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# From inexperience to proficiency: age-related improvements shape the use of novel anthropogenic food subsidies in a long-lived bird

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Worldwide, humans have altered ecosystems not only by reducing and changing the distribution of resources but also by providing new foraging opportunities to wildlife. However, little is known about the early-life development and maintenance of new foraging behaviours, which are crucial for species to adapt to human-induced environmental changes. Using a longitudinal global positioning system (GPS)-tracking dataset from 71 adult and 147 juvenile white storks (*Ciconia ciconia*) tracked for up to 6 years, this study investigates shifts in the exploitation of landfill resources during ontogeny and explores whether selective survival, within-individual improvements or both shape the emergence of this behaviour. Landfill use was found to increase with age. From their second year of life onwards, white storks visit landfills more often than in their first year, forage more in areas with abundant organic waste and reduce their foraging energy expenditure. Overall, this study reveals that the age-related increase in the use of anthropogenic food sources is driven primarily by within-individual improvements operating most strongly in early life, rather than by selective survival of individuals that most frequently and proficiently use landfill sites. As more species rely on anthropogenic food subsidies, this work highlights how opportunistic species cope with and adapt to human-driven environmental change, influencing individual lifetime decisions and potentially impacting population dynamics.

## 1. Introduction

The early years of life are crucial for most animals, especially long-lived species, as they are key to successful recruitment into the reproductive stage and for maintaining healthy populations [1–3]. During these often prolonged immature years, individuals undergo periods of substantial behavioural changes and learning, while frequently experiencing significantly lower

survival compared with adults [4–6]. These processes, namely differential survival and within-individual improvements (i.e. trait amelioration within an individual as it ages [7]), are known to shape population-level ageing patterns [8,9]. However, their relative importance may vary across behaviours [10–13]. For instance, differential survival seems to shape long-distance migration patterns of black kites *Milvus migrans* [14], but has little effect on the local movements or social behaviours of griffon vultures *Gyps fulvus* [15]. In addition, although numerous studies have explored the behavioural differences between juveniles and adults [16–19], there is still limited knowledge on how long it takes for immature individuals to progressively develop adult-like behaviours and increase their foraging proficiency, or which specific traits require the most time to develop fully during maturation (but see [7,14,19–21]).

Low survival in early life is often attributed to a range of factors, including higher predation risk and juveniles' limited ability to locate and secure enough resources for survival [22,23], primarily owing to their inexperience and/or physical immaturity [4,24–26]. Moreover, juveniles often exhibit greater variation in space use compared with older conspecifics, who have a better understanding of resource distribution and can optimize their foraging strategies [5,16,27,28], often outcompeting juveniles at optimal foraging sites [29–32]. Such behavioural changes, which influence foraging performance, can be driven by improvements in skills gained through learning and foraging experience, which develop with age [27,33–35]. Yet, while some individuals may quickly acquire adult-like skills and survive to recruitment, others that are potentially of lower quality may underperform and be more likely to perish [14,17]. To uncover the role of differential survival and individual improvements in the development of foraging behaviours, longitudinal studies are required, particularly in long-lived species. Advances in tracking technology now provide unprecedented opportunities to explore in detail the ontogeny of foraging behaviours—that is, the developmental processes of these behaviours by an individual organism, from its origin to maturity. These tools allow researchers to investigate whether changes in behaviour develop gradually or abruptly and whether they are shaped by selective survival of the most proficient individuals, by within-individual improvements over time or a combination of both processes.

In recent decades, human activities have altered the distribution and availability of foraging resources for wildlife, occasionally creating new foraging opportunities [36–39]. Organic waste from landfill sites and rubbish dumps has become an important food source for many species worldwide [37,40], particularly for opportunistic birds such as storks, gulls, corvids and raptors, such as kites and vultures [30,40–43]. These abundant, predictable and easily accessible resources have reshaped many species' foraging behaviour, allowing individuals to reduce foraging time and energy expenditure [44,45] while improving fitness, survival and population growth [37,40,46,47]. However, these anthropogenic resources carry multiple risks that might impact fitness (e.g. increased exposure to pathogens, poisoning and collision or electrocution hazards [48–50]). In addition, the high concentrations of food and birds at these sites intensify competition, potentially reducing food acquisition for less proficient individuals [30,51]. Understanding how individuals exploit these novel resources is critical for understanding how species cope or adapt to environmental change, especially given the rapid pace of such changes in recent years.

In this study, we investigate shifts in the exploitation of landfill resources during ontogeny using long-term global positioning system (GPS) and accelerometer data from white storks (*Ciconia ciconia*), a long-lived opportunistic species that has recently increased its reliance on landfill food resources [30,44,52,53]. Previous research has shown that adult storks are more proficient than juveniles in using landfill resources, often displaying dominance and securing access to optimal foraging areas. They typically spend more time foraging in landfill zones with higher food availability, achieve greater food intake and exhibit more aggressive behaviour than juveniles [30]. As a long-lived social species that reaches maturity in its third or fourth year, learning is expected to play a significant part in the acquisition of foraging skills. Given the high competition for food at landfill sites [30], it is also likely that more proficient immature individuals may be better able to exploit them and, as a result, experience higher survival rates than less proficient ones. Specifically, this study aimed to investigate (i) age-related differences in the use of predictable anthropogenic food subsidies (PAFS) at the population level; and (ii) whether age-related differences in the use of these resources are driven by the selective survival of proficient individuals and/or by individual learning and improvements during ontogeny. This work provides a mechanistic understanding of how age shapes the exploitation of human-provided food sources that have emerged in recent decades [52], with the potential to unravel the species' ability to adapt to human-driven changes in resource availability.

## 2. Methods

### (a) GPS deployment and tracking data

Fieldwork for the deployment of GPS-tracking devices was conducted in southern Portugal, where approximately 60% of the total Portuguese white stork population resides (approx. 7000 breeding pairs [54]). Between 2016 and 2021, a total of 71 adult white storks and 147 juveniles were GPS-tagged in the region and tracked over time. Adults were captured and tagged either at landfill sites using nylon leg nooses or at their nests using a remotely activated clap-net trap. Individuals were classified as adults if they were in their fourth year or older, with age determined by visual examination of plumage and moult characteristics during handling [55]. They were later confirmed as breeders by identifying their nests through the GPS data and visiting them to verify the presence of eggs and/or chicks. Pre-fledgling juveniles were retrieved from their nests for tagging and promptly returned afterwards. After fledging, they were designated as first-year storks, and thereafter, age was determined based on a 12 month interval starting in June of each year. The nests of tagged adults and juveniles were distributed along a 1–40 km distance gradient from active landfills. All individuals were tagged with GPS/global system for mobile commmunications (GSM) loggers equipped with tri-axial acceleration sensors ('Flyway-50' from Movetech Telemetry

or 'Ornitrack-50' from Ornitela). These devices were deployed as backpacks with a Teflon harness, with a combined weight ranging from 50 to 90 g, representing 1.1–3.7% of the bird's body mass. All tagged birds were resighted in the days following deployment and during the breeding season, and no abnormal behaviours or adverse effects were observed.

The GPS loggers were programmed to record a GPS location every 20 min, along with a tri-axial acceleration burst consisting of nine consecutive measurements at 1 Hz. These acceleration bursts were used to classify bird behaviour and to calculate overall dynamic body acceleration (ODBA, in g, where g is gravitational acceleration), which was used as a proxy for relative energy expenditure [56,57]. Although this sampling frequency is lower than that typically used to estimate absolute energy expenditure, ODBA was used here to compare relative activity levels among individuals and age classes, as all devices operated under identical settings. To classify bird behaviour, the random forest built by Soriano-Redondo *et al*. [44] was used, specific to each tag type [44]. This machine-learning algorithm identifies foraging, resting and flight behaviours from previously classified and validated tri-axial acceleration data [44]. The ODBA was calculated by subtracting each acceleration point from a 4 s running mean for each axis and summing the resulting values across all three axes [44].

## (b) Study period

This study focused on the period between June and September, when large numbers of storks of different ages gather at landfill sites as the breeding season ends and migration starts, providing an opportunity to investigate age-related differences in landfill use [30]. Before June, adults are still mostly attached to their nests, whereas after September, most migratory individuals are already south of the Atlas Mountains. During the study period, landfills in Portugal and Spain were used by both resident and pre-migratory storks and served as stopover sites for individuals already migrating. In Northern Africa, landfills are used both by storks wintering in Morocco and as stopovers for individuals continuing their migration to the Sahel [30,58,59].

For all storks, the study period began on 1 June (the earliest fledging date), except for first-year juveniles, whose study period started on their individual fledging dates, defined as the first day they moved more than 50 m away from their nests for at least two consecutive GPS fixes [50]. Juveniles fledged between 1 June and 24 July and started using landfills in the first days after fledging (electronic supplementary material, figure S1). The study period always ended either on the day when the birds died or when the device stopped transmitting ($n$ = 85), on the day they crossed the Atlas Mountains, after which landfill use is negligible ($n$ = 109), or on 30 September for those that did not migrate beyond the Atlas Mountains ($n$ = 185). Only storks monitored for at least 10 days during each study period were included in the analysis.

## (c) Identification of landfill sites and core areas

All landfill sites visited by tracked storks were identified through visual inspection of GPS data, where repeated, clustered GPS fixes indicated consistent use of specific locations that matched those in the dataset published by Marcelino *et al*. [59], which includes 28 landfills, dumps and waste disposal sites used by GPS-tracked white storks from the Portuguese population while on migration. High-resolution satellite imagery was also used to inspect remaining sites and identify any potential missing landfills. As no landfills were used by our GPS-tracked storks beyond the Atlas Mountains, GPS locations south of this ecological barrier were not included in the analysis (figure 1), consistent with previous findings that few artificial stopovers occur after this point along the migratory route [59]. Within each identified landfill, the core area was defined as a 25 m radius around the dump site where organic waste is deposited [30]. These areas, characterized by the highest abundance and availability of fresh waste, represent the primary foraging sites, where adult storks secure more food than inexperienced first-year juveniles [30]. To systematically identify core areas across all landfills used by GPS-tracked storks, monthly visits were conducted at five landfills in southern Portugal over a 3-year period (2018–2020) to accurately map core areas. The foraging GPS locations of adult storks at these landfills (if >50 GPS locations were available) were then used to calculate a monthly 25% kernel density estimation, from which the centroid was derived. Kernel densities were calculated using the 'kernelUD' function in the 'adehabitatHR' R package [60]. These centroids consistently matched the exact locations of core areas mapped during landfill visits over the years, validating this methodology for identifying core areas. To ensure the robustness of the method outside of Portugal, point visits were further conducted at a small subset of landfills in Spain and northern Morocco, and it was confirmed that the core areas derived from adult storks' GPS locations corresponded well to the observed foraging areas. Therefore, for all remaining landfills in the Iberian Peninsula and northern Morocco, including those with only a single verification visit, monthly core area centroids were determined using all foraging GPS locations of adult storks within each landfill during a given month, resulting in a total of 136 monthly landfill core areas.

## (d) Age-related differences in landfill use

To assess landfill use, all ground locations with GPS-derived speeds below 5 km $h^{-1}$ [50] were classified as either inside (≤1 km from the centroid of the landfill [44]) or outside landfill boundaries (>1 km from the centroid of the landfill [44]), and locations within landfills were further classified as either inside or outside core areas [30]. To minimize potential bias, only days with more than 10 GPS ground locations were considered for analysis. This threshold ensured daily data resolution and reduced the influence of occasional device malfunctions or missed GPS fixes. Age-related differences in landfill attendance were investigated by comparing three metrics: daily and overall landfill attendance, and core area attendance. For each individual in a given year, daily landfill attendance was calculated as the proportion of days during the study period with at least one GPS location classified as inside a landfill site [30,44]. Overall landfill attendance was calculated as the proportion of all

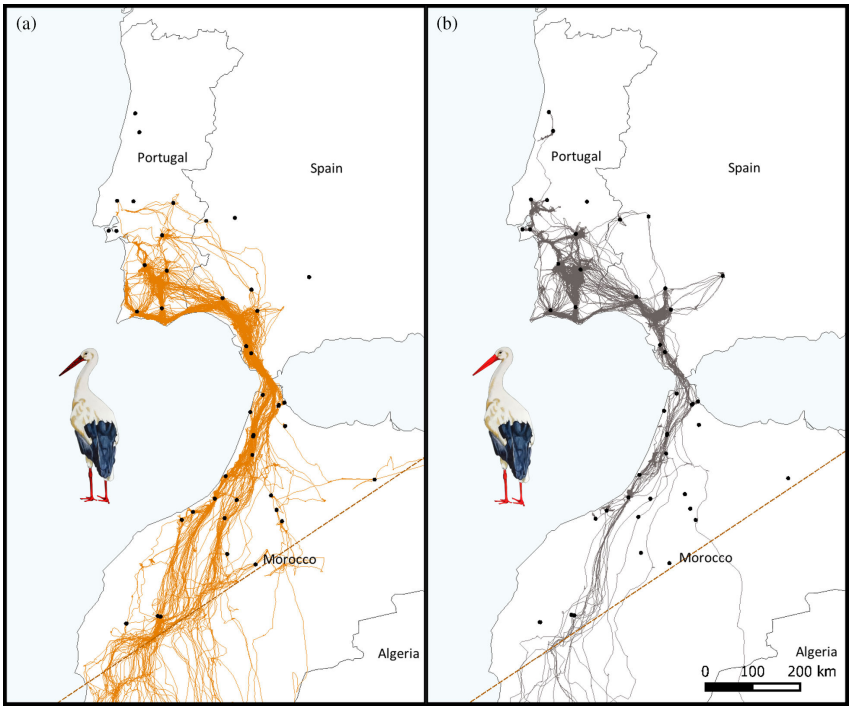


**Figure 1.** Routes used by GPS-tracked white storks between 2016 and 2021 in the Iberian Peninsula and northern Morocco: (a) juveniles (orange tracks) and (b) adults (grey tracks). The black dots represent the landfill sites used by the tracked individuals. The brown dashed lines, following the Atlas Mountains, indicate the southern latitudinal limit of the data included in the analysis.

GPS locations over the study period classified as inside landfill boundaries [30]. Core area attendance was calculated as the proportion of landfill GPS locations classified as within the core areas [30]. In addition, age-related differences in foraging performance at landfill sites were investigated by comparing foraging time and foraging energy expenditure in core areas across age classes. Foraging time was calculated as the proportion of all landfill foraging locations that were located within core areas, while foraging energy expenditure was quantified as the mean ODBA of the foraging locations within core areas.

To analyse these age-related differences, storks were grouped into four age classes: first year (1), second year (2), third year (3) and fourth year or older (≥4; including both tracked individuals of known age and adults of unknown age). Then, five generalized linear mixed-effects models (GLMMs) were fitted using the 'glmmTMB' R package [61] and the 'lmer' function in the 'lme4' R package [62]. The model assumptions were assessed using the 'DHARMa' R package [63]. The first two models examined individual daily landfill attendance (proportion of days visiting landfills) and overall landfill attendance (proportion of GPS locations at landfills) as response variables and used a beta family with a logit link to account for overdispersion. The third and fourth models examined core area attendance (proportion of landfill locations in core areas) and foraging time in core areas (proportion of foraging locations within landfills that were inside core areas) as response variables and used a binomial family with a logit link. The fifth model included foraging energy expenditure in core areas (mean ODBA of foraging GPS locations within core areas) as the response variable, using a Gaussian family with an identity link. All models included age class (storks in year 1, 2, 3 or 4 onwards) and month as the explanatory variables, and bird ID and calendar year as random intercepts. Month was included as a fixed effect to account for temporal variation in landfill use during the study period, which could arise from seasonal changes in food availability, migration timing or other factors unrelated to age. *Post hoc* Tukey tests were conducted to assess differences between age classes, using the 'emmeans' R package [64].

## (e) Mechanisms driving age-related changes in landfill use

The roles of selective survival and/or individual learning were investigated as potential mechanisms driving age-related changes in landfill use by white storks. The first mechanism, selective survival, suggests that individual differences in a juvenile's ability to exploit landfill resources during its first year of life may result in differential survival rates. Thus, young storks that survived into the second year of life are predicted to exhibit greater foraging proficiency at using landfills early in life, ultimately leading to an overall increase in landfill use proficiency with age at the population level. This was tested by fitting five GLMMs, in which the five previously used metrics of landfill use were included as response variables, survival ('survived', 'died' or 'undetermined') as the explanatory variable, and calendar year as a random intercept. For the metrics modelled as proportions, overdispersion was detected and model fit was improved by applying a beta family with a logit link. First-year juveniles tracked into their second year were classified as 'survived'. Conversely, individuals were classified as 'died' when GPS devices transmitted stationary locations or when accelerometer data showed no activity, and in most cases, carcasses and tracking devices were subsequently recovered. Birds for which transmission was abruptly lost (mostly during the crossing of the Sahara Desert), without clear signs of mortality, were classified as 'undetermined'. While these birds could have perished during migration, they were not confirmed mortalities owing to the lack of GSM coverage. Including this category allowed for the comparison with the other two groups and excluded a possible bias in the detection of mortalities in the desert.

The second mechanism, individual learning, states that the higher proficiency in landfill use by adults compared with juveniles is driven by within-individual improvements that arise throughout life. To explore this, two complementary analyses were conducted using all juveniles tracked for at least their first 2 years, as well as those tracked into adulthood (up to their sixth year). First, it was investigated whether individuals tagged as juveniles and followed across multiple years exhibited age-related differences in landfill use. Five GLMMs were fitted using the same response metrics of landfill use and the same model distributions as in the age-related differences analysis. All models included age class (storks in year 1, 2, 3 or 4) and month as explanatory variables, with bird ID and calendar year as random intercepts. Age classes corresponding to storks in years 5 and 6 were excluded from the analysis owing to small sample sizes. Additionally, landfill use metrics calculated for adults of unknown age were included in the figures as a reference group. Second, within-individual improvements were examined explicitly by quantifying year-to-year changes in each landfill use metric for the same individual. For each bird, the change in each metric between consecutive years was calculated as the absolute difference between the value in year $t$ and the value in year $t - 1$. These individual changes were then modelled as response variables in linear mixed-effects models (LMMs), with age transition (1–2, 2–3 and 3–4 years) included as a categorical fixed effect without an intercept, so that each age transition had its own estimated mean improvement. This allowed direct testing of whether the improvement during each transition differed from zero. Bird ID and calendar year were included as random intercepts.

## 3. Results

Between 2016 and 2021, 71 adult and 147 first-year white storks were tracked for up to 6 years. In total, 29 first-year juveniles were tracked to their second year, 10 to their third year, 4 to their fourth year, 3 to their fifth year and 2 to their sixth year. The GPS-tracked storks foraged at 45 different landfill sites across the Iberian Peninsula and northern Morocco (figure 1).

### (a) Age-related differences in landfill use

Significant age-related differences in all metrics of landfill attendance and foraging performance were found when comparing first-year storks with older age classes (figure 2, electronic supplementary material, table S1). Second-year storks were significantly more likely to visit landfills daily compared with first-year storks (predicted values ± s.e.; year 1 = 0.35 ± 0.02; year 2 = 0.58 ± 0.04; $p \leq 0.001$; figure 2a), while no significant differences in daily landfill attendance were found among the remaining older age classes (electronic supplementary material, table S2). Overall landfill attendance of second-year storks was also significantly higher than for first-year storks (year 1 = 0.14 ± 0.01; year 2 = 0.21 ± 0.03; $p \leq 0.001$; figure 2b), and there were no significant differences among the older age classes (electronic supplementary material, table S2). Within landfills, core area attendance was generally low (mean ± s.d. = 0.11 ± 0.06), although it increased gradually with age, with significant differences detected between first-year and second-year storks and between third-year and fourth-year or older individuals (figure 2c; electronic supplementary material, table S2). Fourth-year or older storks were almost twice as likely to access these areas compared to first-year storks (year 1 = 0.08 ± 0.01; year ≥4 = 0.16 ± 0.01; $p \leq 0.001$; figure 2c). Foraging time within core areas also showed a gradual increase with age, with significant sequential differences observed between all age classes (figure 2d; electronic supplementary material, table S2). Fourth-year or older storks spent over twice as much time foraging in these areas compared with first-year juveniles (year 1 = 0.12 ± 0.01; year ≥4 = 0.29 ± 0.02; $p \leq 0.001$; figure 2d). Finally, foraging energy expenditure in core areas was significantly higher for first-year storks compared with second-year storks (year 1 = 0.17 ± 0.01; year 2 = 0.15 ± 0.01; $p \leq 0.001$; figure 2e), with no differences observed among the older age classes (electronic supplementary material, table S2). Monthly variation in landfill use was accounted for in all models but did not affect the significance of the age-related patterns (electronic supplementary material, table S2).

### (b) The role of selective survival in driving age-related changes in landfill use

Landfill attendance and foraging performance during the first year of life did not differ significantly among storks classified as survived, died or undetermined in the second year of life (figure 3, electronic supplementary material, table S3). First-year storks that survived to their second-year were as likely to visit landfill sites as those that did not survive or whose fate was unknown, both for daily landfill attendance (predicted values ± s.e.; survived = 0.33 ± 0.04; died = 0.35 ± 0.04; $p = 0.655$; undetermined = 0.31 ± 0.03; $p = 0.282$; figure 3a) and overall landfill attendance (survived = 0.12 ± 0.02; died = 0.13 ± 0.02; $p = 0.805$; undetermined = 0.11 ± 0.01; $p = 0.499$; figure 3b). Similarly, no significant differences were observed in core area attendance among the three groups (survived = 0.07 ± 0.01; died = 0.06 ± 0.01; $p = 0.656$; undetermined = 0.07 ± 0.01; $p = 0.741$; figure 3c), nor in the foraging time in core areas (survived = 0.11 ± 0.02; died = 0.10 ± 0.02; $p = 0.480$; undetermined = 0.11 ± 0.02; $p = 0.427$; figure 3d) or in the foraging energy expenditure in core areas (survived = 0.18 ± 0.01; died = 0.18 ± 0.01; $p = 0.913$; undetermined = 0.17 ± 0.01; $p = 0.057$; figure 3e). These patterns were consistent when accounting for monthly variation in landfill use, indicating that first-year foraging behaviour had no detectable influence on survival to the second year (electronic supplementary material, table S4).

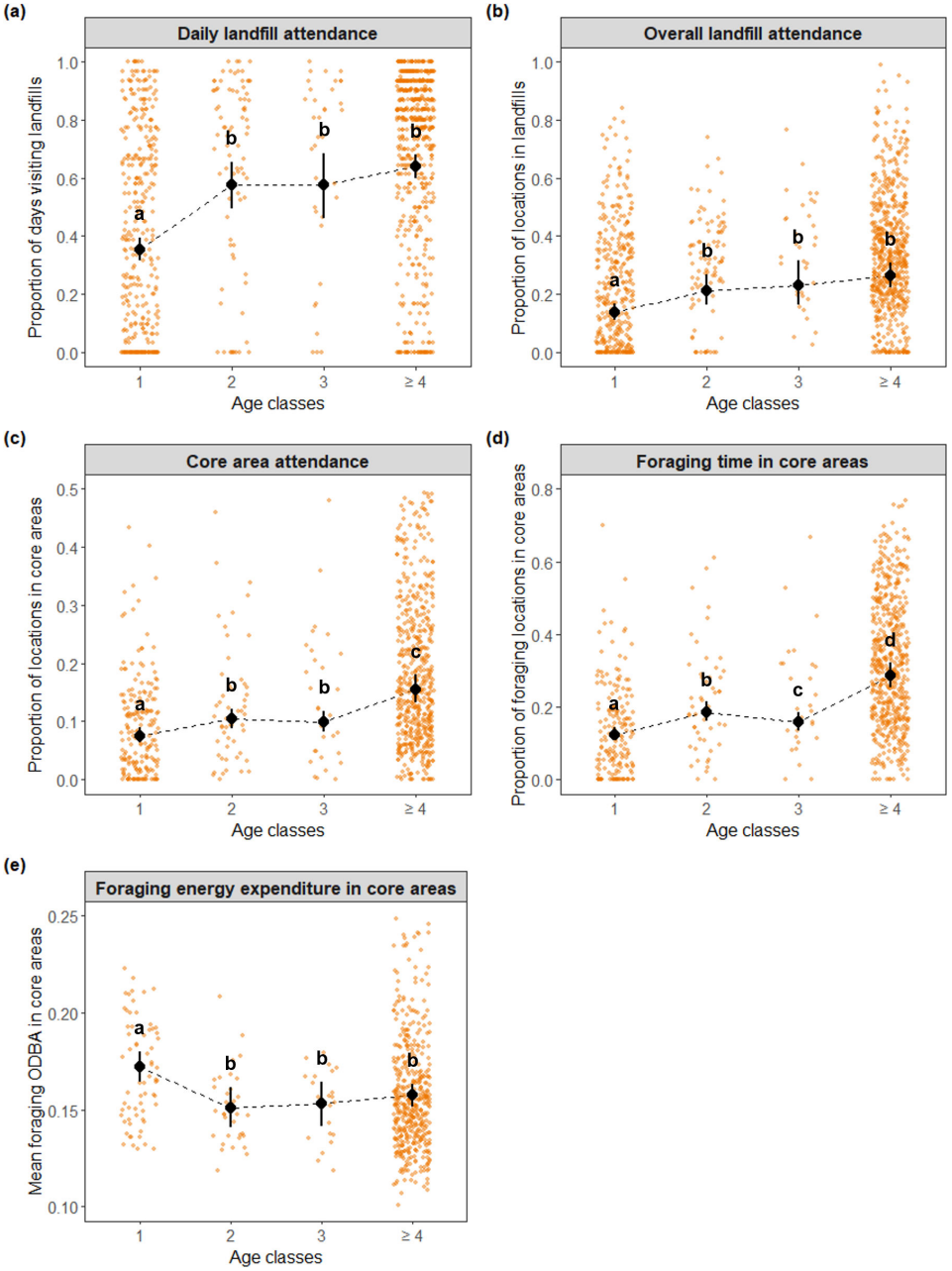


**Figure 2.** Predicted values and 95% confidence intervals of the GLMMs explaining age-related differences in (a) daily, (b) overall and (c) core area landfill attendance, as well as (d) foraging time and (e) foraging energy expenditure in core areas for GPS-tracked white storks. Orange dots represent the raw data. Different letters indicate significant pairwise differences between age classes (age classes sharing a letter do not differ significantly).

## (c) The role of individual learning in driving age-related changes in landfill use

Significant within-individual improvements in landfill use were observed, with age-related increases in landfill attendance and foraging performance occurring primarily between the first and second years (figure 4, electronic supplementary material, tables S5–S7). Storks rapidly increased their daily (predicted values ± s.e.; year 1 = 0.36 ± 0.02; year 2 = 0.59 ± 0.05; $p \leq 0.001$; figure 4a) and overall (year 1 = 0.13 ± 0.01; year 2 = 0.20 ± 0.03; $p \leq 0.001$; figure 4b) landfill attendance between their first 2 years. Although no additional significant improvements were detected among older age classes (figure 4f, electronic supplementary material, tables S6 and S7), storks in their fourth year were almost twice as likely to visit landfills daily (year 4 = 0.65 ± 0.10; figure 4a) and spent almost twice as much time there (year 4 = 0.26 ± 0.7; figure 4b). Within landfills, juvenile storks showed significant improvements in both their ability to access and forage in core areas between their first and second years (figure 4f, electronic supplementary material, table S7). As storks aged, they became significantly more likely to attend core areas (year 1 = 0.07 ± 0.01; year 2 = 0.10 ± 0.01; $p \leq 0.001$; figure 4c), and their time spent foraging in these areas also increased (year 1 = 0.11 ± 0.01; year 2 = 0.16 ± 0.02; $p \leq 0.001$; figure 4d). Individuals in their fourth year spent almost twice as much time in core areas (year 4 = 0.13 ± 0.02; figure 4c) and more than twice as much time actively foraging there compared to their first year (year 4 = 0.24 ± 0.03; figure 4d). Lastly, substantial within-individual improvements in foraging efficiency occurred during the first two years of life (figure 4f, electronic supplementary material, table S7), as mean foraging ODBA in core areas significantly decreased from the first to the second year (year 1 = 0.17 ± 0.01; year 2 = 0.15 ± 0.01; $p \leq 0.001$; figure 4e). No further reductions in

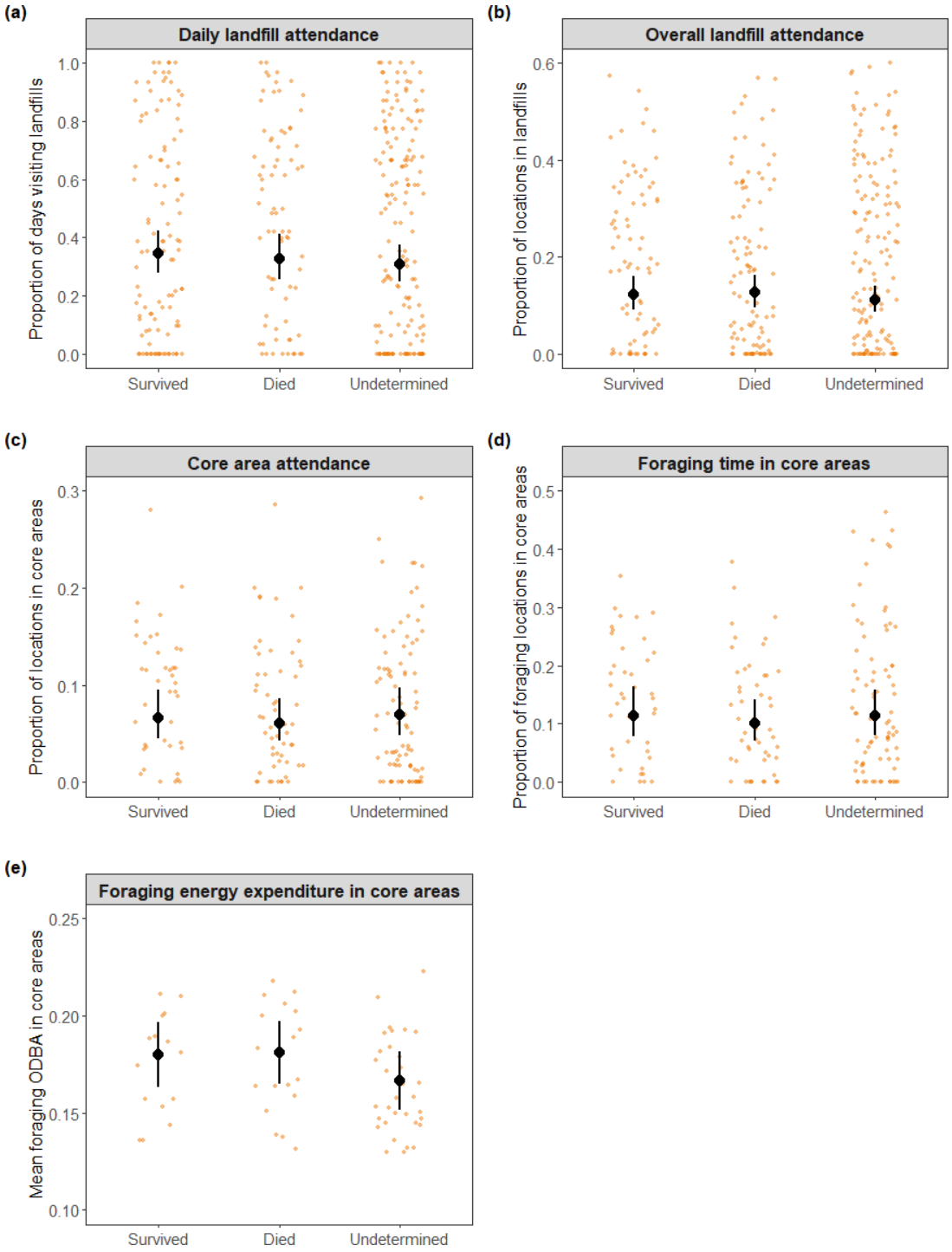


**Figure 3.** Predicted values and 95% confidence intervals of the GLMMs explaining age-related differences in (a) daily, (b) overall and (c) core area landfill attendance, as well as (d) foraging time and (e) foraging energy expenditure in core areas for GPS-tracked juvenile white storks with distinct survival outcomes in their first year (survived, died or undetermined). Orange dots represent raw data. No significant differences in landfill attendance and foraging performance at landfills were detected between the three groups.

energy expenditure were observed among older age classes (figure 4e). Monthly variation in landfill use was accounted for in all models and did not affect the significance of the age-related patterns (electronic supplementary material, table S6).

## 4. Discussion

Food waste disposal is the primary global source of PAFS [37]. An estimated 30–40% of food produced for human consumption is currently wasted [65], creating abundant, spatially and temporally predictable resources that are increasingly exploited by a growing number of species worldwide [37,40]. Using a comprehensive longitudinal GPS-tracking dataset from a long-lived generalist species, this study provides evidence that, at the population level, age-related increases in landfill use are primarily driven by individual learning during early life rather than by selective survival of individuals that most frequently and proficiently use landfill sites. From their second year onwards, white storks visited landfill sites more often and spent

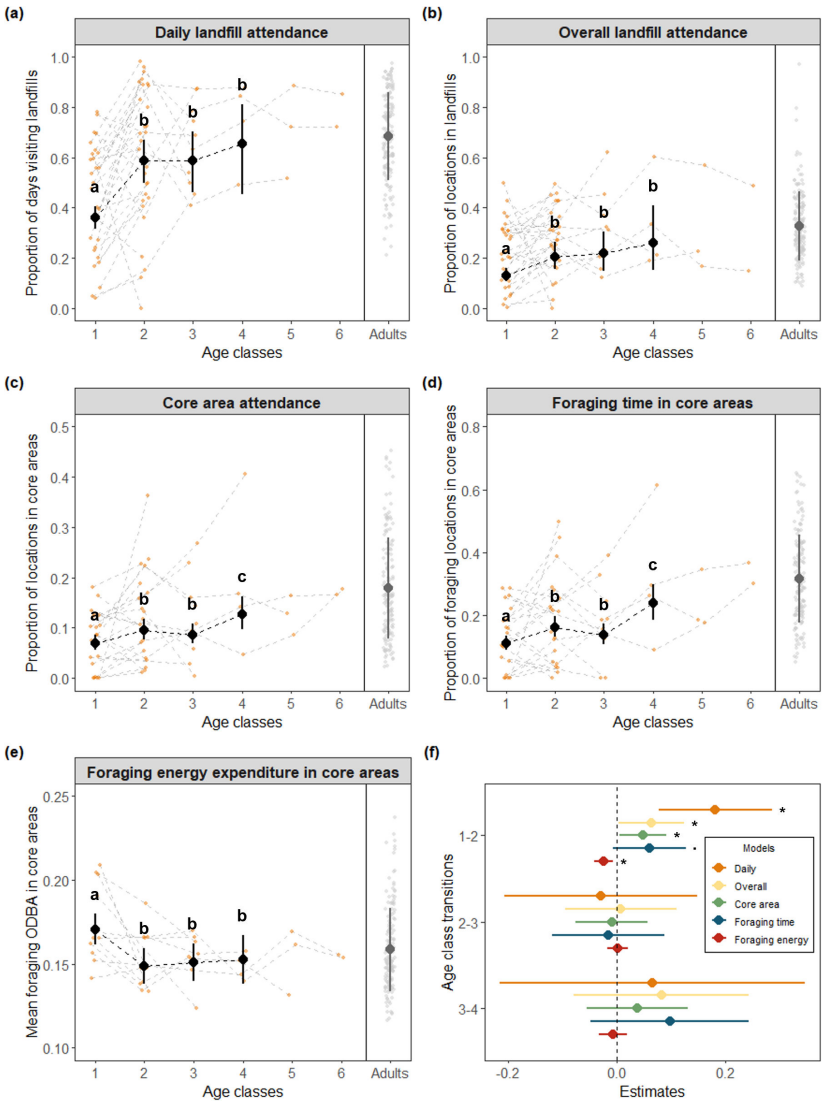


**Figure 4.** Predicted values and 95% confidence intervals of the GLMMs explaining age-related differences in (a) daily, (b) overall and (c) core area landfill attendance, as well as (d) foraging time and (e) foraging energy expenditure in core areas of GPS-tracked juvenile white storks for up to six continuous years of tracking. (f) Estimates and 95% confidence intervals of the LMMs quantifying within-individual improvements in each metric between consecutive age classes. In (a–e), orange and grey dots represent raw data of juveniles and adults, respectively. The grey lines connecting the orange dots indicate the individual changes in landfill use. Different letters indicate significant pairwise differences between age classes (age classes sharing a letter do not differ significantly). The mean and standard deviation for adults of unknown age are shown as reference values. In (f), significant improvements are indicated with '*' and marginally significant with '.'.

considerably more time there (>50% increase) compared with their first year. Additionally, they became more likely to access landfill core areas where the waste is dumped, while expending less energy when foraging at these sites.

The use of landfills as key foraging areas for white storks is a well-documented but relatively recent behaviour, particularly in Western Europe and North Africa [30,44,52,66,67]. Despite the potential risks of foraging in these sites [40,68], the visits been shown to be a time- and energy-saving strategy because individuals both reduce foraging time and increase foraging efficiency [44]. As a result, thousands of storks now heavily rely on these artificial feeding areas not only in their breeding grounds and during winter but also during migration [30,59,66,69]. Here, we show that landfill use starts at an early age, soon after fledging (electronic supplementary material, figure S1) and during their first migratory journey [59], suggesting that young birds quickly recognize landfills as predictable foraging areas. This might reflect the landfill-based diet of stork nestlings [44]. Nonetheless, landfill use by juveniles is significantly lower than that of older birds: first-year storks were almost half as likely to visit landfill sites daily compared with second-year storks and older age classes, with daily attendance rising from 35% of days in first-year birds up to 64% in older individuals. Similarly, overall landfill attendance (proportion of locations within landfills) increased significantly from 14 to 26%. One possible explanation for this age-related increase in the use of landfills might be intraspecific competition. Despite the abundance of food, competition at these sites may promote a foraging hierarchy where age and physical maturity are critical attributes [29,70]. Indeed, Martins *et al*. [30] showed evidence of strong competition for food at landfills, with adult storks dominating and outcompeting first-year juveniles in food acquisition, and consuming nearly four times more food than juveniles. In such competitive environments, young storks must rapidly develop efficient foraging behaviours that are essential for their survival. Social information and learning, whether from parents or older individuals, may help mitigate early-life inexperience and improve survival prospects [71–74].

Overall, our results demonstrate that patterns of landfill use in younger immature white storks differ from those of older mature individuals. Yet, while key foraging-related traits change over time, the strongest within-individual improvements

occurred between the first and the second year of life. These changes are probably driven by individual improvements in physical attributes (e.g. increased size, strength or coordination) and the rapid accumulation of experience (e.g. learning to locate and secure food) [5,16,24–26]. This pattern suggests that certain behaviours may become established as soon as juveniles leave the nest and start exploring their environment [4,73]. Nevertheless, later-life changes in resource use may still result from either cumulative experience or senescence [75,76]. As individual lifespans were not fully covered, it remains unclear whether age-related improvements in landfill use extend beyond maturity, stabilize or decline later in life, emphasizing the need for lifelong tracking to characterize later-life behavioural trajectories [15].

A widely accepted hypothesis is that higher juvenile mortality compared with adults results from inferior foraging skills, creating strong selection pressure for rapid attainment of adult-level efficiency [4,5,73]. First-year white storks experience significantly higher mortality [19,77,78]; hence, selective survival in early life could contribute to age-related differences in landfill use [14,17]. Nonetheless, we found no evidence that individuals surviving into the second year exhibited higher landfill attendance or better foraging performance during their first year. Thus, the selection of the most proficient landfill-user individuals does not seem to be the mechanism driving age-related changes in landfill use at the population level. Various factors may instead affect survival into the second year, including the selection of wintering grounds [79], and pressures operating at those areas, particularly in Sub-Saharan Africa, where no landfill sites are available, potentially selecting for individuals with other distinct foraging skills. Furthermore, juvenile mortality may be strongly influenced by stochastic events. Predation, disease or power line collisions and electrocution are particularly relevant for large birds such as storks and represent a major source of anthropogenic mortality [2–4,80–82]. These factors could mask any potential survival benefits associated with superior landfill foraging ability.

Owing to the challenges of obtaining individual lifelong tracking data, most studies investigating the ontogeny of foraging behaviour, space use and resource exploitation rely on dichotomous comparisons between juveniles and adults of unknown age or focus only on short early-life stages, such as the nestling period or the initial months after fledging [5,11,78,83]. Despite our relatively small sample size of first-year storks tracked for up to 6 years, this study provides insights into the mechanisms underlying the development of resource-use behaviours. In addition, even with acceleration data recorded at a relatively low sampling frequency (1 Hz), we detected consistent age-related improvements in foraging energy expenditure, reinforcing the robustness and reliability of our findings. Advances in GPS-tracking technology will soon enable lifelong monitoring of individuals, which is essential for disentangling the roles of individual learning and selective survival in shaping the development of animal behaviour [14,15].

Human activities often lead to shifts in food availability for animals, introducing new resources and foraging opportunities [37,84,85]. Previous research suggests that ecological novelty fosters behavioural innovations, allowing species to adapt to anthropogenic changes [86,87]. Our study reveals that population-specific behaviours, such as the increasing reliance of white storks on landfills and human-provided resources, can emerge through rapid individual improvements during early life. However, contrasting patterns in other species illustrate the complexity of these dynamics; for instance, juvenile Steppe Eagles (*Aquila nipalensis*) are attracted to human-altered areas while adults tend to avoid them [88]. Although young storks appear capable of developing foraging skills independently, their social nature suggests that learning is probably enhanced through interactions with conspecifics [74]. If foraging strategies in white storks are socially learnt, innovative skills that help them thrive in landfills could spread rapidly within social groups and be sustained over generations as cultural traditions [89,90]. Social learning may therefore be a crucial mechanism for enabling the exploitation of anthropogenic food sources, with significant implications for behavioural adaptation to human-driven environmental changes.

## 5. Conclusion

Our study reveals how age-related improvements shape the use of landfills in a long-lived opportunistic species, demonstrating that the exploitation of anthropogenic food resources develops over time, with the strongest effects occurring in early life. Within-individual improvements, rather than selective survival, play a key part in increasing foraging specialization at landfills, which has been shown to have far-reaching consequences for individual fitness [91]. Anthropogenic food subsidies have profoundly altered animal behaviour, leading to the loss of migration and improving survival [53]. However, forthcoming changes in waste management, prompted by European Union directives (1999/31/UE and 2018/850/UE), will probably pose significant challenges to these species owing to a substantial reduction in available resources (see [92] for evidence of decreased stork productivity following the implementation of bird deterrent measures at a landfill). With landfill closures on the horizon, further research is needed to understand how these changes influence bird migratory decisions and foraging behaviour. In addition, comprehensive longitudinal studies like this one are essential to understand and predict the adaptive capacity of animal populations to human-induced environmental changes.

Ethics. All animal handling and device deployment procedures were approved by the Institute for Nature Conservation and Forests in Portugal (license numbers: 493/2016/CAPT; 661-663/2017/CAPT; 548-550/2018/CAPT; 247-250/2019/CAPT; 364-368/2020/CAPT; 198-202/2021/CAPT) and carried out in agreement with their recommendations.

Data accessibility. The tracking data used in this study can be found on Dryad [93].

Supplementary material is available online [94].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. B.H.M.: conceptualization, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; A.M.A.F.: conceptualization, funding acquisition, methodology, validation, writing—review and editing; A.S.-R.: conceptualization, data curation, methodology, validation, writing—review and editing; M.A.: data curation, investigation, validation, writing—

review and editing; I.C.: conceptualization, data curation, funding acquisition, investigation, methodology, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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