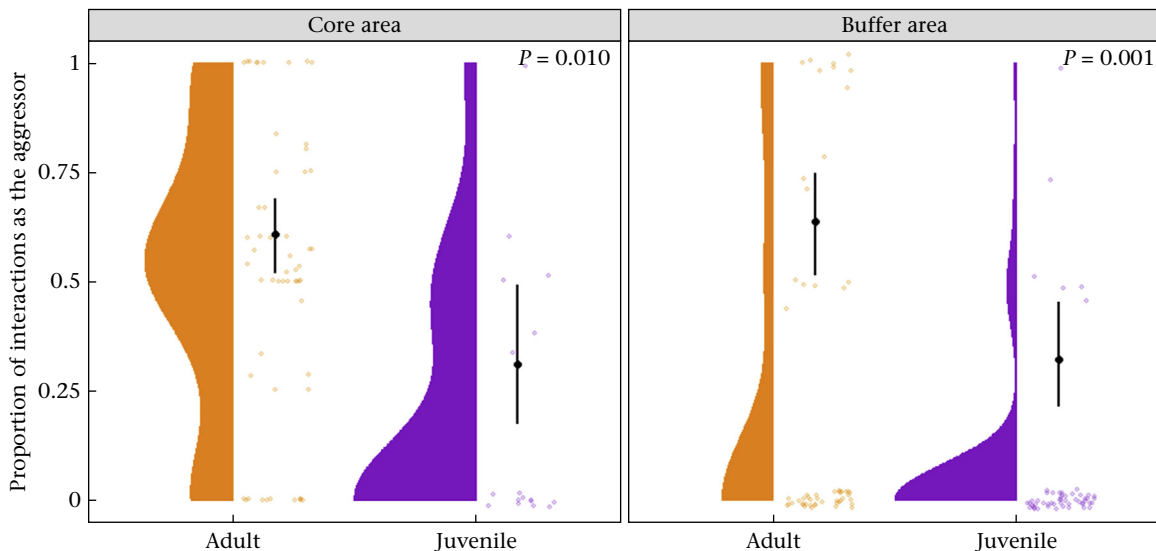

Figure 6. Predicted values and 95% confidence intervals of the estimates from the GLMMs explaining the influence of age (adult or juvenile) and landfill area (core or buffer area) in determining aggressiveness (N = 55 adults per landfill area; N = 17 and 55 juveniles per landfill area) of white storks using landfills during the premigratory period. Orange and purple areas represent the density distribution of dominance for adult and juvenile birds, respectively. Dots represent raw individual data.

the estimates. Still, both adult and juvenile stork estimates exhibited comparable levels of variability, indicating that the eventual impact of pseudoreplication was minimal. Therefore, this study shows that, as expected from dominance hierarchies in food access (Richner, 1989; Tibbetts et al., 2022), age is a determining attribute in the hierarchical structure of white storks, with adults dominating and monopolizing landfill food resources.

The use of landfill food waste has been shown to provide a wide range of benefits to white stork populations, most notably enabling individuals to save foraging time and energy (Soriano-Redondo et al., 2021), improve breeding success and boost population growth (Bialas et al., 2020; Djerdali et al., 2008; Gilbert, 2015; López-García et al., 2021). Furthermore, the year-round availability of food waste in landfills, particularly when other resources are scarce, is facilitating the use and defence of nests by adults during the nonbreeding season, probably allowing for the establishment of resident populations (Catry et al., 2017; Gilbert et al., 2016). Indeed, most of the Portuguese breeding population is now resident (62% by 2015), no longer carrying out the annual migration to Africa (Catry et al., 2017).

In the first few months of independent life, the development of foraging skills is critical for juvenile survival (Daunt et al., 2007; Lindström, 1999; Orgeret et al., 2016; Sæther et al., 2013). Adult dominance in access to food waste may force juveniles to seek resources outside landfills, where they will be more exposed to environmental seasonality and natural resource depletion, which is known to induce migratory decisions in birds (Newton, 2007). Hence, the high intraspecific competition at landfill sites during the premigratory period suggests that food availability is restricted to adults and the ability to compete for these resources is unlikely to override the urge to migrate among inexperienced birds (Chernetsov et al., 2004). With fewer conspecific adult storks foraging in natural habitats, there will be fewer social learning opportunities for juveniles, delaying the acquisition of vital foraging skills (Franks & Thorogood, 2018; van Schaik, 2010). Furthermore, as the number of nonmigratory adults increases due to year-round food availability at landfill sites (Catry et al., 2017; Tortosa et al., 2002), the resulting lack of experienced birds migrating and leading the way to profitable natural foraging areas may be driving juveniles into suboptimal foraging grounds during the winter. Ultimately, the reduced number of adult birds on wintering grounds may even contribute to the inefficient exploitation of resources by juvenile birds, which will probably affect their body condition and increase mortality.

Overall, our findings provide strong evidence that anthropogenic food subsidies can affect age classes differently, with adults benefiting more than juveniles. This age-structured access to landfill resources may have potential carryover effects on population dynamics (Oro et al., 2013; Plaza & Lambertucci, 2017). After significant population declines until the 1980s, white storks are now increasing across Europe (BirdLife International, 2016). In recent decades, the exponential growth of this species in some southern European countries, mostly assisted by landfill resources, has increased the potential for human–wildlife conflicts in agricultural and urban areas (Molina & Del Moral, 2006; Rosa et al., 2005, p. 41), as well as the transmission of pathogens and diseases from landfill sites (Höfle et al., 2020). Therefore, to avoid future conflicts, specific management measures are needed to reduce the amount of organic food waste available at landfill sites.

Author Contributions

Bruno Herlander Martins: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original draft, Writing - Review and editing, Visualization. **Andrea Soriano-Redondo**: Conceptualization, Methodology, Validation, Data curation, Writing - Review and editing. **Aldina M. A. Franco**: Conceptualization, Methodology, Validation, Writing - Review and editing, Supervision, Funding acquisition. **Inês Catry**: Conceptualization, Methodology, Validation, Investigation, Data curation, Writing - Review and editing, Supervision, Funding acquisition.

Data Availability

The tracking data used in this study are stored in Movebank (http://www.movebank.org, study names 'White Stork Adults and Juveniles 2016', 'White Stork Adults 2017', 'White Stork Juveniles 2017', 'White Stork Adults 2018', 'White Stork Juveniles 2018', 'White Stork Adults 2019', 'White Stork Juveniles 2019', 'White Stork Adults 2020', 'White Stork Juveniles 2020') and will be available in the Movebank Data Repository (https://doi.org/10.5441/001/1.137cn005) after a 1 year embargo, or on request. Behavioural data obtained through video recordings are available as Supplementary Material.

Declaration of Interest

None.

Acknowledgments

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2023.10.011.

References

Acácio, M. (2021). *The determinants of dispersal and migratory movements of long-lived birds (Unpublished doctoral thesis)*. University of East Anglia.

Acácio, M., Catry, I., Soriano-Redondo, A., Silva, J. P., Atkinson, P. W., & Franco, A. M. A. (2022). Timing is critical: Consequences of asynchronous migration for the performance and destination of a long-distance migrant. *Movement Ecology, 10*(1), 1–16. https://doi.org/10.1186/s40462-022-00328-3

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters, 14*(9), 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Arizaga, J., Resano-Mayor, J., Villanúa, D., Alonso, D., Barbarin, J. M., Herrero, A., Lekuona, J. M., & Rodríguez, R. (2018). Importance of artificial stopover sites through avian migration flyways: A landfill-based assessment with the white stork Ciconia ciconia. *Ibis, 160*(3), 542—553. https://doi.org/10.1111/ibi.12566

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1). https://doi.org/10.18637/jss.v067.i01

Bécares, J., Blas, J., López-López, P., Schulz, H., Torres-Medina, F., Flack, A., Enggist, P., Höfle, U., Bermejo, A., & De la Puente, J. (2019). *Migración y ecología espacial de la cigüeña blanca en España. Monografía n.o 5 del programa Migra*. SEO/BirdLife. https://doi.org/10.31170/0071

Bialas, J. T., Dylewski, Ł., & Tobolka, M. (2020). Determination of nest occupation and breeding effect of the white stork by human-mediated landscape in Western Poland. *Environmental Science and Pollution Research, 27*(4), 4148—4158. https://doi.org/10.1007/s11356-019-06639-0

BirdLife International. (2016). Ciconia ciconia. *The IUCN Red List of Threatened Species*. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22697691A86248677.en

Blanco, G. (1994). Seasonal abundance of Black kites associated with the rubbish dump of Madrid, Spain. *Journal of Raptor Research, 28*(4), 242—245.

Blanco, G. (1996). Population dynamics and communal roosting of White Storks foraging at a Spanish refuse dump. *Waterbirds, 19*(2), 273—276. https://doi.org/10.2307/1521871

Bocheński, M., & Jerzak, L. (2006). Behaviour of the white stork *Ciconia ciconia*: A review. In P. Tryjanowski, T. H. Sparks, & L. Jerzak (Eds.), *The white stork in Poland: Studies in biology, ecology and conservation* (pp. 295—324). Bogucki Wydawnictwo Naukowe.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist, 161*(1), 1—28. https://doi.org/10.1086/343878

Campioni, L., Dias, M. P., Granadeiro, J. P., & Catry, P. (2020). An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: Timings and destinations change progressively during maturation. *Journal of Animal Ecology, 89*(1), 29—43. https://doi.org/10.1111/1365-2656.13044

Catry, I., Encarnação, V., Pacheco, C., Catry, T., Tenreiro, P., da Silva, Luís, P., Leão, F., Bally, F., Roda, S., Silvério, L., Capela, C., Alonso, H., Saldanha, S., Urbano, O., Saraiva, J., Encarnação, P., Sequeira, N., Mendes, M., Monteiro, P., … Moreira, F. (2017). Recent changes on migratory behaviour of the White stork (*Ciconia ciconia*) in Portugal: Towards the end of migration? *Airo, 24*(January), 28—35.

Chernetsov, N., Berthold, P., & Querner, U. (2004). Migratory orientation of first-year white storks (Ciconia ciconia): Inherited information and social interactions. *Journal of Experimental Biology, 207*(6), 937—943. https://doi.org/10.1242/jeb.00853

Daunt, F., Afanasyev, V., Adam, A., Croxall, J. P., & Wanless, S. (2007). From cradle to early grave: Juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biology Letters, 3*(4), 371—374. https://doi.org/10.1098/rsbl.2007.0157

Diamond, J., & Bond, A. B. (1991). Social behavior and the ontogeny of foraging in the kea (*Nestor notabilis*). *Ethology, 88*(2), 128—144. https://doi.org/10.1111/j.1439-0310.1991.tb00268.x

Djerdali, S., Tortosa, F. S., Hillstrom, L., & Doumandji, S. (2008). Food supply and external cues limit the clutch size and hatchability in the White Stork *Ciconia ciconia*. *Acta Ornithologica, 43*(2), 145—150. https://doi.org/10.3161/000164508X395252

Elliott, A., Garcia, E. F. J., & Boesman, P. F. D. (2020). White stork (Ciconia ciconia), version 1.0. In J. del Hoyo, A. Elliot, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Birds of the world*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.whisto1.01.

Ellis, E. C., Goldewijk, K. K., Siebert, S., Lightman, D., & Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography, 19*(5), 589—606. https://doi.org/10.1111/j.1466-8238.2010.00540.x

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., & Snyder, P. K. (2005). Global consequences of land use. *Science, 309*(5734), 570—574. https://doi.org/10.1126/science.1111772

Franks, V. R., Ewen, J. G., McCready, M., & Thorogood, R. (2018). Copy parents or follow friends? Juvenile foraging behaviour changes with social environment. *BioRxiv*. https://doi.org/10.1101/429688

Franks, V. R., & Thorogood, R. (2018). Older and wiser? Age differences in foraging and learning by an endangered passerine. *Behavioural Processes, 148*, 1—9. https://doi.org/10.1016/j.beproc.2017.12.009

Gilbert, N. I. (2015). Movement and foraging ecology of partially migrant birds in a changing world *(Unpublished doctoral thesis)*. University of East Anglia.

Gilbert, N. I., Correia, R. A., Silva, J. P., Pacheco, C., Catry, I., Atkinson, P. W., Gill, J. A., & Aldina, A. M. (2016). Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. *Movement Ecology, 4*(1), 1—13. https://doi.org/10.1186/s40462-016-0070-0

Grecian, J. W., Lane, J. V., Michelot, T., Wade, H. M., & Hamer, K. C. (2018). Understanding the ontogeny of foraging behaviour: Insights from combining marine predator biologging with satellite-derived oceanography in hidden Markov models. *Journal of the Royal Society Interface, 15*(143). https://doi.org/10.1098/rsif.2018.0084

Höfle, U., Jose Gonzalez-Lopez, J., Camacho, M. C., Solà-Ginés, M., Moreno-Mingorance, A., Manuel Hernández, J., De La Puente, J., Pineda-Pampliega, J., Aguirre, J. I., Torres-Medina, F., Ramis, A., Majó, N., Blas, J., & Migura-Garcia, L. (2020). Foraging at solid urban waste disposal sites as risk factor for cephalosporin and colistin resistant *Escherichia coli* carriage in white storks (*Ciconia ciconia*). *Frontiers in Microbiology, 11*(July), 1—13. https://doi.org/10.3389/fmicb.2020.01397

Kaufmann, J. H. (1983). On the definitions and functions of dominance and territoriality. *Biological Reviews, 58*(1), 1—20. https://doi.org/10.1111/j.1469-185X.1983.tb00379.x

Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution, 14*(9), 343—348. https://doi.org/10.1016/S0169-5347(99)01639-0

López-García, A., Sanz-Aguilar, A., & Aguirre, J. I. (2021). The trade-offs of foraging at landfills: Landfill use enhances hatching success but decrease the juvenile survival of their offspring on white storks (Ciconia ciconia). *Science of the Total Environment, 778*. https://doi.org/10.1016/j.scitotenv.2021.146217

Lundberg, P. (1985). Dominance behaviour, body weight and fat variations, and partial migration in European blackbirds *Turdus merula*. *Behavioral Ecology and Sociobiology, 17*(2), 185—189. https://doi.org/10.1007/BF00299250

Marcelino, J., Moreira, F., Franco, A. M. A., Soriano-Redondo, A., Acácio, M., Gauld, J., Rego, F. C., Silva, J. P., & Catry, I. (2021). Flight altitudes of a soaring bird suggest landfill sites as power line collision hotspots. *Journal of Environmental Management, 294*, Article 113149. https://doi.org/10.1016/j.jenvman.2021.113149

Marchetti, K., & Price, T. (1989). Differences in the foraging of juvenile and adult birds: The importance of developmental constraints. *Biological Reviews, 64*, 51—71. https://doi.org/10.1111/j.1469-185X.1989.tb00638.x

Mendez, L., Prudor, A., & Weimerskirch, H. (2017). Ontogeny of foraging behaviour in juvenile red-footed boobies (*Sula sula*). *Scientific Reports, 7*(1), 1—11. https://doi.org/10.1038/s41598-017-14478-7

Molina, B., & Del Moral, J. C. (2006). *La Cigüeña blanca en España: VI censo internacional (2004)*. SEO/BirdLife.

Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P., & Fagan, W. F. (2013). Social learning of migratory performance. *Science, 341*(August), 999—1003. https://doi.org/10.1126/science.1237139

Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J., & Dickman, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography, 24*(1), 1—11. https://doi.org/10.1111/geb.12236

Newton, I. (2007). *The migration ecology of birds*. https://doi.org/10.1016/B978-0-12-517367-4.X5000-1

Novaes, W. G., & Cintra, R. (2013). Factors influencing the selection of communal roost sites by the black vulture *Coragyps atratus* (Aves: Cathartidae) in an urban area in Central Amazon. *Zoologia, 30*(6), 607—614. https://doi.org/10.1590/S1984-46702013005000014

Orgeret, F., Weimerskirch, H., & Bost, C. A. (2016). Early diving behaviour in juvenile penguins: Improvement or selection processes. *Biology Letters, 12*(8), Article 20160490. https://doi.org/10.1098/rsbl.2016.0490

Oro, D., Genovart, M., Tavecchia, G., Fowler, M. S., & Martínez-Abraín, A. (2013). Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters, 16*(12), 1501—1514. https://doi.org/10.1111/ele.12187

Patenaude-Monette, M., Bélisle, M., & Giroux, J. F. (2014). Balancing energy budget in a central-place forager: Which habitat to select in a heterogeneous environment? *PLoS One, 9*(7), 1—12. https://doi.org/10.1371/journal.pone.0102162

Plaza, P. I., & Lambertucci, S. A. (2017). How are garbage dumps impacting vertebrate demography, health, and conservation? *Global Ecology and Conservation, 12*, 9—20. https://doi.org/10.1016/j.gecco.2017.08.002

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/.

Real, E., Oro, D., Martínez-Abraín, A., Igual, J. M., Bertolero, A., Bosch, M., & Tavecchia, G. (2017). Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird. *Journal of Avian Biology, 48*(11), 1462—1470. https://doi.org/10.1111/jav.01454

Richner, H. (1989). Phenotypic correlates of dominance in carrion crows and their effects on access to food. *Animal Behaviour, 38*(4), 606—612. https://doi.org/10.1016/S0003-3472(89)80005-3

Riotte-Lambert, L., & Weimerskirch, H. (2013). Do naive juvenile seabirds forage differently from adults? *Proceedings of the Royal Society B: Biological Sciences, 280*(1768). https://doi.org/10.1098/rspb.2013.1434

Rosa, G., Encarnação, V., & Candelária, M. (2005). *V Censo Nacional Cegonha-branca Ciconia ciconia (2004) - integrado no VI Censo Mundial de Cegonha-branca* (p. 41). SPEA/ICNF. Vi.

Rotics, S., Turjeman, S., Kaatz, M., Zurell, D., Wikelski, M., Sapir, N., Fiedler, W., Eggers, U., Resheff, Y. S., Jeltsch, F., & Nathan, R. (2021). Early-life behaviour predicts first-year survival in a long-distance avian migrant. *Proceedings of the Royal Society B: Biological Sciences, 288*(1942). https://doi.org/10.1098/rspb.2020.2670

Sæther, B. E., Coulson, T., Grøtan, V., Engen, S., Altwegg, R., Armitage, K. B., Barbraud, C., Becker, P. H., Blumstein, D. T., Dobson, F. S., Festa-Bianchet, M., Gaillard, J. M., Jenkins, A., Jones, C., Nicoll, M. A. C., Norris, K., Oli, M. K., Ozgul, A., & Weimerskirch, H. (2013). How life history influences population

dynamics in fluctuating environments. *American Naturalist, 182*(6), 743—759. https://doi.org/10.1086/673497

van Schaik, C. P. (2010). Social learning and culture in animals. In P. Kappeler (Ed.), *Animal behaviour: Evolution and mechanisms* (pp. 623—653). Springer. https://doi.org/10.1007/978-3-642-02624-9.

Searle, S. R., Speed, F. M., & Milliken, G. A. (1980). Population marginal means in the linear model: An alternative to least squares means. *American Statistician, 34*(4), 216—221. https://doi.org/10.1080/00031305.1980.10483031

Soriano-Redondo, A., Acácio, M., Franco, A. M. A., Martins, B. H., Moreira, F., Rogerson, K., & Catry, I. (2020). Testing alternative methods for estimation of bird migration phenology from GPS tracking data. *Ibis, 162*(2), 581—588. https://doi.org/10.1111/ibi.12809

Soriano-Redondo, A., Franco, A. M. A., Acácio, M., Martins, B. H., Moreira, F., & Catry, I. (2021). Flying the extra mile pays-off: Foraging on anthropogenic waste as a time and energy-saving strategy in a generalist bird. *Science of the Total Environment, 782*, Article 146843. https://doi.org/10.1016/j.scitotenv.2021.146843

Tauler-Ametller, H., Hernández-Matías, A., Pretus, J. L. L., & Real, J. (2017). Landfills determine the distribution of an expanding breeding population of the endangered Egyptian Vulture *Neophron percnopterus*. *Ibis, 159*(4), 757—768. https://doi.org/10.1111/ibi.12495

Thyberg, K. L., & Tonjes, D. J. (2016). Drivers of food waste and their implications for sustainable policy development. *Resources, Conservation and Recycling, 106*, 110—123. https://doi.org/10.1016/j.resconrec.2015.11.016

Tibbetts, E. A., Pardo-Sanchez, J., & Weise, C. (2022). The establishment and maintenance of dominance hierarchies. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 377*(1845), Article 20200450. https://doi.org/10.1098/rstb.2020.0450

Tortosa, F. S., Caballero, J. M., & Reyes-López, J. (2002). Effect of rubbish dumps on breeding success in the White Stork in Southern Spain. *Waterbirds, 25*(1), 39—43. https://doi.org/10.1675/1524-4695(2002)025[0039:eordob]2.0.co;2

van Donk, S., Shamoun-Baranes, J., van Der Meer, J., & Camphuysen, K. C. J. (2019). Foraging for high caloric anthropogenic prey is energetically costly. *Movement Ecology, 7*(1), 1—12. https://doi.org/10.1186/s40462-019-0159-3

Van den Bossche, W., Berthold, P., Kaatz, M., Nowak, E., & Querner, U. (2002). *Eastern European White Stork populations: Migration studies and elaboration of conservation measures.* German Federal Agency for Nature Conservation.

Votier, S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, J., Guilford, T., Hamer, K. C., Jeglinski, J. W. E., Morgan, G., Wakefield, E., & Patrick, S. C. (2017). Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B: Biological Sciences, 284*(1859). https://doi.org/10.1098/rspb.2017.1068, 0—6.

Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., Newton, J., Votier, S. C., & Hamer, K. C. (2015). Long-term individual foraging site fidelity — why some gannets don't change their spots. *Ecology, 96*(11), 3058—3074. https://doi.org/10.1890/14-1300.1

Weiser, E. L., & Powell, A. N. (2010). Does garbage in the diet improve reproductive output of Glaucous Gulls. *Condor, 112*(3), 530—538. https://doi.org/10.1525/cond.2010.100020

Wunderle, J. M. (1991). Age-specific foraging proficiency. *Current Ornithology, 8*(January), 273—324.

Appendix

Table A1
Ethogram of white stork behaviours identified in the videos and corresponding time budget categories

Behaviour	Description	Category
Searching	The stork moves around while trying to find things to eat	Foraging
Looking	The stork stands while trying to find things to eat	Foraging
Pecking	The stork moves or stands while biting and picking up small pieces of food	Foraging
Probing	The stork moves or stands while inserting the slightly open mandible deep into the substrate to obtain food	Foraging
Handling	The stork moves or stands while holding a piece of food in its beak and trying to swallow it	Foraging
Feeding	The stork stands while repeatedly taking nourishment from things to eat	Foraging
Vigilant	The stork stands while keeping careful watch for possible danger or difficulties	Alert
Warning	The stork stands while performing threats towards other birds	Alert
Pacing	The stork moves away from something or from other birds at a steady and consistent speed	Alert
Running	The stork quickly moves away from something or from other birds	Alert
Flapping	The stork moves the wings up and down agitated and preparing to fly away from something or from other birds	Alert
Jumping	The stork flaps its wings and pushes itself off the ground repeatedly to move away from something or from other birds	Alert
Resting	The stork stands while ceasing movement	Inactive
Preening	The stork stands while tidying and cleaning the feathers with the beak	Inactive
Wandering	The stork moves around slowly with no clear purpose of finding things to eat	Inactive

Table A2
Results of post hoc Tukey tests to assess foraging proficiency differences between landfill areas

GLMM Response	Contrasts	Estimate	SE	z	P
Foraging time	Adult Core area − Juvenile Core area	1.329	0.143	9.326	**<0.001**
	Adult Core area − Adult Buffer area	1.027	0.095	10.858	**<0.001**
	Adult Core area − Juvenile Buffer area	1.123	0.095	11.813	**<0.001**
	Adult Core area − Adult Outer area	4.959	0.278	17.818	**<0.001**
	Adult Core area − Juvenile Outer area	4.099	0.199	20.646	**<0.001**
	Juvenile Core area − Adult Buffer area	−0.302	0.141	−2.140	0.267
	Juvenile Core area − Juvenile Buffer area	−0.205	0.141	−1.457	0.692
	Juvenile Core area − Adult Outer area	3.630	0.297	12.241	**<0.001**
	Juvenile Core area − Juvenile Outer area	2.770	0.224	12.385	**<0.001**
	Adult Buffer area − Juvenile Buffer area	0.096	0.093	1.027	0.909
	Adult Buffer area − Adult Outer area	3.932	0.278	14.168	**<0.001**
	Adult Buffer area − Juvenile Outer area	3.071	0.198	15.553	**<0.001**
	Juvenile Buffer area − Adult Outer area	3.836	0.278	13.816	**<0.001**
	Juvenile Buffer area − Juvenile Outer area	2.975	0.198	15.054	**<0.001**
	Adult Outer area − Juvenile Outer area	−0.861	0.327	−2.628	0.091
Alert time	Adult Core area − Juvenile Core area	−1.496	0.142	−10.554	**<0.001**
	Adult Core area − Adult Buffer area	0.356	0.107	3.331	**0.011**
	Adult Core area − Juvenile Buffer area	−0.625	0.097	−6.450	**<0.001**
	Adult Core area − Adult Outer area	3.698	0.342	10.798	**<0.001**

Table A2 (*continued*)

GLMM Response	Contrasts	Estimate	SE	z	P
	Adult Core area − Juvenile Outer area	1.450	0.140	10.329	**<0.001**
	Juvenile Core area − Adult Buffer area	1.851	0.145	12.735	**<0.001**
	Juvenile Core area − Juvenile Buffer area	0.871	0.138	6.293	**<0.001**
	Juvenile Core area − Adult Outer area	5.193	0.356	14.574	**<0.001**
	Juvenile Core area − Juvenile Outer area	2.946	0.171	17.156	**<0.001**
	Adult Buffer area − Juvenile Buffer area	−0.980	0.102	−9.593	**<0.001**
	Adult Buffer area − Adult Outer area	3.342	0.344	9.716	**<0.001**
	Adult Buffer area − Juvenile Outer area	1.095	0.144	7.597	**<0.001**
	Juvenile Buffer area − Adult Outer area	4.322	0.341	12.673	**<0.001**
	Juvenile Buffer area − Juvenile Outer area	2.075	0.137	15.143	**<0.001**
	Adult Outer area − Juvenile Outer area	−2.247	0.356	−6.316	**<0.001**
Inactive time	Adult Core area − Juvenile Core area	−1.699	0.519	3.277	**0.013**
	Adult Core area − Adult Buffer area	−2.024	0.136	−14.918	**<0.001**
	Adult Core area − Juvenile Buffer area	−1.121	0.142	−7.885	**<0.001**
	Adult Core area − Adult Outer area	−6.302	0.244	−25.880	**<0.001**
	Adult Core area − Juvenile Outer area	−4.599	0.159	−28.931	**<0.001**
	Juvenile Core area − Adult Buffer area	−3.723	0.509	−7.316	**<0.001**
	Juvenile Core area − Juvenile Buffer area	−2.820	0.511	−5.519	**<0.001**
	Juvenile Core area − Adult Outer area	−8.001	0.547	−14.628	**<0.001**
	Juvenile Core area − Juvenile Outer area	−6.299	0.515	−12.228	**<0.001**
	Adult Buffer area − Juvenile Buffer area	0.903	0.104	8.718	**<0.001**
	Adult Buffer area − Adult Outer area	−4.278	0.222	−19.256	**<0.001**
	Adult Buffer area − Juvenile Outer area	−2.575	0.124	−20.737	**<0.001**
	Juvenile Buffer area − Adult Outer area	−5.181	0.227	−22.835	**<0.001**
	Juvenile Buffer area − Juvenile Outer area	−3.478	0.132	−26.299	**<0.001**
	Adult Outer area − Juvenile Outer area	1.702	0.236	7.221	**<0.001**
Food intake	Adult Core area − Juvenile Core area	1.264	0.165	7.669	**<0.001**
	Adult Core area − Adult Buffer area	0.974	0.087	11.206	**<0.001**
	Adult Core area − Juvenile Buffer area	0.870	0.084	10.387	**<0.001**
	Juvenile Core area − Adult Buffer area	−0.290	0.175	−1.661	0.345
	Juvenile Core area − Juvenile Buffer area	−0.395	0.173	−2.277	0.103
	Adult Buffer area − Juvenile Buffer area	−0.104	0.102	−1.021	0.737
Aggressiveness	Adult Core area − Juvenile Core area	1.230	0.395	3.115	**0.010**
	Adult Core area − Adult Buffer area	−0.132	0.277	−0.476	0.964
	Adult Core area − Juvenile Buffer area	1.185	0.304	3.892	**<0.001**
	Juvenile Core area − Adult Buffer area	−1.362	0.437	−3.115	**0.010**
	Juvenile Core area − Juvenile Buffer area	−0.045	0.456	−0.098	1.000
	Adult Buffer area − Juvenile Buffer area	1.317	0.354	3.716	**0.001**

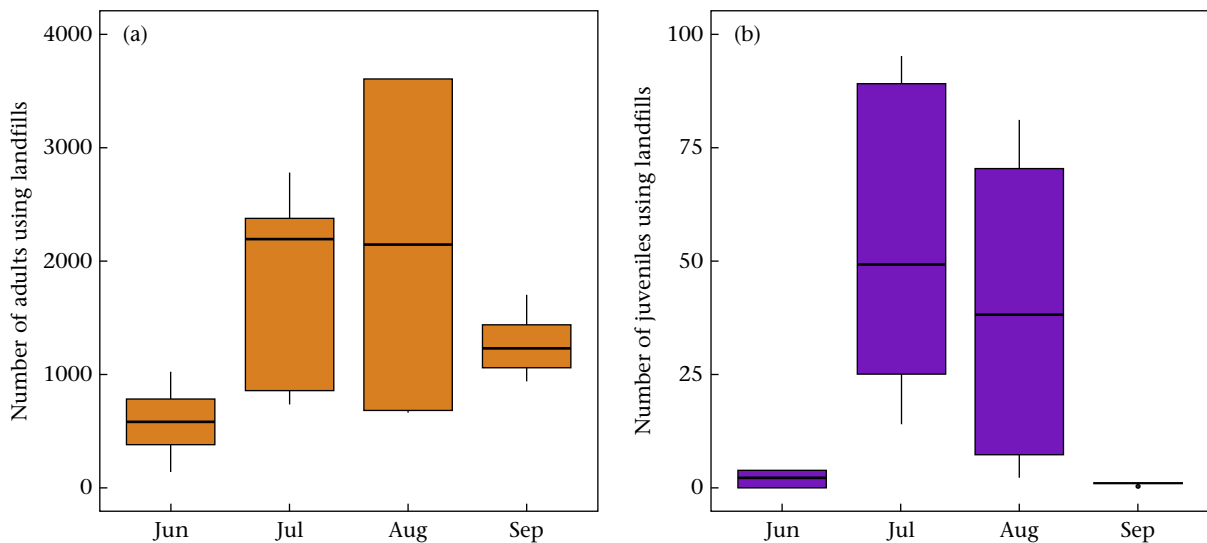Significant *P* values are shown in bold.

Figure A1. Total number of (a) adult and (b) juvenile white storks counted monthly at the five landfills in southern Portugal during the 2020 premigratory period (June to September). Middle, lower and upper hinges of the box plots correspond to the median, 25th and 75th percentiles, respectively. Whiskers correspond to the 95% confidence intervals and the dots is an outlier.
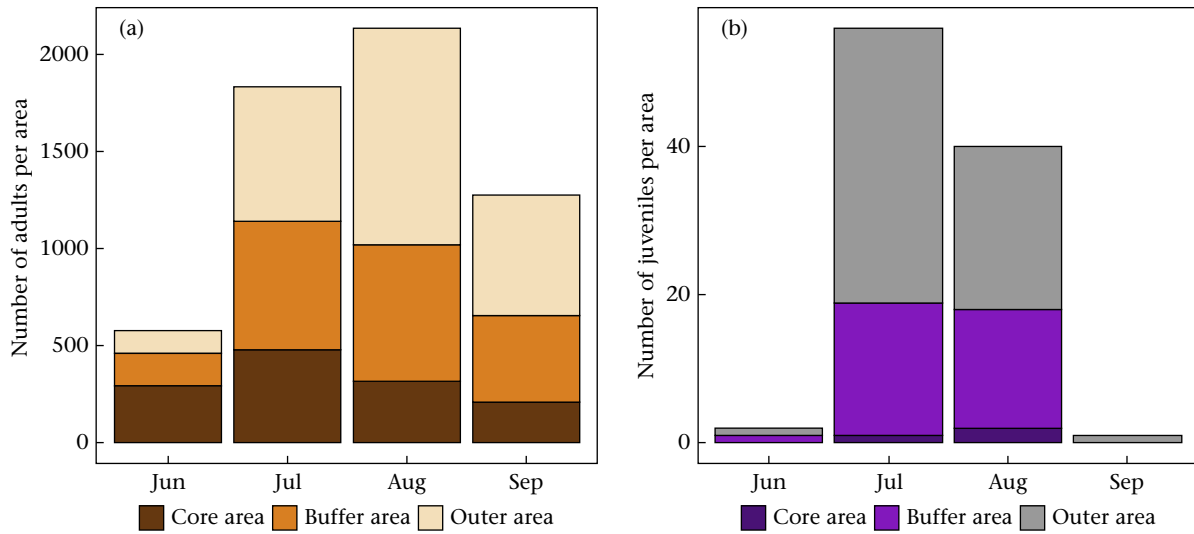
Figure A2. Monthly average estimate of the number of (a) adult and (b) juvenile white storks per landfill area (core, buffer and outer area) at the five landfills in southern Portugal during the 2020 premigratory period (June to September).
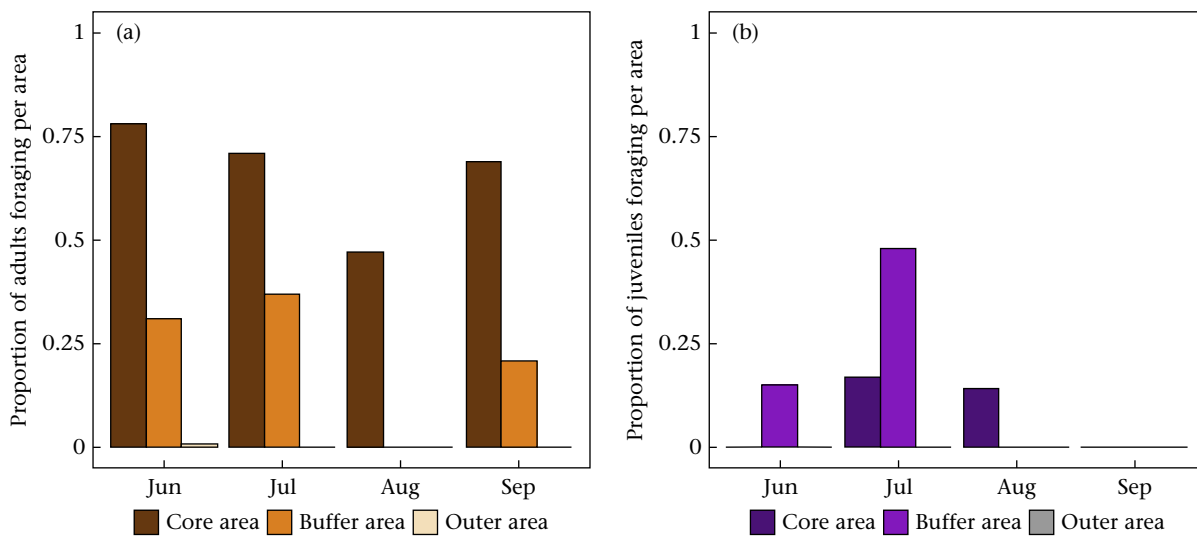

Figure A3. Monthly average estimate of the proportion of (a) adult and (b) juvenile white storks foraging per landfill area (core, buffer and outer area) at the five landfills in southern Portugal during the 2020 premigratory period (June to September).