Ecological and evolutionary implications of anthropogenic food subsidies on wildlife: The white stork as a case study

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Abstract

Human activities are causing widespread depletion of natural resources while generating substantial food subsidies that offer new foraging opportunities for wildlife. These changes in food availability are reshaping ecosystems and influencing individual behaviours and population dynamics of species worldwide. Landfill sites are now recognized as one of the most important predictable anthropogenic food subsidies and are increasingly associated with enhanced fitness, survival, and abundance of opportunistic species. This thesis combines extensive GPS tracking, behavioural video recordings at landfills, and long-term breeding data to explore the drivers and mechanisms underlying changes in the foraging behaviour of the opportunistic white stork (*Ciconia ciconia*), particularly in the increased use of landfill resources. In the first study, I explore age-related differences in landfill use and demonstrate that adult storks visit landfills considerably more often than juveniles, exhibit higher feeding success, and display greater aggression towards conspecifics. Consequently, juveniles are outcompeted by adults and displaced from accessing these food sources. In further investigation into the ontogeny of landfill use, I reveal that landfills become crucial foraging sites for storks early in life. The increase in this new foraging behaviour is then driven by the development of individual foraging skills during the first few years and refined as individuals mature, resulting in better performance in the use of these resources in adulthood. Finally, when exploring the influence of landfill resources on the breeding performance and population dynamics of storks, I found that breeding near landfills advances the laying dates, positively affecting clutch sizes and fledgling numbers. Proximity to landfills is also decisive for increased fledgling body condition. Consequently, variations in the abundance and distribution of nests further revealed a notable increase in the overall number of nests in just six years, particularly in the areas closer to landfill sites, indicating a dynamic interplay between landfill resources, breeding success, and population dynamics. Overall, this research provides valuable insights into the intricate relationship between anthropogenic food subsidies, foraging behaviour, life traits, and population dynamics of opportunistic bird species. Moreover, it provides a basis for understanding the consequences of anthropogenic food waste on wildlife, guiding future conservation efforts and management of wildlife populations in the context of changing ecosystems.

Resumo

As atividades humanas estão a causar um esgotamento generalizado dos recursos naturais e ao mesmo tempo a gerar subsídios alimentares substanciais que oferecem novas oportunidades de alimentação para a vida selvagem. Estas mudanças na disponibilidade de alimentos estão a remodelar os ecossistemas e a influenciar os comportamentos individuais e as dinâmicas populacionais das espécies em todo o mundo. Os aterros sanitários são agora reconhecidos como um dos mais importantes subsídios alimentares antropogénicos previsíveis e estão cada vez mais associados a um aumento da aptidão, sobrevivência e abundância de espécies oportunistas. Esta tese combina um extenso seguimento de indivíduos por GPS, gravações de vídeos comportamentais nos aterros sanitários e dados de reprodução a longo prazo para explorar os fatores e mecanismos subjacentes às mudanças no comportamento de procura de alimento da oportunista cegonha-branca (*Ciconia ciconia*), particularmente no aumento do uso dos recursos dos aterros sanitários. No primeiro estudo, exploro as diferenças relacionadas com a idade no uso dos aterros sanitários e demonstro que as cegonhas adultas visitam os aterros com muito mais frequência do que os juvenis, apresentam maior sucesso alimentar e mostram maior agressividade para com os membros da mesma espécie. Consequentemente, os juvenis são superados pelos adultos e impedidos de aceder a estas fontes de alimento. Numa investigação mais aprofundada sobre a ontogenia do uso dos aterros sanitários, revelo que os aterros se tornam locais de alimentação cruciais para as cegonhas logo no início da vida. O aumento deste novo comportamento de procura de alimento é depois impulsionado pelo desenvolvimento das habilidades individuais de alimentação durante os primeiros anos e refinado à medida que os indivíduos amadurecem, resultando num melhor desempenho no uso destes recursos na idade adulta. Por fim, ao explorar a influência dos recursos dos aterros sanitários no desempenho reprodutor e na dinâmica populacional das cegonhas, verifiquei que a reprodução perto dos aterros antecipa as datas de postura, afetando positivamente o tamanho das ninhadas e o número de crias. A proximidade aos aterros também é decisiva para o aumento da condição corporal das crias. Consequentemente, as variações na abundância e distribuição dos ninhos revelaram ainda um aumento notável no número total de ninhos em apenas seis anos, particularmente nas áreas mais próximas dos locais de aterros sanitários, indicando uma interação dinâmica entre os recursos dos aterros, o sucesso reprodutor e a dinâmica populacional. No geral, esta investigação fornece informações valiosas sobre a complexa relação entre os subsídios alimentares antropogénicos, o comportamento de procura de alimento, as características de vida e a dinâmica populacional de espécies de aves oportunistas. Além disso, fornece uma base para compreender as consequências do desperdício alimentar humano sobre a vida selvagem, orientando futuros esforços de conservação e gestão de populações de animais selvagens no contexto da mudança dos ecossistemas.

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Chapter 1

General introduction

1.1 Food availability and animal foraging behaviour

Food availability and its role in animal foraging behaviour is an elemental aspect of ecology, determining the survival, reproduction, and distribution of countless species across diverse ecosystems (Fox et al., 2001; Stephens et al., 2007). Foraging behaviour describes the different strategies employed by organisms to obtain and make use of energy and nutrients, which is a result of the dynamic interaction between environmental cues, physiological requirements, and evolutionary pressures (Kramer, 2001). In this thesis, I explore the complex relationship between food availability and foraging behaviour, unravelling the adaptive responses of species to face the challenges posed by ongoing human-driven environmental changes.

Food availability as a driving force

One of the primary determinants of animal foraging behaviour, shaping the strategies adopted by species to secure their sustenance, is the availability of food resources (Fox et al., 2001; Martin, 1987; Stephens et al., 2007). In any given ecosystem, the landscape is dynamic and defined by the abundance, distribution, and accessibility of food resources that organisms must learn to exploit (Martin, 1987). Seasonal fluctuations, geographical variations, and the unpredictable nature of resources require adaptive foraging strategies to ensure the survival and reproduction of individuals, populations, and species (Pyke et al., 1977).

The concept of optimal foraging theory provides a theoretical framework for understanding how animals maximise their energy gains while minimising the costs associated with foraging (Stephens & Krebs, 1986). Animals constantly face the challenge of balancing the energy spent searching for food with the energy obtained from consumption (Pyke et al., 1977). Therefore, evolutionary pressures can shape foraging behaviours that optimise this energetic balance, leading to different strategies observed across species (Kramer, 2001).

Diversity in foraging strategies

Animals exhibit a remarkable variety of foraging strategies, perfectly adjusted to their ecological niche and the specific challenges posed by their environment (Schoener, 1971). Overall, animals can be broadly classified into generalist and specialist foragers, which can also be based on the spatial and temporal distribution of food resources (Kramer, 2001).

Generalist foragers have flexible diets and can exploit a broad range of food sources (Büchi & Vuilleumier, 2014; Fridley et al., 2007). They are often opportunistic and adaptable to various environments, which enables them to effectively cope with fluctuations in food availability (Abrams, 2006; Carnicer et al., 2008). In contrast, specialist foragers exhibit a high degree of specialisation in their dietary requirements, often relying on a specific type of food (Bolnick et al., 2003). These specialisations often arise as a result of evolutionary adaptations geared toward exploiting a specific niche within an ecosystem; survival is therefore intrinsically linked to the availability of specific food sources, making these species more vulnerable to environmental changes (Araújo et al., 2011; Bolnick et al., 2003).

The spatial and temporal distribution of food resources can further play a crucial role in shaping foraging behaviour (Morris, 2003; Mueller & Fagan, 2008). This is because some animals may engage in territorial foraging, where they establish and defend territories rich in resources, while others undertake long-distance journeys to exploit seasonal peaks in food availability across different locations (Newton, 2007).

Ontogeny of foraging behaviour

The development of foraging strategies throughout the life cycle of individuals involves behavioural changes that usually depend on individual skills and preferences related to food acquisition (Riotte-lambert et al., 2013; Sergio et al., 2014; Yoda et al., 2004). Thus, the ontogeny of foraging behaviour is a dynamic and complex process that can be influenced by genetic and environmental factors, as well as life experience (De Grissac et al., 2016; Patrick et al., 2015; Sergio et al., 2014; Wakefield et al., 2015).

Key aspects of the ontogeny of foraging behaviour include understanding the inborn behaviours that individuals exhibit without the need for learning or experience (Marchetti & Price, 1989; Pyke, 1984). Yet, many foraging behaviours are learned through experience and observation (Marchetti & Price, 1989; Wunderle, 1991). Young individuals may initially rely on innate behaviours, but may also later refine and adapt their foraging strategies based on experience and knowledge of their environment (Marchetti & Price, 1989; Wunderle, 1991). Learning can thus occur through trial and error, observation of conspecifics, or responses to environmental cues (Grecian et al., 2018; Wakefield et al., 2015).

The ontogeny of foraging behaviour often progresses through distinct developmental stages that can be influenced by physical and cognitive development and nutritional needs (Lindström, 1999; Sæther et al., 2013). Also, social learning plays a role, as juveniles can learn from older, more experienced conspecifics or other species, gaining valuable information about food sources and foraging techniques (Marchetti & Price, 1989; Wunderle, 1991).

Variations in the availability and distribution of food resources can shape the ontogeny of foraging behaviour and lead to adjustments in their foraging strategies (Baert et al., 2022; Campioni et al., 2020; Guilford et al., 2011). Foraging behaviour, therefore, requires adaptability throughout life, as it increases the survival and reproduction capacity of individuals in different ecological conditions (Kramer, 2001).

Behavioural responses to changing environments

Adapting to changing environments is fundamental to the survival of all species, but the unprecedented challenges posed by the intensification of agricultural landscapes are leading to population declines in species unable to adjust their behavioural processes to track and use the resources that become available (Rosalino et al., 2014). As human actions continue to rapidly reshape landscapes and alter ecosystems, the delicate balance between food availability and wildlife behaviour is increasingly disrupted (Wong & Candolin, 2015). Habitat destruction, climate change, and pollution contribute to drastic shifts in the distribution and abundance of food resources, challenging the adaptive capacity of numerous species (Venter et al., 2016). Consequently, foraging behaviours are forced to adapt very quickly, leading to potential mismatches between the timing of resource availability and the timing of foraging activities (Schlaepfer et al., 2002). In fact, the costs of these disruptions in responses to the environment can even extend beyond individual species, influencing entire ecosystems and the intricate web of interactions that sustains them (Scheffers et al., 2016).

1.2 Impacts of human-driven changes in food availability for wildlife

Anthropogenic activities are considered the main driver of ongoing global environmental change, posing an increasing threat to wildlife (Foley et al., 2005; Nelson et al., 2006; Newbold et al., 2015). The cumulative impact of human actions is profoundly transforming ecosystems and the availability of natural resources, resulting in substantial variations in the abundance and distribution ranges of many species (Brook et al., 2008; Ellis et al., 2010; Powers & Jetz, 2019; Venter et al., 2016).

Habitat loss and fragmentation, mainly driven by urban expansion, agricultural intensification, and the overexploitation of natural resources, are rapidly diminishing and restricting the use of vital food sources and nesting sites, significantly influencing species behaviour (Fahrig, 2003; Fischer & Lindenmayer, 2007; Li et al., 2022; Simkin et al., 2022). Simultaneously, human-induced climate change is exerting a substantial impact on wildlife, forcing species to adapt to continuous fluctuations in temperature and precipitation, which determine the availability and distribution of resources and affect animal movement patterns (Fontúrbel et al., 2021; Sala et al., 2000; Simkin et al., 2022; Stuart Chapin & Díaz, 2020; Walther et al., 2002). Moreover, industrialization and the intensification of agricultural and livestock production are releasing a variety of pollutants into the environment, contaminating soils, food resources, and water supplies, further disrupting animal behaviour and the ecological and evolutionary processes of wildlife populations (Bertram et al., 2022; Marlatt et al., 2022; Sharma et al., 2019). All these threats are interconnected and collectively contribute to the current biodiversity extinction crisis (Brook et al., 2008; Pereira et al., 2012; Phalan et al., 2011).

Alongside the widespread depletion of natural resources and declines in wildlife populations resulting from the intense appropriation of primary productivity, human activities are also generating large amounts of food waste and providing accessible resources to multiple species capable of adapting and benefiting from these changes (Oro et al., 2013). Currently, up to 30–40% of all food produced for human consumption is wasted (Parfitt et al., 2010), and regions with the highest concentration of human population and the highest production of food waste are those most affected by these anthropogenic subsidies (Oro et al., 2013). Hence, human food waste offers abundant food sources and new foraging opportunities for a wide range of species worldwide, which are highly predictable in both space and time, as well as easier to exploit than natural resources (Bartumeus et al., 2010; Cortés-Avizanda et al., 2012; Gilbert et al., 2016). Anthropogenic food subsidies play an increasingly important role in the diet of several generalist and opportunistic species that take advantage from such resources and promote changes in their life histories (Oro et al., 2013). Therefore, the exploitation of human food waste is strongly influencing the behaviour of these species and allowing their numbers to increase, while also promoting cascading effects across food webs and ecosystems, potentially reducing the goods and services they provide (Cortés-Avizanda et al., 2012; Newsome et al., 2015; Rodewald et al., 2011). Although reducing food waste and feeding a growing global human population remains a challenge, understanding the resilience and adaptability of wildlife to these new ecosystem changes is an emerging issue for global conservation efforts (FAO, 2017; Thyberg & Tonjes, 2016).

1.3 Predictable anthropogenic food subsidies

All food resources that are provided intentionally (e.g., bird feeders) or unintentionally (e.g., organic food waste) through human activities and that become consistently accessible to wildlife are known as Predictable Anthropogenic Food Subsidies (PAFS; Oro et al., 2013). The most common predictable food sources that are made available to wildlife include the disposal of organic remains in landfills, fisheries discards and crop leftovers. All these PAFS can directly affect individuals as they learn to anticipate and exploit these resources, leading to changes in their behaviour and ecology. This, in turn, can cause cascading effects on populations and ecosystems, influencing population dynamics, community structure, and even evolutionary processes (Figure 1.1).

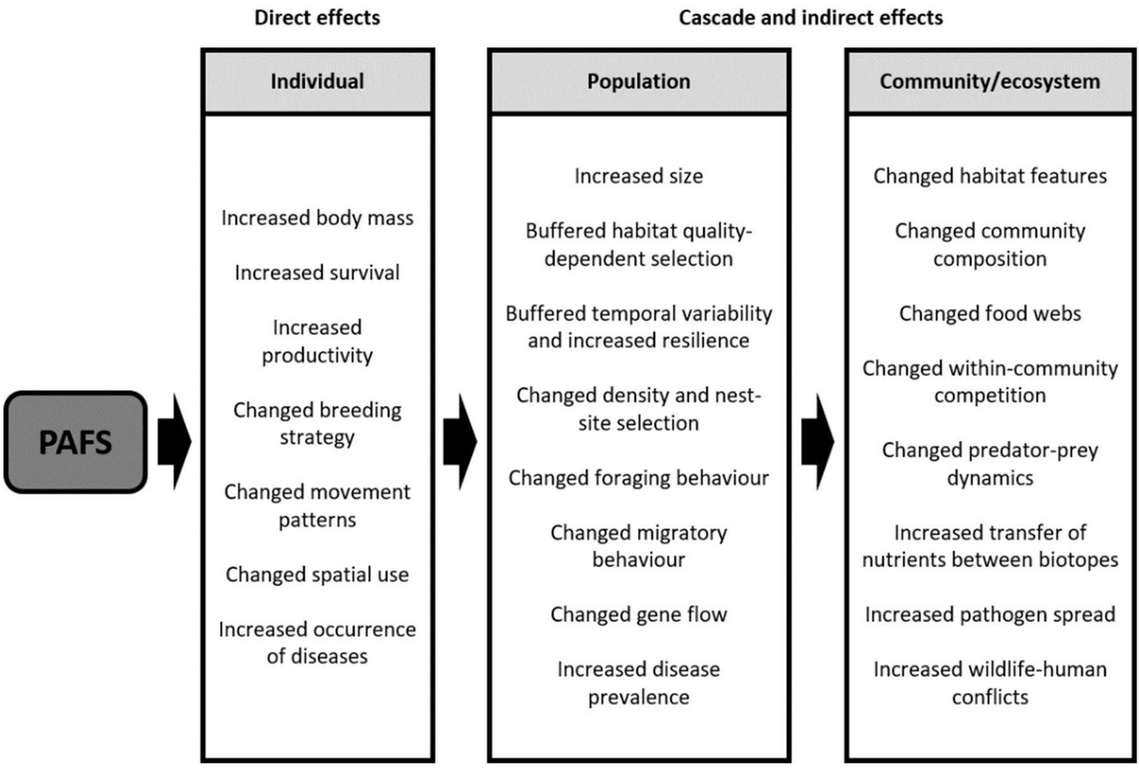

Figure 1.1 – Web of potential effects of PAFS at individual, population, community and ecosystem levels. Adapted from Oro et al., 2013).

In the context of evolutionary implications, PAFS can exert selective pressures on life history traits of species that exploit these subsidies. For example, animals that learn to adapt to human-provided food sources may experience changes in their foraging behaviour, movement patterns, breeding strategies, or even their body condition over generations (Bartumeus et al., 2010; Plaza & Lambertucci, 2017). From an ecological perspective, PAFS can alter the competitive dynamics among species, potentially leading to shifts in community structure and biodiversity (Newsome et al., 2015; Tauler-Ametller et al., 2017). Species that are better able to exploit anthropogenic food sources may further outcompete others, leading to changes in the abundance and distribution of different species within an ecosystem (Duhem et al., 2008).

Moreover, the use of PAFS can vary according to social interactions, age and individual personality (Deygout et al., 2010; Oro et al., 2013). Thus, understanding the implications of PAFS at different levels is crucial for effective conservation and management strategies. Also, responsible management of these subsidies is essential to minimise negative ecological impacts and maintain the health and balance of ecosystems considering the ongoing global environmental changes.

1.4 Landfill use implications for wildlife

Worldwide, open-air landfill sites, where millions of tonnes of food waste are discarded, constitute one of the most significant PAFS exploited by many species, especially birds (Oro et al., 2013; Plaza & Lambertucci, 2017). Landfills can thus gather abnormally high densities of opportunistic species, mostly birds, with hundreds or thousands of individuals.

The superabundance of organic waste in landfills offers opportunistic species a food source with great repeatability in space and time, which is renewed daily and allows for a reduction in foraging times and necessary feeding intervals (Plaza & Lambertucci, 2017; Soriano-Redondo et al., 2021; van Donk et al., 2019). This, in turn, can result in improved breeding parameters and survival, as well as influence annual movement patterns and species geographical ranges (Gilbert et al., 2016; Marcelino et al., 2023; Patenaude-Monette et al., 2014; Plaza & Lambertucci, 2017). Nevertheless, while the majority of studies highlight the positive effects of these high-value anthropogenic food sources, landfill use can also entail detrimental impacts that remain poorly explored. Questions persist regarding the nutritional quality of the food, which might negatively affect the physiological condition of individuals, neonatal growth rates, and overall breeding productivity (de la Casa-Resino et al., 2014; Höfle et al., 2020; Pineda-Pampliega et al., 2021; Plaza & Lambertucci, 2017). Moreover, feeding on waste might increase accidental ingestion of hazardous waste (e.g. plastic) as well as exposure to contaminants and pathogens that increase species physiological stress and reduce survival, ultimately further spreading diseases and increasing human-wildlife conflicts (Becker et al., 2015; Gómez et al., 2016; Lopes et al., 2021; Plaza & Lambertucci, 2017).

Overall, landfill sites can increase the carrying capacity of surrounding areas, reducing emigration and promoting immigration from non-subsidized areas, thereby increasing population sizes and density of opportunistic species (López-García & Aguirre, 2023; Payo-Payo et al., 2015; Plaza & Lambertucci, 2017). However, landfills can also act as ecological traps, as exploiting these resources may affect population dynamics through increased predation risk or by altering interference competition mediated by density-dependence processes (Araújo et al., 2011; Real et al., 2017).

Furthermore, in recent years, evidence has demonstrated that the availability of abundant food from anthropogenic food subsidies, such as food waste from landfills, is increasingly playing a key role in shaping the movements of different species (Plaza & Lambertucci, 2017). Landfill sites are also more heavily used along migratory routes and are even prompting a complete change in the migration patterns of some species as they become more sedentary (Flack et al., 2016; Marcelino et al., 2023; Rotics et al., 2017). Therefore, assessing alterations in movement patterns in response to food availability in landfills is critical for understanding the ability of species to adapt to rapid environmental change and for clarifying the conservation implications associated with the potential significant reduction of these new resources.

As a result of human population growth and increasing demand for resources, reducing food waste is a top priority for governments and essential for meeting environmental sustainability goals. According to the European Union´s Directive, waste must be reduced to 10% of present levels by 2035 (EU Directive 2018/850). Nonetheless, the consequences of removing these anthropogenic subsidies are uncertain and may differ between species (Newsome & van Eeden, 2017). For example, no short-term effects were observed on the breeding success of Egyptian vultures (*Neophron percnopterus*), one year following a landfill closure (Katzenberger et al., 2019). However, yellow-legged gulls (*Larus michahellis*) experienced significant declines in both breeding success and body mass over the subsequent three years after landfill closure (Steigerwald et al., 2015). Therefore, monitoring the impacts of landfill closures on species that rely heavily on these resources is critical for their conservation and management.

1.5 Study system

This thesis investigates the implications of landfill food waste on the foraging behaviour and breeding decisions of the white stork (*Ciconia ciconia*), an opportunistic species that now relies heavily on these resources in southern Portugal. The white stork has become a successful species in exploiting landfill resources year-round in the Iberian Peninsula (Catry et al., 2017). This success may have contributed to an increase in the number of resident individuals within a population that was entirely migratory (Catry et al., 2017; Molina & Del Moral, 2006), and to the exponential growth of the breeding population (Encarnação, 2015; Molina & Del Moral, 2006). As a long-lived bird with an extensive immature stage (3–5 years), this species has a long period to refine and potentially adapt its foraging behaviour, along with its movements, before breeding begins. However, the individual differences in the use of landfill resources and the subsequent cascading effects on the population have not yet been investigated.

Study species

The white stork is a large, long-lived distinctive wading bird and a highly adaptable and opportunistic species (Elliott et al., 2020; Hancock et al., 1992). Its breeding range extends throughout the Palearctic and west-central Asia, while its wintering area is mainly in sub-Saharan Africa (Elliott et al., 2020). As a carnivore, it consumes a wide variety of animal prey, with the most common food items including insects, earthworms, amphibians, reptiles, and small mammals (Elliott et al., 2020; Hancock et al., 1992). White storks feed mainly during the day, obtaining most of their food from the ground, among low vegetation and shallow waters, but their diet varies greatly according to season, location, and prey availability (Elliott et al., 2020; Hancock et al., 1992). It primarily prefers habitats in areas with open wetlands, particularly grassy areas that are wet or periodically flooded, such as riverbanks, marshes, swamps, ditches, grassland, and meadows, while it tends to avoid areas with taller vegetation cover, such as forests and shrublands (Elliott et al., 2020; Hancock et al., 1992). On their African wintering grounds, white storks also use grasslands, wetlands, and farmlands (Elliott et al., 2020; Hancock et al., 1992).

As a gregarious bird, breeding pairs typically gather in small groups for foraging, and nesting in colonies is frequent (Elliott et al., 2020; Hancock et al., 1992). Most white storks are monogamous and pair for life; however, extra-pair copulation can occur (Elliott et al., 2020; Hancock et al., 1992). The breeding period is from the beginning of March to the first days of July (Elliott et al., 2020). A pair raises a single clutch per year, in which the female usually lays four eggs at two-day intervals, although clutches of 1 – 7 eggs have been recorded (Elliott et al., 2020). The chicks fledge after about two months and usually start breeding when they are 3 – 5 years old (Elliott et al., 2020; Hancock et al., 1992). In their first winter, the plumage of young storks is already similar to that of the adults (Elliott et al., 2020; Hancock et al., 1992).

Although currently a common species in Europe, white stork populations suffered a sharp decline until the 1980s due to severe droughts in the Sahel and habitat loss in the Iberian

Peninsula resulting from agricultural changes (Carrascal et al., 1993; Catry et al., 2017; Senra & Alés, 1992). Since then, several initiatives across Europe have been undertaken to restore and enhance the populations of this species, contributing to their recovery (Schaub et al., 2004). Moreover, guaranteed and year-round food availability from anthropogenic sources, initially with the introduced red-swamp crayfish, highly abundant in rice fields, and later with the emergence of landfill resources, has likely facilitated the expansion, population growth, and establishment of overwintering populations in Iberia (Catry et al., 2017; Ferreira et al., 2019).

In Portugal, the number of breeding pairs increased from 3,302 in 1994 to 11,691 by the time of the last census in 2014 (Encarnação, 2015). During that same period, the number of resident storks also significantly increased, from around 1,000 to over 14,000 individuals, which represented approximately 60% of the breeding population at the time (Catry et al., 2017). Their ability to exploit year-round food from landfills undoubtedly plays a major role in shifting their foraging behaviour and suppressing migratory behaviour, as 80% of overwintering individuals in Iberia congregate near landfill sites (Catry et al., 2017; Tortosa et al., 2002). Previous studies have also shown that the continuous availability of food in landfills has facilitated year-round nest use, influencing their home-ranges and movement behaviour during the breeding and wintering seasons (Gilbert et al., 2016).

Therefore, remaining in the breeding area throughout the year and nesting near predictable food sources helps individuals avoid the costs associated with distances covered throughout the year, particularly during migration, and ensures the benefits of early arrival at the breeding grounds (Soriano-Redondo et al., 2023; Visser et al., 2009). On the other hand, this strategy may also expose individuals to periods of low resource abundance and unfavourable weather conditions (Berthold, 2001). Overall, the strategy adopted by each individual may impact subsequent survival, fitness, and offspring productivity, potentially driving the suppression of migratory behaviour and leading to different dynamics between individuals nesting near and far from landfills (Soriano-Redondo et al., 2023).

Study area

The Iberian Peninsula currently hosts some of the most stable and abundant populations of white storks in Europe (BirdLife International, 2016; Elliott et al., 2020), forming a crucial part of one of the most significant migratory routes for the species (BirdLife International, 2016; Elliott et al., 2020). Hence, all the research conducted for this thesis was performed in southern Portugal, covering the main distribution area of the species in the country (Encarnação, 2015). This region is characterised by a Mediterranean climate and is predominantly occupied by mosaics of arable land, agroforestry areas, pastures, and other intensive agricultural lands, which represent the most important habitats for this species in Portugal (Encarnação, 2015). Additionally, landfill resources are highly available at different sites evenly spread across the study area and further along the migration route (Marcelino et al., 2023). This creates an ideal study system for understanding how individuals change their foraging behaviour, moving from the consumption of natural resources to the exploitation of food waste in landfills, and how these resources influence the breeding and population dynamics of the white stork.

To accomplish this, hundreds of adult and juvenile individuals were tagged with GPS tracking devices in several colony sites throughout the study area (Figure 1.2), and the use of landfills was assessed over several years. Regular visits were made to all landfills in the study area (Figure 1.2), and behavioural data was collected from hundreds of storks foraging at these sites. In addition, monitoring and collection of breeding data from hundreds of pairs was also carried out over six years in the different colony sites (Figure 1.2).

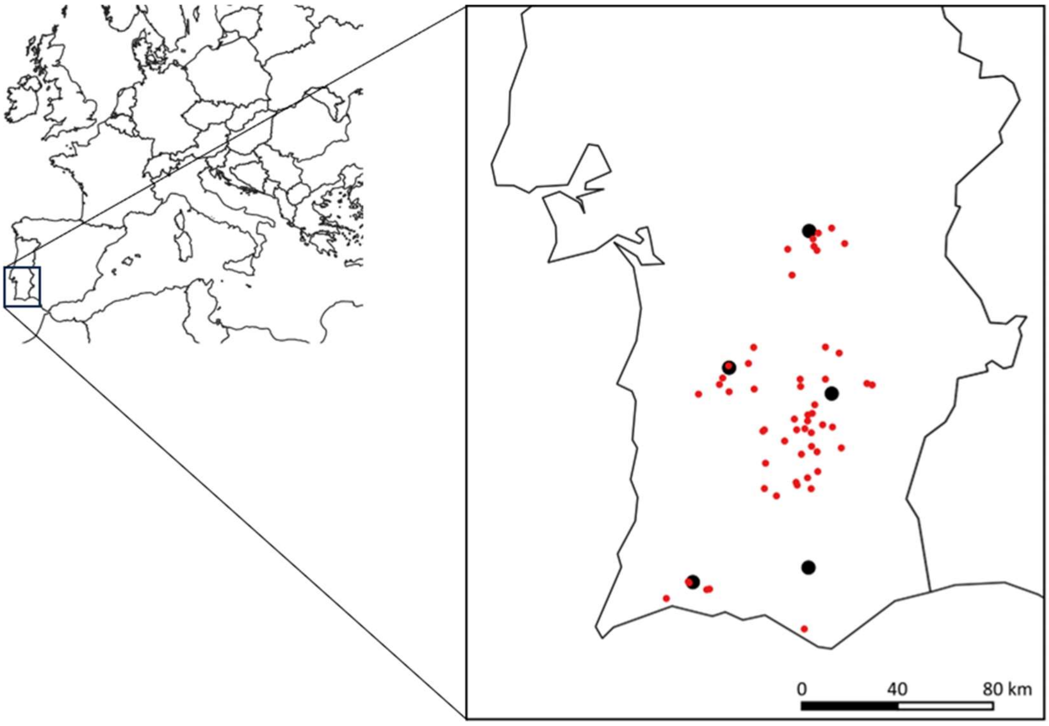

Figure 1.2 – Framing of the study area with the location of landfill sites (black dots) and monitored colony sites (red dots).

1.6 Thesis structure

This thesis explores the influence of landfill food resources on the foraging behaviour and breeding decisions of a long-lived opportunistic bird species. I combine data on individual landfill use, obtained from several years of GPS tracking of hundreds of white storks in different life stages, with behavioural data from videos recorded at landfills and breeding data from long-term monitoring to understand the factors and mechanisms driving the intensive exploitation of these resources by this species. In Chapter 2, I analyse age-related differences in landfill use between juvenile and adult white storks. In Chapter 3, I delve deeper into the ontogeny of this foraging behaviour, examining age-related changes in landfill use and foraging performance among storks as they mature, from fledging to adulthood. In Chapter 4, I investigate the influence of nest distance to landfill resources on the storks´ breeding decisions and their population dynamics.

The emergence of landfill food waste as predictable anthropogenic food subsidies is supporting growing populations of opportunistic species and shaping their foraging behaviour. However, although individuals can vary in their ability to use these resources, the factors that influence this variability within species are still poorly understood. In Chapter 2, I combine GPS tracking data and behavioural video recordings of hundreds of adult and juvenile white storks across different landfill sites to investigate age-related differences in landfill attendance, access to resources, and foraging efficiency at landfills. This chapter is published in *Animal behaviour*.

For most animals, early life is a critical period in which the development of foraging behaviour can have significant ecological and evolutionary implications. While foraging ability is generally associated with age and experience, particularly in long-lived species, the ontogeny of foraging behaviour remains unclear. In Chapter 3, I use long-term GPS tracking data of hundreds of white storks tracked from fledging to adulthood to investigate age-related changes in landfill use and examine whether differential use is driven by individual selective survival or ontogenic development.

An increasing number of species use landfill resources throughout their annual cycles, yet the influence of these resources on individual breeding decisions, breeding success, and population dynamics remains to be determined. In Chapter 4, I investigate how the nest distance to landfills is related to the breeding performance and demography of the white stork population by using long-term breeding data from hundreds of nests spread across a gradient of distance to landfill sites.

Lastly, in the general conclusions (Chapter 5), I summarise the main findings of this thesis, discuss how it has contributed to understanding the influence of predictable anthropogenic food subsidies on foraging behaviour, and identify potential future research directions and food waste management measures.

I present each chapter in the style of standalone publications for peer-reviewed journals, with references and supplementary information presented at the end of each chapter.

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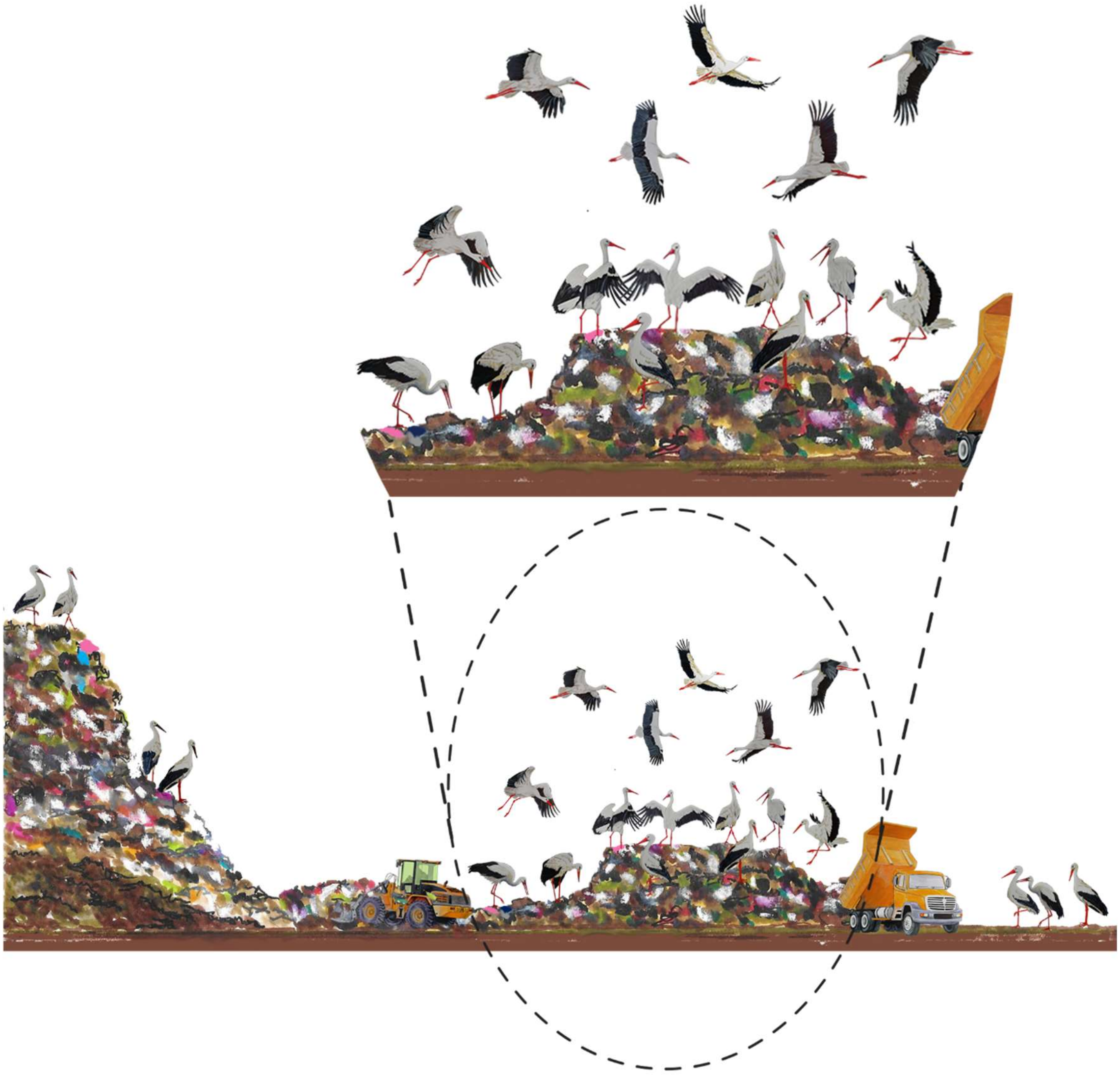
Chapter 2

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



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

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Abstract

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 pre-migratory 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 pre-migratory 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.

2.1 Introduction

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 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 naive 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). 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 (i) landfill attendance, (ii) access to food resources and (iii) foraging proficiency (behaviour time budgets, feeding success and agonistic interactions), during the pre-migratory 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.

2.2 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 pre-migratory 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 pre-migratory 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 non-migratory birds. The pre-migratory 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; Figure 2.1). 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 pre-migratory 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 pre-migratory 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 pre-migratory 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 pseudo-replication, 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 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 S2.1), to facilitate interpretation and guarantee consistency. All behaviours were then merged into three main categories (‘foraging’, ‘alert’ or ‘inactive’; Table S2.1), 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 pre-migratory 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 pre-migratory period) and the second model included the overall landfill attendance (individual proportion of GPS locations in landfills during the pre-migratory 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 pre-migratory 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.

2.3 Results

Landfill use during the pre-migratory period

Tracking data for 68 adult and 67 juvenile white storks tagged in southern Portugal were obtained during the pre-migratory 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 (Figure 2.1). 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 annual cycle, while all juveniles alive at the end of the pre-migratory period migrated to Africa.

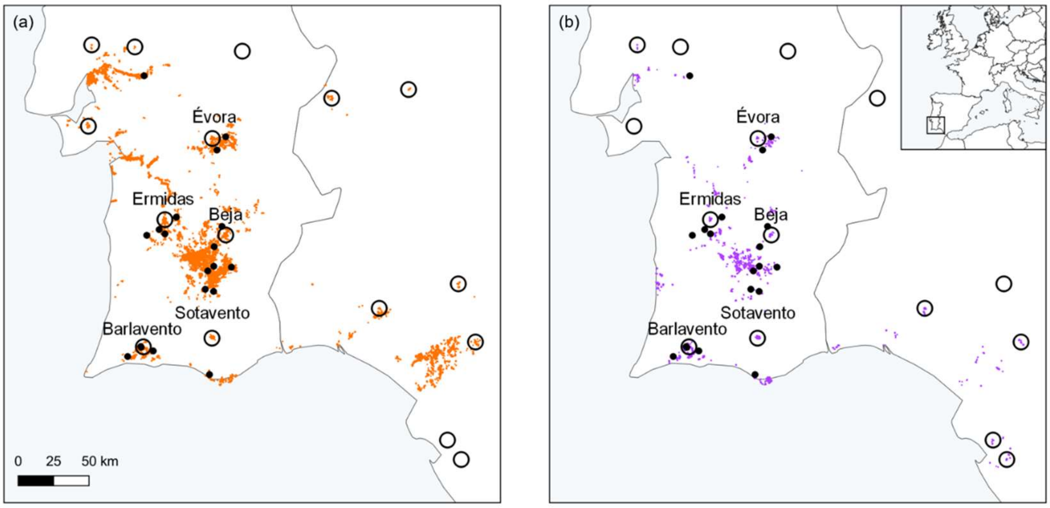

Figure 2.1 - Total ground GPS locations of (a) adult (*N* = 68) and (b) juvenile (*N* = 67) tracked white storks during their pre-migratory periods between 2018 and 2020. Black circles and dots indicate landfills and nesting sites, respectively.

Monthly counts at landfills confirmed the regular use of these sites by thousands of storks during the pre-migratory period (Figure S2.1). 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 (Figure S2.1).

Landfill attendance and access to food resources

Tracking data showed clear age-related differences in daily landfill attendance during the pre-migratory period (Table 2.1). The proportion of days adult storks visited landfills was twice as high as for juveniles (predicted values ± SE: adults = 0.57 ± 0.11; juveniles = 0.29 ± 0.19; *P* < 0.001; Figure 2.2a). However, the overall landfill attendance (proportion of GPS locations in landfills) of adult storks was not significantly higher than that of juveniles (predicted values ± SE: adults = 0.27 ± 0.08; juveniles = 0.20 ± 0.18; *P* = 0.068; Figure 2.2b).

Table 2.1 - Parameters of the GLMs explaining the influence of age (adult or juvenile) of GPS-tagged white storks in determining landfill attendance during the pre-migratory 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.

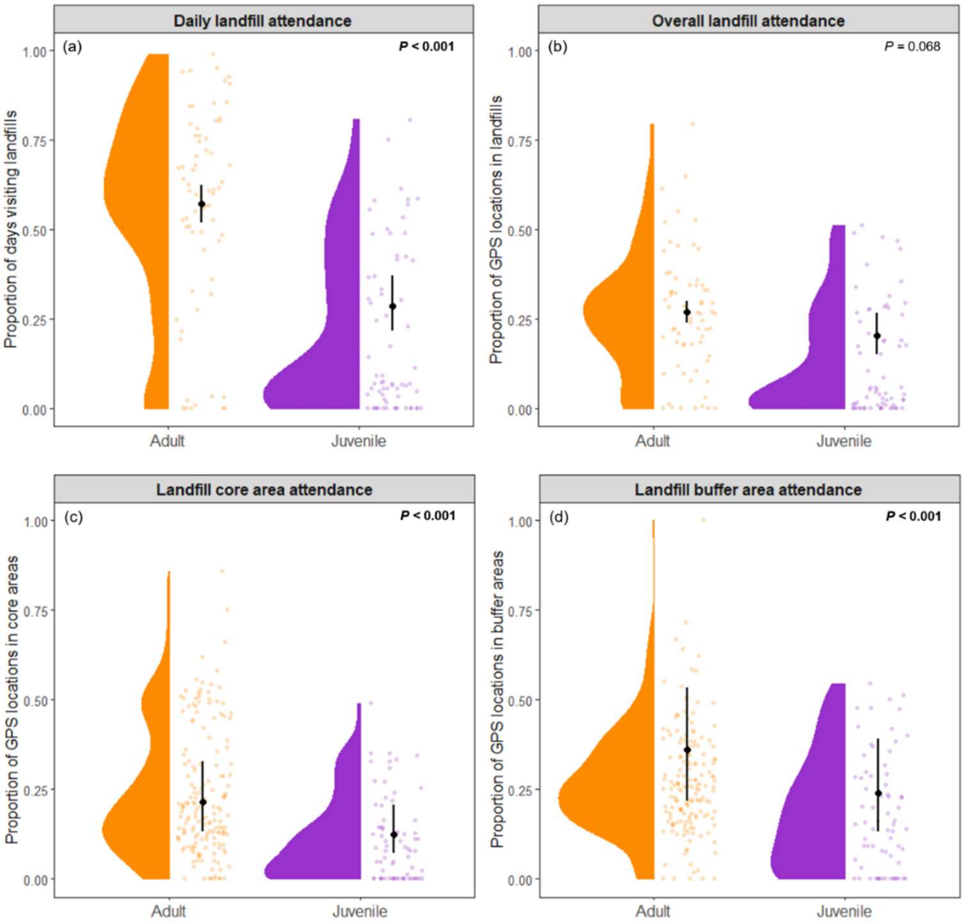

Figure 2.2 - Predicted values and 95% confidence intervals of the estimates from the GLMs and GLMMs explaining the influence of age (adult or juvenile) of tagged white storks in determining (a) daily landfill attendance and (b) overall landfill attendance (*N* = 68 adults, *N* = 67 juveniles); and in determining (c) landfill core area attendance and (d) landfill buffer area attendance (*N* = 61 adults, *N* = 47 juveniles) during the pre-migratory period. Orange and purple areas represent the density distribution of attendance for adult and juvenile birds, respectively. Dots represent raw individual data.

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 2.2). The proportion of adult stork GPS locations in landfill core feeding areas was nearly twice as high as that of juveniles (predicted values ± SE: adults = 0.22 ± 0.29; juveniles = 0.12 ± 0.31; $P < 0.001$; Figure 2.2c). In the adjacent buffer areas, the proportion of GPS locations was also considerably higher for adults (predicted values ± SE: adults = 0.36 ± 0.36; juveniles = 0.24 ± 0.37; $P < 0.001$; Figure 2.2d). Juvenile storks were mainly restricted to the outer areas of the landfill sites (Figure 2.3).

Table 2.2 - Parameters of GLMMs explaining the influence of age (adult or juvenile) of GPS-tagged white storks in determining access to landfill resources during the pre-migratory 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.

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 (Figure S2.2). 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/m^2, respectively), along the decreasing gradient of food availability.

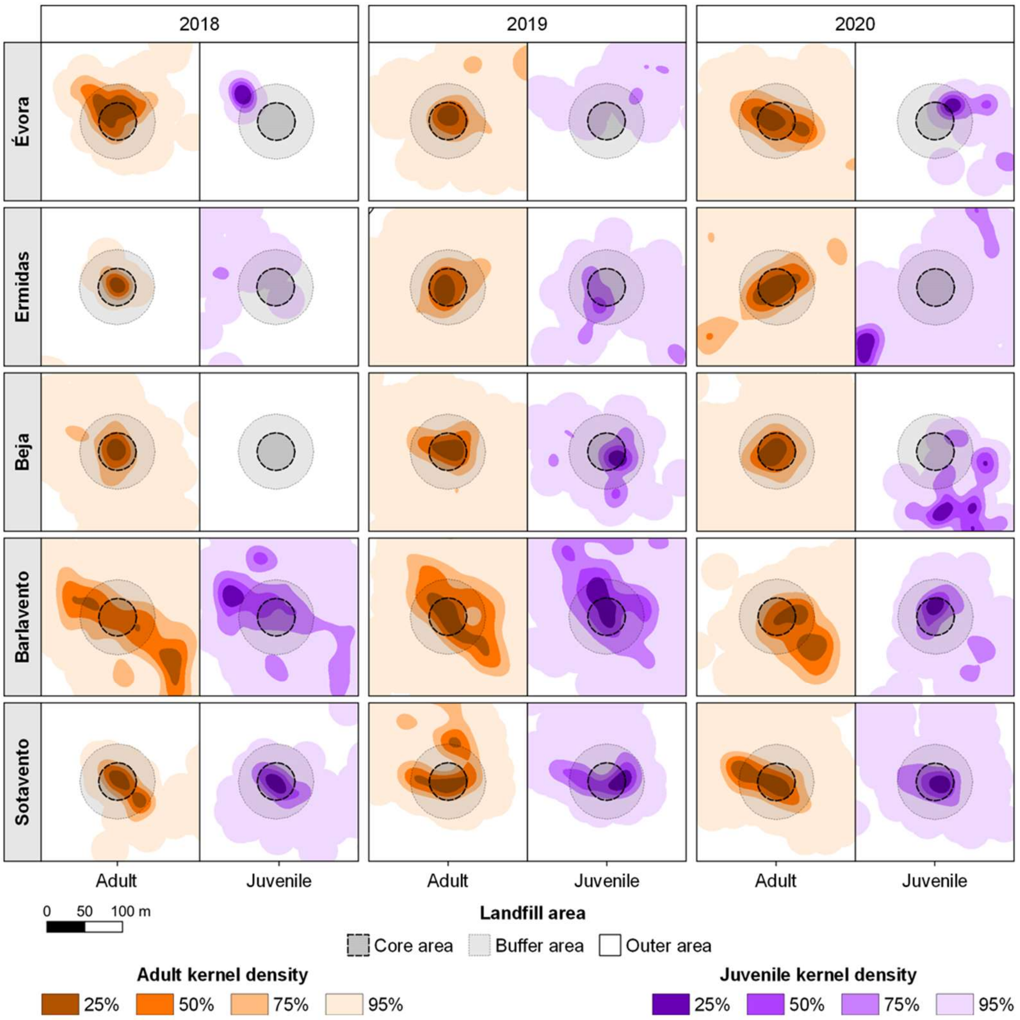

Figure 2.3 - Kernel utilisation distributions (KUD) calculated from the combined data of GPS-tracked adult (*N* = 61) and juvenile (*N* = 47) white storks that used the five landfills in southern Portugal during the 2018–2020 pre-migratory periods. Density of GPS locations decreases along the decreasing gradient of food availability (core > buffer > outer areas). Colours represent specific KUD contours; landfill areas are represented by black dashed circles.

Landfill foraging proficiency

Video recording analysis showed that foraging proficiency was influenced by bird age and landfill area (Table 2.3, Table S2.2). 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 non-existent (adults = 0.01 ± 0.32; juveniles = 0.03 ± 0.25; *P* = 0.091; Figure 2.4a). 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; Figure 2.4b). 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; Figure 2.4c). 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 (Figure S2.3).

Table 2.3 - 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 pre-migratory 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.

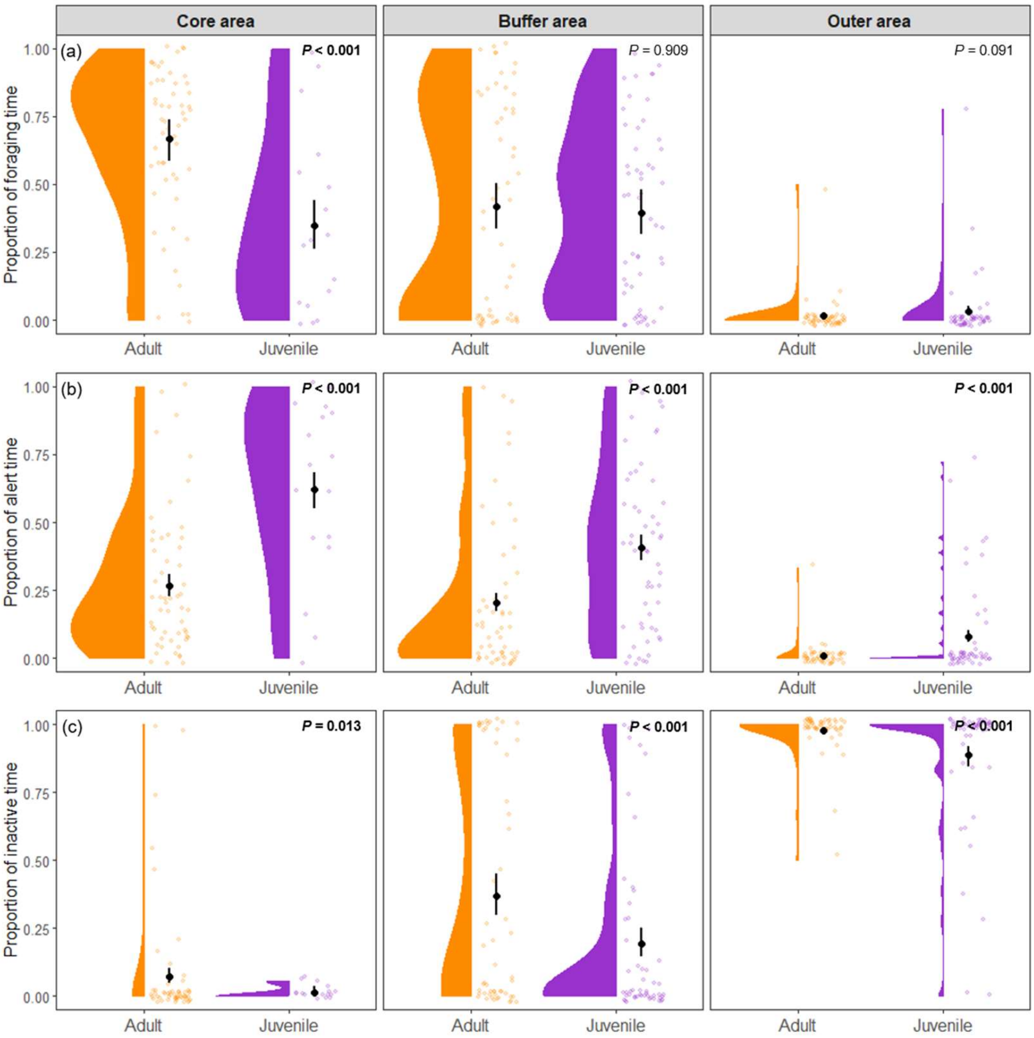

Figure 2.4 - Predicted values and 95% confidence intervals of the estimates from the GLMMs explaining the influence of age (adult or juvenile) and landfill area (core, buffer or outer area) in determining (a)

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 pre-migratory period. Orange and purple areas represent the density distribution of behaviour time budgets for adult and juvenile birds, respectively. Dots represent raw individual data.

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; Figure 2.5).

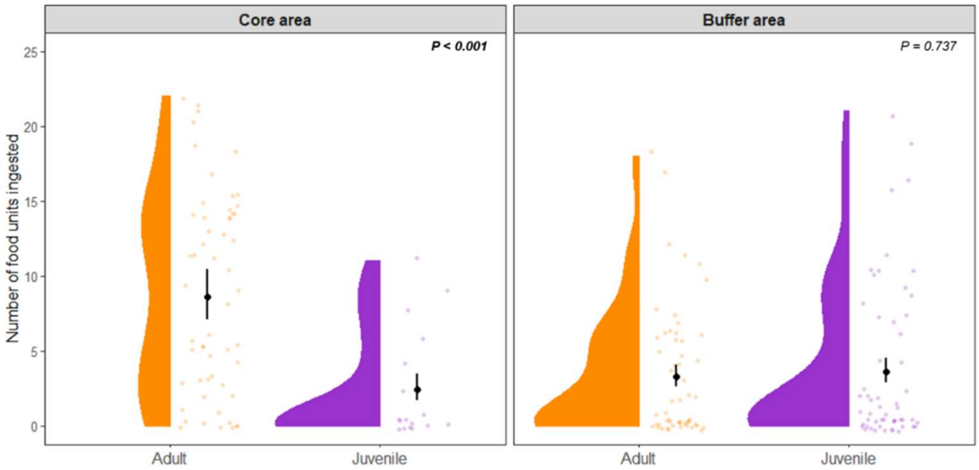

Figure 2.5 - Predicted values and 95% confidence intervals of the estimates from the GLMMs explaining the influence of age (adult or juvenile) and landfill area (core or buffer area) in determining food intake (*N* = 55 adults per landfill area; *N* = 17 and 55 juveniles per landfill area) of white storks using landfills during the pre-migratory period. Orange and purple areas represent the density distribution of food intake for adult and juvenile birds, respectively. Dots represent raw individual data.

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 (Figure 2.6).

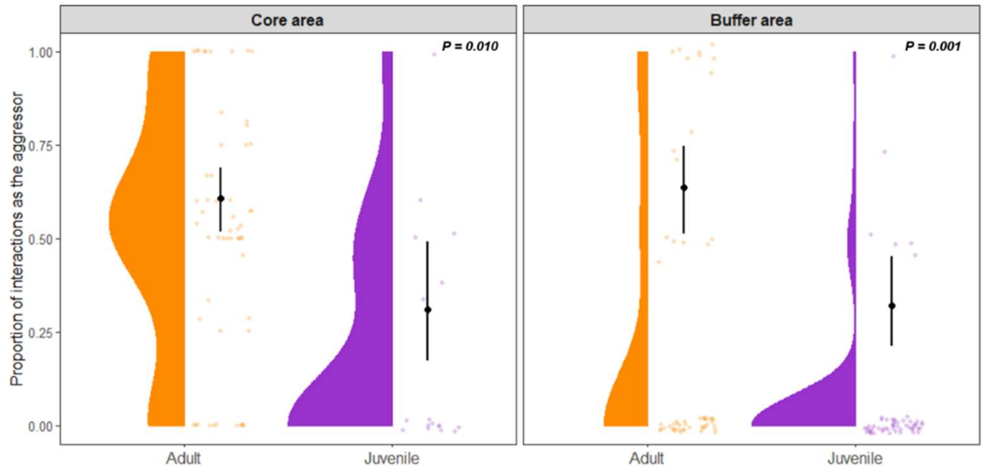

Figure 2.6 - Predicted values and 95% confidence intervals of the estimates from the GLMMs explaining the influence of age (adult or juvenile) and landfill area (core or buffer area) in determining aggressiveness (*N* = 55 adults per landfill area; *N* = 17 and 55 juveniles per landfill area) of white storks using landfills during the pre-migratory period. Orange and purple areas represent the density distribution of dominance for adult and juvenile birds, respectively. Dots represent raw individual data.

2.4 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 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 pre-migratory 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 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 pre-migratory 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 pseudo-replication influencing the estimates. Still, both adult and juvenile stork estimates exhibited comparable levels of variability, indicating that the eventual impact of pseudo-replication 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 non-breeding 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 pre-migratory 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 non-migratory 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 carry-over 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), 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.

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Chapter 2 Supplementary Materials

Figure S2.1 - Total number of adult and juvenile white storks counted monthly at the five landfills in southern Portugal

Figure S2.2 - Monthly average estimate of the number of adult and juvenile white storks per landfill area at the five landfills in southern Portugal

Figure S2.3 - Monthly average estimate of the proportion of adult and juvenile white storks foraging per landfill at the five landfills in southern Portugal

Table S2.1 - Ethogram of white stork behaviours and corresponding time budget categories

Table S2.2 - Results of post hoc Tukey tests to assess foraging proficiency differences between landfill areas

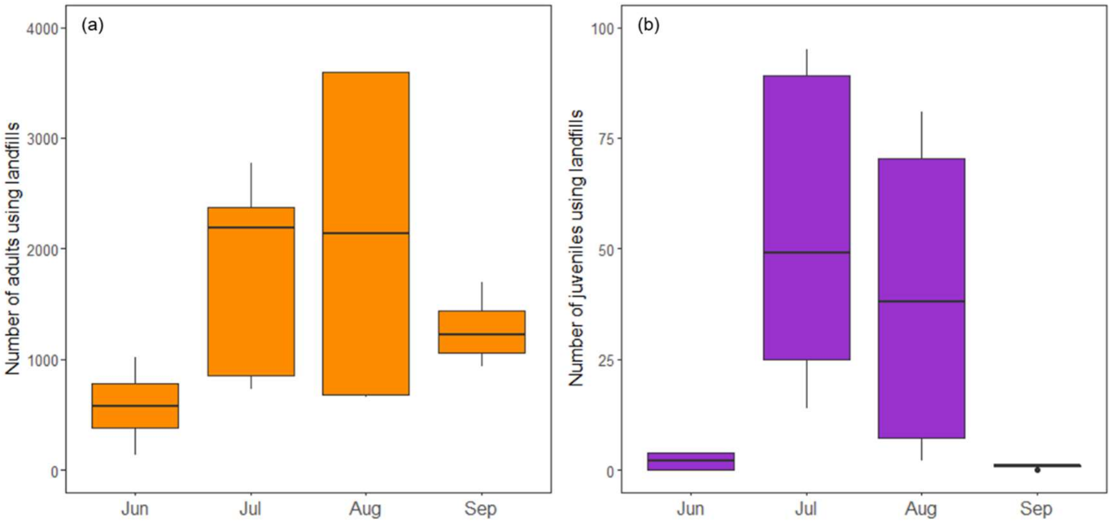

Figure S2.1 - Total number of (a) adult and (b) juvenile white storks counted monthly at the five landfills in southern Portugal during the 2020 pre-migratory period (June to September). Middle, lower and upper hinges of the box plots correspond to the median, 25th and 75th percentiles, respectively. Whiskers correspond to the 95% confidence intervals and the dots is an outlier.

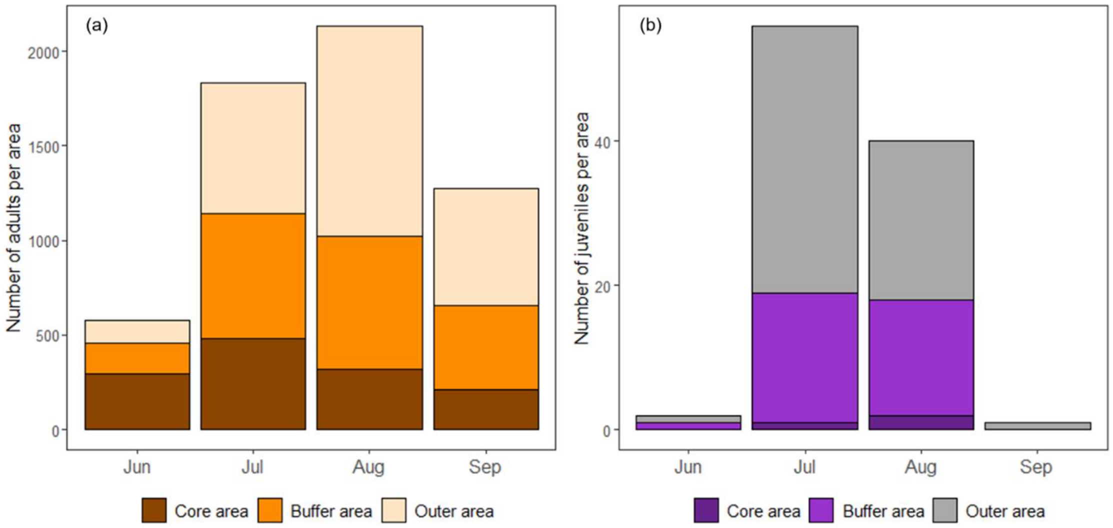

Figure S2.2 - Monthly average estimate of the number of (a) adult and (b) juvenile white storks per landfill area (core, buffer and outer area) at the five landfills in southern Portugal during the 2020 pre-migratory period (June to September).

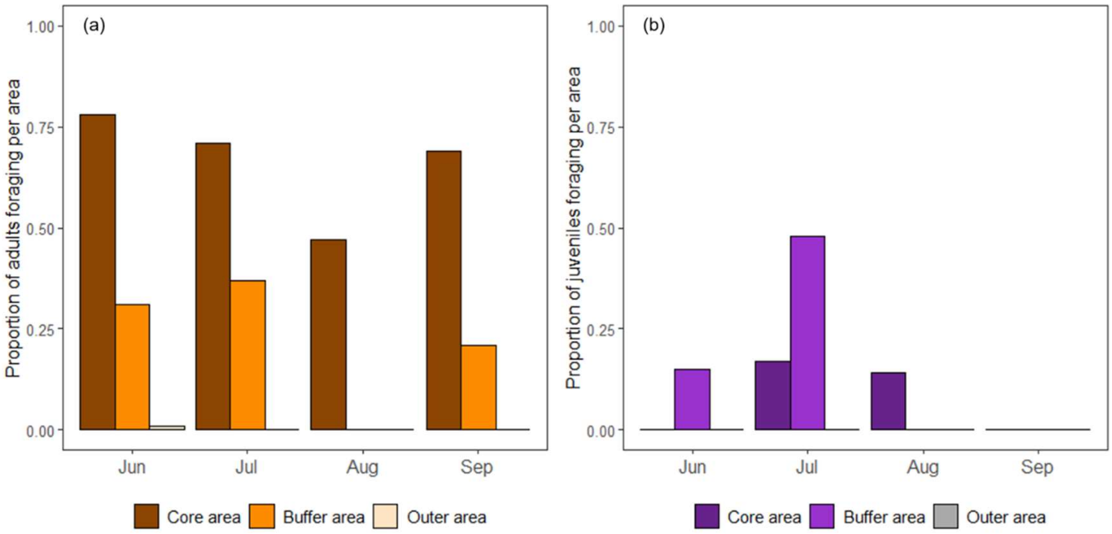

Figure S2.3 - Monthly average estimate of the proportion of (a) adult and (b) juvenile white storks foraging per landfill area (core, buffer and outer area) at the five landfills in southern Portugal during the 2020 pre-migratory period (June to September).

Table S2.1 - 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 S2.2 - 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**
	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.

Chapter 3

Landfill use is driven by individual age-related improvements in the foraging behaviour of a long-lived bird species

Landfill use is driven by individual age-related improvements in the foraging behaviour of a long-lived bird species

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Abstract

Early life is a critical period for most animals, during which the development of foraging behaviour can have important ecological and evolutionary implications. Although it is known that foraging ability in long-lived species is higher in adulthood, the ontogeny of foraging behaviour is still unclear. This study uses long-term GPS tracking data from over 200 white storks (*Ciconia ciconia*), a long-lived opportunistic bird species, to investigate how foraging on landfill resources evolves with age and whether differential landfill use is driven by selective survival or ontogenic development. Our findings reveal that landfills are soon used as foraging sites during exploratory behaviour in early life. However, age-related disparities in landfill use emerge, with storks from their second year onwards being more than half as likely to visit landfills daily and spending considerably more time there than storks in their first year. Additionally, older storks are gradually more likely to access landfill areas with higher food availability, spending more time foraging in those areas and reducing energy expenditure. In this process, there is no evidence of selective survival favouring fledglings with a higher propensity for foraging at landfills. Instead, the rapid acquisition and refinement of the ability to exploit these resources occur as individuals mature, resulting in improved foraging performance when using landfills in adulthood. Therefore, landfill food waste can shape the foraging behaviour of species from an early age, influencing individual life decisions over time and potentially impacting population dynamics.

3.1 Introduction

The first years of life are critical for most animals, especially for long-lived species (Daunt et al., 2007; Lindström, 1999; Orgeret et al., 2016; Sæther et al., 2013). Juveniles typically experience higher mortality than adults, directly influencing age structure, population dynamics, and the persistence of individual traits (Charlesworth, 1994; Stearns, 1992). Higher juvenile mortality is often attributed to their limited ability to find and acquire enough food to survive (Marchetti & Price, 1989; Wunderle, 1991), primarily due to their inexperience and/or physical immaturity (Daunt et al., 2007; Fayet et al., 2015; Le Vaillant et al., 2012; Zimmer et al., 2011). These age-related disparities may result in experienced adults outcompeting young individuals for optimal foraging sites (Kaufmann, 1983; Marchetti & Price, 1989; Wunderle, 1991), potentially leading to the selective survival of individuals more likely to develop specific foraging skills (Daunt et al., 2007; Orgeret et al., 2016). Such findings align with a gradual ontogenetic shift in feeding ecology and behaviour (Carravieri et al., 2017; Grecian et al., 2018; Votier et al., 2017). Nevertheless, the ontogeny of foraging behaviour remains largely unclear.

During the first years of life, inexperienced individuals generally develop their movement strategies, refine foraging behaviours, and enhance their overall movement and foraging performance (Penteriani et al., 2015; Riotte-Lambert & Weimerskirch, 2013; Sergio et al., 2014; Yoda et al., 2004). As a result, juveniles often exhibit greater individual variation in space use compared to their older conspecifics, who possess better knowledge about the spatial distribution of resources (De Grissac et al., 2016; Sergio et al., 2014; Votier et al., 2017; Wakefield et al., 2015). Moreover, recent evidence is increasingly revealing patterns in several long-lived seabirds that are consistent with an "exploration-refinement" foraging mechanism as they age (Baert et al., 2022; Campioni et al., 2020; Guilford et al., 2011; Wakefield et al., 2015). Therefore, the development of foraging behaviour is likely determined by inherent individual abilities and by learning and experience acquired in the first years of life. Still, it remains unknown whether changes in foraging behaviour occur gradually or abruptly and whether they are driven by the selective survival of the best performers, improvements within individuals, or a combination of both.

In recent decades, human activities have been changing the distribution of food resources by consistently generating and disposing large quantities of food waste worldwide, thereby providing new foraging opportunities for wildlife (Ellis et al., 2010; Oro et al., 2013; Parfitt et al., 2010). Among these predictable anthropogenic food subsidies, the disposal of organic waste in landfills has emerged as one of the main resources used by many species (Oro et al., 2013; Plaza & Lambertucci, 2017). Landfill sites are increasingly attracting and gathering larger numbers of individuals, especially bird species like storks, gulls, kites and vultures (Blanco, 1994; Langley et al., 2021; Martins et al., 2024; Tauler-Ametller et al., 2017). However, this heightened exploitation of food waste carries now a significant potential for increasing human-wildlife conflicts, the transmission of pathogens and diseases, and the transfer of contaminants to natural habitats (Plaza & Lambertucci, 2017).

Landfills, by providing highly valuable food sources that are renewed daily and consistently deposited in the same locations (Oro et al., 2013; Plaza & Lambertucci, 2017; Thyberg & Tonjes, 2016), enable species to shorten their foraging time and energy expenditure (Soriano-Redondo et al., 2021; van Donk et al., 2019). This, in turn, leads to changes in the movements, behaviours, and geographical ranges of species (Gilbert et al., 2016; Marcelino et al., 2023; Patenaude-Monette et al., 2014; Plaza & Lambertucci, 2017), intensifying intraspecific competition mediated by density-dependent processes within the restricted areas of landfill sites (Araújo et al., 2011). Consequently, this can result in diminished food acquisition and the exclusion of less proficient individuals, with detrimental costs for individual fitness (Araújo et al., 2011; Martins et al., 2024). However, foraging on landfill resources is increasingly associated with enhanced fitness, survival, and the abundance of several opportunistic species (Newsome et al., 2015; Oro et al., 2013; Plaza & Lambertucci, 2017; Weiser & Powell, 2010). Nonetheless, it remains unknown how these species adapt and shift their behaviour over their lifetimes, transitioning from foraging across a wide range of natural food sources to efficiently exploiting landfill resources.

In this study, we used long-term GPS tracking data from white storks (*Ciconia ciconia*), an opportunistic species that heavily relies on landfill resources (Martins et al., 2024; Soriano-Redondo et al., 2021), to investigate the ontogeny of a relatively recent foraging behaviour. The Iberian white stork population has substantially increased in recent decades, taking advantage of the new anthropogenic resources available at landfill sites (Molina & Del Moral, 2006; Rosa et al., 2005). This population is now partially migratory, with a growing number of mature individuals remaining in the breeding areas during the winter, likely due to the year-round abundance of food resources accessible at landfills (Catry et al., 2017; Gilbert et al., 2016; Soriano-Redondo et al., 2023; Tortosa et al., 2002). Even so, the vast majority of juveniles continue to migrate (Acácio et al., 2022; Bécares et al., 2019; Martins et al., 2024). Since white storks are long-lived social birds that reach maturity in their third year of life, early learning may play an important role in the acquisition of their foraging skills (Bocheński & Jerzak, 2006; Elliott et al., 2020). With adult storks exhibiting more proficient use of landfill resources compared to juveniles, often holding a dominant behaviour and having increased access to optimal landfill foraging areas (Martins et al., 2024), it is now essential to explore and understand the developmental process of this foraging behaviour.

To understand the ontogeny of foraging behaviour on landfill resources, we used a 6-year GPS tracking dataset with tri-axial acceleration, which allowed us to determine the behaviour and energy expenditure of the storks. Specifically, we investigated (i) age-related changes in landfill use, that is, how the storks´ ability to attend landfill sites and access their optimal foraging areas, as well as how foraging time and energy spent foraging within these areas vary with age, and (ii) whether age-related changes are driven by individual selective survival and/or individual development. This work provides a mechanistic understanding of how age can shape foraging behaviour and individual foraging performance in the exploitation of new anthropogenic food sources, while also unravelling the ability of species to respond to intense ongoing changes in food availability.

3.2 Methods

Study system and GPS deployment

Fieldwork was conducted in southern Portugal, covering the entire area where the latest census identified approximately 7,000 white stork breeding pairs, which represented around 60% of the total population in this country (Encarnação, 2015). Additionally, in this region, landfill resources are highly accessible year-round at five different sites spread across the area. In total, 71 adults and 147 first-year juveniles were GPS-tagged and tracked between 2016 and 2021. Adults were captured and tagged at landfill sites using leg loop traps or at their nests using a remotely activated clap net trap. Each year, adults were 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 were promptly returned afterwards. All individuals were tagged with GPS/GSM loggers 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 90g, representing 1.1-3.7% of the bird´s body mass. Loggers were programmed to transmit a GPS location every 20 minutes, along with a tri-axial acceleration burst of 9 consecutive GPS locations at 1 Hz. These acceleration bursts provided data for assessing bird behaviour and calculating overall dynamic body acceleration (ODBA, g), which serves as a proxy for energy expenditure (Gleiss et al., 2011; Shepard et al., 2008). To determine bird behaviour, a random forest machine-learning algorithm specific for each tag type was trained to identify foraging, resting and flight behaviours from manually classified and validated tri-axial acceleration data (Soriano-Redondo et al., 2021). ODBA was calculated by subtracting each acceleration point from a running mean of 4 seconds for each axis and summing the resulting values across all three axes (Soriano-Redondo et al., 2021). All fledging juveniles were classified as first-year birds, and thereafter, age was determined based on the 12-month interval between Junes of successive years. All mature adults of unknown age were classified as birds at least in their fourth year or older.

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.

GPS tracking data

This study focused on the period between June and September, during which large numbers of storks of different ages gather at landfill sites for foraging as the breeding season ends (Martins et al., 2024). In this partially migratory population, storks are either remaining close to their breeding areas and exploiting landfill resources (residents), which is now common among adults, or using these sites as stopovers while migrating to wintering grounds in Africa (Arizaga et al., 2018; Marcelino et al., 2023; Martins et al., 2024). Landfills are mainly available in Europe and Northern Africa (Morocco) and are not used beyond the Atlas Mountains (Marcelino et al., 2023), thus all GPS locations south of this ecological barrier were discarded (Figure 3.1). The study period always started on the 1st of June (the earliest fledging date), except for first-year juveniles that started on their fledging dates (when individuals moved more than 50 meters away from their nests, Martins et al. 2024). Then, it ended either on the day birds died or the device stopped transmitting, on the day birds crossed the Atlas Mountains, or on the last day of September for birds that did not migrate beyond the Atlas Mountains. Only storks that were tracked for a minimum of 10 days in a given year and that moved beyond the closest landfill to their nest were included.

Classification of landfill areas

All landfill sites visited by the tracked storks were identified through a visual inspection of GPS data. To specifically focus on GPS locations indicative of potential foraging site selection, those at nests or in flight were excluded. The remaining ground locations were then categorized as either inside or outside a landfill. Following Martins et al. 2024, the "core area" at each landfill was defined as the range within a 25-meter radius around the location where organic waste was discarded (dump site). This optimal foraging area is characterized by a high concentration of fresh waste and increased resource availability, where adult storks regularly access and exploit food more efficiently than juveniles (Martins et al., 2024). Therefore, the GPS dataset of adult birds within the landfills was used to determine dump sites over the years and establish core areas. Initially, only the GPS locations at the five landfills in southern Portugal were considered, as monthly visits were conducted there over several years and the dump sites were accurately identified in the field. For all adult birds at each of these landfills, their monthly centroids were estimated based on the 25% kernel of at least 50 foraging GPS locations, and they consistently overlapped with the precise locations of known dump sites. Thus, whenever landfills were not directly visited, dump sites were identified only if one or more adults had used that landfill in a given month, and were determined as the centroids of all their foraging GPS locations pooled together. Monthly core areas were then defined around these centroids, and each GPS location of all tracked storks within the corresponding landfills was categorized as either inside or outside a core area.

GPS data analysis

Age-related changes in the ability to attend landfill sites were investigated by comparing the daily and overall landfill attendance between storks in their first, second, and third years, as well as storks from their fourth year onwards combined with adults of unknown age (hereafter age classes). For each individual in a given year, daily landfill attendance was determined as the proportion of days with at least one GPS location at a landfill site and overall landfill attendance as the proportion of all GPS locations in landfills (Martins et al., 2024). Afterwards, age-related changes in the ability to access optimal foraging areas (core areas) were investigated by comparing the core area attendance between age classes. Considering only the subset of data within landfills where core areas were defined, core area attendance was determined for each individual in a given year as the proportion of GPS locations in those areas (Martins et al., 2024). Furthermore, age-related changes in foraging performance at landfill sites were also investigated by comparing the foraging time and foraging energy expenditure in core areas between age classes. Again, the same subset of data was considered, and for each individual in a given year, foraging time in core areas was determined as the proportion of foraging GPS locations in core areas, while foraging energy expenditure was determined as the mean foraging ODBA value calculated from the foraging GPS locations in core areas.

The role of individual selective survival as a driver of landfill use was investigated by assessing whether the ability of first-year juveniles to exploit these resources was related to their survival outcomes. Each juvenile tracked up to the second year was classified as a "survivor". Conversely, individuals were classified as “dead” whenever the GPS device transmitted locations without movement or activity, and the bird carcass was later recovered.

In cases where the data suggested potential mortality due to the abrupt loss of transmission, but death was not confirmed, individuals were classified as “undetermined”.

The role of individual development was investigated by assessing whether juvenile storks with multiple years of landfill use improved their ability to exploit these resources within the first two years. Additionally, it was also investigated whether storks tracked over the years further improved their ability to use landfill resources as they aged and matured.

Statistical analysis

Age-related changes in landfill use were investigated through five generalised linear mixed-effects models (GLMMs), using the ´glmer´ function in the ´lme4´ R package (Bates et al., 2015). The first four models included daily landfill attendance (individual proportion of days visiting landfills), overall landfill attendance (individual proportion of GPS locations in landfills), core area attendance (individual proportion of GPS locations in core areas), and foraging time in core areas (individual proportion of foraging GPS locations in core areas) as response variables with a binomial structure. The last model included foraging energy expenditure in core areas (individual mean foraging ODBA in core areas) as the response variable with a gaussian response. All models included age classes as a factor (storks in their 1st, 2nd, 3rd or 4th year onwards) as the explanatory variable. Bird ID and calendar year were included as random effects. We further performed post hoc Tukey tests to assess differences between age classes, using the ´emmeans´ package (Searle et al., 1980).

To explore evidence of selective survival as a driver of landfill use and understand whether the juvenile storks that were more likely to exploit landfill resources during their first year survived longer, we fitted five GLMMs. The models included the five previously used metrics with the same response structures and in all models, survival (survivor, dead or undetermined) was specified as the explanatory variable and calendar year as a random effect.

To explore evidence of individual development as a driver of landfill use and understand whether juvenile storks improved their ability to use landfill resources within their first two years, we again fitted five GLMMs with the same metrics. In parallel, to understand whether juveniles tracked over the years further improved their ability to exploit these resources, we fitted five more GLMMs. Stork age was specified as a continuous explanatory variable in all models, with its quadratic term included to account for potential non-linear relationships for the later five models. Bird ID and calendar year were set as random effects in all models. Additionally, landfill use metrics calculated for adults of unknown age over the years were also included in these figures as a reference group.

3.3 Results

Between 2016 and 2021, we collected GPS data from 79 adult and 147 juvenile white storks tracked for up to six years. From their first year of life, all GPS-tracked storks used 45 different landfills across the Iberian Peninsula and northern Morocco until they crossed the Atlas Mountains while migrating to their wintering grounds in sub-Saharan Africa (Figure 3.1). The dataset of all first-year juveniles included 8,427 tracking days (mean 57 ± 28 days per individual). Afterwards, there was a sharp decline in the number of tracked individuals due to juvenile mortality or devices no longer transmitting. From their second to sixth years, our dataset included 2,533 (88 ± 30, n = 29), 1,137 (114 ± 14, n = 10), 457 (114 ± 16, n = 4), 366 (122 ± 0, n = 3), and 244 (122 ± 0, n = 2) tracking days, respectively. The dataset of all adult storks (≥4 years) included 19,272 tracking days (mean 112 ± 21 days per stork year).

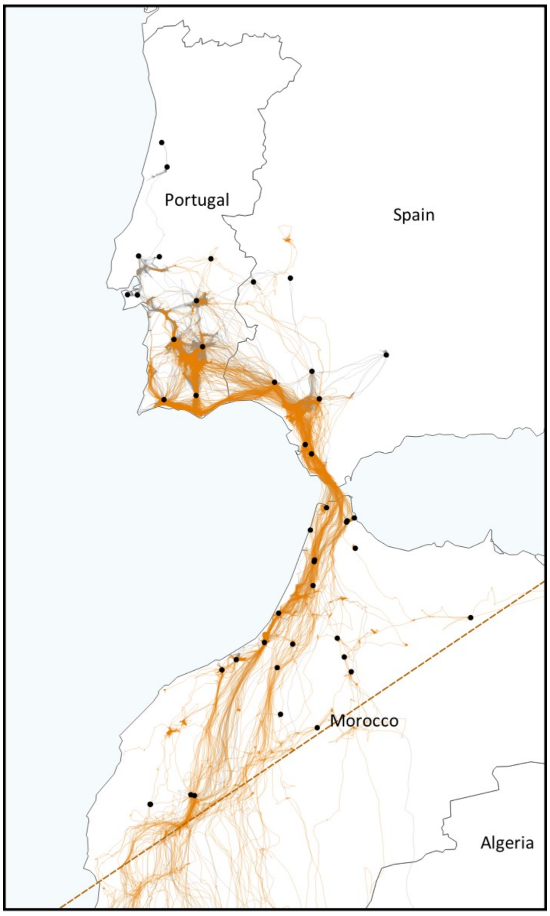

Figure 3.1 - Routes and landfills used by GPS-tracked juvenile (orange tracks) and adult (grey tracks) white storks over the years in the Iberian Peninsula and northern Morocco. The black dots represent the landfill sites. The brown dashed line, following the Atlas Mountains, indicates the southern limit latitude for including GPS data in the analysis.

Age-related changes in landfill use

Significant age-related differences in landfill use were found between first-year juveniles and all subsequent age classes (Table 3.1). Second-year storks were more than half as likely to attend landfills daily compared to first-year juveniles (predicted values ± SE; 1st year storks = 0.39 ± 0.11; 2nd year storks = 0.61 ± 0.12; P = < 0.001; Figure 3.2a), and this likelihood was equally high in the older age classes (Table S3.1). Additionally, the proportion of GPS locations in landfills was significantly higher for second-year storks compared to first-year juveniles (1st year storks = 0.19 ± 0.07; 2nd year storks = 0.22 ± 0.08; P = < 0.001; Figure 3.2b), and it was consistently elevated in older age classes (Table S3.1). Within landfills, core area attendance was generally low, yet there was a gradual age-related increase (Table S3.1), with older storks being twice as likely to attend these areas compared to first-year juveniles (1st year storks = 0.07 ± 0.02; 4th year or older storks = 0.14 ± 0.05; P = < 0.001; Figure 3.2c). Similarly, there was a gradual increase across all age classes in the proportion of time foraging in core areas (Table S3.1), with older storks spending more than half as much time foraging in these areas as first-year juveniles (1st year storks = 0.12 ± 0.04; 4th year or older storks = 0.28 ± 0.07; P = < 0.001; Figure 3.2d). Lastly, foraging energy expenditure in core areas was significantly lower for second-year storks compared to first-year juveniles (1st year storks = 0.17 ± 0.01; 2nd year storks = 0.15 ± 0.02; P = < 0.001; Figure 3.2e), and it was consistently lower across older age classes as well (Table S3.1).

Table 3.1 - Parameters of GLMMs explaining differences in landfill use between age classes of GPS-tracked white storks.

GLMM response	Explanatory variable	Estimate	SE	*df*	*z/t*	*P*
Daily landfill attendance	Intercept	-0.466	0.115		-4.039	**< 0.001**
	Year 2	0.918	0.072		12.733	**< 0.001**
	Year 3	0.824	0.096		8.567	**< 0.001**
	Year ≥ 4	1.176	0.108		10.928	**< 0.001**
Overall landfill attendance	Intercept	-1.482	0.113		-13.17	**< 0.001**
	Year 2	0.241	0.014		16.84	**< 0.001**
	Year 3	0.205	0.018		11.14	**< 0.001**
	Year ≥ 4	0.240	0.024		10.15	**< 0.001**
Core area attendance	Intercept	-2.583	0.089		-29.144	**< 0.001**
	Year 2	0.520	0.047		11.110	**< 0.001**
	Year 3	0.394	0.055		7.144	**< 0.001**
	Year ≥ 4	0.805	0.060		13.424	**< 0.001**
Foraging time in core areas	Intercept	-2.000	0.082		-24.276	**< 0.001**
	Year 2	0.557	0.066		8.394	**< 0.001**
	Year 3	0.333	0.074		4.496	**< 0.001**
	Year ≥ 4	1.069	0.079		13.524	**< 0.001**
Foraging energy expenditure in core areas	Intercept	0.174	0.003	92.517	51.722	**< 0.001**
	Year 2	-0.020	0.005	166.413	-3.879	**< 0.001**
	Year 3	-0.018	0.006	129.745	-3.110	**0.002**
	Year ≥ 4	-0.015	0.004	189.083	-3.936	**< 0.001**

The reference level for age classes is 'Year 1'. Significant *P* values are shown in bold.

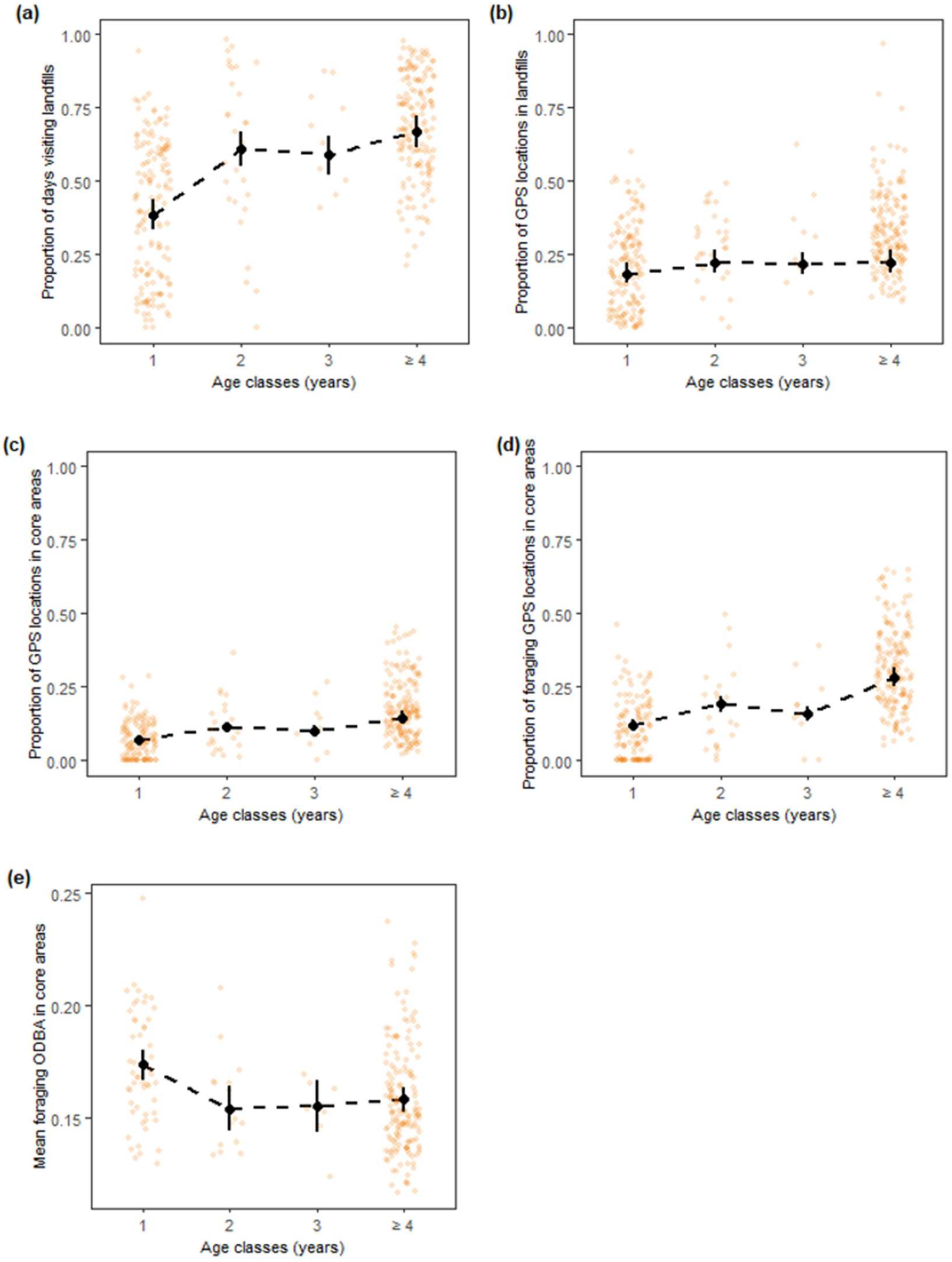

Figure 3.2 - Predicted values and 95% confidence intervals of the GLMMs estimates explaining age-related differences in (a) daily and (b) overall landfill attendance; and differences within landfills in (c) core area attendance, (d) foraging time, and (e) foraging energy expenditure in core areas for GPS-tracked white storks. Orange dots represent raw individual data.

Mechanisms driving landfill use changes

There were no differences found in landfill use among first-year juveniles related to their survival outcomes (Table 3.2). Both storks that survived up to the second year and those with confirmed or undetermined mortality were equally likely to visit landfills daily (predicted values ± SE; survivor = 0.43 ± 0.18; dead = 0.38 ± 0.14; p = 0.261; undetermined = 0.39 ± 0.13; p = 0.429; Figure 3.3a). Additionally, they exhibited similar proportions of GPS locations in landfills (survivor = 0.22 ± 0.12; dead = 0.15 ± 0.08; p = 0.313; undetermined = 0.20 ± 0.09; p = 0.562; Figure 3.3b). Even within landfills, they were just as likely to access the core areas (survivor = 0.08 ± 0.05; dead = 0.07 ± 0.04; p = 0.467; undetermined = 0.09 ± 0.04; p = 0.486; Figure 3.3c), spend the same period of time there foraging (survivor = 0.14 ± 0.09; dead = 0.12 ± 0.06; p = 0.368; undetermined = 0.11 ± 0.18; p = 0.873; Figure 3.3d), and expend identical amounts of energy foraging in these areas (survivor = 0.18 ± 0.03; dead = 0.17 ± 0.03; p = 0.914; undetermined = 0.17 ± 0.02; p = 0.452; Figure 3.3e).

Table 3.2 - Parameters of GLMMs explaining differences in landfill use among GPS-tracked juvenile white storks with distinct survival outcomes in their first year.

GLM Response	Explanatory variable	Estimate	SE	*df*	*z/t*	*P*
Daily landfill attendance	Intercept	-0.263	0.192		-1.369	0.171
	Dead	-0.247	0.220		-1.125	0.261
	Undetermined	-0.168	0.212		-0.790	0.429
Overall landfill attendance	Intercept	-1.262	0.179		-7.051	**< 0.001**
	Dead	-0.205	0.203		-1.008	0.313
	Undetermined	-0.115	0.198		-0.580	0.562
Core area attendance	Intercept	-2.445	0.170		-14.353	**< 0.001**
	Dead	-0.150	0.206		-0.727	0.467
	Undetermined	0.132	0.190		0.696	0.486
Foraging time in core areas	Intercept	-1.821	0.172		-10.550	**< 0.001**
	Dead	-0.193	0.215		-0.900	0.368
	Undetermined	0.031	0.195		0.160	0.873
Foraging energy expenditure in core areas	Intercept	0.176	0.007	49.000	24.746	**< 0.001**
	Dead	-0.001	0.010	49.000	-0.109	0.914
	Undetermined	-0.007	0.009	49.000	-0.758	0.452

The reference level for survival is ‘Survivor’. Significant *P* values are shown in bold.

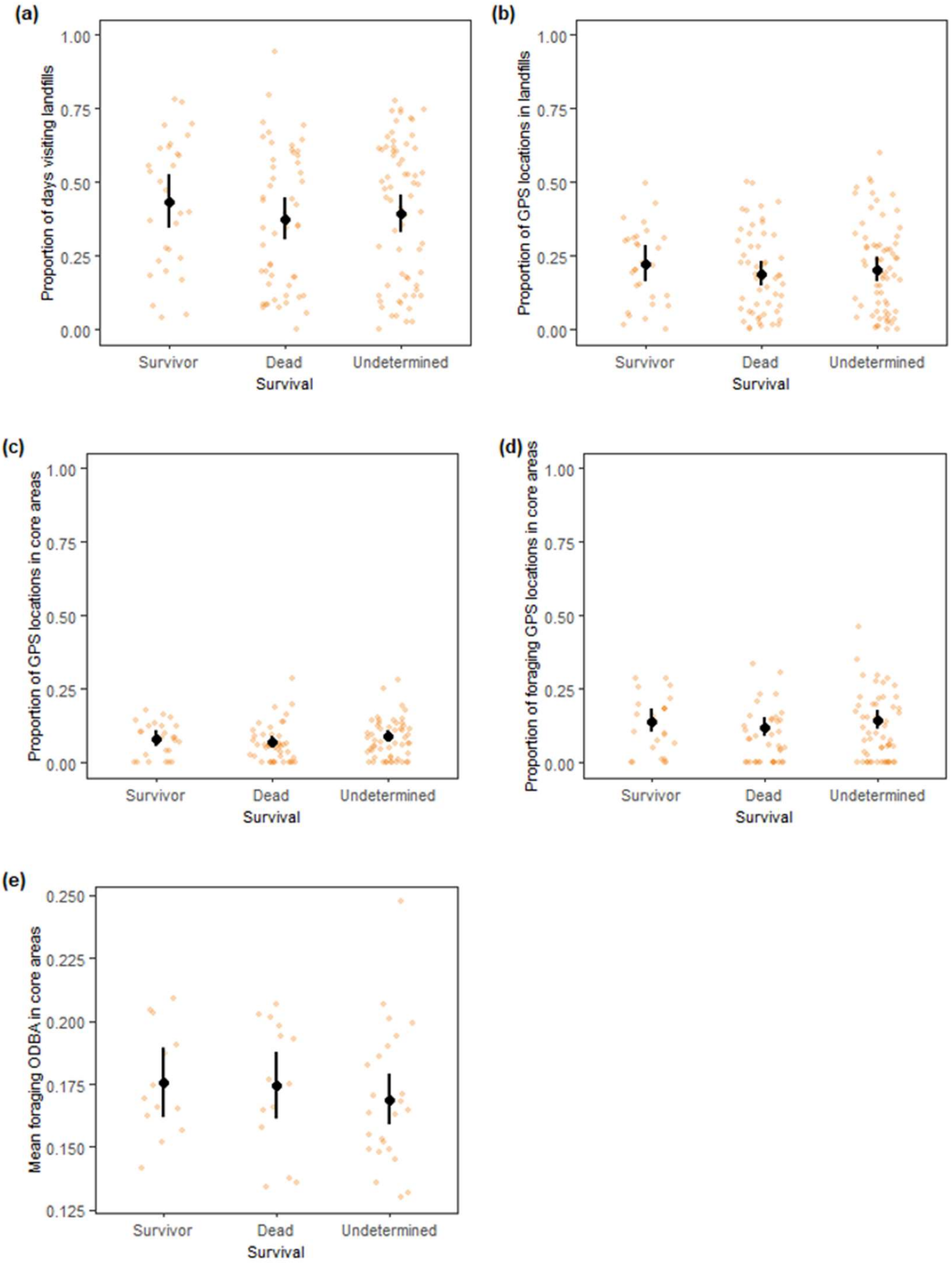

Figure 3.3 - Predicted values and 95% confidence intervals of the GLMMs estimates explaining age-related differences in (a) daily and (b) overall landfill attendance; and differences within landfills in (c) core area attendance, (d) foraging time, and (e) foraging energy expenditure in core areas among GPS-tracked juvenile white storks with distinct survival outcomes in their first year. Orange dots represent raw individual data.

When considering only juvenile storks tracked over multiple years, significant age-related developments in landfill use were observed, not only from the first to the second years but also over subsequent years as they aged and matured (Table 3.3). Storks rapidly became more than half as likely to attend landfills daily from the first to second years (predicted values ± SE; 1st year = 0.40 ± 0.20; 2nd year = 0.62 ± 0.18; $p = < 0.001$; Figure 3.4a), with this upward trend persisting over the years and resulting in almost twice the attendance from the fourth year onwards (1st year = 0.45 ± 0.17; 4th year = 0.70 ± 0.17; $p = < 0.001$; Figure 3.4a). Furthermore, the proportion of GPS locations in landfills increased by almost half from the first to second years (1st year = 0.19 ± 0.10; 2nd year = 0.27 ± 0.12; $p = < 0.001$; Figure 3.4b), and this trend continued to be evident up to the fourth year as well (1st year = 0.21 ± 0.09; 4th year = 0.30 ± 0.13; $p = < 0.001$; Figure 3.4b). Within landfills, storks were substantially more likely to attend core areas in the second year compared to the first (1st year = 0.07 ± 0.06; 2nd year = 0.10 ± 0.08; $p = < 0.001$; Figure 3.4c), with this increasing trend evident over the years and almost doubling by the sixth year (1st year = 0.08 ± 0.07; 6th year = 0.15 ± 0.14; $p = 0.002$; Figure 3.4c). Similarly, the proportion of time foraging in core areas increased significantly from the first to second years (1st year = 0.12 ± 0.10; 2nd year = 0.18 ± 0.13; $p = < 0.001$; Figure 3.4d), and this increase was once again clear over the years, surpassing twice the initial duration by the sixth year (1st year = 0.14 ± 0.10; 6th year = 0.32 ± 0.22; $p = < 0.001$; Figure 3.4d). Finally, foraging energy expenditure in core areas decreased significantly from the first to second years (1st year = 0.18 ± 0.03; 2nd year = 0.15 ± 0.03; $p = 0.002$; Figure 3.4e), and this downward trend persisted over the years until stabilising at a level consistent with the average reference value for adult storks of unknown age.

Table 3.3 - Parameters of GLMMs explaining differences in landfill use of GPS-tracked juvenile white storks within their first two years and over the years as they age and mature.

GLMM Response	Explanatory variable	Estimate	SE	*df*	*z/t*	*P*
Daily landfill attendance	Intercept	-0.414	0.210		-1.971	**0.049**
(in the first two years)	Age	0.921	0.092		9.972	**< 0.001**
Daily landfill attendance	Intercept	-0.184	0.170		-1.080	0.280
(over the years)	Age	0.564	0.067		8.437	**< 0.001**
	Age^2	-0.076	0.015		-5.227	**< 0.001**
Overall landfill attendance	Intercept	-1.420	0.160		-8.856	**< 0.001**
(in the first two years)	Age	0.404	0.048		8.423	**< 0.001**
Overall landfill attendance	Intercept	-1.326	0.140		-9.454	**< 0.001**
(over the years)	Age	0.349	0.035		9.853	**< 0.001**
	Age^2	-0.061	0.003		-23.764	**< 0.001**
Core area attendance	Intercept	-2.568	0.237		-10.815	**< 0.001**
(in the first two years)	Age	0.370	0.074		5.008	**< 0.001**
Core area attendance	Intercept	-2.450	0.218		-11.263	**< 0.001**
(over the years)	Age	0.031	0.054		0.585	0.559
	Age^2	0.022	0.007		3.042	**0.002**
Foraging time in core areas	Intercept	-1.965	0.224		-8.776	**< 0.001**
(in the first two years)	Age	0.470	0.092		5.112	**< 0.001**
Foraging time in core areas	Intercept	-1.855	0.208		-8.904	**< 0.001**
(over the years)	Age	0.028	0.057		0.497	0.619
	Age^2	0.039	0.010		3.950	**< 0.001**
Foraging energy expenditure in core areas	Intercept	0.177	0.009	7.123	20.054	**< 0.001**
(in the first two years)	Age	-0.031	0.008	13.175	-3.916	**0.002**
Energy expenditure in core areas	Intercept	0.175	0.007	8.282	26.770	**< 0.001**
(over the years)	Age	-0.022	0.005	33.206	-3.938	**< 0.001**
	Age^2	0.003	0.001	31.548	2.947	**0.006**

Significant *P* values are shown in bold.

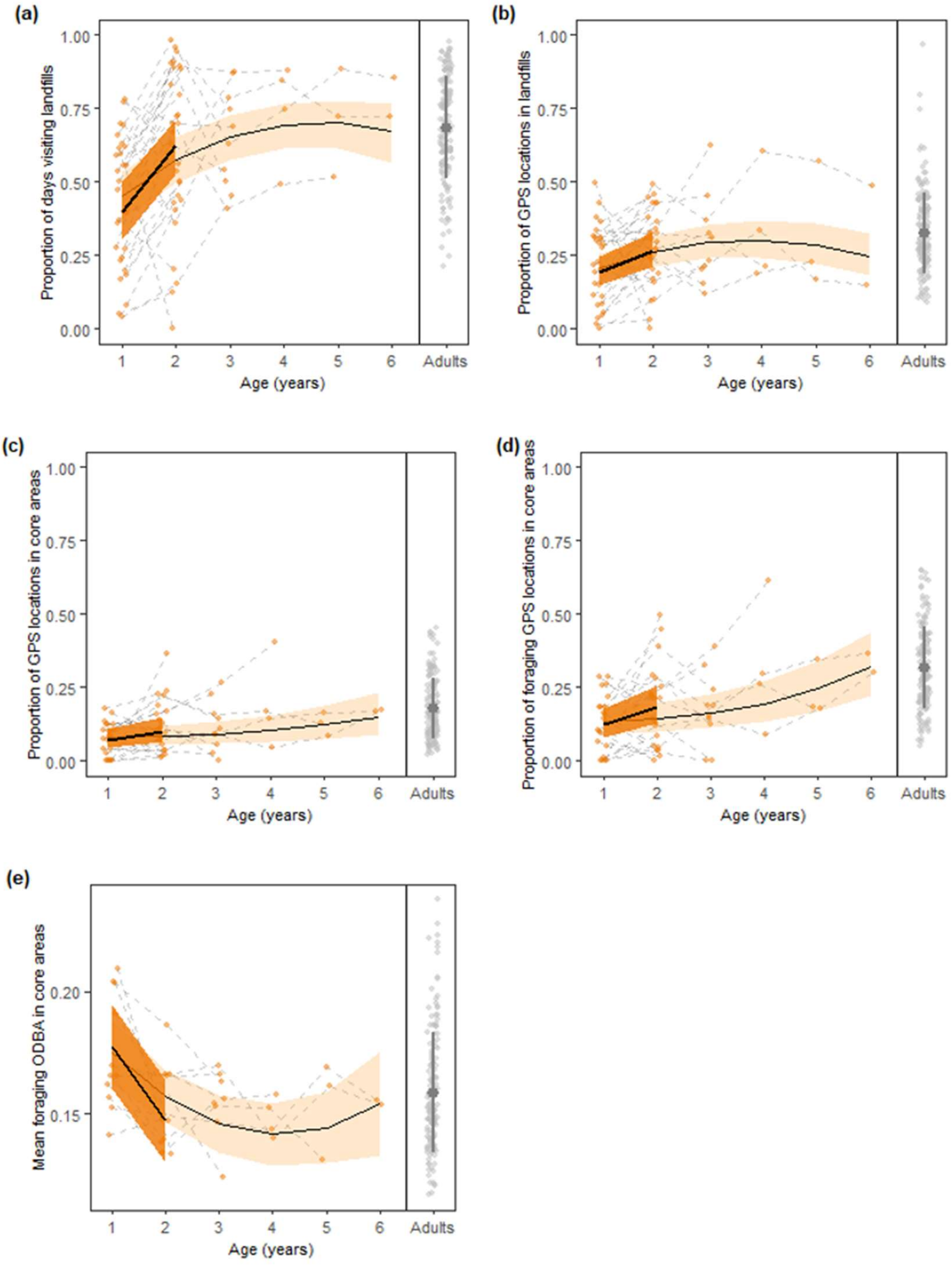

Figure 3.4 - Predicted values and 95% confidence intervals of the GLMMs estimates explaining age-related differences in (a) daily and (b) overall landfill attendance; and differences within landfills in (c) core area attendance, (d) foraging time, and (e) foraging energy expenditure in core areas of GPS-tracked juvenile white storks within their first two years and over the years as they age and mature. Orange and grey dots represent raw data of juvenile and adults, respectively. The mean and standard deviation for adults are shown as reference values.

3.4 Discussion

Using GPS tracking data from a long-lived opportunistic bird species, this study provides evidence that landfill use is closely tied to age and suggests that the development of this foraging behaviour is primarily driven by individual developments during the early life stages rather than selective survival. From their second years onwards, white storks visited landfill sites more often and extended the time spent there compared to their first years. Additionally, they were gradually more likely to access the landfill core areas, which are characterized by higher food availability, and exhibited an overall enhancement in foraging performance. While no evidence was found to support the selective survival of individuals with a higher propensity to exploit landfill food waste during their first year of life, individual development, likely resulting from learning and experience, emerged as a significant driver for the increased ability of storks to exploit these resources. This trend persisted over the six years in which the tracked storks matured and gained experience. These findings further support the hypothesis that foraging behaviour and foraging site specialization in long-lived species are linked to an exploration-refinement process.

From an early age, white storks started visiting and exploring landfill sites, showing similar patterns of foraging site selection to those of adults, as is expected of species that rely on social information and behavioural cues from experienced individuals (Galef & Giraldeau, 2001; Marchetti & Price, 1989; Mendez et al., 2017). Even during their first migratory journeys, most individuals used landfills as main stopover sites, confirming that juveniles soon identify landfills as profitable food sources and that their migratory behaviours are early shaped by these resources (Marcelino et al., 2023). However, landfill use was considerably lower than that of adult birds, consistent with what was known for the pre-migratory period (Martins et al., 2024). Thus, despite the abundance of food at landfills, intraspecific competition at these sites may promote a complex foraging hierarchy in the population dominance structure, in which age and physical maturity are usually critical attributes (Kaufmann, 1983; Tibbetts et al., 2022). Ultimately, as juveniles can be outcompeted by mature birds (Martins et al., 2024), this may be an additional factor leading to the migration of most young individuals to sub-Saharan Africa.

We show clear age-related differences in landfill use between first-year storks and all other following age classes. Storks from their second year onwards were more than half as likely to visit landfill sites daily compared to first-year storks (rising from 39% of the days in first-year storks up to 67% at older ages), and they were also significantly more likely to spend their time at landfills (increasing from 19% up to 22% of the total GPS locations in landfills). This rapid increase in landfill use, mostly occurring within the first two years of life, suggests that this stage is crucial for the development of fidelity to landfills as the main foraging sites. Within landfills, storks from older age classes were gradually more likely to access landfill resources in core areas, along with spending more time foraging in these areas. Furthermore, storks from their second year onwards expended less energy foraging compared to first-year storks. These findings indicate a progressive improvement in access to resources and foraging performance at landfill sites, supporting the idea that foraging skills are acquired slowly with age.

Individual selective survival did not prove to be a significant driver of changes in landfill use, as juveniles with higher landfill attendance or better performance at these sites were not associated with enhanced survival. First-year survival is generally low, primarily due to the underdevelopment of foraging and migration skills resulting from immaturity and inexperience (Marchetti & Price, 1989; Newton, 2008; Wunderle, 1991). However, heightened mortality during this life stage may be strongly influenced by stochastic events throughout early life development, initial exploratory behaviours, and migration (Daunt et al., 2007; Lindström, 1999; Sæther et al., 2013). Therefore, these different challenges may mitigate the potential significance of individual variability in early foraging skills for divergent mortality outcomes. Some implications of such challenges are indeed known to pose a particular survival risk for inexperienced juveniles facing their first long and risky journeys soon after fledging (Rotics et al., 2016, 2021). Moreover, the increased exploitation of landfill resources may be leading to shifts in migratory strategies from early life to adulthood, thereby further enhancing the survival of older birds as the suppression of long journeys diminishes annual displacement and lowers energy and fitness costs (Flack et al., 2016; Soriano-Redondo et al., 2023). In fact, wintering in Europe and relying more on these anthropogenic resources is proving to be less demanding compared to the challenges faced in sub-Saharan Africa, potentially improving the survival of juveniles (Rotics et al., 2017).

Nevertheless, individual development seems to play a key role as a driver of changes in landfill use and of proficient foraging behaviour at these sites. There were substantial increases in landfill attendance, access to their resources, and foraging performance at landfill sites among individuals tracked for at least the first two years. Trends towards more pronounced increases were also evident among all birds tracked up to six years. These findings support the exploration-refinement foraging hypothesis while also unravelling the developmental process suggested in other long-lived species (Grecian et al., 2018; Votier et al., 2017; Wakefield et al., 2015), which has even been proposed to explain inter-individual differences in migratory behaviour (Baert et al., 2022; Campioni et al., 2020; Guilford et al., 2011; Sergio et al., 2014). Hence, profitable foraging sites are identified early during exploratory behaviours, and foraging behaviour is shaped by the acquisition and improvement of the ability to exploit and compete for resources as individuals mature. This process is further refined throughout life. Moreover, the early development of efficient foraging behaviour may be a consequence of the need to locate and obtain enough food for self-maintenance and breeding, as it typically determines the age of first reproduction in many long-lived species (Forslund & Pärt, 1995; Krüger, 2005).

Our study reveals that the use of landfill resources in a long-lived opportunistic bird species increases rapidly early in life. This foraging behaviour becomes later refined as individuals age and mature, enabling them to efficiently exploit these resources in adulthood. These findings highlight the vulnerability of species relying heavily on landfill food waste, anticipating significant challenges due to the expected substantial reduction of these resources under European Union directives (1999/31/UE and 2018/850/UE). Consequently, such species will need to undergo a drastic shift in their foraging behaviour towards natural food sources. However, alternative foraging resources may be insufficient to support these populations in the future. As a result, we predict a potential increase in mortality due to the substantial reduction in benefits directly linked to the use of landfill resources. This, in turn, could result in a decrease in the current size of populations, making evident the profound impact of human activities on species behaviour and population dynamics.

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Chapter 3 Supplementary Materials

Table S3.1 - Results of post-hoc Tukey tests to assess differences between age classes

Table S3.1 - Results of post-hoc Tukey tests to assess differences between age classes.

GLMM Response	Contrasts	Estimate	SE	*z/t*	*P*
Daily landfill attendance	Year 1 – Year 2	-0.918	0.072	-12.733	**< 0.001**
	Year 1 – Year 3	-0.824	0.096	-8.567	**< 0.001**
	Year 1 – Year 4	-1.176	0.108	-10.928	**< 0.001**
	Year 2 – Year 3	0.094	0.092	1.021	0.737
	Year 2 – Year 4	-0.258	0.106	-2.439	0.070
	Year 3 – Year 4	-0.351	0.107	-3.276	**0.006**
Overall landfill attendance	Year 1 – Year 2	-0.241	0.014	-16.840	**< 0.001**
	Year 1 – Year 3	-0.205	0.018	-11.137	**< 0.001**
	Year 1 – Year 4	-0.240	0.024	-10.151	**< 0.001**
	Year 2 – Year 3	0.036	0.016	2.224	0.117
	Year 2 – Year 4	0.001	0.021	0.069	0.999
	Year 3 – Year 4	-0.035	0.020	-1.776	0.285
Core area attendance	Year 1 – Year 2	-0.520	0.047	-11.110	**< 0.001**
	Year 1 – Year 3	-0.394	0.055	-7.144	**< 0.001**
	Year 1 – Year 4	-0.805	0.060	-13.424	**< 0.001**
	Year 2 – Year 3	0.129	0.049	2.598	0.046
	Year 2 – Year 4	-0.285	0.052	-5.487	**< 0.001**
	Year 3 – Year 4	-0.411	0.053	-7.706	**< 0.001**
Foraging time in core areas	Year 1 – Year 2	-0.557	0.066	-8.394	**< 0.001**
	Year 1 – Year 3	-0.333	0.074	-4.496	**< 0.001**
	Year 1 – Year 4	-1.069	0.079	-13.524	**< 0.001**
	Year 2 – Year 3	0.224	0.068	3.297	**0.005**
	Year 2 – Year 4	-0.511	0.072	-7.122	**< 0.001**
	Year 3 – Year 4	-0.735	0.072	-10.250	**< 0.001**
Energy expenditure in core areas	Year 1 – Year 2	0.020	0.005	3.828	**0.001**
	Year 1 – Year 3	0.018	0.006	3.073	**0.014**
	Year 1 – Year 4	0.015	0.004	3.849	**< 0.001**
	Year 2 – Year 3	-0.001	0.006	-0.185	0.997
	Year 2 – Year 4	-0.004	0.005	-0.763	0.871
	Year 3 – Year 4	-0.003	0.006	-0.477	0.964

Significant *P* values are shown in bold.

Chapter 4

Nest distance to landfill resources shapes breeding performance and population dynamics in a long-lived opportunistic bird species

Nest distance to landfill resources shapes breeding performance and population dynamics in a long-lived opportunistic bird species

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Abstract

Intensification of human activities and widespread appropriation of primary productivity are leading to extensive degradation of natural resources and declines in wildlife populations. Simultaneously, these activities are generating large quantities of food waste, which becomes highly available to species that can adapt and benefit from these changes. Landfill sites are now among the most abundant and predictable anthropogenic food subsidies in the world, sustaining increasing numbers of opportunistic species and shifting their behaviour and demography. While many bird species incorporate landfill resources into their annual life cycle, the influence of proximity to these profitable food sources on individual breeding decisions, breeding success, and population demographics is still poorly understood. This was investigated for a long-lived opportunistic bird species, the white stork (*Ciconia ciconia*), using extensive breeding data collected over six years from hundreds of nests spread along a gradient of distance to landfill sites. Proximity to landfills was associated with earlier laying dates, and a gradual breeding delay was observed as distance increased. Although there was no further effect of proximity to landfills on subsequent breeding parameters, early laying resulted in positive cascading effects, including larger clutch sizes and increased numbers of fledglings. Proximity to landfills was also associated with enhanced fledgling fitness, with a gradual decrease in fledgling body condition noted as distance increased. Additionally, early laying dates resulted in improved fledgling fitness, regardless of nest location. The spatial-temporal analysis further revealed a significant shift in the abundance and distribution of white stork nests, characterized by a notable increase in areas near landfills, contrasting with a slight decrease in areas distant from landfill sites. This study provides evidence of a dynamic interaction between landfill resources, breeding success, and the abundance and distribution of white storks, thus helping to understand the influence of anthropogenic food sources on opportunistic bird species and guiding future conservation and management efforts.

4.1 Introduction

Food availability plays a crucial role in determining the demography and distribution of many bird species (Martin, 1987). Natural variations in resource availability provide vital cues for individuals to adjust their energy expenditure and breeding decisions, contributing to the selection of optimal nesting sites and determining the appropriate level of investment in offspring (Ruffino et al., 2014). Beyond these natural fluctuations, the ongoing intensification of human activities is leading to widespread habitat degradation and significant transformations in food availability. This, in turn, results in dramatic individual fitness losses, population declines or displacements, and, in some extreme cases, even species extinctions (Ceballos et al., 2017; Powers & Jetz, 2019; Venter et al., 2016).

Together with the depletion of natural resources resulting from primary productivity extractions, human activities are now generating new predictable anthropogenic food subsidies (PAFS), and many species are adapting and benefiting from these changes (Oro et al., 2013). Through the widespread daily disposal of large amounts of food waste, humans are actively reshaping the distribution and abundance of resources for wildlife, with estimates suggesting that around one-third of global food production is wasted every year (Parfitt et al., 2010). This waste mostly ends up being dumped in landfills around the world, making these sites one of the most important PAFS that influence population dynamics, food webs, and inter- and intra-species interactions (Oro et al., 2013; Plaza & Lambertucci, 2017). Hence, understanding the cascading effects of these new food sources is increasingly important.

Exploiting landfill resources enables wildlife to access valuable and reliable food supplies, reducing the energy costs usually associated with foraging on natural resources (Soriano-Redondo et al., 2021; van Donk et al., 2019). This results in several advantages for landfill scavengers at both individual and population levels (Oro et al., 2013; Plaza & Lambertucci, 2017), including significant enhancements in body condition and breeding success for species relying on these resources (Auman et al., 2008; Djerdali et al., 2016; Steigerwald et al., 2015; Tortosa et al., 2003). Access to landfill sites is particularly important during the breeding season, given the increased demands associated with nest construction, egg laying, and chick rearing, which require greater energy intake while constraining the daily movements of breeding birds (Bryant, 1988; Tinbergen & Dietz, 1994). Furthermore, a reduction in the time spent foraging provides breeders with more time to address the needs of their offspring (e.g., protection from predators or adverse weather conditions), thereby enhancing productivity and increasing offspring survival throughout the nestling period (Annett & Pierotti, 1999; Kilpi & Öst, 1998; Steigerwald et al., 2015).

Nesting site selection and timing of breeding are crucial factors influencing the breeding success and overall fitness of birds (Birkhead, 1977; Horn, 1968; Perrins, 1970). According to Optimal Foraging Theory (Schoener, 1971), the advantages of foraging in landfills during the breeding season should diminish as the distance from nests to landfill sites increases, yet the quality of the natural resources in the areas surrounding the nests may also be decisive for decision-making and breeding success (A. López-García et al., 2023; Orłowski et al., 2019; Sergio & Newton, 2003). Overall, birds with greater access to abundant and predictable food sources typically lay earlier, which often results in larger clutches, higher breeding success, and improved fledgling fitness (Robb et al., 2008; Tortosa et al., 2003). This, in turn, may eventually lead to higher survival rates in the post-fledging period (Rotics et al., 2021). Therefore, landfill sites are expected to promote the aggregation of breeding pairs towards their surroundings (Bialas et al., 2020; Alejandro López-García & Aguirre, 2023).

Here, we studied the consequences of using landfill resources on the breeding success, distribution and abundance of the white stork (*Ciconia ciconia*), a long-lived generalist and opportunistic bird species. In Iberian Peninsula, white stork populations have significantly increased in the last few decades, primarily supported by access to new anthropogenic resources available at landfill sites (Encarnação, 2015; Molina & Del Moral, 2006; Rosa et al., 2005). Currently, large numbers of storks regularly visit landfills throughout the year, as foraging on organic food waste from landfills is a time and energy saving strategy (Soriano-Redondo et al., 2021). Nevertheless, there appears to be an attendance gradient during the breeding season determined by the distance of nests to landfill sites (Soriano-Redondo et al., 2021). However, the influence of variations in the exploitation of these resources on individual breeding parameters, as well as on population abundance and distribution, remains poorly understood.

Unravelling the dynamics of species using landfill resources is crucial for effective conservation and management strategies. Therefore, our aim was to investigate the influence of nest distance to landfill resources on (i) breeding success, (ii) the body condition of fledglings, and (iii) the abundance and distribution of the white storks. We hypothesize that breeding pairs nesting closer to landfills lay earlier, experience higher breeding success, and produce fledglings in better body condition. Consequently, we also expect an increase in the number of nests in locations closer to landfill sites.

4.2 Methods

Study area and data collection

This study was conducted in southern Portugal, specifically targeting the region that supports the predominant white stork population in this country, which has experienced remarkable growth, rising from less than 2,000 breeding pairs in 1984 to around 12,000 by 2014 (Encarnação, 2015). This increase is mainly attributed to the use of landfill resources, allowing the white stork population to capitalize on the abundant resources available at the five landfill sites distributed throughout this region (Catry et al., 2017). Hence, the study area was defined within a buffer radius of 40 km from each of these landfills, resulting in an approximate area of 21,800 km^2 (Figure 4.1). All data was collected during the breeding seasons of six consecutive years (2018-2023), involving intensive monitoring of all nests at 54 different colony sites distributed along a distance gradient from the landfills (Figure 4.1). For each colony site, a central coordinate was assigned, and all occupied nests within a 200-meter radius of that location were considered. Distances to the centroids of the nearest landfills were then calculated from these locations. Due to frequent changes in nest occupancy and uncertainty in determining if breeding pairs occupy the same nests in multiple years, a unique identification was given to each surveyed nest annually. Nests were inspected at least once a week from February to March to confirm occupancy and determine laying dates. Regular visits were made from March to July to collect data on clutch size and the number of fledglings. Nest monitoring was performed using a camera attached to a pole or a drone. Additionally, for the entire subset of nests accessible by ladder, all fledglings around 45 to 55 days old were retrieved from the nests for wing measurement and weighing, and they were immediately returned afterwards. Furthermore, data was obtained on the location of all the nests recorded in the 2014 breeding census (Encarnação, 2015). The number of occupied nests at each colony site was then determined for both that year and 2020, as this was the year in which all the sites were also visited and the nests recorded during this study.

Ethics

Birds inspected for biometrics were handled for 5-10 minutes, strictly following ethical standards for animal practices as defined by the current European legislation (Directive 2010/63/EU; European Union 2010). All work, including animal manipulation, was approved by the relevant authority, the Institute for Nature Conservation and Forests (ICNF, Portugal), which provided the research permits (license numbers: 548-550/2018/CAPT; 247-250/2019/CAPT; 364-368/2020/CAPT; 198-202/2021/CAPT, 541-545/2022/CAPT, 505-509/2023/CAPT) during the study period.

Data analysis

The influence of nest distance to landfill sites on breeding success was investigated by comparing the laying date, clutch size, and number of fledglings along a distance gradient. The laying date was defined as the day the first egg of the clutch was laid, and nests where no laying occurred were not included in these analyses. Clutch size was given as the maximum number of eggs laid, and the number of fledglings was determined by counting live chicks that were at least 40 days old. The influence of nest distance to landfills on the body condition of fledglings was investigated by comparing their body condition index. Following Marcelino et al. 2023, this index was calculated as the standardized residuals of a linear model correlating wing length (mm) and weight (g). Moreover, the influence of distance to landfills on the spatio-temporal changes in the abundance and distribution of white stork nests was investigated by comparing the nest occupancy variation index. This index was calculated as the difference in the number of occupied nests recorded at each colony site between the 2014 breeding census and the 2020 count performed in this study. To address the challenge of independent colony sampling and account for potential nesting site selection effects, habitat information from the Corine Land Cover 2018 database was extracted for the entire study area. This approach allowed all the colony sites to be grouped based on latitude and habitat differences. Hence, all colony sites were first classified into three latitude classes (northern, central, and southern nests). The proportion of each land cover group within a 2km buffer around every colony site was then estimated. Lastly, they were all pooled together into ten different habitat groups whenever they exhibited similar cover distributions (Table S4.1).

Statistical analysis

All the analyses were performed by fitting generalised linear mixed-effects models (GLMMs), using the ‘glmer’ function in the ‘lme4’ R package (Bates et al., 2015). To determine the influence of nest distance to landfill sites on breeding success, we first fitted a model including the laying date as the response variable with a Gaussian error structure and nest distance to the landfill as the explanatory variable. We then fitted two models, including the clutch size with a Gaussian error structure and the number of fledglings with a Poisson error structure, as the response variables. The explanatory variables of both models included nest distance to the landfill, as well as the laying date and their interaction. To account for the annual stochastic effects of weather and variability in the quality of natural habitats around the nests, the three models were set with the breeding year and colony habitat group as random effects. To determine the influence of nest distance to landfills on the body condition of fledglings, we fitted a model including the fledglings body condition index as the response variable with a Gaussian error structure. Also here, nest distance to the landfill, the laying date, and their interaction were included as the explanatory variables. To take into consideration the annual climate effects as well as variations in the quality of the natural habitats around the nests along with differences between siblings, the breeding year and the nest ID within the colony habitat group were set as random effects. To determine the influence of distance to landfills on the abundance and distribution of nests, we fitted a model including the nest occupancy variation index as the response variable with a Gaussian error structure, and the nest distance to the landfill as the explanatory variable. The colony habitat group was set as a random effect to account for the variations in the quality of the habitats around the nests. For all response variables with multiple explanatory variables, the AIC and AIC weights of all models were compared (Burnham & Anderson, 2002), and those with the lowest AIC and highest AIC weight were selected. When the fit of the models was equally good (delta AIC <2), the most parsimonious model was selected, in which the interactions were dropped as they were not significant.

4.3 Results

Breeding data was collected annually from an average of 182 ± 80 nests per year (with confirmed laying), resulting in the survey of 1172 white stork nests during the study. Nests were distributed along a distance gradient of 1 to 40km to the landfill sites (Figure 4.1). Body condition data was collected from an average of 44 ± 31 fledglings per year, in a total of 222 fledglings from 155 nests over the study period. Overall, colony sites revealed a widespread preference for non-irrigated and permanently irrigated arable land, agroforestry areas with pastures and cork oak forests, and other agricultural areas (Table S4.1).

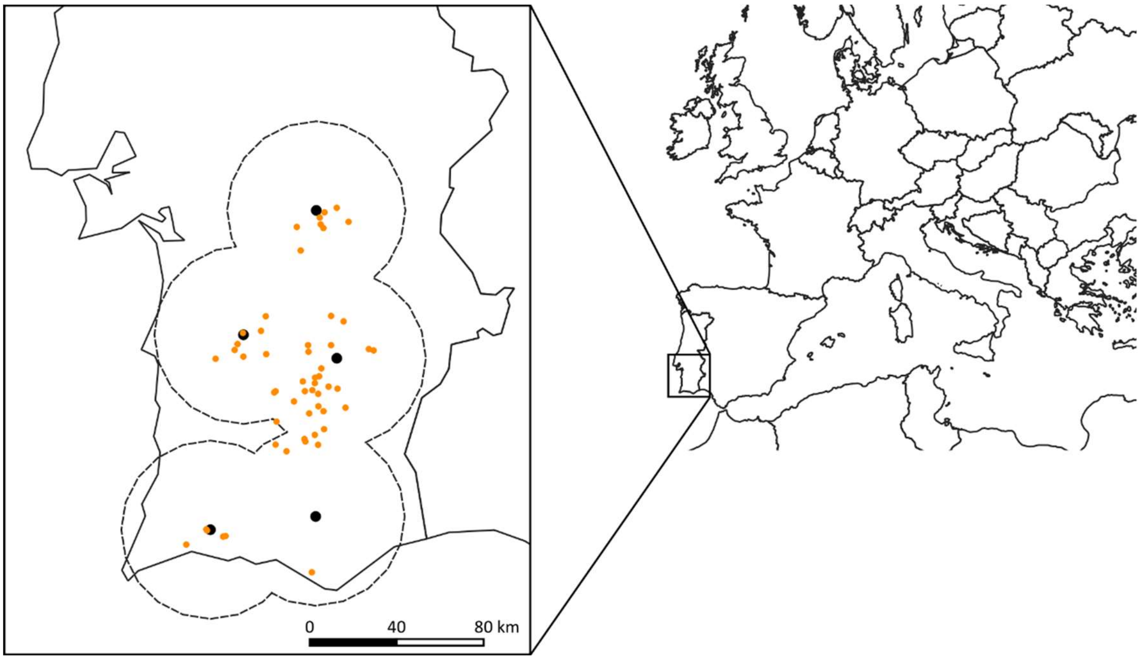

Figure 4.1 – Map of the study area in southern Portugal, including a 40 km buffer zone (dashed line) around the location of each landfill site (black dots) and the location of the white stork colony sites (orange dots).

Influence of nest distance to landfills on breeding success

Breeding parameters revealed that the average laying date was March 14th ± 10 days (ranging from February 18th to April 21th), the average clutch size was 4.18 ± 0.71 eggs (ranging from 3 to 6 eggs), and the average number of fledglings was 1.42 ± 1.12 (ranging from 0 to 4 fledglings). The laying date was highly influenced by the proximity of nests to landfill sites (Table 4.1). Breeding pairs nesting closer to landfills laid their eggs significantly earlier, around the beginning of March, while those nesting gradually further away exhibited a delay in their laying dates until around the end of March (Figure 4.2a). Clutch size and the number of fledglings were also influenced by the proximity of nests to landfill sites and by laying date (Table S4.2), but once accounting for laying date, there was no further significant influence of nest distance to landfills (Table 4.1). Breeding pairs laying their eggs earlier exhibited significantly larger clutch sizes, averaging around 5 eggs, while those laying later showed a gradual reduction in clutch sizes, dropping to only 3 eggs (Figure 4.2b). Similarly, breeding pairs laying earlier exhibited a significantly larger number of fledglings, averaging around 3 chicks, while those laying later experienced a gradual decrease in their average number of fledglings, dropping to less than 1 chick (Figure 4.2c).

Table 4.1 - Parameters of GLMMs explaining the influence of nest distance to landfill sites on breeding parameters.

GLMM response	Explanatory variable	Estimate	SE	*df*	*z/t*	*P*
Laying date	Intercept	67.779	1.698	17.729	39.928	**< 0.001**
	Nest distance to landfill	0.336	0.072	36.917	4.639	**< 0.001**
Clutch size	Intercept	6.144	0.168	182.905	36.56	**< 0.001**
	Nest distance to landfill	-0.005	0.004	14.300	-1.20	0.25
	Laying date	-0.026	0.002	993.761	-12.03	**< 0.001**
Number of fledglings	Intercept	2.031	0.200		10.151	**< 0.001**
	Nest distance to landfill	-0.002	0.003		-0.790	0.429
	Laying date	-0.023	0.003		-8.111	**< 0.001**

Significant *P* values are shown in bold.

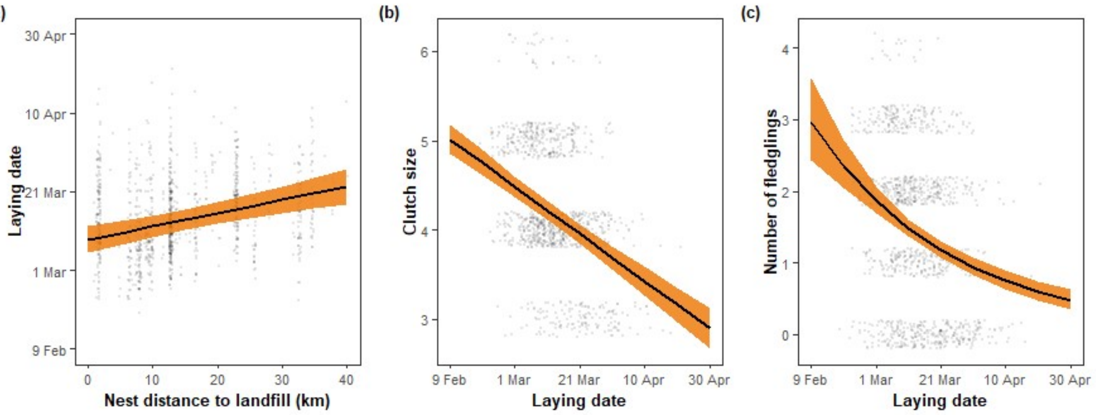

Figure 4.2 – Predicted values and 95% confidence intervals of GLMMs estimates explaining (a) differences related to the nest distance to landfills on the laying date, (b) differences related to the laying date on clutch size, and (c) differences related to the laying date on the number of fledglings.

Influence of nest distance to landfills on the body condition of fledglings

Fledglings presented an average wing length of 431 ± 43 mm (ranging from 340 to 523 mm), and an average weight of 3379 ± 463 g (ranging from 1975 to 4725 g). The body condition of fledglings was highly influenced by the proximity of nests to landfill sites and by laying date (Table 4.2; Table S4.3). Breeding pairs nesting closer to landfills had fledglings with significantly better body condition, while those nesting gradually further away showed a decrease in offspring fitness (Figure 4.3a). Furthermore, breeding pairs laying their eggs earlier produced fledglings with significantly better body condition compared to those laying later (Figure 4.3b).

Table 4.2 - Parameters of GLMMs explaining the influence of nest distance to landfill sites and of laying date on the body condition of fledglings.

GLMM response	Explanatory variable	Estimate	SE	*df*	*z/t*	*P*
Body condition index	Intercept	2.808	0.674	93.051	4.167	**< 0.001**
	Nest distance to landfill	-0.016	0.007	112.676	-2.258	**0.026**
	Laying date	-0.035	0.009	116.235	-3.767	**< 0.001**

Significant *P* values are shown in bold.

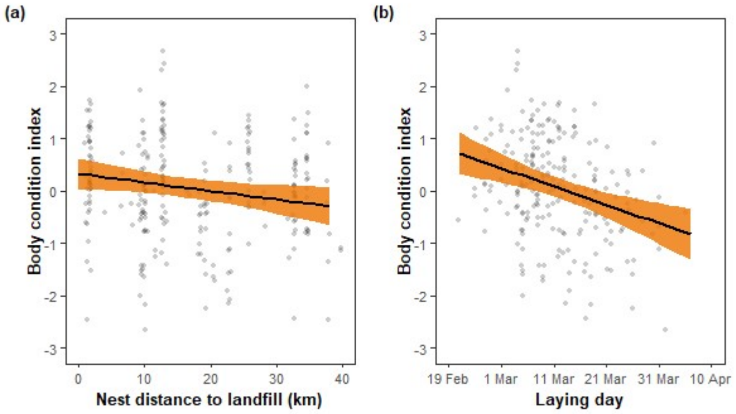

Figure 4.3 – Predicted values and 95% confidence intervals of GLMMs estimates explaining differences related to (a) the nest distance to landfill sites and (b) the laying date in the body condition index of fledglings.

Influence of nest distance to landfills on the abundance and distribution of nests

The variation in the number of nests recorded in 2014 and 2020 showed an average increase of 7 ± 12 nests per colony site (ranging from an increase of 42 up to a decrease of 12 nests). The abundance and distribution of nests were influenced by their proximity to landfill sites (Table 4.3). The number of breeding pairs nesting closer to landfills was significantly higher than those nesting gradually further away, with a pronounced increase in the number of nests at the colony sites closest to landfills and even a slight decrease in the number of nests at greater distances (Figure 4.4).

Table 4.3 - Parameters of GLMMs explaining the influence of distance to landfill sites on the abundance and distribution of nests.

GLMM response	Explanatory variable	Estimate	SE	*df*	*t*	*P*
Nest occupancy variation index	Intercept	19.953	2.954	10.574	6.754	**< 0.001**
	Nest distance to landfill	-0.715	0.147	8.891	-4.876	**< 0.001**

Significant *P* values are shown in bold.

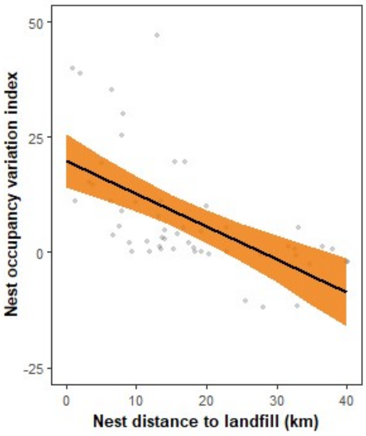

Figure 4.4 – Predicted values and 95% confidence intervals of GLMMs estimates explaining differences related to nest distance to landfill sites in the nest occupancy variation index.

4.4 DISCUSSION

Using extensive breeding data from a wide geographical area, this study shows a clear influence of the nest distance to landfill resources on the breeding performance and population demographics of the white stork, a long-lived opportunistic bird species. Proximity to landfill sites induced early laying dates, which were highly correlated with larger clutch sizes and a greater number of fledglings. Moreover, proximity to landfills played a crucial role in enhancing the body condition of fledglings. Notably, this proximity was also associated with an increasing number of nests and a population concentration around landfill sites over the years. Together, these findings reveal the rapid cascading effects resulting from the use of landfill resources on the breeding success and population dynamics of white storks. Simultaneously, these results suggest a scarcity of high-quality natural resources capable of surpassing the advantages provided by these new anthropogenic food sources.

The widespread selection of nesting sites on arable land, along with agroforestry and other agricultural areas observed in this study is consistent with previous studies reporting the habitat preferences of the white stork in southern Portugal in recent years (Encarnação, 2015). In Europe, this species was reported to prefer rural areas with pastures and cork oak agroforests, while avoiding agricultural fields, arable lands, and urban areas (Alonso et al., 1991; Carrascal et al., 1993; Alejandro López-García & Aguirre, 2023; Zurell et al., 2018), yet these preferences seem to have shifted in recent decades due to habitat degradation, with arable land now emerging as a potential alternative sub-optimal nesting area (Bialas et al., 2021; Alejandro López-García & Aguirre, 2023; Orłowski et al., 2019). The presence and use of landfill resources now disrupts natural habitat preferences, as these sites are recognized to ensure a stable food supply for many species, thereby reducing the proportion of high-quality foraging habitat required near nests (Evans & Gawlik, 2020; Oro et al., 2013; Tauler-Ametlller et al., 2019).

We present evidence of significant differences in laying dates influenced by the distance of nests to landfill sites. Breeding pairs nesting closer to landfills were more likely to lay their eggs in early March, with a gradual delay observed as the distance increased. However, neither clutch size nor the number of fledglings were directly influenced by the proximity of nests to landfills. Nonetheless, in both cases, the laying date proved to be a highly decisive factor for these breeding parameters. Although the effect of food abundance is often related to an earlier laying date, larger clutch size, and increased breeding success (Robb et al., 2008; Siikamäki, 1998; Tortosa et al., 2003), the primary consequence is likely to be in determining the laying date, subsequently triggering cascading effects on the other breeding parameters. This is particularly likely as individuals breeding earlier in the season generally produce larger clutches and experience greater productivity than later breeders (Daan et al., 1989; Perrins, 1970; Robb et al., 2008).

Despite no direct influence on productivity, nest distance to landfills had a significant effect on the body condition of fledglings, in addition to the effect of laying date. Fledglings from breeding pairs nesting closer to landfills had higher body condition, with a gradual decline in fledgling body condition noted as the distance to landfills increased. Additionally, regardless of nest location, early laying dates positively influenced fledgling body condition. Thus, landfills can probably shape the nesting site selection of breeding pairs, influencing the decision between having to maximise the delivery of natural prey to their offspring or reducing foraging effort by exploiting abundant food sources at these sites, a behaviour typical of birds with access to supplementary feeding (Robb et al., 2008). Birds may travel longer distances to exploit food waste at landfill sites, as these food sources reduce the energetic cost of foraging and enhance parental investment in nest attendance (Gilbert et al., 2016; Moritzi et al., 2001; Soriano-Redondo et al., 2021). Nevertheless, the distances covered by breeding birds are likely to determine how often offspring are fed and the nature of the food they acquire, thereby influencing their body condition (Pineda-Pampliega et al., 2021). Furthermore, the high correlation observed between the laying date and the body condition of the fledglings reinforces that the cascading effects of early laying can contribute not only to breeding success but also to the fitness of their offspring.

Finally, considerable changes were observed in the abundance and distribution of nests related to the proximity of landfill sites. In just six years, the number of breeding pairs and occupied nests increased by an average of 7 nests per colony site, with this growth being more substantial in areas closest to landfill sites, while at greater distances there was even a slight decline. This indicates a shift in the centres of abundance of white storks towards areas closer to landfill resources. These population changes have also been observed in other generalist and opportunistic species, such as gulls and vultures, attracted by the abundance and constant renewal of organic waste at landfills (Belant et al., 1993; Monsarrat et al., 2013; Tauler-Ametller et al., 2017). These anthropogenic food sources reduce species reliance on natural prey and the need to select high-quality habitats (A. López-García et al., 2023; Payo-Payo et al., 2015; Tauler-Ametller et al., 2017), thereby diminishing intraspecific competition and conflicts over food resources and nesting sites in natural areas (Corman et al., 2016; Restani et al., 2001). Therefore, the improved breeding success and higher fledgling fitness when nesting near landfills certainly contribute to population growth and an increasing demand for the areas surrounding these sites.

In summary, our findings provide strong evidence that proximity to landfill sites enhances productivity and offspring fitness in bird species capable of exploiting these resources. As a result, this facilitates the rapid increase of the breeding population, leading to an increased demand for nesting sites in areas closer to landfills. This highlights the potential for heightened human-wildlife conflicts, as well as a full range of evolutionary and ecological implications for wildlife associated with intensive landfill use (Oro et al., 2013; Plaza & Lambertucci, 2017). Despite these concerns, it is noteworthy that certain species are effectively capitalizing on the human redistribution of food resources during a time when many species are experiencing significant population decreases. After steep population declines until the 1980s, white stork numbers are now increasing across Europe (BirdLife International, 2016), and their ability to adapt to human-transformed landscapes and benefit from organic waste plays a crucial role in this recovery (Catry et al., 2017; Encarnação, 2015; Molina & Del Moral, 2006). With new European Union directives aimed at reducing the amount of organic food waste available at landfill sites (1999/31/UE and 2018/850/UE), there is likely to be a detrimental impact on white stork populations and several other species that rely on these resources. Therefore, to mitigate potential conflicts or population collapses, specific management measures are necessary to gradually reduce the availability of organic food waste at landfills or alternatively, allow access to moderate quantities of food waste while enhancing the quality of suitable habitats.

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Chapter 3 Supplementary Materials

Table S4.1 - Latitude classes, proportion of each land cover group within a 2km buffer around every colony site, and corresponding habitat groups.

Table S4.2 - Model selection to determine the influence of nest distance to landfill sites on clutch size and the number of fledglings.

Table S4.3 - Model selection to determine the influence of nest distance to landfill sites on the body condition index of fledglings.

Table S4.1 - Latitude classes, proportion of each land cover group within a 2km buffer around every colony site, and corresponding habitat groups.

Latitude	Land cover group %	Land cover group code	Land cover group description	Number of colony sites	Habitat group
Northern	60	211	Non-irrigated arable land	5	N1
	20	244	Agro-forestry areas		
	10	212	Permanently irrigated land		
	10	NA	Others		
	50	211	Non-irrigated arable land	3	N2
	20	221	Vineyards		
	20	223	Olive groves		
	10	NA	Others		
Central	50	212	Permanently irrigated land	5	C1
	25	244	Agro-forestry areas		
	15	211	Non-irrigated arable land		
	10	NA	Others		
	60	223	Olive groves	3	C2
	20	212	Permanently irrigated land		
	10	244	Agro-forestry areas		
	10	NA	Others		
	50	211	Non-irrigated arable land	7	C3
	30	223	Olive groves		
	15	212	Permanently irrigated land		
	5	NA	Others		
	80	211	Non-irrigated arable land	17	C4
	10	244	Agro-forestry areas		
	5	324	Transitional woodland-shrub		
	5	NA	Others		
	60	244	Agro-forestry areas	8	C5
	20	231	Pastures		
	10	211	Non-irrigated arable land		
	10	NA	Others		
Southern	40	323	Sclerophyllous vegetation	2	S1
	30	324	Transitional woodland-shrub		
	15	311	Broad-leaved forest		
	15	NA	Others		
	40	242	Complex cultivation patterns	3	S2
	30	222	Fruit trees and berry plantations		
	15	111	Continuous urban fabric		
	15	NA	Others		
	30	324	Transitional woodland-shrub	1	S3
	20	323	Sclerophyllous vegetation		
	20	243	Agricultural land with natural vegetation		
	30	NA	Others		

Table S4.2 - Model selection to determine the influence of nest distance to landfill sites on clutch size and the number of fledglings.

GLMM Response	GLMM Explanatory	AIC	Δ AIC	Weights
Clutch size				
Mcs 1	**Nest distance to landfill + Laying date**	**1991.2**	**0.0**	**0.658**
Mcs 2	Nest distance to landfill * Laying date	1992.5	1.3	0.342
Mcs 3	Nest distance to landfill	2174.0	182.8	< 0.001
Mcs 4	Null	2177.4	186.2	< 0.001
Number of fledglings				
Mnf 1	**Nest distance to landfill + Laying date**	**3204.6**	**0.0**	**0.648**
Mnf 2	Nest distance to landfill * Laying date	3205.8	1.2	0.352
Mnf 3	Nest distance to landfill	3269.5	64.9	< 0.001
Mnf 4	Null	3271.9	67.3	< 0.001

Significant values are shown in bold.

Table S4.3 - Model selection to determine the influence of nest distance to landfill sites on the body condition index of fledglings.

GLMM Response	GLMM Explanatory	AIC	Δ AIC	Weights
Body condition index				
Mbci 1	**Nest distance to landfill + Laying date**	**541.9**	**0.0**	**0.726**
Mbci 2	Nest distance to landfill * Laying date	543.9	2.0	0.270
Mbci 3	Nest distance to landfill	552.6	10.7	0.003
Mbci 4	Null	556.4	14.5	< 0.001

Significant values are shown in bold.

Chapter 5

General conclusions

5.1 Summary of main findings

The ecological consequences of anthropogenic activities on wildlife populations are increasingly recognised for their importance, with landfill resources standing out as notable examples of human-induced changes in food availability. However, it remains unclear how opportunistic species, such as the white stork, adapt and shift from consuming a wide range of natural food sources to exploiting human food waste at landfill sites.

In Chapter 2, I combined several fine-scale methods to explore differences in landfill use between juvenile and adult white storks. The study shows that age determines landfill attendance, access to food, and foraging proficiency at these sites. Adults visit landfills more often than juveniles and are found there in higher numbers. Adults are also more likely to access and feed in the best landfill areas, where resources are more abundant, while juveniles are displaced to the areas with lower food availability. Furthermore, adults achieve higher feeding success and exhibit dominance over juvenile individuals. These findings suggest that the disparity in landfill use between adults and juveniles is due to a lack of experience and foraging skills that likely develop with age, enabling storks to proficiently exploit landfill resources in adulthood.

In Chapter 3, I delved further into the ontogeny of landfill use by examining GPS data of white storks tracked over multiple years, from fledgling to adulthood. This study reveals that the foraging behaviour of storks is strongly associated with age. In the very first two years, there is a rapid increase in landfill attendance and in the total time spent at landfill sites. As storks get older, individuals show considerable improvements in their skills, increasing their ability to access landfill resources and their foraging performance at these sites. I did not find evidence supporting the selective survival of individuals with a higher propensity to exploit landfill food waste early in life, but I found that the acquisition and refinement of the ability to exploit these resources occurs as individuals age, resulting in a higher effectiveness when using landfill resources in adulthood. This trend is evident not only during the first two years but also as storks mature and gain experience over time. These findings support the hypothesis that foraging behaviour and foraging specialisation is driven by continuous learning and refinement, rather than an early selection of individuals with an inherent ability to exploit profitable food sources.

In Chapter 4, I used long-term breeding data of white storks across a broad geographic breeding area and showed that nest distance to landfill resources influences stork breeding performance and population demographics. Storks lay their eggs earlier when they are closer to landfill sites, and early laying is strongly associated with larger clutch sizes and a larger number of fledglings. Furthermore, fledglings from nests closer to landfills present better body condition, even when accounting for the effect of laying date. Notably, over just six years, the overall number of nests increased significantly, with this growth being more substantial in areas closest to landfills, while at greater distances there was even a slight decline. This indicates that population growth is directed towards landfill sites over time. Hence, my results highlight the cascading effects of the use of landfill resources on the breeding success and population dynamics of species increasingly relying on these food sources.

Overall, in this thesis, I provide important knowledge for understanding the development process of landfill use by white storks and its wider implications for population dynamics, which can be extrapolated to other opportunistic species.

5.2 Broader context of this PhD research

GPS tracking as a tool for animal ecology and conservation

Animal GPS tracking is revolutionising the fields of animal ecology and conservation by providing researchers with invaluable data on wildlife movement patterns, habitat use, and foraging behaviour (Katzner & Arlettaz, 2020). This information is especially important for understanding wildlife movement patterns and some of their specific behaviours, identifying critical habitats, and developing effective management measures to mitigate the impacts of human activities. Modern GPS tracking devices are increasingly lightweight and incorporated with sensors that allow large amounts of information to be recorded about the movements, behaviours, and energy expenditure of animals with high spatial-temporal resolution. They transmit globally and have a lifespan of several years, enabling new avenues of research in movement ecology and behavioural ecology, particularly by tracking an increasing number of individuals over multiple years. The value of this set of new tracking data is undeniable, but while many ecological studies are pointing out different conservation implications, only a small proportion of these studies are explicitly incorporated into government conservation and management assessments (Fraser et al., 2018). Nonetheless, a large part of government conservation planning documents relies on movement data, highlighting its importance for conservation (Fraser et al., 2018). Recent studies are using GPS tracking for applied conservation purposes, such as identifying potential sites for key biodiversity areas (Beal, et al., 2021), informing the design of protected areas (Choi et al., 2019), and quantifying political responsibility for the conservation of migratory species across countries (Beal, et al., 2021; Guilherme et al., 2023). Despite the increasing incorporation of movement data in studies, there are still large gaps in knowledge for which the importance of new studies using these technologies is evident (Chapter 2 and Chapter 3), especially in the face of rapid environmental changes.

The determinants of foraging behaviour

The development of foraging behaviour is influenced by several individual attributes primarily linked to life experience, the ability to obtain food, and physical maturation, which in turn are related to age (Marchetti & Price, 1989; Wunderle, 1991). Experience can be especially relevant when selecting foraging grounds, with adults often repeatedly and efficiently exploring the same areas based on learned, predictable habitat features (Votier et al., 2017; Wakefield et al., 2015). In young birds, specialised foraging skills on specific resources are likely acquired during individual exploratory behaviour early in life (Bolnick et al., 2003; Marchetti & Price, 1989;

Wunderle, 1991). The findings presented in Chapter 2 and Chapter 3 show that juveniles exhibit similar foraging site preferences to adults and can start using landfills shortly after fledging. This behaviour aligns with the expected pattern in birds that use social information and behavioural cues from older and more experienced individuals to identify and exploit profitable foraging sites (Franks & Thorogood, 2018; Marchetti & Price, 1989). Remarkably, the results from these chapters provide evidence that the widespread use of landfill resources and the subsequent aggregation of high densities of individuals at landfill sites promote changes in foraging dynamics, intensifying intraspecific competition for these food sources (Real et al., 2017), and establishing an age-determined hierarchy in the population dominance structure (Kaufmann, 1983; Tibbetts et al., 2022). These findings suggest that anthropogenic food subsidies can affect age classes differently, disproportionately favouring adults over juveniles. Consequently, this age-specific access to landfill resources may have enduring effects on population dynamics (Oro et al., 2013; Plaza & Lambertucci, 2017). As different species are increasingly responding to changes in food availability by seeking resources in landfills, these results suggest that this situation may be transversal to other species.

The ontogeny of foraging behaviour

The developmental period that long-lived birds undergo before reaching breeding maturity can be relatively long, lasting up to four years in white storks. During this maturation period, individuals might have distinct habitat preferences, along with differences in foraging and migratory behaviours (Baert et al., 2022; Guilford et al., 2011; Sergio et al., 2014). The first few years of life should allow these long-lived species to learn the main foraging sites, and subsequently, foraging behaviour and migratory decisions tend to become fixed with age and experience, although they can be refined whenever possible (Campioni et al., 2020; Grecian et al., 2018; Votier et al., 2017). However, this age-related variation has often been simplified into a dichotomous comparison between newborn juveniles and adults of unknown age.

Consequently, limited knowledge exists regarding whether these variations occur gradually or abruptly, and whether they result from improvements within individuals, selective survival of those with better performance, or a combination of both factors. In Chapter 3, the results reveal no evidence of selective survival favouring fledglings most likely to forage in landfills. Instead, individuals rapidly acquire and refine the ability to exploit these resources as they mature, resulting in enhanced foraging performance when using landfills in adulthood. These findings reveal fundamental information about the mechanisms driving the intensive use of landfill resources by white storks. Nonetheless, further research is required to ascertain whether these mechanisms are also applicable to other long-lived animals exploiting a range of food subsidies.

The cascading effects of landfill use on species

The ongoing supply of organic waste in landfills is currently a major attraction for several species (Plaza & Lambertucci, 2017). Animals may travel considerable distances and adjust their movement patterns to access these food sources (Gilbert et al., 2016; Marcelino et al., 2023; Soriano-Redondo et al., 2021; Spelt et al., 2021). Meanwhile, several opportunistic bird species, including vultures, gulls, and storks, have started nesting near landfill sites, taking advantage of the predictable food availability (Duhem et al., 2008; López-García & Aguirre, 2023; Monsarrat et al., 2013; Tauler-Ametller et al., 2017). Foraging at landfills is associated with larger clutches and egg sizes, as well as improved body condition of breeders and higher offspring survival rates (Djerdali et al., 2016; Pineda-Pampliega et al., 2021; Steigerwald et al., 2015; Tortosa et al., 2002). These factors collectively contribute to promoting population growth and a shift in species distribution. However, due to the lack of long-term data to evaluate the influence of landfills on individual breeding parameters and thus gain a deeper understanding of potential cascading effects on population dynamics, there is still much to learn about the trade-offs of exploiting landfill resources. To better understand the influence of anthropogenic food sources on opportunistic bird species and to inform future conservation efforts, Chapter 4 offers insightful information on the dynamic interaction between landfill resources, breeding success, and population dynamics of the white stork. The findings provide strong evidence that proximity to landfills is highly associated with earlier laying dates, leading to positive effects such as larger clutch sizes and increased numbers of offspring. Proximity to landfills is also associated with improved body condition of the fledglings. Therefore, landfill resources can facilitate an increase in the breeding population, with a higher demand for nesting sites near landfills. This highlights the need to investigate the main issues that may arise from these population increases to avoid serious human-wildlife conflicts and to address all possible evolutionary and ecological consequences for species associated with the intensive use of anthropogenic food subsidies.

Broader applicability of this PhD research

Although the assessment of the implications of the use of landfill resources in this thesis focused on white storks in the Iberian Peninsula, the approaches used and the results obtained are broadly applicable to other species and study systems. While there has been increased attention to the need to evaluate the effects of predictable anthropogenic food subsidies on wildlife (Oro et al., 2013), especially those available in landfill sites (Plaza & Lambertucci, 2017), this thesis provides pioneering insights into several research gaps. These include understanding key factors that influence age variability in landfill use, the mechanisms that drive changes in foraging behaviour at landfill sites, and the cascading effects on populations resulting from the intensive use of landfill resources. The methods employed in this thesis collectively contribute to a comprehensive understanding of the complex interactions between age-related foraging behaviour, individual learning, and population dynamics in a species reliant on landfill resources. Therefore, this thesis reveals significant ecological consequences of anthropogenic food subsidies, shedding light on the potential challenges associated with the benefits of landfill use by wildlife, and highlighting the need for proactive management strategies to balance the coexistence of human activities and wildlife populations in an evolving landscape.

5.3 Future studies and implications

Integrating GPS tracking data and behavioural data

Research on wildlife and ecosystems greatly benefits from integrating individual GPS tracking data with detailed behavioural information (Katzner & Arlettaz, 2020; Tomkiewicz et al., 2010). GPS tracking enables precise monitoring of individual movement and habitat use over time, while behavioural data make it possible to understand a range of activities, including foraging, breeding patterns, and interactions with the environment. Currently, the large number of precise locations transmitted, along with behavioural information assessed from data provided by GPS devices with tri-axial acceleration sensors, is already very detailed and reliable. This level of detail allows for fine-scale assessment of landfill use and foraging performance at these sites (Chapter 2 and Chapter 3). Nevertheless, these devices do not record even more detailed data, such as selected food items, amounts of food intake, interactions with other individuals, or breeding parameters. Therefore, there is still a need to complement and confirm certain information with direct observations in the field (Chapter 2 and Chapter 4).

Influence of foraging strategy on fitness and survival

Recognizing the fitness and survival consequences of different foraging strategies is crucial for understanding their potential impact on population dynamics (Daunt et al., 2007; Lindström, 1999; Sæther et al., 2013). For instance, the strategy of using landfill resources early, compared to the exploitation of other natural resources, can be decisive in the fitness and survival of white storks during their long migratory journeys, significantly shaping their movements and even enabling individuals in poor body condition to successfully reach wintering areas (Marcelino et al., 2023). Moreover, as the Iberian white stork population transitions to residency, relying on landfills entails less time and energy expenditure compared to the foraging strategy of long-distance migrants, who depend on natural food sources during the winter

(Soriano-Redondo et al., 2023). This variance in foraging behaviour results in disparities in breeding fitness and exposes individuals to varying mortality risks throughout the year (Soriano-Redondo et al., 2023), which need to be further assessed. While GPS-tracking data is essential for identifying the timing and location of bird mortality throughout their annual cycle, the reliability of these devices remains insufficient for determining mortality causes. Additionally, device failures are still common, making it challenging to ascertain the fate of individuals whose transmitters have ceased functioning without confirmation of mortality, whether during migration or during wintering areas like the Sahel region. Therefore, despite the resulting limitations highlighted in Chapter 3, it is imperative to approach survival-related assessments with caution to avoid misinterpretation of results. Future research efforts may eventually address this issue by employing more reliable tracking devices, although they entail higher costs, while considering the balance between the number of individuals that can be tagged and the estimated tracking period expected. Moreover, very little is still known about the potential long-term negative effects on wildlife resulting from the intensive use of landfill resources, such as the effects of toxicants and the development of diseases. Although some studies have already indicated changes in certain risk factors (Höfle et al., 2020; Plaza & Lambertucci, 2017), the impact on survival has not yet been fully accounted for.

Understanding how bird species adapt to changes in food availability

Tracking birds throughout their lives is essential to understand their interactions with the environment and the mechanisms of adaptation to environmental change. For instance, long-term tracking has made it possible to identify different age-related responses to resource availability (Chapter 2), and reveal the drivers of changes in landfill use as individuals mature (Chapter 3). Still, there is a need to extend the life of tracking devices or, alternatively, to have the ability to exchange obsolete devices for new ones in order to study individuals over longer periods of time. Given the low survival rates of first-year juveniles, tracking birds from their first year of life to maturity has proven to be an even more challenging task. Maximising the number of GPS-tracked years per individual could be achieved by targeting and deploying devices on immatures with a higher survival probability. This would increase the overall sample size and would help identify other possible mechanisms behind variations in foraging behaviour through the maturation stage. Moreover, continuous and enduring monitoring of species is crucial for comprehending the state and evolution of population dynamics. Carrying out extensive monitoring of breeding parameters and individual dispersal over the years makes it possible to assess population changes in space and time (Chapter 4) and evaluate their trends.

The white stork serves as an exceptional case study for understanding species adaptation to environmental changes. With adults capable of living up to 39 years (Fransson et al., 2023), this species now has a significant portion of the Iberian population that has lost its migratory behaviour, attributed to the high food availability in the breeding range (Catry et al., 2017). Although adult storks can exhibit different migratory phenotypes, with the majority being residents and intensively using landfill resources, first-year juveniles migrate to Africa and then rapidly increase their landfill use while also changing their migratory strategies (Chapters 2 and 3). Given that age-structured access to landfill food waste is forcing juveniles to seek resources beyond landfills and exposing them to environmental seasonality, it may likely be a key factor influencing their migratory decisions. Therefore, perhaps by continuing to study the movements and foraging behaviour of white storks as they age, it may be possible to unravel the mechanisms driving the change in migratory behaviour.

In light of the prevailing environmental changes, it is of utmost importance to understand how species modify their migratory behaviour. The abundant food supply in landfills has drastically altered the movement and migratory patterns of white storks and several other species reliant on these sites. Nevertheless, this resource is on the verge of depletion, as recent European Directives dictate that by 2030, only around 10% of human waste should be discarded on open-air landfill sites (1999/31/UE and 2018/850/UE). It is unclear what will happen to species that rely on landfills during this adaptation phase and then after these resources are completely unavailable.

In the event of a sharp decline in food availability, such species will need to undergo a drastic change in their foraging behaviour towards natural food sources. However, alternative foraging sources might not be enough in the future to sustain these increasing populations. As tracking data suggests that adults are not flexible enough to revert their natural migratory patterns, juveniles may be the drivers of future changes in the population. By adapting to the new conditions and through generational shifts, the population can transition towards migration. This is because better-performing immature individuals will migrate to regions of Africa with greater food availability, enhancing their chances of survival compared to less-performing juveniles that remain in Iberia.

In the absence of this primary food source, white storks are likely to alter their foraging strategies, shifting towards increased use of agricultural lands (Langley et al., 2021; Zorrozua et al., 2020), and relying more on invasive crayfish at rice fields for winter survival (Ferreira et al., 2019). Since storks are already considered pests by farmers, especially when present at rice fields (author´s pers. information), this will likely increase human-wildlife conflicts. Even so, as landfills in Morocco will be unaffected by European legislation, birds will still have access to this resource through short-distance migrations. Landfill closure, in turn, could result in a decrease in the current size of populations (Steigerwald et al., 2015). Hence, to avoid future conflicts or the collapse of populations, specific management measures are needed to gradually reduce the amount of organic food waste available at landfill sites or, instead, agree the level of supplementary food sources that should be made available for storks and other animals that have become reliant on this abundant supply.

Overall, this thesis offers valuable insights into the complex interactions between landfill resources, foraging behaviour, life traits, and the population dynamics of an opportunistic bird species. Hopefully, this research will stimulate researchers to further investigate and disentangle the influence of anthropogenic food subsidies, individual experience, and social learning on the adaptation of species to ongoing environmental changes.

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Appendix 1

Testing alternative methods for estimation of bird migration phenology from GPS tracking data

Publication

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Short communication

Testing alternative methods for estimation of bird migration phenology from GPS tracking data

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The development and miniaturization of GPS tracking devices has enabled a better understanding of migration phenology, but it can be challenging to identify where and when migration starts and ends, and researchers rely on multiple methods to infer it. Here, we use GPS tracks of 18 trans-Saharan migrant White Storks *Ciconia ciconia* to determine how the choice of method influences the estimation of migratory timing and discuss its implications. We evaluate and provide R code for the implementation of five alternative methods: spatial threshold, absolute displacement, spatio-temporal displacement, net squared displacement and change point analysis. Spatial threshold, absolute displacement and spatio-temporal displacement methods produce, in most cases, significantly different estimates of migration timing and duration as compared with net squared displacement and change point analysis.

Keywords: biologging, birds, GPS, GSM loggers, migration phenology, migratory timing.

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Migration phenology, the timing of seasonal movements between breeding and non-breeding areas, is of paramount importance for many biological processes and has been linked to bird population declines (Møller *et al.* 2008, Both *et al.* 2010, Newson *et al.* 2016). Migration timing has been used to assess the impacts of weather conditions, climate change or anthropogenic food subsidies on individuals and populations (Vansteelant *et al.* 2015, Flack *et al.* 2016, Usui *et al.* 2017). For example, arrival dates of some bird species to the breeding grounds are advancing in response to climate change, which has been shown to have fitness consequences, with birds failing to raise their offspring at the peak of food abundance (Both *et al.* 2006) or facing increased interspecific competition for nesting sites (Ahola *et al.* 2007). However, estimating the timing and duration of migration is challenging and the impact of choosing alternative methodological approaches remains largely unknown.

The study of migration phenology has long relied on the observation or capture of the first arriving or last departing birds from the breeding or wintering grounds (Lukas & Marc 2003, Shamoun-Baranes *et al.*, 2006). In the last few decades, the development and miniaturization of tracking devices has allowed scientists to infer arrival and departure times at the individual level and at greater spatial resolution. GPS devices, in particular, can provide very detailed information on movement and behaviour during individuals' annual cycles. GPS data have revealed fitness advantages of earlier migration onset (Rotics *et al.* 2016), costs of early departure from the wintering grounds (Rotics *et al.* 2018), effects of weather conditions on migration timing (Vansteelant *et al.* 2015, 2017, Illan *et al.* 2017), and the relationship between start of migration and migratory route (Hewson *et al.* 2016).

Such detailed movement data also present new analytical challenges. Several methods have been used to determine the timing of migration using GPS data (examples in Table S1 of Appendix S1). To establish the transitions between non-migratory and migratory behaviours, and thus the start, end and duration of migration, researchers use a range of methods of varying complexity. These methods can be broadly classified into five: spatial threshold (S), absolute displacement (AD), spatio-temporal displacement (SD), net squared displacement (NSD) and change point analysis (CPA).

The simplest one is the S method, in which birds reach or leave the breeding or wintering grounds after crossing *Y* latitude or boundary (López-López *et al.* 2010, Hewson *et al.* 2016, Illan *et al.* 2017, King *et al.* 2017, Monti *et al.* 2018). The AD method, which may incorporate a spatial threshold as well, sets the start of migration as the first day at which daily displacement (i.e. distance between roosting sites) reaches or exceeds a specific threshold distance, and the end of migration as the last day that daily displacement reaches that distance (Oppel *et al.* 2015, Flack *et al.* 2016, Burnside *et al.* 2017). Rotics *et al.* (2016) combined the AD and S methods by setting the start of autumn migration journeys for White Storks *Ciconia ciconia* breeding in Germany as the bird's first flight day (>100 km displacement) southwards (AD method) and the end of autumn migration as the day birds crossed 17.5°N southwards (S method).

The SD method includes both spatial and displacement thresholds, as well as a temporal threshold. Thus, migration starts on the first day of T days where daily displacement is $>X$ that leads to the crossing of the Y spatial threshold, and finishes on the first day after T days where daily displacement is $<X$, after crossing the Y spatial threshold (Rodríguez-Ruiz *et al.* 2014, Vansteelant *et al.* 2015, 2017, Rotics *et al.* 2018). For example, Vansteelant *et al.* (2017) studied the migratory journeys of European Honey Buzzards *Pernis apivorus* breeding in the Netherlands and determined that migration started on the first day after the last period of three or more consecutive stationary days in the breeding range (> 51°N) and finished on the first day after the first period of three or more consecutive stationary days in the non-breeding range (<10°N).

The NSD method has been widely used for mammals but also in some bird studies (Singh *et al.* 2016, Buechley *et al.* 2018). To determine the start and end of migration, NSD calculates the square of the straight-line distance between the track starting location and each subsequent point. It estimates the start or end of migration as a function of the distance between seasonal ranges and the proportion of the total movement distance (see Singh *et al.* 2016 and Spitz *et al.* 2017 for a detailed explanation).

Variations of CPA methods have been used to determine migration phenology in MacQueen's Bustards *Chlamydotis macqueenii* and Montagu's Harriers *Circus pygargus* (Limiñana *et al.* 2007, Madon & Hingrat 2014). CPA methods segment the tracks in time series based on abrupt changes in behaviour. These breakpoints can be estimated using regressions or change point algorithms (see Madon & Hingrat 2014 for a detailed explanation and R scripts).

In this study, we use these five techniques to determine the start, end and duration of migration. We compare the results obtained by the five methods and quantify the differences between methods at an individual level. Moreover, we also test whether the method of choice could influence estimates of migratory timing at a population level. To do so, we use a dataset of juvenile and adult White Storks tagged with GPS/GSM transmitters from Portugal to their wintering sites in sub-Saharan Africa and back.

METHODS

Tagging and tracking White Storks

For this study we selected GPS tracks of 18 White Storks (five adults in 2017, eight juveniles in 2017 and five juveniles in 2018) breeding in southern Portugal that performed trans-Saharan migrations. Juveniles were first-year birds tagged before fledging and adults were breeding birds (>3 years old). Birds were tagged with GPS/GSM loggers (Movetech Telemetry and Ornitela, both tag fixes have negligible location error). Adult birds were caught at landfill sites using nylon leg nooses and in nests using a remotely activated clap net. Juvenile birds were taken from the nest for tag deployment and returned afterwards. The devices were back-mounted using a Teflon harness (further details in Gilbert *et al.* 2016). The mass of the tags plus the harness was ~90 g, 1.8–3.7% of the birds' body mass. The tags collected GPS positions every ~20 min.

Spatial threshold method (S)

Sub-Saharan migratory White Storks breeding in Portugal cross three main geographical barriers to reach their wintering grounds: the Mediterranean Sea, the Atlas mountains and the Sahara desert. We therefore established the start of autumn migration as the first day the birds crossed the first barrier, the Mediterranean Sea at the Strait of Gibraltar at 36°N, southwards, and the end of migration was defined as the first day birds crossed the south of the Sahara desert at 18°N, southwards. The start of spring migration was established as the first day birds crossed 18°N northwards and the end was the first day birds crossed 36°N northwards (R code provided in Appendix S2).

Absolute displacement method (AD)

The start of autumn migration was the first day a bird moved >60 km between consecutive roosting sites that led to the crossing of 36°N southwards. The 60-km threshold was defined as a conservative estimate of daily distance travelled during migration, based on the White Stork dataset. The end of autumn migration was the last day the bird moved >60 km between consecutive roosting sites after crossing 18°N southwards. The start and end of spring migration was set as the first day a bird moved >60 km between roosting sites that led to the crossing of 18°N and 36°N northwards, respectively (R code provided in Appendix S3).

Spatio-temporal displacement method (SD)

The start of autumn (and spring) migration was the first day a bird moved during three consecutive days >60 km between consecutive roosting sites that led to the crossing of the breeding (or wintering) range boundary

(90% kernel probability density). The end of autumn (and spring) migration was the last day the bird moved during three consecutive days >60 km between consecutive roosting sites after crossing the wintering (or breeding) range boundary.

Net squared displacement method (NSD)

To determine migratory timing, we first fit several movement models to our tracks using the R package 'MigrateR' (Spitz *et al.* 2017). The start and end of migration was calculated as the date at which the top model predictions (depending on the individual migrant, mix-migrant or disperser) reached $p \times \delta$ and $(1 - p) \times \delta$, respectively, where δ represents the distance separating seasonal ranges and p (0.05) is the threshold fraction of total distance moved (Spitz *et al.* 2017) (R code provided in Appendix S5).

Change point analysis method (CPA)

We followed Madon and Hingrat (2014) to perform a change point analysis. To determine the transitions between non-migratory and migratory states, we used the Pruned Exact Linear Time algorithm. Next, we manually classified 30% of the track segments into migratory or non-migratory and used a supervised classification tree to classify the remaining 70% (R code provided in Appendix S6).

Statistical analyses

To quantify the degree to which the methods were consistent when estimating migration phenology for each individual, we calculated the intraclass correlation coefficient (ICC) for the start and end of autumn and spring migration. The ICC varies from 0 to 1, for low to high correlation within each individual. To calculate the ICC, we used the R package 'ICC' (Wolak 2015).

To assess population-level differences among methods, we performed generalized linear mixed models (GLMMs), with start, end and duration of migration as response variables (log-transformed), method as an explanatory variable and individual as a random factor. The date of start and end of migration were included in the models as calendar date (1 January = 1). Next, we performed multiple comparisons using Tukey contrasts to determine which methods provided different estimates of migration phenology.

RESULTS

Spatial range of migration

The start and end of the migratory period varied depending on the threshold method. Using the S method, the location of the migration start and end was delimited by 36°N and 18°N (Fig. 1a and Appendix S2). Using the AD method, departure and arrival locations ranged from the breeding grounds in Portugal to the Strait of Gibraltar (Fig. 1b and Appendix S3). The SD method set the arrival and departure of the breeding grounds in the south of Portugal, and movements between the breeding site and the Gibraltar Strait were classified as migratory (Fig. 1c and Appendix S4). The NSD and CPA methods had the highest spatial variability between individuals in departure and arrival locations from and to the breeding grounds, ranging from the south of Portugal to the south of Morocco (Fig. 1d,e and Appendixes S5 and S6). The location of the start and end of migration in the wintering grounds showed great variability amongst individuals, ranging from 12°N to 18°N when using the AD, SD, NSD or CPA methods (Fig. 1).

Timing and duration of migration

The median start of autumn migration ranged from 3 August with the AD method to 10 August with the NSD method (Fig. 2a). Although it showed high consistency among methods (ICC = 0.89), the model estimates differed significantly ($P = 0.011$) due to differences between the SD and NSD methods ($P = 0.003$). The end of autumn migration ranged from 22 August with the S method to 4 September with the CPA method (Fig. 2c), and it showed a low consistency (ICC = 0.56) and significant differences among multiple methods ($P < 0.001$, see Appendix 7 for Tukey contrasts). Spring migration had a similar pattern. The start of the migration ranged from 12 January with the NSD method to 25 January with the S method (Fig. 2b) and it showed high consistency (ICC = 0.92), but still with significant differences ($P = 0.019$), due to different estimates between the S and NSD methods ($P = 0.004$). The end of spring migration ranged from 7 February (NSD) to 17 April (SD) (Fig. 2d) and showed low consistency (ICC = 0.55) and significant differences among multiple methods ($P < 0.001$, see Appendix 7 for Tukey contrasts).

Overall, the S, AD and SD methods yielded similar results (Fig. 3), except for estimates of the duration of autumn migration under the S and SD methods ($P < 0.001$). The NSD and CPA methods also produced similar estimates (Fig. 3) except, similarly, for the duration of autumn migration ($P = 0.03$). Nevertheless, these two groups of methods predicted different migratory timings; the estimates of S, AD and SD differed from the estimates of NSD and CPA in most cases (Fig. 3, see Appendix 7 for further details).

DISCUSSION

We found substantial differences between methods in the estimation of the start, end and duration of

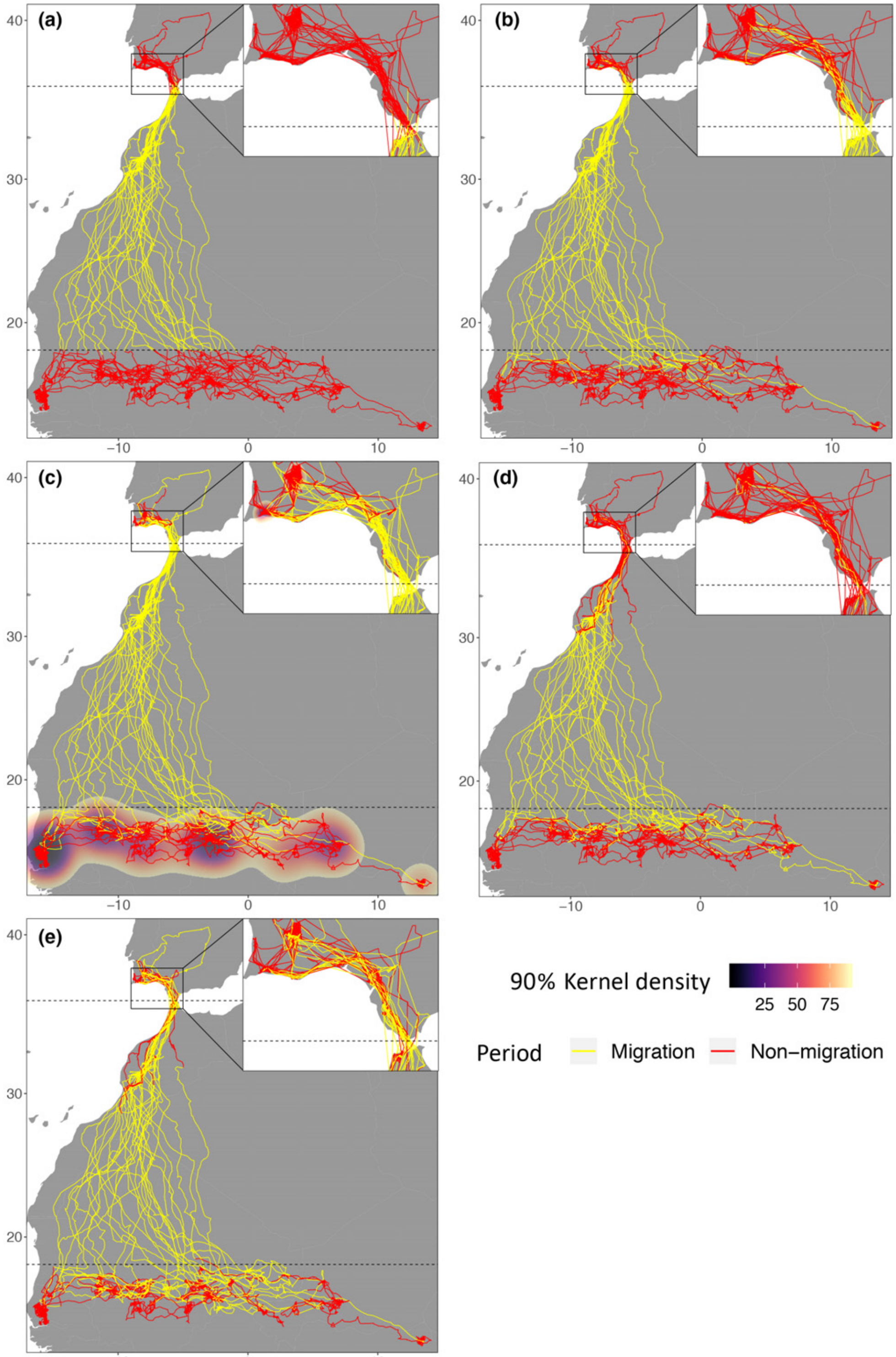


Figure 1. Annual movements of 18 White Storks classified as migratory or non-migratory according to the (a) spatial threshold (S), (b) absolute displacement (AD), (c) spatio-temporal displacement (SD), (d) net squared displacement (NSD) and (e) change point analysis (CPA) methods. Dashed lines represent spatial thresholds (36°N and 18°N) used in the S and AD methods. [Colour figure can be viewed at wileyonlinelibrary.com]

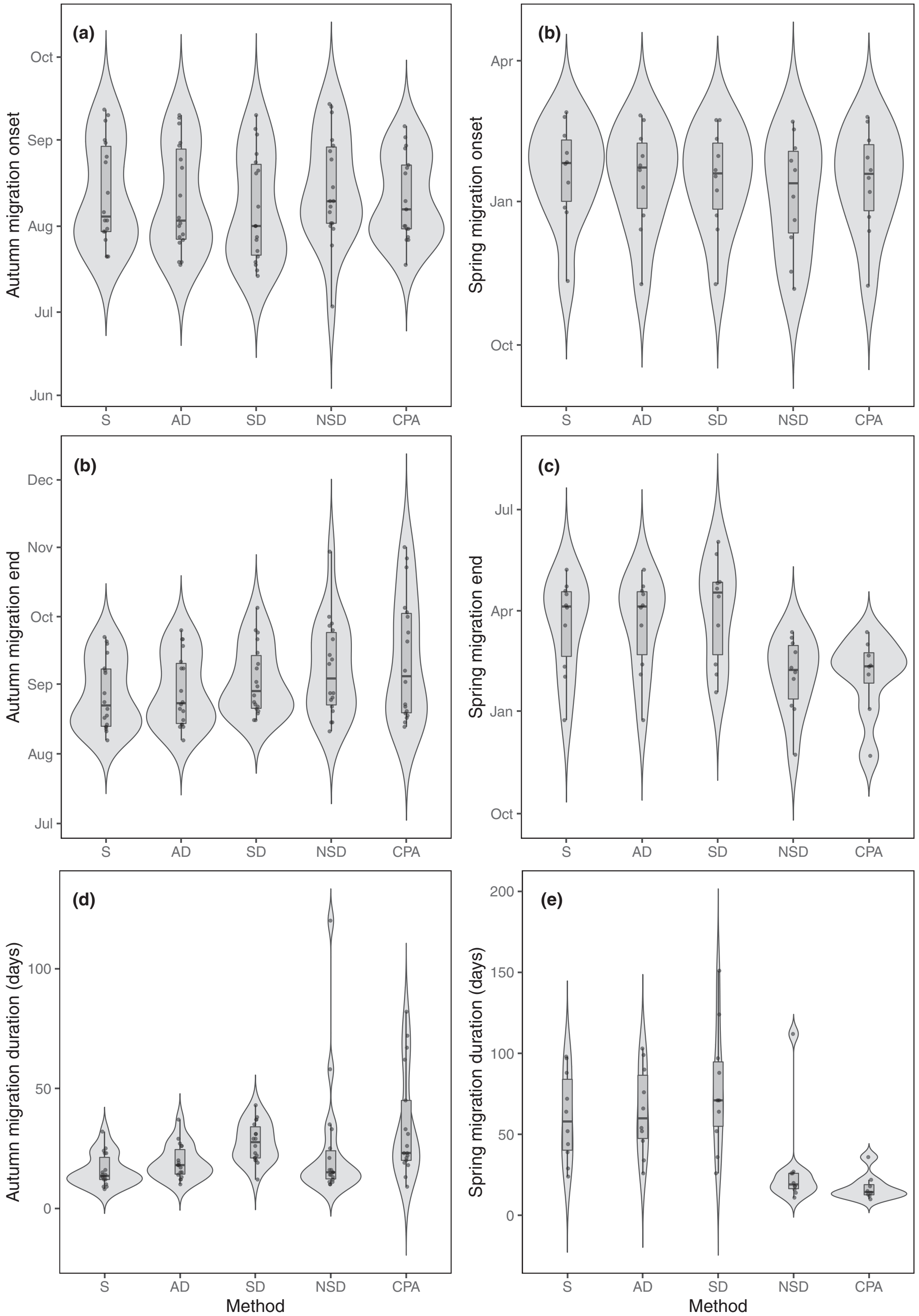


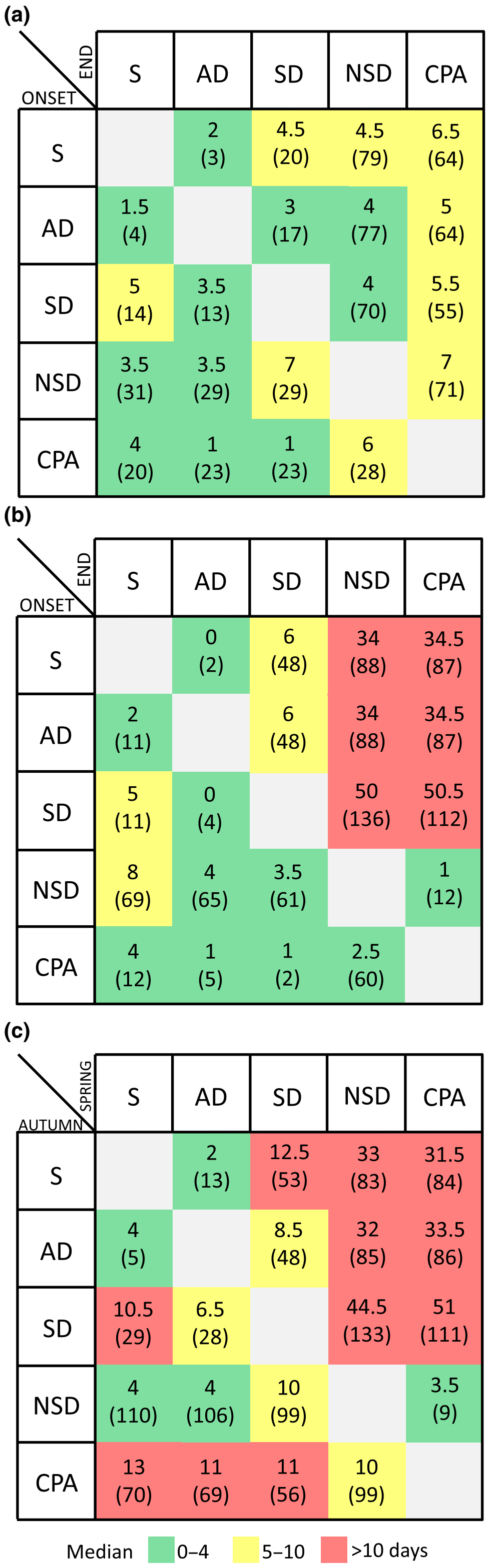
Figure 2. Violin plots of the distribution density of the start of (a) autumn and (b) spring migration; end of (c) autumn and (d) spring migration; and duration in days of (e) autumn and (f) spring migration obtained using different methods. Middle, lower and upper hinges of the boxplot correspond to the median, 25th and 75th percentiles, respectively. Whiskers correspond to the 95% confidence intervals. S, spatial threshold method; AD, absolute displacement method; SD, spatio-temporal displacement method; NSD, net squared displacement method; CPA, change point analysis.

migration of juvenile and adult White Storks tracked from their breeding areas in Portugal to their wintering areas in sub-Saharan Africa and back. Both autumn and spring migration are vulnerable to these differences (Figs 2f and 3b), with up to a 12-fold difference in autumn migration duration depending on the method used, from 10 days using the S method to 120 days using the NSD method (Table S3 of Appendix S7). Our study highlights the need to consider carefully the method used to determine migration phenology based on GPS tracking devices and to assess the sensitivity of the data to the method used.

The sensitivity to the method used varied depending on the phenological metric estimated; the start of autumn and spring migrations was more consistently estimated among methods (ICC = 0.89 and 0.92) than the end (ICC = 0.56 and 0.55). Importantly, we found that the NSD and CPA methods were significantly different from the S, AD and SD methods in most estimates. This could be explained by several differences between these two groups of methods: (1) NSD and CPA make minimum *a priori* assumptions, whereas AD and SD require prior assumptions about daily displacement during migration; and (2) NSD and CPA are based only on animal movement, whereas S, AD and SD require ecological knowledge broadly to determine breeding and wintering areas.

Although we do not advocate a one-size-fits-all approach, our results suggest that the low level of ecological knowledge required by the NDS and CPA methods is detrimental to the estimation of the migration phenology of White Storks. The NDS and CPA methods fail to distinguish a realistic threshold in the breeding range, which, in this case, leads to autumn migrations only starting after crossing of the Strait of Gibraltar or spring migrations ending before crossing of the Strait.

The results also show that the S method produced similar estimates to the AD and SD methods, but it does not capture the spatial variability of individual breeding and wintering sites within the species' breeding and wintering ranges. Thus, in the northern hemisphere for species with large wintering or breeding ranges, individuals breeding in the northernmost and wintering in the southernmost areas of their ranges could have their estimated migration period cut short by multiple days.



(a)

END ONSET	S	AD	SD	NSD	CPA
S		2 (3)	4.5 (20)	4.5 (79)	6.5 (64)
AD	1.5 (4)		3 (17)	4 (77)	5 (64)
SD	5 (14)	3.5 (13)		4 (70)	5.5 (55)
NSD	3.5 (31)	3.5 (29)	7 (29)		7 (71)
CPA	4 (20)	1 (23)	1 (23)	6 (28)	

(b)

END ONSET	S	AD	SD	NSD	CPA
S		0 (2)	6 (48)	34 (88)	34.5 (87)
AD	2 (11)		6 (48)	34 (88)	34.5 (87)
SD	5 (11)	0 (4)		50 (136)	50.5 (112)
NSD	8 (69)	4 (65)	3.5 (61)		1 (12)
CPA	4 (12)	1 (5)	1 (2)	2.5 (60)	

(c)

SPRING AUTUMN	S	AD	SD	NSD	CPA
S		2 (13)	12.5 (53)	33 (83)	31.5 (84)
AD	4 (5)		8.5 (48)	32 (85)	33.5 (86)
SD	10.5 (29)	6.5 (28)		44.5 (133)	51 (111)
NSD	4 (110)	4 (106)	10 (99)		3.5 (9)
CPA	13 (70)	11 (69)	11 (56)	10 (99)	

Median 🟩 0–4 🟨 5–10 🟥 >10 days

Figure 3. Median (maximum) difference in number of days of the estimated start and end of (a) autumn and (b) spring migration between methods; and (c) median (maximum) difference in the duration of autumn and spring migrations. S, spatial threshold method; AD, absolute displacement method; SD, spatio-temporal displacement method; NSD, net squared displacement method; CPA, change point analysis. [Colour figure can be viewed at wileyonlinelibrary.com]

Although the AD and SD methods yielded similar results, SD performed better for individuals that had short stops within the breeding or wintering range before the end of migration. Both methods require the establishment of arbitrary thresholds: spatial, displacement and temporal (SD only). Therefore, we suggest (1) a preliminary exploration of the movement data, to estimate the displacement and temporal thresholds during migration; and (2) to use GPS locations obtained during the breeding and wintering periods to perform kernel density estimates that will identify the breeding and wintering area boundaries and reduce the arbitrariness of spatial thresholds adopted.

We recommend that similar studies, comparing the efficacy of these methods in determining the phenology of migration, should be conducted for other bird species. Our results suggest that expert knowledge is needed to determine appropriate spatial, displacement and temporal thresholds. The choice of method used to determine migration phenology can influence the conclusions, especially if parts of the migratory journey are excluded. This is particularly important for studies that examine the start or end of migration at the individual level, or the importance of weather conditions during migration. In this study, some methods would not enable us to account for the crossing of the Mediterranean Sea at the Strait of Gibraltar, an important geographical barrier for White Storks.

In light of the increasing number of species and individuals that have their migratory journeys recorded using GPS data (see Table S1 of Appendix S1 for examples), a certain degree of standardization of the definition of migration, and the method used to estimate it, is required to obtain consistent estimates across studies. To facilitate comparisons between studies, we think that errors associated with estimates of migration phenology should be considered, particularly in interspecific studies that use tracking data from multiple sources. More importantly, we encourage researchers to make data available in data repositories and to report accurately the methods used. We hope this contribution will raise awareness of the challenges associated with the study of migration phenology using GPS tracking data and help researchers find appropriate methods to analyse their data.

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DISCLOSURE OF INTERESTS

The authors declare no competing interests.

Data availability statement

Tracking data are stored in Movebank. R code is available in the Supporting information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. List of methodologies used to estimate migration phenology.

Appendix S2. Spatial threshold method.

Appendix S3. Absolute displacement method.

Appendix S4. Spatio-temporal displacement method.

Appendix S5. Net squared displacement method.

Appendix S6. Change point analysis method.

Appendix S7. Comparison among methods.

Appendix 2

Flying the extra mile pays-off: Foraging on anthropogenic waste as a time and energy-saving strategy in a generalist bird

Publication

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, 146843.

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Flying the extra mile pays-off: Foraging on anthropogenic waste as a time and energy-saving strategy in a generalist bird

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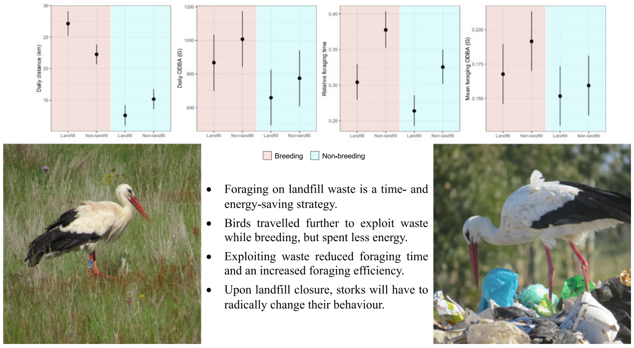
HIGHLIGHTS

- Foraging on landfill waste is a time- and energy-saving strategy.
- Birds travelled further to exploit waste while breeding, but spent less energy.
- Exploiting waste reduces foraging time and an increase in foraging efficiency.
- Upon landfill closure, storks will have to radically change their behaviour.

GRAPHICAL ABSTRACT



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ABSTRACT

Food waste disposal represents a major global source of predictable anthropogenic food subsidies and is exploited by many organisms. However, the energetic cost-benefits of foraging on these food subsidies have remained largely unexplored. Here we investigate the year-round foraging decisions of resident white storks, *Ciconia ciconia*, in Iberia, and assess the energetic and time cost-benefits of foraging on both landfill waste and natural food sources. To do so, we use GPS and acceleration data from 55 individuals tagged in southern Portugal between 2016 and 2019. We find that the probability of attending landfill sites was 60% during the non-breeding season and 44% during the breeding season. Moreover, foraging on landfill waste is a time- and energy-saving strategy; although birds had to travel 20% further to exploit this resource during the breeding period, they spent overall 10% less energy than when foraging on natural prey. We show that this relationship could be mediated by a reduction in foraging time and an increase in foraging efficiency while exploiting landfill waste. Surprisingly, we do not find any evidence that landfill specialists experienced any competitive advantage during landfill exploitation over birds that visit landfills occasionally. These insights are key to predict how species that rely on landfills can be affected by waste reduction initiatives planned by the European Union, and implement the necessary management strategies.

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1. Introduction

Humans produce enormous quantities of food waste; estimates suggest that 30–40% of all food produced is wasted (Parfitt et al., 2010) and deposited in locations where it can be accessible to wildlife. These predictable anthropogenic food subsidies (PAFS), in the form of organic waste on landfills, fisheries discards or crop residuals, generate impacts on animal populations at multiple scales, from the individual to the ecosystem (Oro et al., 2013). Individuals from numerous animal species have modified their movements, activity, geographical range, and home range size in response to PAFS (Gilbert et al., 2016; López-López et al., 2014; Newsome et al., 2015; Patrick et al., 2015; van Donk et al., 2019); which can affect survival and reproduction rates, and subsequently the demography of these populations (Plaza and Lambertucci, 2017).

Landfill sites, in particular, can potentially sustain high densities of scavenging individuals (Oro et al., 2013). The spatial and temporal predictability, accessibility, and nutritional value of anthropogenic food waste can provide abundant food resources for wildlife, and has been shown to be responsible for the demographic explosion of generalist animals (such as foxes, rats and gulls), but also for the sustenance of some endangered species (Plaza and Lambertucci, 2017). Landfill use has been associated with increased body mass in black vultures (*Coragyps atratus*) (Plaza and Lambertucci, 2018), kelp gull (*Larus dominicanus*) nestlings (Lenzi et al., 2019), and grizzly bears (*Ursus arctos horribilis*) (Blanchard, 1987). Landfill use has also been linked to higher reproduction performance; for example, white storks (*Ciconia ciconia*) had larger clutch sizes (Djerdali et al., 2008), glaucous gulls (*Larus hyperboreus*) experienced higher fledging rate (Weiser and Powell, 2010), and laughing gull (*Leucophaeus atricilla*) chick growth and survival was enhanced (Dosch, 1997), compared to conspecifics foraging in more natural landscapes.

According to the optimal foraging theory animals choose to forage in sites that maximize energy intake while minimizing energy and time expenditure (Stephens and Krebs, 1986; Ydenberg et al., 1994). Landfill waste offers large quantities of high-energy food (Patenaude-Monette et al., 2014; van Donk et al., 2019) but is localised in space; hence trade-offs exist between time spent in landfills sites and energetic costs of travelling, especially for central-place foragers during the breeding season (Gilbert et al., 2016). Foraging in landfill sites is likely to exacerbate inter and intraspecific competition (through agonistic interactions and food-robbing), which increases energetic costs, since they attract large numbers of individuals and at high densities (Oro et al., 2013). On the other hand, on natural heterogeneous landscapes, prey is often patchily distributed and intraspecific competition is likely to be low since individuals tend to forage in smaller groups (Catry et al., 2017). These dynamics could lead to the emergence of individual foraging strategies and specialisation, with less competitive individuals avoiding landfill sites. Despite many studies focusing on the fitness benefits for individuals exploiting landfill waste, the energetic cost-benefits of landfill use have not yet been fully quantified.

Use of landfill resources, together with the global increase of temperature due to climate change, has likely facilitated the establishment of non-migratory white stork populations in Iberia (Catry et al., 2017). Resident individuals rely on food waste disposal sites for foraging and no longer complete their annual migrations to and from their sub-Saharan wintering grounds. In two decades the number of resident white storks in Portugal has increased from 1187 individuals (18% of the breeding population) in 1995 to 14,434 (62% of the breeding population) in 2015 (Catry et al., 2017). White storks' use of landfill resources in Iberia has been investigated, and evidence shows that storks nesting close to landfill sites heavily relied on them (Gilbert et al., 2016). Moreover, breeding success for these individuals was higher than for individuals nesting further away (Gilbert, 2015).

While this increasing number of white storks in Iberia is widely attributed to their high adaptability and behavioural plasticity, new EU directives (1999/31/UE and, more recently, 2018/850/UE), regulating waste disposal, can greatly revert this trend. These directives have established new circular economy targets aiming to reduce municipal waste landfilled to 10% in the next decade. Recent evidence shows that landfill closure can lead to a decline on survival, body mass, egg volume and/or clutch size in several gull species (Payo-Payo et al., 2015; Pons and Migot, 1995; Steigerwald et al., 2015) (but see Katzenberger et al., 2019). Therefore, it is crucial to understand foraging decisions, and how animals search for and exploit landfill waste, as opposed to natural prey, to predict how animal populations might respond when food waste is drastically reduced, and to develop appropriate conservation and management strategies.

Here we investigate (i) the foraging decisions of resident white storks feeding on PAFS and natural food sources in Iberia; (ii) the energetic and time cost-benefits of these foraging decisions during the breeding and non-breeding seasons; and (iii) whether birds highly specialised on landfills gain a competitive advantage while exploiting PAFS, by increasing their foraging efficiency and decreasing the foraging time necessary to meet their energetic requirements, over birds that only visit landfills occasionally. These insights will be key to understand the drivers of landfill use and to predict how storks — and to some extent other birds found regularly in large numbers at landfills (e.g. egrets, herons, gulls and some raptors) — may be affected by reductions in PAFS. This understanding is key for a species that has substantially increased in numbers in the last decades due to the exploitation of landfills (Catry et al., 2017), and for which density dependent effects of food depletion are associated with high nestling mortality (Denac, 2006; Zurell et al., 2015).

In this study we examine 4 years of GPS and tri-axial acceleration data from resident white storks in Iberia and determine their behaviour, energy expenditure, foraging decisions, and landfill use. We use structural equation models (SEM) (Lefcheck et al., 2016; Lefcheck, 2016) to understand the relationships among foraging movements, energy expenditure and behaviour. We hypothesize that the choice of food resources (anthropogenic waste or natural prey) will lead to different foraging strategies, for example at landfills sites birds will reduce the time devoted to foraging and increase energy efficiency given the spatiotemporal predictability of organic waste deposition. Moreover, we predict that foraging strategies might differ between the breeding and non-breeding season, as breeding birds will have to return to the nest frequently, so their foraging range will be reduced, and landfill sites might then be outside the range. In this context, fundamental trade-offs between energetic and nutritional requirements in parental provisioning strategies are expected (Wright et al., 1998). Finally, we predict that landfill specialists will have competitive advantage over birds that only use landfills occasionally.

2. Material and methods

2.1. Bird capture and GPS tracking

Our dataset included GPS data with tri-axial acceleration from 55 resident adult white storks, tagged between 2016 and 2019 in southern Portugal. Resident individuals overwintered in the Iberian Peninsula and did not cross the Strait of Gibraltar. Storks were tagged with 'Flyway 50' GPS/GSM loggers from Movetech Telemetry (4 different models varying slightly in weight) and 'Ornitrack-50' GPS/GSM loggers from Ornitela. Adult birds were caught at multiple landfill sites using nylon leg nooses, and at several breeding colonies using a remotely activated clap net at the nests. Birds were measured and ringed, and the devices were mounted on the back of the birds as backpacks with a Teflon harness. The tag and harness together weighted 60–90 g, which represented 1.5–3.7% of a given bird's body mass at the time of tagging. Most birds were resighted in the days following tag deployment and no abnormal behaviour or adverse effects due to tagging were observed. The procedure was approved by the Instituto da Conservação da

Natureza e Florestas (Portugal). The tags were programmed to record 9 consecutive GPS positions at 1 Hz every 20 min, and concurrently a 9 s tri-axial acceleration burst at 1 Hz. We kept the first GPS position recorded, thus location and acceleration matched. GPS data was visually examined to detect potential outliers, which were subsequently removed, together with the associated acceleration burst. We identified 75 nest locations for the tagged birds across the years after visually inspecting the GPS tracks and visiting the sites. The nests were situated between 1.5 and 40.2 km away from the closest landfill site (mean = 17. 3 km).

2.2. Data selection and processing

From each acceleration burst we derived two metrics, ODBA (overall dynamic body acceleration, 1 G = 9.8 m/s^2), a proxy of energy expenditure invested in locomotion, and behaviour (Gleiss et al., 2011; Shepard et al., 2008b). ODBA was obtained from tri-axial acceleration bursts by subtracting the smoothing of total acceleration, using a running-mean of 4 s, from the total acceleration, as recommended in Gleiss et al. (2011) and Shepard et al. (2008a, 2008b). To determine the bird behaviour at each burst, we used the tri-axial acceleration data to train random forest machine-learning algorithms (R package 'randomForest' ver. 4.6 (Liaw and Wiener, 2002)). Movetech Telemetry tags and Ornitela tags differ in their sensor characteristics (e.g. position of the sensor and axes orientation) hence we created device specific algorithms. We characterised four behaviours: foraging, resting (including preening), flapping, and soaring flight (including gliding and orographic and thermal soaring). To train the algorithm we manually labelled 250 tri-axial acceleration bursts for each behaviour and tag type; 70% of the data was used for training the algorithm and 30% for testing it. To label the training data we compiled information from several sources: (i) 9 tags that were programmed to continuously record GPS and acceleration data which allowed a detailed understanding of the birds' movements and behaviour, (ii) video recordings of captive white storks that were fitted with the tracking devices, and (iii) from the 9 consecutive GPS locations that allowed to infer birds' speed and movement during the acceleration burst. The random forest model had 96% accuracy for Movetech Telemetry tags data and 97% accuracy for Ornitela tags data. For this study, flapping and soaring flight were aggregated and considered as flying, as both behaviours occurred infrequently, representing only 5.7% of locations.

Landfill sites were determined through visual inspection of satellite images, and in all cases, they were confirmed by visits or contact with local authorities. Each GPS location was classified as either inside or outside a landfill. Subsequently, using the behavioural and GPS data, we created daily foraging strategy metrics for each individual stork. We only included in the analyses days with more than 10 daylight GPS positions and acceleration bursts (median GPS positions per day was 29) and with more than 4 positions classified as 'foraging' to guarantee representative metrics.

We built two different datasets for the subsequent analyses. First, to assess individual and seasonal differences in attendance to landfill sites, we created a 'daily attendance dataset'. In this dataset each day was classified as a 'landfill attendance day' when at least one foraging location occurred on a landfill in the corresponding 24-h period, or as a 'non-landfill attendance day' when no foraging locations occurred on landfills. Second, to understand the foraging movements, behaviour and energy expenditure of feeding on anthropogenic waste or natural prey we built a 'daily foraging strategy dataset' that only included days where birds displayed either one or the other strategy, thus removing days where birds foraged on both waste and natural prey. To do so, we created a variable, 'foraging site' with two levels: 'landfill foraging day', when 70% of the daily foraging positions occurred in landfill sites, and 'non-landfill foraging day', when 70% of the foraging positions for a given day occurred outside landfill sites. We chose this threshold as it ensured birds spent most of the day in one of the two areas, while it minimized the number of days that had to be removed from the dataset to less than 20%.

The activity and energetic trade-offs between foraging on landfills vs natural prey were explored using several metrics: (i) daily distance travelled (km), calculated as the summed distance between consecutive locations for each day; (ii) daily relative flight time, calculated by dividing the number of burst classified as flying by the total of bursts obtained in a day; (iii) mean ODBA (G) as a proxy of daily energy expenditure (Gleiss et al., 2011), calculated as the mean ODBA of the accelerometer bursts obtained in a day; (iv) daily relative foraging time, calculated by dividing the number of burst classified as foraging by the total of burst in a day; and (v) mean foraging ODBA (G), as a proxy for foraging efficiency (lower mean foraging ODBA values indicate higher foraging efficiency), calculated as the daily mean ODBA for the foraging bursts. Daily distance travelled and relative flight time were highly correlated (Pearson correlation = 0.75), which indicates that the metrics

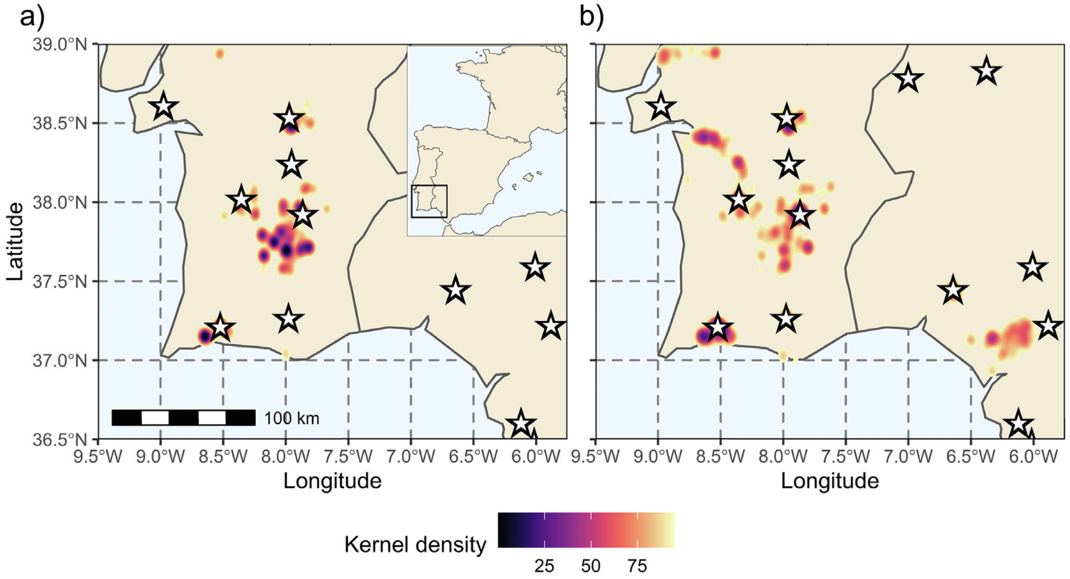

Fig. 1. Foraging areas of tracked white storks in southern Iberia (Portugal and Spain) between 2016 and 2019 during a) the breeding and b) the non-breeding periods. Stars indicate landfill sites.

were largely insensitive to the number of fixes; we only retained daily distance travelled in further analyses.

To account for the potential effect of season on the foraging site choice (landfill sites or non-landfill sites), we located the nesting site of each individual, and using the GPS data, we defined the beginning of the breeding season as the first three consecutive days that an individual occupied the nest; and the end of the breeding period as last three consecutive days the nest was occupied.

To explore if birds that visited landfill sites more often had a competitive advantage when exploiting this resource, we used the 'daily attendance dataset' to create a landfill specialisation index, from 0 (natural prey specialist; never visits landfill sites) to 1 (waste specialist; only forages on landfill sites), for each individual. We divided the number of days that the bird attended a landfill by the total numbers of days that the bird was tagged.

2.3. Statistical analysis

To understand seasonal variability in foraging site attendance we fitted a generalised linear mixed-effects model (GLMM) with foraging site attendance (landfill or non-landfill) as the response variable and season (breeding or non-breeding) as the explanatory variable, using the *glmmPQL* function with a binomial structure (R package 'MASS' ver. 7.3 (Ripley et al., 2013)); the model included bird ID nested in tag type (5 levels: 4 types of Movetech tags and 1 type of Ornitela tag) as random effects and an autocorrelation structure of order 1 to account for the potential temporal correlation between consecutive days. Subsequently, to understand the potential constraints of reproduction in the choice of foraging site, we used the data from the breeding season to fit a GLMM with a binomial structure, using the *glmer* function (R package 'lme4' ver. 1.1-21 (Bates et al., 2015)). We considered foraging site attendance as the response variable, and included as explanatory variables, distance from the nest site to the closest landfill site, and its quadratic term, to account for potential non-linearity in the relationship; we also included bird ID nested in tag type as random effects. We used the R package 'MASS' when the inclusion of an autocorrelation structure was necessary as 'lme4' does not allow the implementation of GLMMs with that structure.

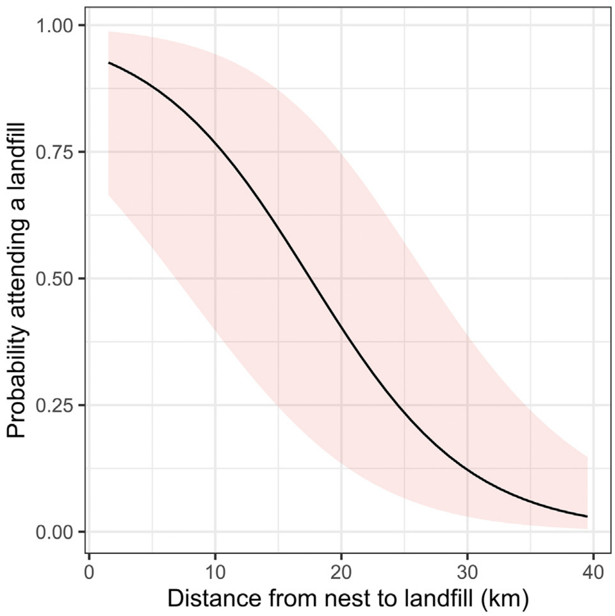

Fig. 2. Estimates from GLMMs explaining the probability of white storks attending a landfill during the breeding season as a function of the distance from the nesting site to the closest landfill.

Using the 'daily foraging strategy dataset', we explored the effect of landfill use on time and energy budgets, by implementing 3 linear mixed-effects models (LMM) with daily distance travelled (km), mean ODBA (G), and mean foraging ODBA (G) as response variables and foraging site (landfill or non-landfill), season (breeding or non-breeding), and its interaction, as explanatory variables, using the *lme* function (R package 'nlme' ver. 3.1 (Pinheiro et al., 2017)). The model with daily distance travelled as response variable, included an additional covariate, the number of GPS positions, to account for its the potential effect on the response. We implemented a GLMM with the *glmmPQL* function for relative foraging time with a binomial structure that included foraging site, season, and its interaction as fixed effects as well. All four models included bird ID nested in tag type as random effects and an

Table 1

Estimates from LMMs and GLMM explaining (a) total distance travelled, (b) mean overall dynamic body acceleration (mean ODBA), (c) relative foraging time, and (d) mean foraging ODBA. Reference level for season is 'breeding', and for foraging site is 'landfill'.

	Estimate	SE	*t*	*p*
(a) Distance travelled				
Fixed effects				
Intercept	20.32	1.50	13.58	<0.001
Season	−13.90	0.81	−17.15	<0.001
Foraging site	−5.001	0.71	−7.07	<0.001
Season:Site	7.65	0.87	8.83	<0.001
GPS positions	0.23	0.04	6.05	<0.001
Random effects				
Bird ID | Tag type	4.98			
Tag type	0.01			
AR(1)	0.50			
Residual variance	15.50			
Marginal R^2	0.08			
Conditional R^2	0.17			
(b) Mean ODBA				
Fixed effects				
Intercept	0.09	0.01	10.36	<0.001
Season	−0.02	0.00	−16.24	<0.001
Foraging site	0.01	0.00	12.57	<0.001
Season:Site	0.00	0.00	−1.78	0.0755
Random effects				
Bird ID | Tag type	0.01			
Tag type	0.02			
AR(1)	0.54			
Residual variance	0.03			
Marginal R^2	0.17			
Conditional R^2	0.46			
(c) Relative foraging time				
Fixed effects				
Intercept	−0.83	0.06	14.08	<0.001
Season	−0.20	0.03	−5.82	<0.001
Foraging site	0.33	0.03	11.91	<0.001
Season:Site	−0.03	0.03	−0.90	0.3694
Random effects				
Bird ID | Tag type	0.25			
Tag type	0.05			
AR(1)	0.59			
Residual variance	1.58			
Marginal R^2	0.01			
Conditional R^2	0.03			
(d) Foraging ODBA				
Fixed effects				
Intercept	0.17	0.01	15.46	<0.001
Season	−0.02	0.002	−9.59	<0.001
Foraging site	0.02	0.002	15.42	<0.001
Season:Site	−0.02	0.002	−8.71	<0.001
Random effects				
Bird ID | Tag type	0.01			
Tag type	0.02			
AR(1)	0.32			
Residual variance	0.03			
Marginal R^2	0.15			
Conditional R^2	0.44			

autocorrelation structure of order 1. Subsequently, we calculated for each model the coefficient of determination R^2 (Nakagawa et al., 2017).

We explored the relative contribution of individuals' foraging decisions into the overall energy expenditure when using different foraging sites and during different seasons. To do so, we implemented multigroup analysis for piecewise SEM with foraging site and season as grouping variables, using the functions *psem* and *multigroup* (R package 'piecewiseSEM' ver. 2.1 (Lefcheck et al., 2016; Lefcheck, 2016)). The SEM included two sub-models: 1. an LMM with mean ODBA as the response variable, and daily distance travelled, relative foraging time and mean foraging ODBA as explanatory variables; and 2. a GLMM with relative foraging time as the response variable, and mean foraging ODBA as explanatory variables. Both models included random effects and autocorrelation structure as described above. The global structure of the SEM model was well supported according to the global goodness-of-fit: Fisher's C = 0.098 with $p = 0.952$.

To test the role of landfill specialisation on landfill exploitation we selected only days classified as landfill foraging days. We modelled a LMM with mean foraging ODBA and a GLMM with relative foraging time as the response variables, and season and specialisation index as explanatory variables. We used random effects and an autocorrelation structure as previously specified. Normality of the residuals was checked for all LMMs performed.

3. Results

We obtained two datasets of movement and acceleration data; the 'daily attendance dataset' contained data of 12,616 stork-days (median ± SE; 162 ± 28 days per individual); and the 'daily foraging strategy dataset' of 10,183 stork-days (136 ± 22 days per individual, see detailed information in Tables S1 and S2). During both the breeding and non-breeding season foraging occurred in southern Portugal, but during the non-breeding season white storks increased their foraging range towards southern Spain (Fig. 1). All individuals but one foraged both on landfill sites and outside of landfill sites. The probability of attending landfill sites varied with season (estimate = 0.63; SE = 0.07; $p < 0.001$); it was 60% during the non-breeding season and 44% during the breeding season. Moreover, during the breeding season, the probability of attending a landfill was constrained by the distance from the nest to the closest landfill site (estimate = −0.16; SE = 0.03; $p < 0.001$) in a linear way (quadratic term was non-significant; $\chi2 = 2.882$; $p = 0.09$), with individuals nesting closer to a landfill site foraging there more often (Fig. 2).

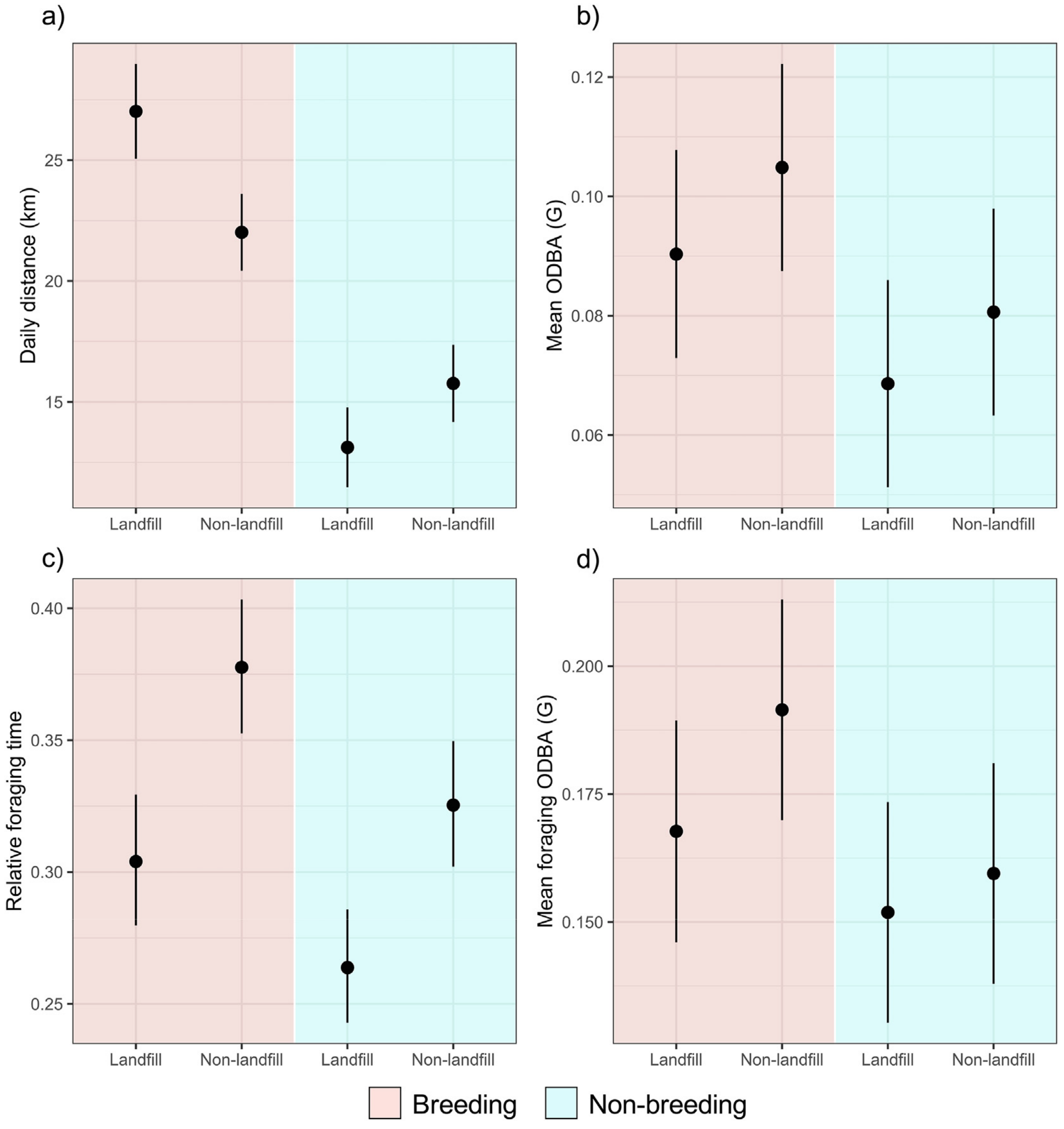

Fig. 3. Predicted values and 95% confidence intervals from GLMMs explaining (a) daily distance travelled, (b) mean overall dynamic body acceleration (ODBA), (c) relative foraging time, and (d) mean foraging ODBA of foraging white storks, as a function of season (breeding or non-breeding) and foraging site (landfill or non-landfill).

Table 2
Estimates from structural equation models (SEM) explaining the relationship among total distance travelled, mean overall dynamic body acceleration (ODBA), relative foraging time, and mean foraging ODBA. Estimates for (a) the whole model, (b) breeding period outside landfills, (c) non-breeding period outside landfills, (d) breeding period in landfills, and (e) non-breeding period in landfills.

	Predictor	Estimate	SE	*p*
(a) Model-wide interactions				
Response				
Mean ODBA	Distance travelled			<0.001
Mean ODBA	Relative foraging time			<0.001
Mean ODBA	Foraging ODBA			<0.001
Relative foraging time	Foraging ODBA			<0.001
(b) Breeding, non-landfill				
Response				
Mean ODBA	Distance travelled	0.0005	0.0000	<0.001
Mean ODBA	Relative foraging time	0.1049	0.0020	<0.001
Mean ODBA	Foraging ODBA	0.3150	0.0091	<0.001
Relative foraging time	Foraging ODBA	0.8266	0.2827	0.0035
(c) Non-breeding, non-landfill				
Response				
Mean ODBA	Distance travelled	0.0005	0.0000	<0.001
Mean ODBA	Relative foraging time	0.1016	0.0020	<0.001
Mean ODBA	Foraging ODBA	0.2536	0.0091	<0.001
Relative foraging time	Foraging ODBA	1.6589	0.3157	<0.001
(d) Breeding, landfill				
Response				
Mean ODBA	Distance travelled	0.0006	0.0000	<0.001
Mean ODBA	Relative foraging time	0.0985	0.0068	<0.001
Mean ODBA	Foraging ODBA	0.2218	0.0184	<0.001
Relative foraging time	Foraging ODBA	−0.0627	0.5119	0.9026
(e) Non-breeding, landfill				
Response				
Mean ODBA	Distance travelled	0.0004	0.0000	<0.001
Mean ODBA	Relative foraging time	0.0691	0.0033	<0.001
Mean ODBA	Foraging ODBA	0.1696	0.0085	<0.001
Relative foraging time	Foraging ODBA	−0.7308	0.2773	0.0085

White storks travelled further during the breeding season to visit landfill sites (estimate ± SE; 27.02 ± 0.98 km) than when foraging outside landfill areas (22.01 ± 0.79 km); while during the non-breeding season, storks travelled less overall, and birds that used landfills travelled shorter distances (13.11 ± 0.82 km) than those feeding outside of landfills (15.76 ± 0.80, Table 1, Fig. 3). The results for mean ODBA, relative foraging time and mean foraging ODBA were similar. The three parameters were higher during the breeding season in days that birds foraged outside landfill sites (mean ODBA 0.10 ± 0.01 G; relative foraging time 0.37 ± 0.05; mean foraging ODBA 0.19 ± 0.01 G, Table 1, Fig. 3), and decreased during the non-breeding season and in days that birds foraged in landfill sites, reaching the lowest values when both conditions occurred (mean ODBA 0.07 ± 0.01 G; relative foraging time 0.26 ± 0.05; mean foraging ODBA 0.15 ± 0.01 G, Table 1, Fig. 3). Thus, mean ODBA, relative foraging time, and mean foraging ODBA decreased 34.6%, 30.1%, and 12.4%, respectively, from the days that birds foraged outside landfills during the breeding season to days that birds foraged in landfills during the non-breeding season.

The multigroup analysis for piecewise SEM indicated that mean ODBA increased when white storks had to travel further, when they spent a higher proportion of time foraging, and for storks that presented higher mean foraging ODBA (Table 2). The effect was stronger when foraging occurred outside of landfills during the breeding season (Fig. 4). The relationship between relative foraging time and mean foraging ODBA differed depending on the foraging site (Table 2). When foraging on outside of landfills, an increase on mean foraging ODBA led to a significant increase in relative foraging time; while on landfill sites, an increase on mean foraging ODBA led to slight decrease in foraging time (Fig. 5).

Finally, we did not find any relationship between relative foraging time and landfill specialisation, and between mean foraging ODBA and landfill specialisation when birds foraged on landfill waste (Table 3).

4. Discussion

This study unravels some of the mechanisms that determine landfill use in a generalist and opportunistic species. In Iberia, expansion and population growth of white storks is widely attributed to their high adaptability and behavioural plasticity, which allow them to efficiently use opportunities provided by anthropized environments such as landfills (Catry et al., 2017; Elliott et al., 2020). Here, we show that foraging on landfill waste is a time- and energy-efficient strategy for white storks compared to foraging on natural habitats. Remarkably, although storks had to travel further to exploit this resource during the breeding period, they spent overall less energy in terms of locomotion than when foraging on natural prey (Fig. 3). Our results indicate that this could be mediated by a reduction in foraging time and an increase in foraging efficiency (i.e. a decrease in mean foraging ODBA) while exploiting landfill waste (Fig. 3). These findings contrasts with previous evidence from herring gulls (*Larus argentatus*), which increase energy expenditure 34% when foraging on PAFS compared to natural prey (van Donk et al., 2019). These differences between species are likely to be ascribed to their flight mode; while herring gulls tend to use flapping flight, which is energetically costly, white storks soar, which allow them to fly longer distances to reach landfill sites at a cheaper energetic cost, especially at certain times of day when flight conditions (e.g. uplift) are favorable (Duriez et al., 2014).

Nevertheless, we find that white storks experience constraints during the breeding season and reduce landfill attendance to 44% of days compared to 60% in the non-breeding period. This reduction is mostly a function of distance to nest location, as location white storks nesting further to landfill sites visit them less often than birds nesting closer (Fig. 2). These differences in foraging site preference indicate that the energetic compensation of longer flights, with increased foraging efficiency and decreased foraging time at landfill sites, compensate for longer flights only up to a certain limit, after which it is no longer beneficial to travel further to forage at landfills.

The hindrance imposed by reproduction is reflected on all the parameters that we studied; storks increased distance travelled, energy expenditure, foraging time, and mean foraging ODBA during the breeding season (Fig. 3). These parameters are likely to increase in response to the spatial restrictions that impose returning to the nest frequently and the higher energetic demands derived from raising chicks (Johst et al., 2001). On the contrary, during the non-breeding period, storks are not constrained by nest location and often roost closer to landfill sites, thus reducing daily distances travelled. Moreover, foraging just to meet their own energy demands could be leading to a reduction in foraging time and daily energy expenditure.

Our results show that daily energy expenditure is highly influenced by distance travelled, foraging time and foraging efficiency, with higher energy expenditure with increasing distance travelled and foraging time and decreasing foraging efficiency (Fig. 4). The slopes of these relationships were maintained when foraging at landfill sites and non-landfill sites, both during the breeding and non-breeding season. However, in all cases the intercept was lower when foraging at landfill sites, indicating that there could be other unaccounted factors decreasing the daily energy expenditure on days that birds forage at landfill sites, such as a reduction on flight energetics, a change of flight mode (soaring vs flapping), or a decrease on time spent preening.

Interestingly, we found that the relationship between relative foraging time and energy efficiency differed depending on the foraging site. At natural sites, birds with high levels of energy expenditure (low energy efficiency) during foraging, increased the time spent foraging. On the contrary, at landfill sites, birds that were less energy-efficient during foraging spent less time foraging, this effect was stronger during the non-breeding season (Fig. 5). This divergence is likely to steam from the different characteristics of foraging on landfill waste versus natural prey. Individuals foraging at landfill sites, where large numbers of white storks congregate, are likely to experience easy access to food but also density

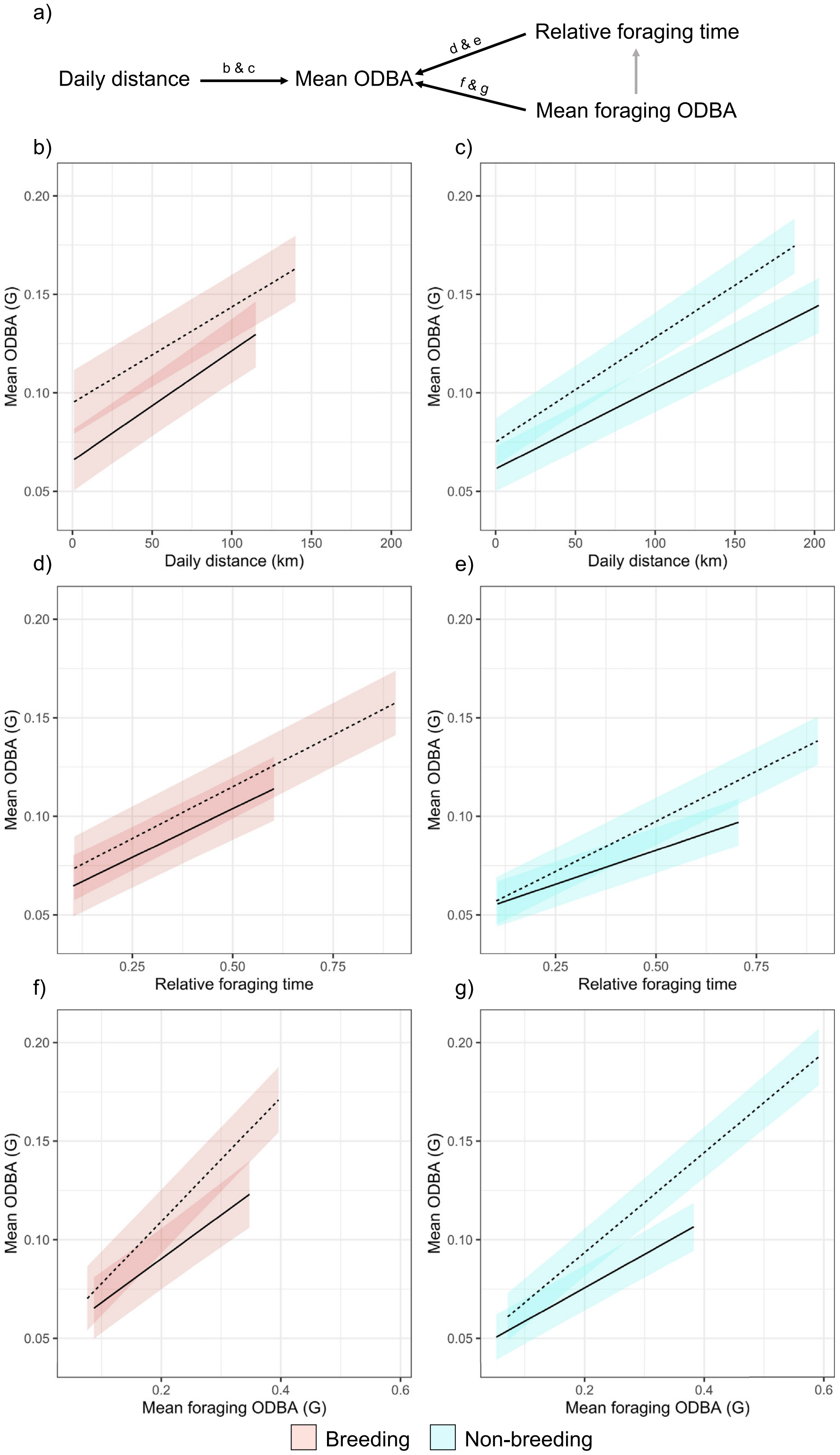

Fig. 4. (a) Graphical explanation of the structural equation model (SEM) showing the relative contribution of white storks' foraging decisions into the mean overall dynamic body acceleration (ODBA). Black arrows indicate relationships represented in the figure and the grey arrow relationship not represented in the figure. Mean ODBA as a function of daily distance travelled for (b) the breeding season and (c) the non-breeding season; mean ODBA as a function of relative foraging time for (d) the breeding season and (e) the non-breeding season; and mean ODBA as a function of mean foraging ODBA for (f) the breeding season and (g) the non-breeding season. Solid line on landfill sites and dashed line on non-landfill sites.

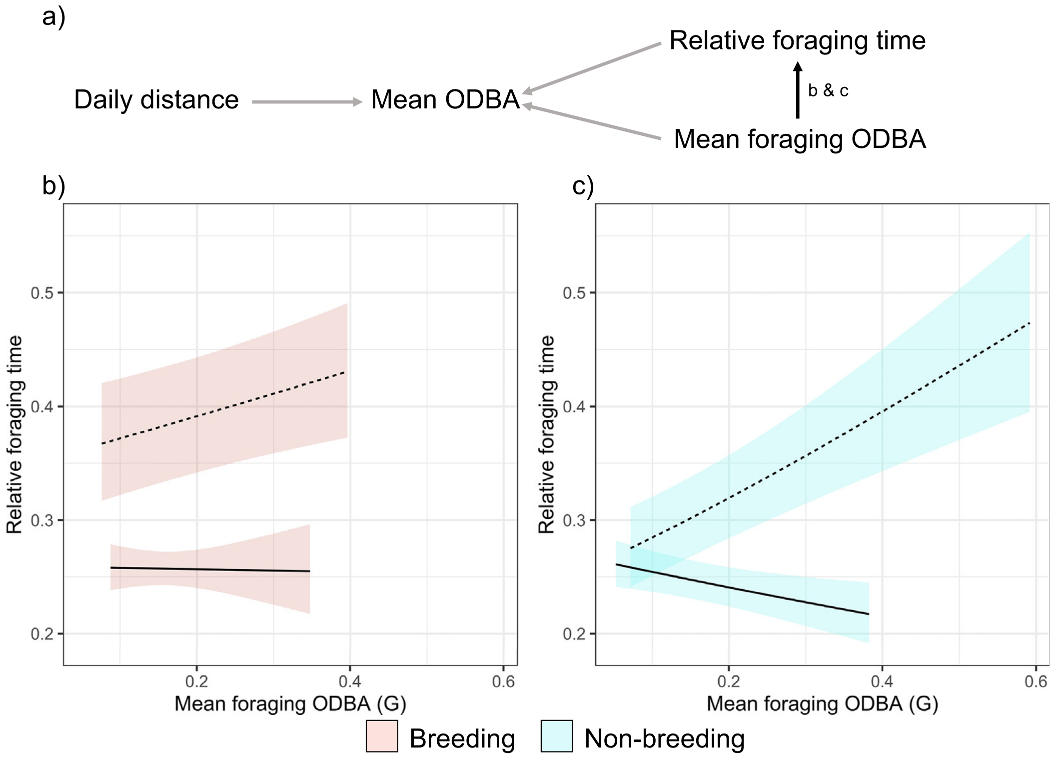

Fig. 5. (a) Graphical explanation of the structural equation model (SEM) showing the relative contribution of white storks' foraging decisions into the mean overall dynamic body acceleration (ODBA). Black arrows indicate relationships represented in the figure and the grey arrow relationship not represented in the figure. Relative foraging time as a function of mean foraging ODBA for (b) the breeding season and (c) the non-breeding season. Solid line on landfill sites and dashed line on non-landfill sites.

dependence effects, such as direct competition from conspecifics (Oro et al., 2013). This could lead to an increase of energy expenditure during foraging due to antagonistic interactions with other individuals, but also to a reduction in foraging time, since birds could be displaced from optimal foraging sites (Burger, 1981). On natural areas, however, white storks hunt large invertebrates and small vertebrates and do not aggregate in such large numbers (Elliott et al., 2020). Thus, an increase of mean foraging ODBA is likely to be linked to active hunting, which could then favor an increase in relative foraging time.

Table 3
Estimates from GLMM and LMM explaining (a) relative foraging time, and (b) mean foraging overall dynamic body acceleration (ODBA), while foraging on landfills. Reference level for season is 'breeding'.

	Estimate	SE	*t*	*p*
(a) Relative foraging time				
Fixed effects				
Intercept	−1.21	0.11	−11.29	<0.001
Season	−0.03	0.09	−0.28	0.7795
Specialisation index	0.31	0.19	1.65	0.1062
Season:Specialisation index	−0.11	0.14	−0.79	0.4323
Random effects				
Bird ID | Tag type	0.14			
Tag type	0			
AR(1)	0.25			
Residual variance	1.01			
(b) Foraging ODBA				
Fixed effects				
Intercept	0.16	0.01	11.22	<0.001
Season	−0.02	0.01	−2.51	0.0120
Specialisation index	0.01	0.01	0.42	0.6756
Season:Specialisation index	0.01	0.01	0.82	0.4142
Random effects				
Bird ID | Tag type	0.01			
Tag type	0.02			
AR(1)	0.10			
Residual variance	0.03			

Surprisingly, we did not find any evidence that landfill specialists experienced any competitive advantage during landfill exploitation in terms of foraging time and energy efficiency. Thus, our results suggest that landfill use is mainly driven by distance from the nest to the nearest landfill site, rather than by the ability of individuals to exploit this resource. Therefore, it is likely that white storks compete for nests located in close proximity to landfill sites (Itonaga et al., 2011; Janiszewski et al., 2015).

In this study we have quantified one of the aspects required to define optimal foraging strategies: time allocation and energy expenditure related to locomotion. However, we could not quantify energy intake, a key aspect for energetic balances. Natural prey is patchily distributed, and energetic values can be variable. For example, the energetic value of red-swamp crayfish (*Procambarus clarkii*), an invasive alien species that occurs in rice fields and is widely consumed by white storks (Ferreira et al., 2019; Negro et al., 2000; Tablado et al., 2010), is ~3 kJ/g (Elvira et al., 1996). On the other hand, landfill waste is abundant, easily accessible and predictable in space and time, and highly energetic (up to 10–25 kJ/g (van Donk et al., 2019, 2017)). Recent evidence shows that white stork nestlings in Iberia whose parents exploit landfill sites present better body condition and nutritional status than nestlings whose parents feed on natural resources, which complements our findings (Pineda-Pampliega et al., 2021).

Landfill waste exploitation can also have associated costs, such as higher exposure to heavy metals, poisons, pathogens, and plastics (Ahlstrom et al., 2018; de la Casa-Resino et al., 2014; Plaza and Lambertucci, 2017; Tongue et al., 2019). For example, a recent study of white storks in Iberia found that nestlings from birds foraging on landfill waste had a higher presence of antibiotic-resistant *Escherichia coli* than nestlings from birds feeding on natural resources (Pineda-Pampliega et al., 2021); while another found that nestlings from white storks near landfill sites presented higher blood levels of lead, mercury, selenium, iron, zinc, and arsenic, which can be toxic at high concentrations (de la Casa-Resino et al., 2014). Moreover, the occurrence of plastics in landfills can lead to their ingestion, which can damage the digestive organs of the birds (Peris, 2003).

Overall, our study shows that white storks nesting in the proximity of landfill sites and foraging there frequently save energy and time, thus exploiting landfill waste can be an advantageous strategy. Increased breeding success and population growth driven by waste exploitation has been described for other bird species (Bialas et al., 2020; Djerdali et al., 2008; Gilbert, 2015; Tauler-Ametller et al., 2017), thus a potential reduction of landfill waste could have dramatic impacts on the population, since alternative food resources might not be available to meet the energetic requirements of such large number of individuals (but see Katzenberger et al., 2019). In light of the European Union directives that will lead to a substantial reduction of landfill waste in the next few years, our results indicate that species that heavily rely on landfill waste will be severely affected and will have to radically change their behaviour, for example by increasing foraging time and energy expenditure while foraging, affecting energetic and time balances. However, it is currently unknown whether alternative foraging resources will be able to sustain these populations in the future.

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CRediT authorship contribution statement

ASR conceived the study, carried out the statistical analyses, and drafted the manuscript; AMAF and FM coordinated the study, and critically revised the manuscript; MA processed data, collected field and behavioural data, and critically revised the manuscript; BHM collected field and behavioural data, and critically revised the manuscript; IC conceived the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.146843.

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Appendix 3

Fitness, behavioral, and energetic trade-offs of different migratory strategies in a partially migratory species

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ARTICLE

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Fitness, behavioral, and energetic trade-offs of different migratory strategies in a partially migratory species

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Abstract

Alternative migratory strategies can coexist within animal populations and species. Anthropogenic impacts can shift the fitness balance between these strategies leading to changes in migratory behaviors. Yet some of the mechanisms that drive such changes remain poorly understood. Here we investigate the phenotypic differences, and the energetic, behavioral, and fitness trade-offs associated with four different movement strategies (long-distance and short-distance migration, and regional and local residency) in a population of white storks (*Ciconia ciconia*) that has shifted its migratory behavior over the last decades, from fully long-distance migration toward year-round residency. To do this, we tracked 75 adult storks fitted with GPS/GSM loggers with tri-axial acceleration sensors over 5 years, and estimated individual displacement, behavior, and overall dynamic body acceleration, a proxy for activity-related energy expenditure. Additionally, we monitored nesting colonies to assess individual survival and breeding success. We found that long-distance migrants traveled thousands of kilometers more throughout the year, spent more energy, and >10% less time resting compared with short-distance migrants and residents. Long-distance migrants also spent on average more energy per unit of time while foraging, and less energy per unit of time while soaring. Migratory individuals also occupied their nests later than resident ones, later occupation led to later laying dates and a lower number of fledglings. However, we did not find significant differences in survival probability. Finally, we found phenotypic differences in the migratory probability, as smaller sized individuals were more likely to migrate, and they might be incurring higher energetic and fitness costs than larger ones. Our results shed light on the shifting migratory strategies in a partially migratory population and highlight the nuances of anthropogenic impacts on species behavior, fitness, and evolutionary dynamics.

KEYWORDS
breeding success, GPS tracking, movement, overall dynamic body acceleration, survival

INTRODUCTION

The migratory strategies of many animal species are rapidly changing due to anthropogenic influences, such as land transformation and climate change (Cox, 2010; Maclean et al., 2008; Sutherland, 1998; Visser et al., 2009). These changes are multifaceted and can encompass modifications in the timing of migration departure and arrival (Cotton, 2003; Gordo & Sanz, 2006; Jenni & Kéry, 2003), the shortening or diversion of migratory routes (Eichhorn et al., 2009; Sutherland, 1998), or the complete disruption of migration and the transition toward residency (Plummer et al., 2015; Pulido & Berthold, 2010; Satterfield et al., 2015). Ultimately, these adjustments can influence ecological and evolutionary processes at multiple scales, from the individual to the ecosystem (Dingle, 2014; Nathan et al., 2008).

Substantial within-population variability can exist in the propensity to migrate, with some individuals from the population being resident and others migrating (Chambon et al., 2018; Lok et al., 2017; Sanz-Aguilar et al., 2012). In many species and populations, migration strategies form a continuum and many alternative strategies coexist, such as long-, medium-, or short-distance migrations, ranging movements, or localized residency, which generates partially migratory populations (Reid et al., 2018). Several studies have shown that migration is energetically costly, with individuals traveling longer distances incurring higher energy costs, often measured using the overall dynamic body acceleration (ODBA) (Flack et al., 2016; Somveille et al., 2018). Additionally, migration has been shown to increase mortality in a diverse range of taxa (Buchan et al., 2020; Klaassen et al., 2016; Rotics et al., 2017; Sillett & Holmes, 2002, but see Conklin et al., 2017). Yet, in some cases, selective pressures on survival fluctuate, with migrants presenting lower survival rates in years with average climatic conditions, but higher survival in years with extreme weather events (Acker, Burthe, et al., 2021; Acker, Daunt, et al., 2021; Sanz-Aguilar et al., 2012).

The migratory strategy might also affect breeding performance. For instance, in European shags (*Gulosus aristotelis*) and older Eurasian spoonbills (*Platalea leucorodia*) individuals performing longer migrations breed later than short-distance migrants or resident individuals, and late breeders have lower reproductive outcomes (Grist et al., 2017; Lok et al., 2017). Therefore, innovations in the migration strategy can be under strong selection if they provide individual fitness advantages over the rest, and can be retained and spread across the population through social learning or evolutionary change (de Zoeten & Pulido, 2020; Newton, 2008). In extreme cases, partial migration can become an unstable strategy and migration could even disappear if migratory individuals suffer increased fitness-associated costs.

The advantages for an individual of adopting either a migratory or a resident strategy can be dependent upon its phenotype (Chapman et al., 2011). For example, in house finches (*Carpodacus mexicanus*), small individuals that cannot endure extremely cold temperatures, or large individuals less able to tolerate heat, migrate to areas with milder climates (Able & Belthoff, 1998; Belthoff & Gauthreaux Jr., 1991). Density-dependent intraspecific competition can also play a role in maintaining partial migration (Chapman et al., 2011; Lundberg, 1987, 2013); in blue tits (*Cyanistes caeruleus*) and blackbirds (*Turdus merula*) smaller subordinate individuals migrate to avoid competition for limited resources, while larger dominant individuals remain in the breeding grounds year-round (Lundberg, 1985; Nilsson et al., 2008; Smith & Nilsson, 1987). This leads to a frequency-dependent evolutionary stable state and can induce highly dynamic temporal patterns on the ratio of resident to migratory individuals in the population (Chapman et al., 2011). Differences in the trophic niche specialization among individuals can also explain differential migration strategies, with individuals whose trophic niche is more affected by seasonal changes being more prone to migrate (Aparicio, 2000). In such cases, partial migration results in an evolutionarily stable strategy, where the fitness consequences for individuals that migrate are balanced against the consequences of remaining in the breeding area throughout the year (Buchan et al., 2020; Chapman et al., 2011).

Additionally, human activities can alter the trade-offs between migratory strategies by providing a competitive advantage or disadvantage to individuals following a certain strategy (Buchan et al., 2020). However, the mechanisms that tip the balance between strategies remain largely unknown. The white stork (*Ciconia ciconia*) provides a unique opportunity to study the factors favoring the emergence of residency, as it displays a range of migratory strategies with different effects in terms of behavior, energetics, and fitness. For example, a comparison across eight white stork populations following diverse migratory strategies revealed that energy expenditure invested in locomotion increased with distance traveled (Flack et al., 2016), while a study on juvenile white storks found that individuals that migrated to Africa presented a lower survival, and increased movements, foraging range, and energy than those overwintering in Europe (Rotics et al., 2017).

Here, we assess the phenotypic differences, trade-offs, and fitness consequences of migration in adult white storks from a partially migratory population breeding in Portugal that is transitioning toward residency (Catry et al., 2017; Gilbert et al., 2016). Whereas juvenile white storks perform annual migrations to Africa during their first year of life, when they reach adulthood, individuals show a range of fixed seasonal migratory strategies (Acácio et al., 2022; Catry et al., 2017; Marcelino et al., 2023). Some individuals are year-round residents, remaining either locally or regionally in Southwest Europe; others migrate during the wintering period to Northwest Africa or the sub-Sahara region (Catry et al., 2017). Markedly, the number of white storks breeding in Portugal has increased substantially in the last two decades, from approximately 3300 individuals in 1994 to 11,700 in 2017 (Catry et al., 2017). Simultaneously, the percentage of resident individuals has steeply increased, from 18% in 1995 to 62% in 2015 (Catry et al., 2017). This shift toward residency is likely to have been due to increased food availability (Catry et al., 2017) and milder temperatures during the winter in the breeding grounds. Landfill waste has become a key food resource for white storks, with individuals attending landfill sites on 44% of the days during the breeding season, and 60% of the days during the wintering season (Soriano-Redondo et al., 2021).

Current trends suggest that partial migration in the Portuguese white stork population is not an evolutionarily stable strategy, as residents are disproportionally increasing in numbers (Catry et al., 2017). Thus, this provides a rare opportunity to investigate the ecological and evolutionary consequences of different migratory strategies throughout the annual cycle. Specifically, we investigated (1) the behavioral differences and estimated energetic costs, measured through ODBA, of birds undertaking various migratory strategies; (2) the fitness consequences of migration in terms of survival and reproduction; and (3) whether individual phenotype affects the migratory probability of adult white storks. We predict that migratory individuals will present higher energy expenditure because most evidence suggests that migrating is energetically costly (Flack et al., 2016). We also predict that migrants will suffer higher fitness costs (Buchan et al., 2020; Rotics et al., 2017), as is reflected by the current population shift toward residency.

MATERIALS AND METHODS

Fieldwork

We captured, measured, blood-sampled, ringed, and tagged 75 breeding adult white storks in Southern Portugal between 2016 and 2020 (4 in 2016, 13 in 2017, 8 in 2018, 43 in 2019, and 7 in 2020). Storks were captured either at their nest using remotely activated clap nets or at landfill sites using nylon leg nooses. GPS/GSM loggers (Movetech Telemetry and Ornitela) were mounted on the backs of the birds as backpacks with a Teflon harness; the total weight of the logger and harness was 60–90 g, 1.5%–3.7% of the bird body mass. The loggers were programmed to record GPS positions and tri-axial acceleration samples every 20 min at 1 Hz for 9 s. At deployment, morphometric measurements (wing, tarsus, and bill length ± 1 mm and weight ± 1 g) were taken for each individual. Blood (<50 μL) was collected from the medial metatarsal vein and a few drops were preserved in vials with ethanol for molecular sexing. All birds were colored-ringed following a unique scheme. All procedures were performed under license of the Instituto da Conservação da Natureza e Florestas, Portugal (license numbers: 493/2016/CAPT, 661/2017/CAPT, 662/2017/CAPT, 548/2018/CAPT, 549/2018/CAPT, 248/2019/CAPT, 365/2020/CAPT, 366/2020/CAPT, and 367/2020/CAPT). Approval from an ethics committee was not required for this study.

Nesting sites were identified for all adults by visually inspecting GPS tracks, and they were visited weekly during the breeding season in subsequent years to determine stork breeding parameters (i.e., laying date, and number of fledglings). Nests were visited annually during the breeding season after the logger stopped recording to assess if this was due to tag failure or bird mortality; this was a reliable method due to high levels of nest faithfulness. Moreover, when an individual was not found in the nest it had used in the previous year, other nests of the colony and nearby colonies were also visited to confirm if the individual had not moved to a neighboring nest. In total, ~420 nests were monitored on a weekly basis during the 2016–2020 breeding seasons.

GPS and acceleration data

We used the 9 s tri-axial acceleration bursts to calculate two movement parameters: ODBA (G), a proxy of energy expenditure invested in locomotion, and bird behavior (Gleiss et al., 2011; Shepard et al., 2008). Following Soriano-Redondo et al. (2021), to calculate ODBA we subtracted the smoothing of the acceleration, using a running mean of 4 s, from the total acceleration. To estimate the bird behavior at each burst we trained two random forest machine-learning algorithms, one for Movetech Telemetry tags and the other for Ornitela tags, using 1000 manually labeled tri-axial acceleration bursts encompassing four behaviors: foraging, resting, soaring and flapping (for details see Soriano-Redondo et al., 2021). The random forest models had 96% accuracy for Movetech Telemetry tags and 97% accuracy for Ornitela tags.

Characterization of migration strategies

We used the GPS trajectories to classify the migratory strategy of each individual every year. We visually examined the GPS data to detect and remove potential outliers. Storks were classified as resident or migratory depending on whether they remained in Southwest Europe or crossed the Strait of Gibraltar after the breeding period. Birds were subsequently classified into four subcategories depending on their wintering grounds. Resident birds were categorized as either local when they remained in proximity to the nest year around (i.e., <50 km away from it); or regional, when they ranged further away from the nest across Southwest Europe (i.e., >50 km away from the nest). We chose this threshold as it ensured that birds classified as local did not commute between different areas in Portugal and always remained close to their nesting site. Migrants who crossed the Strait of Gibraltar and spent the winter in Northwest Africa were classified as Northwest African, and sub-Saharan when they crossed the Sahara Desert as well and wintered in the Sahel.

To establish the migratory phenology of tracked birds we followed Soriano-Redondo et al. (2020). Each annual cycle was divided into four seasons: autumn, wintering, spring, and breeding. For migratory individuals, we defined the start of autumn and spring (i.e., migrations) as the first day a bird moved >60 km between roosts for 3 days consecutively, which led to the departure of the breeding range during autumn migration, and the wintering range during spring migration. The end of autumn and spring was the last day the bird moved >60 km between roosts for 3 days consecutively, after departing from the wintering range during autumn migration, and from the breeding range during spring migration. For resident individuals, we derived the thresholds between periods using the median date of the thresholds of the migratory birds. The start of the autumn period was the 4 August and the end was on 5 September; the start of the wintering period began on 6 September and the end was on 12 December; the start of the spring period was on 13 December and the end was on 22 January; and the start of breeding period was on 23 January and the end was on 3 August.

Breeding parameters estimation

The nest occupation date was determined using the GPS locations, and was defined as the first day that a bird visited its nest for 3 days consecutively. Laying date and number of fledglings were determined by regularly examining the nests using a camera attached to a pole, or by using a drone.

Statistical analysis

We explored the potential effects of migratory strategy (four levels: local, regional, Northwest Africa, and sub-Saharan) on bird movements and ODBA. To do that, we first fitted a linear mixed model (LMM) with annual displacement (i.e., the sum of all the distances moved throughout the year) as the response variable and migratory strategy as explanatory variables. To control for potential differences in tag recordings and individual behavior, we included the number of GPS positions as a fixed factor and individual IDs as a random effect. Second, to understand the implications of the different migratory strategies on the annual energy expenditure, we fitted a linear mixed effects model with mean annual ODBA as the response variable, migratory strategy as the explanatory variable, and individual ID nested in tag type (five levels: four tag types from Movetech Telemetry and one from Ornitela) as a random effect. We included tag type to account for different sensitivities of the tags to record the acceleration measures. Third, to understand the differences in ODBA linked to foraging, resting, soaring, and flapping among the four migratory strategies, we fitted four LMM with mean annual ODBA during foraging, resting, soaring, and flapping as response variables and migratory strategy as an explanatory variable, and individual ID nested in tag type as a random effect. To implement the models, we used the R package *lme4* (Bates et al., 2015, p. 4). To assess the differences between migratory strategies, whenever this variable was significant in the model, we performed Tukey's contrasts.

To understand the behavioral budgets associated with each migratory strategy we fitted generalized LMMs (GLMMs) with Beta distribution, using the R package *glmmTMB* (Brooks et al., 2017). The response variable was the mean proportion of time per day spent performing a certain behavior in an annual cycle. Thus, we fitted four models with the proportion of time foraging, resting, soaring, and flapping. In each, the explanatory variable was migratory strategy and individual ID nested in tag type was a random effect. In the cases in which migratory strategy was significant, we assessed the differences between groups by implementing Tukey's contrasts.

To understand at which stage of the seasonal cycle differences in the bird ODBA, movements, and behavior occurred, we fitted the same models as previously used, with migratory strategy and individual ID (nested in tag type for the ODBA and behavior parameters), but including season as well (four levels: autumn, wintering, spring, and breeding) and the interaction of migratory strategy and season as fixed effects. In this case, the response variables were seasonal displacement, mean seasonal ODBA, mean seasonal ODBA during foraging, resting, soaring, and flapping, and mean proportion of time per day spent foraging, resting, soaring, and flapping during the season. For seasonal displacement, because the duration of the season differed depending on the bird, we also included the duration as a covariate. We implemented Tukey's contrasts to assess the differences between seasons and migratory strategies.

We assessed the direct and indirect effects of the migratory strategies on the subsequent breeding performance. We tested whether migratory strategy directly affected the number of fledglings produced and/or whether there was a cascading effect, with migratory strategy affecting the number of fledglings through changes in nesting and laying dates, as has been reported in other species (Grist et al., 2017; Lok et al., 2017). To do so, we fitted a structural equation model containing three linear models (Figure 1) using the *piecewiseSEM* R package (Lefcheck, 2016; Lefcheck et al., 2016). We fitted an LMM with nest occupation date (day of the year) as a response variable, migratory strategy as the explanatory variable and individual ID as the random effect. This was followed by a LMM model linking laying date (as the response) and nest occupation date as a fixed effect, and with individual ID as the random effect. Last, we fitted a GLMM with a Poisson distribution with the number of fledglings as the response, laying date and migratory strategy as covariates, and individual ID as a random effect. The direct and indirect relationships were also tested outside the structural equation model to extract the effects.

Finally, to determine whether the probability of migration was linked to individual characteristics, we fitted a generalized linear model (GLM) with a binomial link function, with migration probability (resident or migrant) as the response variable, and wing length, sex, and their interaction as explanatory variables. Wing length is correlated with culmen (Pearson's correlation = 0.629, $p < 0.001$) and tarsus lengths (Pearson's correlation = 0.548, $p < 0.001$), and thus a good proxy of body size. Although males tend to be larger than females, collinearity between sex and wing size was relatively low (variance inflation factor [VIF = 1.83]). All model assumptions were checked using the *DHARMa* R package.

Survival estimation

Survival, GPS signal loss and resighting probabilities were simultaneously estimated by means of multievent capture–recapture models (Pradel, 2005). The multievent framework distinguishes what can be observed in the

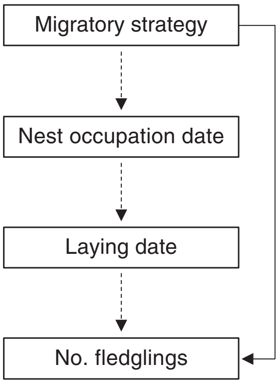

FIGURE 1 Path diagram of piecewise structural equation modeling to establish the direct (solid line) and indirect (dashed lines) relationship between the migratory strategy and the reproductive success.

field from the underlying biological states of the individuals, which must be inferred (Pradel, 2005). Live encounter data were collected during the breeding season of each year between 2016 and 2021 and coded into individual encounter histories. Here, the events were "0" for individuals not observed in a given year. Observed individuals were stratified according to whether they had an active GPS tag or not. We assigned "1" to individuals detected with active GPS devices and "2" to individuals observed alive that either had an inactive GPS device or had lost the GPS device but could be identified by means of rings. In addition to live encountered data, dead recoveries ($n = 10$) were detected by fixed location in GPS signal and confirmed by local scientists. Dead encounters were coded as "3."

We specified the multievent model with three sets of parameters: (1) the initial state probabilities; (2) the state transition probabilities that included the probability of losing the GPS signal and the probability of survival; and (3) the probabilities of resight and recovery. The model included four underlying biological states: two states for live individuals, coded Aa (alive with active GPS) and Ai (alive with inactive GPS), and two states for dead individuals, coded Ra (recently dead with active GPS signal); and LD (long dead).

The multievent model (see details in Appendix S1: Section S3) estimated the probabilities of transition between the states (GPS signal loss and survival) and the probabilities of the events (resighting and recovery). Given our knowledge of the system, our starting model considered the following constraints: initial state probability (τ) was certain for every individual, as all individuals started as alive with an active GPS device deployed ($\tau\_Aa = 1$). Because all recoveries were from individuals with active GPS loggers, we fixed the recovery probability as 1 ($r = 1$). Likewise, the probability of resighting individuals with active GPS devices was fixed to 1 ($p\text{Aa} = 1$). Finally, the model included migratory strategy (resident or migratory) in resighting probability because the probability of resighting individuals without the GPS signal was higher for residents than for migrants. We ran two models, the first model to estimate survival as a function of the migratory strategy with four levels: local, regional, Northwest Africa and sub-Saharan that could not estimate all the parameters due to the small sample size. Thus, we ran a second model, in which we only tested differences in survival between resident and migratory individuals. To test whether there were significant differences between migratory and resident individuals we compared Quasi-Akaike Information Criterion (QAIC) values between this model and a null model, where only recapture probability was influenced by migratory strategy. We ran a goodness-of-fit test (GOF [Choquet et al., 2009]) in R2UCARE (Gimenez et al., 2018) that suggested the presence of transience effects, but this was not significant ($\chi^2 = 9.3$, $df = 4$, p-value $= 0.052$). The remaining tests were not estimable. We used 2.52 as a VIF and used it to correct all models constructed in E-SURGE (Choquet et al., 2005).

RESULTS

We tracked 75 adult white storks (36 males and 39 females) using GPS/GSM loggers equipped with acceleration sensors during a total of 212 annual cycles (78 complete annual cycles), from 2016 to 2021. Individuals displayed four different strategies: they remained in Southwest Europe either locally (Figure 2a) or regionally (Figure 2b), or they migrated and overwintered in Northwest Africa (Figure 2c) or sub-Saharan Africa (Figure 2d). Overall, 58 individuals were residents spending the nonbreeding periods in Southwest Europe (9 locally and 42 regionally, and 7 changed across years), and 16 were migratory and spent the nonbreeding period in Africa (6 in Northwest Africa and 10 in sub-Saharan Africa). With one exception, adult white storks tracked over multiple years were consistent in their tendency to migrate.

Behavioral and energetic consequences of migration

Our results showed that the migratory strategy affected annual displacement (Figure 3a, migratory strategy: $\chi^2 = 313.743$, $p < 0.001$; number of GPS positions: $\chi^2 = 44.931$, $p < 0.001$), with sub-Saharan winterers traveling thousands of kilometers more than all the other storks (Appendix S1: Table S1). A similar pattern was observed in annual ODBA derived from the acceleration sensors (Figure 3b, $\chi^2 = 36.239$, $p < 0.001$): individuals migrating to sub-Saharan countries presented >20% higher ODBA than individuals that migrated to Northwest Africa or that remained in Southwest Europe (Appendix S1: Table S2). Finally, ODBA linked to foraging (Figure 3c, $\chi^2 = 23.172$, $p < 0.001$) and soaring (Figure 3d, $\chi^2 = 70.927$, $p < 0.001$) was also affected by the migratory strategy, but ODBA linked to resting and flapping was not (resting: $\chi^2 = 1.806$, $p = 0.614$; flapping: $\chi^2 = 1.287$, $p = 0.732$). Sub-Saharan migrants presented *a* ~ 10% higher ODBA while foraging, and *a* ~ 25% lower ODBA while soaring than residents and birds that migrated to Northwest Africa (Appendix S1: Tables S3 and S4).

The differences in ODBA could be partly mediated by differences in behavioral budgets. While the proportion of time devoted to foraging and flapping was similar across migratory strategies (Figure 4a; foraging:

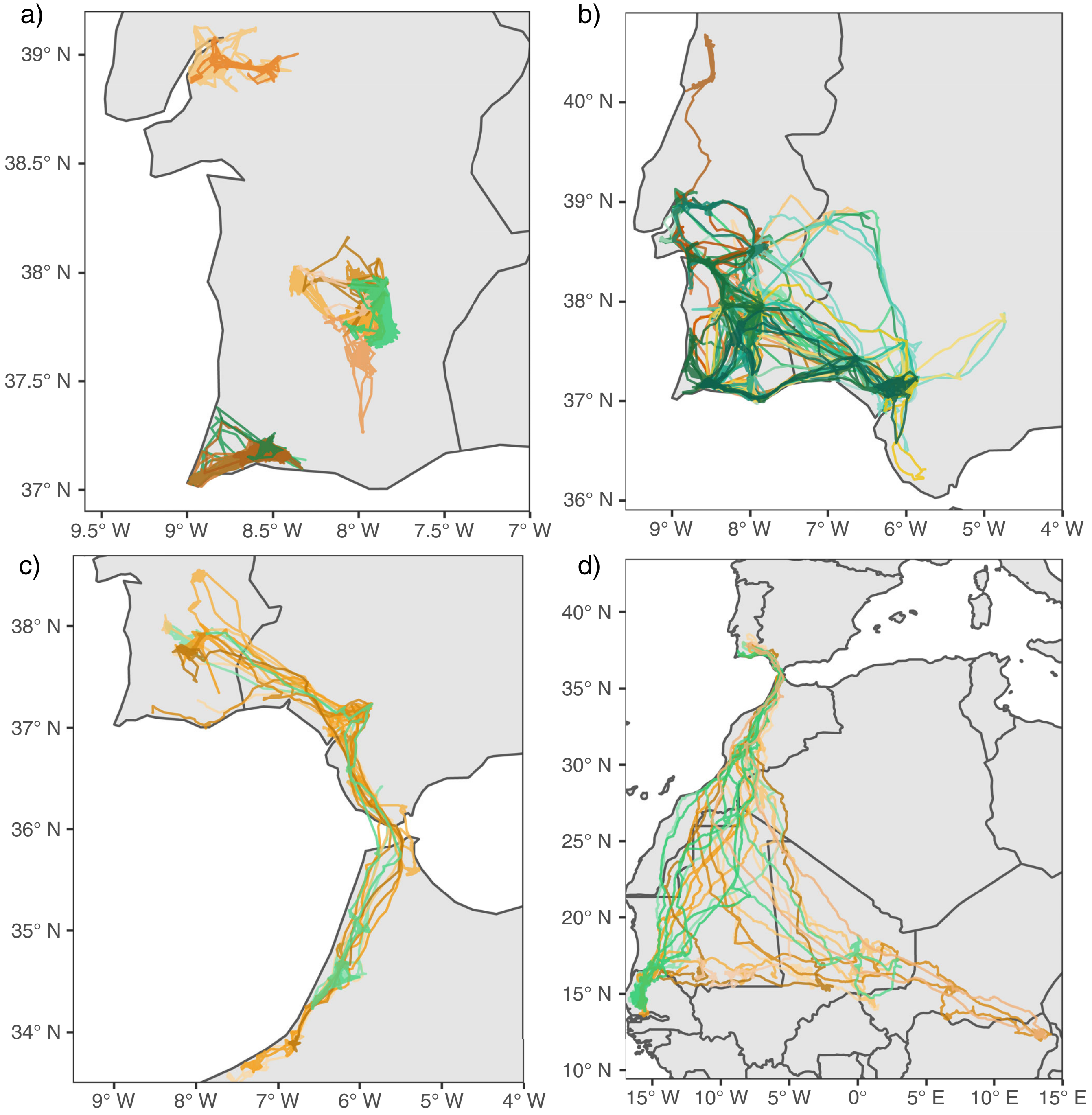

FIGURE 2 Migratory strategies of white storks breeding in Portugal that are resident (a) locally and (b) regionally, and those that migrate to (c) Northwest Africa and (d) sub-Saharan Africa. Shades of green represent males and shades of orange females.

$\chi^2 = 2.178$, $p = 0.536$; Figure 4d, flapping: $\chi^2 = 3.108$, $p = 0.375$), birds that migrated to sub-Saharan Africa spent overall less time resting (Figure 4b, $\chi^2 = 40.2$, $p < 0.001$; Appendix S1: Table S5) and more time soaring (Figure 4c, $\chi^2 = 227.54$, $p < 0.001$; Appendix S1: Table S6) compared with the remaining strategies.

Distance traveled varied depending on season ($\chi^2 = 10.391$, $p = 0.015$; Appendix S1: Figure S1) and migratory strategy ($\chi^2 = 408.161$, $p < 0.001$; Appendix S1: Figure S1), with a significant interaction between them ($\chi^2 = 275.684$, $p < 0.001$; Appendix S1: Figure S1). We controlled for the number of GPS positions ($\chi^2 = 47.154$, $p < 0.001$), and the duration of the season ($\chi^2 = 14.258$, $p < 0.001$). Sub-Saharan migrants traveled longer distances during autumn, spring, and winter than birds that adopted other strategies (Appendix S1: Figure S1, Table S7). ODBA also differed among seasons ($\chi^2 = 232.97$, $p < 0.001$; Appendix S1: Figure S2) and migratory strategies

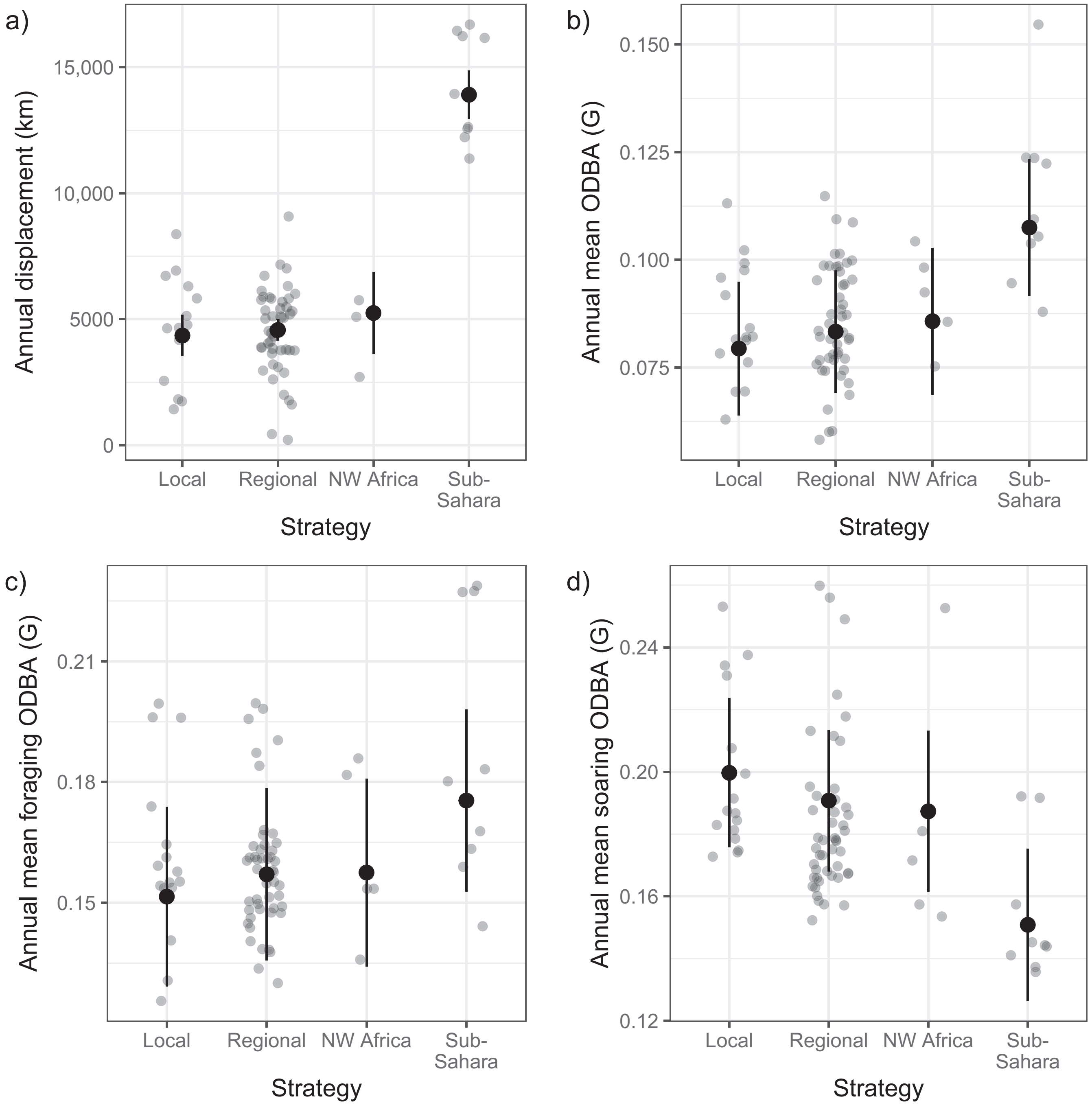

FIGURE 3 Relationship between the migratory strategy and (a) the annual displacement, (b) the annual mean overall dynamic body acceleration (ODBA) (G), and (c) the annual mean foraging ODBA (G). Black dots are predicted estimates from the linear mixed model, vertical lines are the 95% CIs based on fixed-effect uncertainty, and gray dots are raw data. NW Africa, Northwest Africa.

($\chi^2 = 136.40$, $p < 0.001$; Appendix S1: Figure S2), with a significant interaction effect ($\chi^2 = 174.66$, $p < 0.001$; Appendix S1: Figure S2). During both autumn and spring, migratory birds (including sub-Saharan and Northwest Africa winterers) presented higher ODBA than birds that remained in Southwest Europe (both locally and regionally; Appendix S1: Figure S2, Table S8). During the winter, sub-Saharan migrants continued to have higher ODBA than other birds, while during the breeding period all birds had similar levels of ODBA (Appendix S1: Figure S2, Table S8). We also found that ODBA during foraging and soaring varied depending on the season (foraging: $\chi^2 = 190.665$, $p < 0.001$; Appendix S1: Figure S3; soaring: $\chi^2 = 26.219$, $p < 0.001$; Appendix S1: Figure S4) and the migratory strategy (foraging: $\chi^2 = 54.181$, $p < 0.001$; Appendix S1: Figure S3; soaring: $\chi^2 = 40.801$, $p < 0.001$;

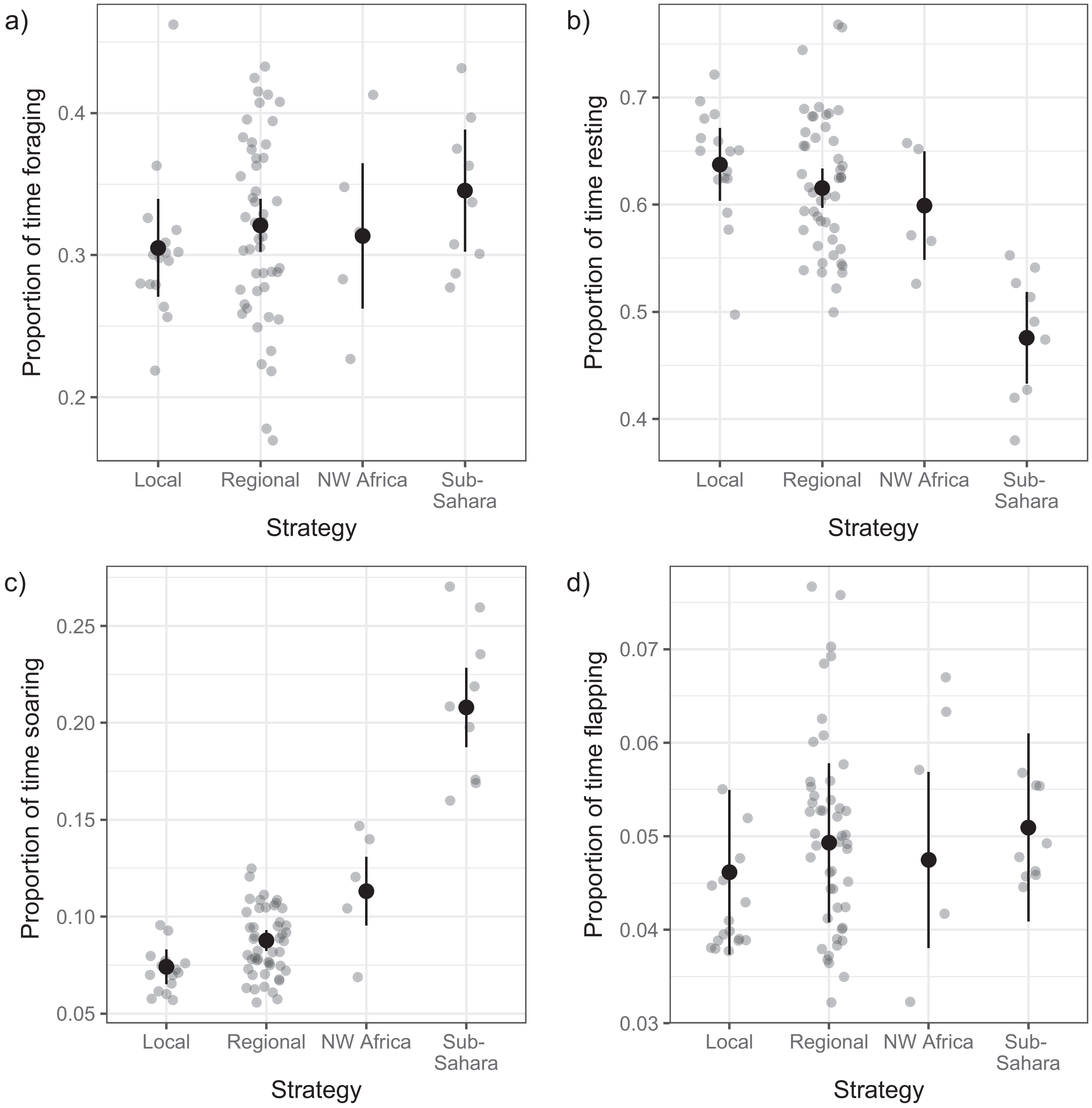

FIGURE 4 Relationship between white storks migratory strategy and the proportion of time (a) foraging, (b) resting, (c) soaring, and (d) flapping. Black dots are predicted estimates from the generalized linear mixed model, vertical lines are the 95% CIs based on fixed-effect uncertainty, and gray dots are raw data. NW Africa, Northwest Africa.

Appendix S1: Figure S4), with a significant interaction effect (foraging: $\chi^2 = 107.219$, $p < 0.001$; Appendix S1: Figure S3; soaring: $\chi^2 = 50.293$, $p < 0.001$; Appendix S1: Figure S4). Interestingly, sub-Saharan migrants had significantly higher ODBA while foraging during the autumn than resident birds, and during the winter in sub-Saharan Africa compared with the other strategies. In the other seasons, however, all birds presented similar levels of ODBA (Appendix S1: Figure S3, Table S9). By contrast, sub-Saharan migrants had significantly lower ODBA while soaring compared with residents and short-distance migrants during both migrations and the wintering period (Appendix S1: Figure S4, Table S10).

Migratory strategy and season also affected the proportion of time devoted to each behavior (Appendix S1: Figures S5–S8, Tables S11–S15). Sub-Saharan birds spent less time resting (Appendix S1: Figure S6, Table S16) and more time soaring (Appendix S1: Figure S7, Table S17) during both migrations and during winter. In addition, they allocated more time to foraging during the winter period and less during the spring (Appendix S1: Figure S5, Table S15). Birds that migrated to Northwest Africa, also increased soaring time and decreased resting time during both migrations, but their behavior during the winter period was similar to that of resident birds (Appendix S1: Figures S6 and S7, Tables S16–S18).

Breeding success

We did not find a direct link between migratory strategy and number of fledglings raised, but we did find an indirect relationship between these two variables (Table 1). The migratory strategy of each individual affected its arrival time to the nest location (Figure 5a, $\chi^2 = 25.697$, $p < 0.001$): birds that moved across Southwest Europe occupied the nest significantly later than birds that remained locally (Tukey's contrasts: local–regional $z = 3.092$, $p = 0.008$), whereas sub-Saharan migrants occupied their nest significantly later than resident birds (Tukey's contrasts: local–sub-Saharan $z = 5.021$, $p < 0.001$; regional–sub-Saharan $z = 3.364$, $p = 0.004$). In turn, a later occupancy of the nest led to a later laying date for those birds (Figure 5b; $\chi^2 = 9.756$, $p = 0.002$), which ultimately reduced breeding success, that is, birds laying eggs later raised a lower number of fledglings (Figure 5c; $\chi^2 = 4.874$, $p = 0.027$).

Survival

We did not find significant differences between residents (local and regional) and migrants (to Northwest and sub-Saharan Africa) in survival probability, as the null model including only the effect of migration in recapture probability presented a lower QAIC_c than the full model (null model $\text{QAIC}_c = 112.88$; full model $\text{QAIC}_c = 114.92$; $\Delta\text{QAIC}_c = 2.05$). However, the full model suggests that residents might be experiencing slightly higher survival than migrants (migrants: survival probability = 0.89, confidence interval [CI] = 0.65–0.97; residents: survival probability = 0.91, CI = 0.83–0.95; Figure 5d), but a larger sample size would be needed to confirm this. The probability of recapture when the signal had been lost was much lower for migrants (0.14) than residents (0.63).

Phenotypic differences in migration strategy

We found that migration probability was affected by wing length, a proxy for individual size ($\chi^2 = 8.371$, $p = 0.004$), but was not affected by sex ($\chi^2 = 0.641$, $p = 0.423$), or the interaction of wing length and sex ($\chi^2 = 0.142$, $p = 0.706$). The significant negative relationship between wing length and migration probability shows that larger birds were more likely to be resident while smaller birds tended to be migratory (Figure 6).

DISCUSSION

In this study we showed the behavioral and energetic trade-offs of different migratory strategies throughout the whole annual cycle of a long-lived bird. While we do not find a direct effect of migration strategy on fitness, we did find that migratory birds occupied their nests later, and later occupation led to delayed laying dates and a lower number of fledglings. We also found that trans-Saharan migrants traveled longer annual distances, spent more time flying and less resting, and incurred higher energetic costs than storks adopting other movement strategies. By contrast, individuals that migrated to Northwest Africa did not differ in behavior or energy expenditure from resident birds (except during spring and autumn). These results are in concordance with previous evidence from juvenile white storks that suggested that wintering in Europe was less demanding compared with sub-Saharan Africa (Rotics et al., 2017).

The behavioral and energetic contrast between birds wintering in Southwest Europe or Northwest Africa and birds traveling to the Sahel is particularly acute during

TABLE 1 Analysis of variance for the structural equation model to establish the direct and indirect relationship between the migratory strategy and the reproductive success.

Response	Predictor	*F*-statistic	*df*	*p*
Nest occupation date	Migratory strategy	25.7	3	**<0.001**
Laying date	Nest occupation date	9.8	1	**0.0018**
No. fledglings	Laying date	5.1	1	**0.0239**
No. fledglings	Migratory strategy	5.1	1	0.0640

Note: Bold values represent $p < 0.05$.

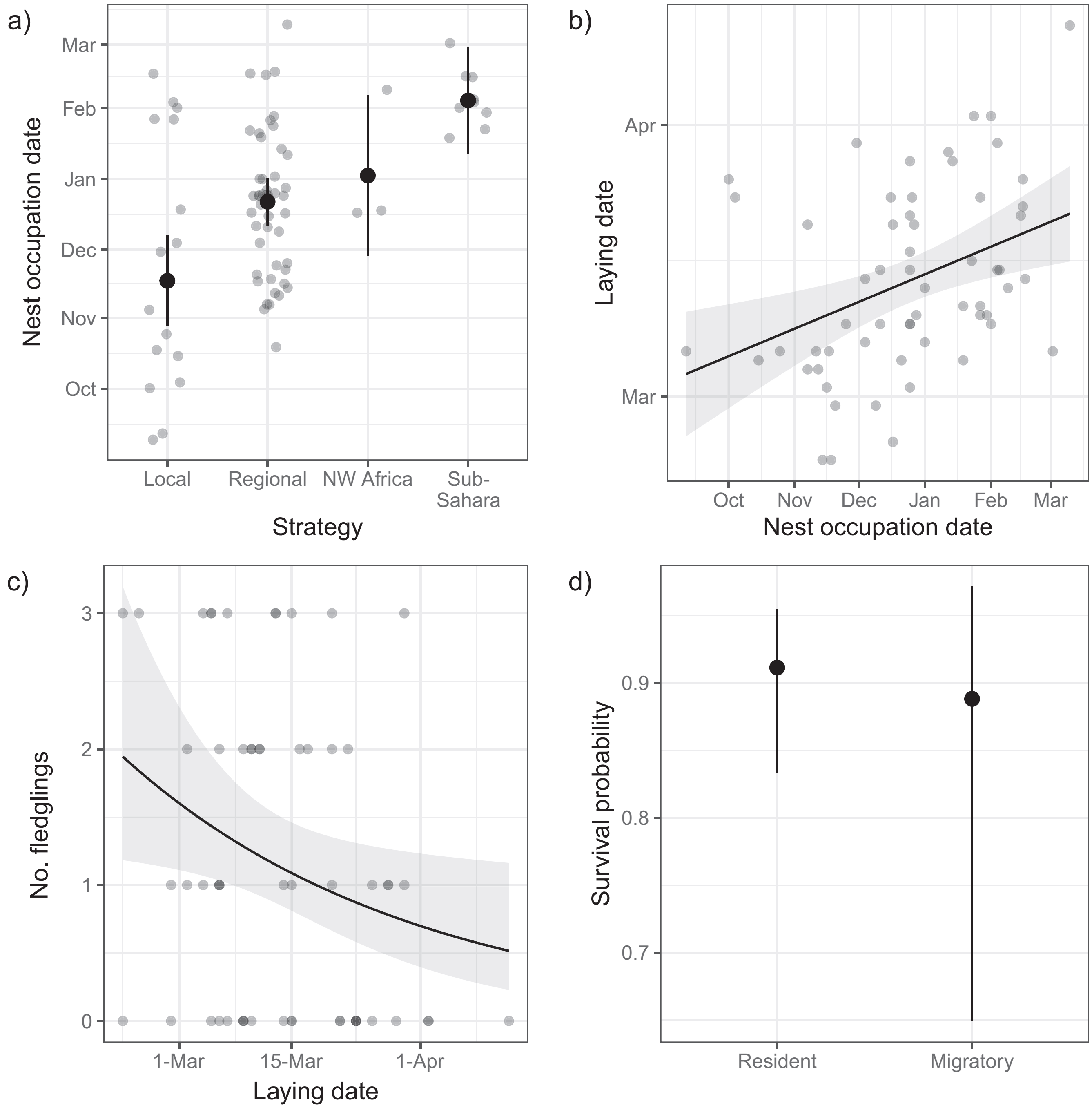

FIGURE 5 (a) Relationship between white storks migratory strategy and the nest occupation date. (b) Relationship between the nest occupation date and the laying date. (c) Relationship between the laying date and the number of fledglings. (d) Survival probability depending on whether the individual remains resident (locally or regionally) or migrates (to Northwest or sub-Saharan Africa). Black dots and black lines are predicted estimates from the (generalized) linear mixed model and multievent capture–recapture model, vertical lines and gray shades are the 95% CIs based on fixed-effect uncertainty, and gray dots are raw data. NW Africa, Northwest Africa.

the winter, but also during spring and autumn, whereas during the breeding period all birds have a similar energy expenditure and behavior. These differences are likely to occur due to several factors. First, the Sahel is 2500 km away from the breeding grounds and reaching this wintering area requires substantial investments in terms of time and energy. Nevertheless, our results also showed that thermal conditions in the Sahel are likely to be more favorable, as reflected by the lower ODBA estimates of individuals while soaring (Flack et al., 2016). Previous evidence from juvenile white storks from Southwest Germany showed similar results, with individuals

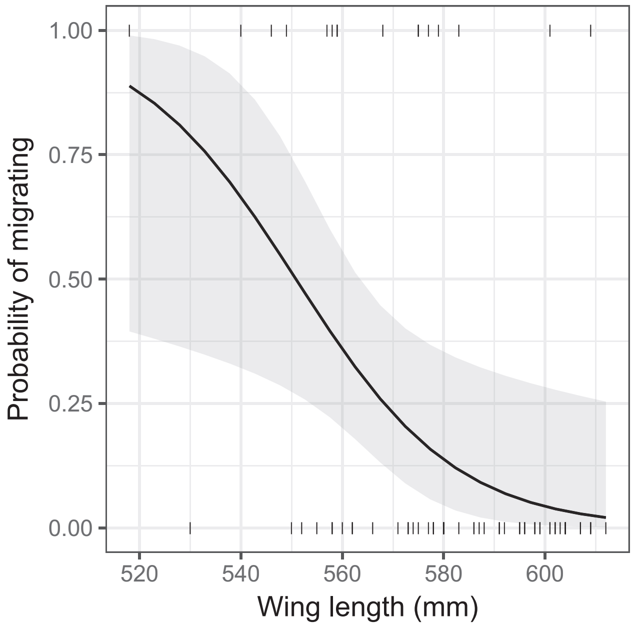

FIGURE 6 Relationship between white stork wing length (in millimeters) and the probability of migrating to Northwest Africa and sub-Saharan Africa. Shading represents 95% CIs and vertical bars are raw data.

overwintering in Northwest Africa moving less during stopover days and having lower ODBA values compared with birds wintering south of the Sahara (Flack et al., 2016). By contrast, residents and individuals that overwintered in Northwest Africa had access to low-cost foraging areas at landfills throughout the year (Ciach & Kruszyk, 2010; Flack et al., 2016; Marcelino et al., 2023), while sub-Saharan migrants forage on natural prey in the Sahel (Elliott et al., 2020), which is likely to be energetically more expensive, as reflected by their higher foraging ODBA. Finally, the longer daylight availability in the Sahel region, compared with Southwest Europe and Northwest Africa during the nonbreeding period, could enable sub-Saharan individuals to increase their diurnal movement activities (Pokrovsky et al., 2021).

Our results show that trans-Saharan migrants present higher ODBA, a proxy for energy expenditure, than storks adopting other movement strategies, but we could not quantify the absolute or relative differences in energy expenditure between migratory strategies, as we could not calibrate the relationship between ODBA and energy expenditure (Halsey & Bryce, 2021). Data on the daily energy expenditure of juvenile white storks (quantified using continuous heart rate and fine-scale movement tracking of the individuals) show that their heart rate increases linearly with ODBA and supports our conclusions (Flack et al., 2020). However, other physiological factors may also influence energy expenditure, the costs for thermoregulation and hydroregulation can be significantly different for individuals overwintering in Southwest Europe and Northwest Africa compared with those in the Sahel affecting the overall higher energy expenditure (Cabello-Vergel et al., 2021). Finally, we could not record other components of energy balance, such as energy intake, which is likely to differ substantially among individuals overwintering in different areas and with different accessibility to landfill resources.

Notably, our results showed that smaller sized individuals are more likely to migrate than larger sized ones, a pattern that is highly consistent over time (i.e., birds used the same wintering grounds every year). However, given the correlational nature of the analysis, we could not establish a direct causality between size and migratory strategy. Nevertheless, several hypotheses could explain these behavioral differences. Smaller birds may be outcompeted at landfill sites, as in these areas birds gather in large numbers that exacerbates competition and aggression (Gilbert et al., 2016; Soriano-Redondo et al., 2021). An alternative, nonexclusive explanation is that smaller individuals are more sensitive to harsher wintering conditions in Southwest Europe and migrate to warmer areas in the Sahel.

Our results suggest that differential fitness between migratory and resident birds is likely to exist and might have influenced the recent increase in the ratio of resident to migratory individuals in the population (Catry et al., 2017). As larger birds tend to be residents, occupy the nest earlier and thus are more likely to reproduce, this could be favoring an overall increase in body size in the population, potentially increasing the prevalence of residency. However, the fast-ongoing population transition toward full residency suggests that other factors may be involved as well. We did not find differences in survival between residents and migrants, but this should be further investigated with larger sample sizes, as the probability of recapture when the GPS signal had been lost was much lower for migrants than residents, and could partially mask the effects on survival.

The availability of landfill waste in Portugal and Spain is expected to decrease substantially in the next few years, as recent EU directives (1999/31/UE and 2018/850/UE) regulating waste disposal have established a reduction of municipal waste landfilled to 10% in the next decade. A dramatic decrease in food availability in the main European wintering areas can have unforeseen consequences for white stork populations. Yet, based on our findings, we predicted an increase in migratory propensity, with only larger individuals being able to remain on the breeding grounds throughout the year. Carry-over effects may include increased mortality and reduced reproduction success, which could slow down the current increase in population numbers and might even lead to a decrease in population size. Our results highlight the nuances of anthropogenic impacts on species behavior, fitness, and evolutionary dynamics.

AUTHOR CONTRIBUTIONS

Andrea Soriano-Redondo, Aldina M. A. Franco and Inês Catry designed the study. Andrea Soriano-Redondo and Ana Payo-Payo performed the analyses. Aldina M. A. Franco, Marta Acácio, Bruno Herlander Martins and Inês Catry collected data. Andrea Soriano-Redondo wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Tracking data (Soriano-Redondo et al., 2023) are available from Movebank at https://doi.org/10.5441/001/1.283.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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