The determinants of dispersal and migratory movements of long-lived birds

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Abstract

Individual movement is influenced by many factors, from intrinsic individual traits to extrinsic environmental conditions. These can determine the onset, duration, and direction of movements, with potential consequences for individual fitness, adaptation to on-going environmental change and, ultimately, species conservation. In this thesis, I combine GPS tracking technology and accelerometery, with remote sensing and weather data, aiming to explore the drivers and mechanisms underlying the movement behaviour of long-lived bird species. The detailed study of individual movement has highly profited from technological advances in GPS tracking equipment, and, here, I show that the accuracy of these devices is not negatively affected by their deployment on large birds. In the first study of the movement ecology of Shoebills *Balaeniceps rex*, I show that their movements are determined by changes in surface water, suggesting different habitat use between adult and immature Shoebills. By exploring the long-distance autumn migrations of White Storks *Ciconia ciconia* travelling over a three-month period, I show that the timing of migration determines the weather conditions storks find *en route*, with implications for migratory performance, energy expenditure, and migration destination. Finally, I describe the ontogeny of migratory strategies of White Storks, to further increase our understanding on the mechanisms underlying this species recent loss of migratory behaviour. I show that the use of anthropogenic food subsidies does not influence the migratory strategy of immature storks, instead storks with lower flight and migratory performance are more likely to decrease migratory distance and become resident. Overall, this research adds to the understanding of how birds respond to the environmental conditions and emphasizes the importance of long-term tracking to study individuals throughout their lives. Additionally, it provides new insights on the mechanisms through which species are adapting to environmental change and highlights the role of individual experience on the loss of migratory behaviour.

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– Chapter 1 –

General introduction

Standing there on the embankment, staring into the current, I realized that

– In spite of all the risks involved –

a thing in motion will always be better than a thing at rest; (…)

that which is static will degenerate and decay, turn to ash,

while that which is in motion is able to last for all eternity.

– Olga Tokarczuk –

1.1 Animal movement and migration

Movement is ubiquitous across the animal world, from small zooplankton performing diel vertical movements in the ocean water column, to large elephants moving across the savannahs. Animal movement has effects on all ecological levels: it affects the moving individual, promotes or impedes intra and inter-specific interactions, it shapes the distribution of populations, and the flow of nutrients, propagules, and pathogens across ecosystems (Shaw, 2020). Animal movement can be subdivided into four basic mechanistic components: i) why individuals move (which asks questions on the internal state of organisms), ii) how do individuals move (analysing the locomotion of individuals), iii) when and where individuals move (studying the navigational skills), and finally iv) what are the external factors that may determine and influence individual movement (e.g., biotic factors – predators and resources, and abiotic factors – environmental conditions and landscape) (Nathan et al., 2008).

The movement ecology of birds has been widely studied, as they are an excellent group to address these questions: bird movements and migrations are fascinating, most species are easy to visually identify in the field, and, through bird ringing and tracking, it is also possible to identify individual birds (Newton, 2008). Whilst birds are generally referred to being either resident or migratory, there are several types of bird movements, including small everyday movements, mostly related to foraging or intra- and inter-specific interactions, larger dispersive movements, including post-breeding dispersal, erratic nomadic movements, and predictable seasonal round-trip migratory movements, often involving several thousand of kilometres (Mueller & Fagan, 2008; Newton, 2008; Shaw, 2020).

Migration is a fascinating phenomenon due to the large scale of the movements observed and the large number of animals that conduct these periodic movements. These long-distance movements are likely driven by the need to track spatially and temporally varying food sources (Somveille et al., 2015), while also avoiding harsh climatic conditions (Boyle et al., 2010). Migration has evolved separately in many animal groups and is likely expressed when the benefits outweigh the costs (Alerstam et al., 2003). An obvious and very important benefit of migration is the occupancy of areas when foraging resources are abundant, and avoidance of areas when resource availability is low, reducing intra-specific competition (Furey et al., 2018; Teitelbaum & Mueller, 2019) and increasing winter survival (Newton, 2008; Winger & Pegan, 2021).

To migrate from the breeding to the non-breeding grounds, species have evolved morphological and physiological adaptations which enable efficient energy accumulation and locomotion, as well as behavioural adaptations that allow for the optimal use of environmental factors (e.g., winds and orientation cues) (Åkesson & Hedenström, 2007; Newton, 2008). Moreover, many young birds migrate thousands of kilometres guided by an inherited genetic program (Åkesson & Helm, 2020; Liedvogel et al., 2011), containing information on the time, direction, and distance of the migratory movements (Thorup et al., 2007, 2020). However, within-population variation in migratory routes and timing is common and can derive from genetic variation in the migratory program, but also from individual interactions with social and environmental factors (Åkesson & Helm, 2020).

In the Northern Hemisphere, a large number of bird species is migratory (Somveille et al., 2015) and many perform long-distance migrations across continents. These long, energy expensive migratory journeys can be dangerous, with risks encountered *en route* (e.g., predation, stochastic weather events), or at arrival at the distant and often unknown wintering grounds. It is therefore not surprising that migration is the season of highest mortality for several species (Buechley et al., 2021; Lok et al., 2015), and that many migratory species seem to be declining (Vickery et al., 2014), whilst species with more diverse movement strategies seem to be more resilient to environmental change (Gilroy et al., 2016).

1.2 The determinants of movement

Individual movement is determined and influenced by many biotic and abiotic factors, such as body condition, competition, environmental factors, amongst others (Nathan et al., 2008). These can establish but also affect the onset, duration, and direction of movements, at small and large spatial scales. For instance, food deprivation can determine the everyday movements of birds (Spiegel et al., 2013) but delay the onset of large migratory movements (Cooper et al., 2015), and the presence of water can govern the short-distance movements of waterfowl (Kleyheeg et al., 2017) but also induce large migratory movements at a continental scale (Roshier et al., 2002).

Timing of movements

The timing of movements, particularly long migratory movements, is crucial to ensure the success of the journey. The onset of migratory movements depends on a variety of cues, both internal (e.g., fuel stores, knowledge of the route) and environmental (e.g., day length, wind direction, social factors) (Alerstam et al., 2003; Winkler et al., 2014), and the phenology of migratory movements has been shaped to enable individuals to take advantage of predictable environmental phenomena during migration and in their destinations (Alerstam et al., 2003; Shamoun-Baranes et al., 2017). In fact, when long-distance migrants start their migratory movements, they use local indicators that allow them to anticipate the conditions in distant sites and at later times (Winkler et al., 2014).

The timing of migration determines the conditions birds find on arrival at the wintering and breeding grounds. If birds arrive too early the boom of foraging resources may have not yet occurred, if they arrive too late the environmental conditions may already have deteriorated, and food availability may be decreasing (Samplonius et al., 2021), which can have detrimental consequences for population growth rates (Both et al., 2006). When arriving at the breeding grounds, early birds may have access to better nest sites and mates (Kokko, 1999), leading to higher breeding success (Gilsenan et al., 2020), but may face worse weather conditions *en route*, leading to higher energetic costs during migration (Rotics et al., 2018).

Many bird species show high individual consistency in the timing of migration (e.g., Gill et al., 2014; Gilsenan et al., 2020), evidencing that endogenous cues govern the start of migratory journeys (Åkesson & Helm, 2020). However, there are also species with individuals capable of adjusting the start of migratory movements in response to environmental conditions, for example, by delaying the start of spring migration if the environmental conditions in the wintering areas are poor and there is lower prey availability (Schlaich et al., 2016; Studds & Marra, 2011). Moreover, some species can adjust their migratory timing to the conditions experienced in the previous year, suggesting a mechanism through which long-distance migrants may be able to adjust the migration phenology to environmental change (Amélineau et al., 2021). Additionally, important shifts in population phenology may arise through individual flexibility in migratory timing (Conklin et al., 2021), therefore it is crucial to understand how environmental conditions influence individual migratory timing, routes and overall migratory behaviour.

Environmental conditions

The environmental conditions individuals experience can determine their movement behaviour, influencing every-day and dispersal movements, as well as long-distance migratory movements. In fact, environmental conditions are the main architects of long-distance migratory movements: changes in climate and food available formulate the onset of migration

(Somveille et al., 2015), whilst landscape features, such as ecological barriers or resource distribution, and weather *en route* shape the migratory flyways (Kranstauber et al., 2015; Vansteelant et al., 2021; Ventura et al., 2020).

Landscape features, such as the presence of ecological barriers (mountain ranges, oceans, or deserts) can significantly alter the movement behaviour of individuals, particularly during long-distance migration. Ecological barriers can impede movement (Santos et al., 2020), cause birds to create detours in their migratory routes (Vansteelant et al., 2017), but it can also lead to changes in movement behaviour, for example, by increasing the length of time birds fly per day (Efrat et al., 2019), or through the induction of non-stop flight behaviour (Gill Jr et al., 2009). On the other hand, when foraging resources are available in the landscape, birds can change their migratory behaviour, by adopting a “fly-forage” migratory strategy (Klaassen et al., 2008).

Weather is extremely important in determining when, to where and how movement occurs (Shamoun-Baranes et al., 2017). Lesser Black-backed Gulls *Larus fuscus* select their foraging habitat according to the weather conditions (Isaksson et al., 2015; Sotillo et al., 2022) and periods of intense rainfall may incite the nomadic movements of waterfowl in semi-arid landscapes (Roshier et al., 2002). Weather conditions can provoke the onset of migration (e.g., daily temperature, Burnside et al., 2021), and enhance migratory performance, by increasing daily speeds and displacements (e.g., tailwinds, Shamoun-Baranes et al., 2003), but it can also hamper migratory progression (Pastorino et al., 2017) and even lead to mortality (Loonstra et al., 2019).

Winds are particularly important during migratory movements, as they can allow birds to fly more efficiently (Bohrer et al., 2012) and minimise energy expenditure (Amélineau et al., 2014; Duriez et al., 2014). Winds can also shape migratory routes (Kranstauber et al., 2015), promote unintended detours (Patchett & Cresswell, 2020) and determine bird’s wintering areas, ultimately influencing population migratory connectivity (Norevik et al., 2020; Vansteelant et al., 2017).

In summary, environmental conditions are crucial in determining bird's movement behaviour, yet how these determine the movement strategies of long-lived birds as they age is not fully known. Moreover, how individuals respond to their environment depends on a number of individual traits, from their age (Harel et al., 2016) to their body condition (Cooper et al., 2015). Only by combining individual and environmental features in movement ecology studies, will it be possible to understand how movement patterns emerge and what mechanisms lead to the development of different migratory behaviours (Shamoun-Baranes et al., 2017).

Individual traits

The internal state of individuals (e.g., health and body condition), or their characteristics (e.g., body size and sex), can have profound effects on their movement behaviour. For example, hunger shapes the individual movement patterns of Griffon Vultures *Gyps fulvus* (Spiegel et al., 2013), and the overall body condition of individuals may influence the migratory decisions of birds (Schmaljohann & Naef-Daenzer, 2011), with lean individuals delaying migration departure (Cooper et al., 2015) or avoiding crossing ecological barriers (Smolinsky et al., 2013). Additionally, individual body size can also impact the movement decisions of the individuals: smaller individuals may be more prone to migrate as a result of their inability to tolerate cold temperatures (Belthoff & Gauthreaux, 1991) or their failure to successfully compete for foraging resources or territories (Smith & Nilsson, 1987).

Individual's sex is often highly correlated with body size and may also determine their movement behaviour. During migration, different sexes may adopt different routes (Deakin et al., 2019), may migrate at different times of the year (Briedis et al., 2019) and even winter in different areas (Bell et al., 2021). However, having sex-specific movement or foraging strategies may disproportionally expose certain individuals to greater risks (Ferrer & Hiraldo, 1992). For example, female Brown Skuas *Catharacta antarctica lonnbergi* forage more frequently on agricultural fields than males, which makes them more vulnerable to culling by farmers (Schultz et al., 2021).

Overall, individual flexibility in movement and foraging behaviour, may increase species resilience to environmental change, when compared with species with less plastic behaviours (Bell et al., 2021; Gilroy et al., 2016). For long-lived species, this flexibility can occur throughout the individual's life, therefore it is important to understand how individuals interact with their environments as they age, and how past experiences may determine the movement strategies adopted in consecutive years.

1.3 The ontogeny of movement

The study of the ontogeny of movement aims to determine how individuals move and interact with their environment as they mature. Overall, older individuals select better foraging locations (Riotte-lambert & Weimerskirch, 2013), have higher foraging efficiency (Fayet et al., 2015; Grecian et al., 2018), better migratory performance (Rotics et al., 2016; Sergio et al., 2014) and are superior at taking advantage of environmental conditions (Harel et al., 2016).

Long-lived birds, in particular, have the ability to learn from past experiences and improve their migratory performance throughout their maturation stage (Campioni et al., 2020; Sergio et al., 2014). Moreover, flock-living birds also have the possibility of learning from conspecifics: Greater Snow Geese *Anser caerulescens atlanticus* select alternative stopover sites, depending on the expected disturbance cause by hunting (Béchet et al., 2003) and younger Whooping Cranes *Grus americana* learn from older individuals new wintering grounds, significantly decreasing the distance they must undertake during migration (Teitelbaum et al., 2016). In some species, juveniles on their first migration are so dependent on the presence of conspecifics that are not able to successfully complete their migration if travelling alone (Chernetsov et al., 2004). Nevertheless, not all species migrate in flocks, and many birds must embark on their first and later migrations without conspecifics.

Migratory performance improvements with age

For many species, the period between fledging and the start of their first migration is quite short, occasionally only a few days long (Wynn et al., 2021). In this brief period, birds must learn to forage and fly with enough efficiency that will allow them to survive on their first migration. Thus, it is unsurprising that first year juveniles have worse migratory performance than adults (Mellone et al., 2013), likely as a result of the poorer navigational skills (Åkesson et al., 2005), slower migratory speeds (Sergio et al., 2014) and poorer flight performance (Harel et al., 2016), with lower soaring/flapping ratios and thus higher flight energetic costs (Rotics et al., 2016).

The first migration is of particular importance as it can establish routes and stopover areas used in subsequent migrations (Åkesson & Weimerskirch, 2005). During their first year, juveniles seem to quickly improve their overall flight performance: White Storks *Ciconia ciconia* on their first autumn migration gradually decrease the amount of energy they spend when flying until resembling adults when arriving at the wintering grounds (Rotics et al., 2016). Likewise, young Wandering Albatrosses *Diomedea exulans* achieve the same daily movement speeds as adults approximately 6 months after fledging (Weimerskirch et al., 2006).

Despite this fast development, it can take several years before birds reach their full migratory performance (Campioni et al., 2020). Few studies manage to track individuals throughout their whole maturation stage, but Sergio et al., 2014 showed an improvement in migratory skills of Black Kites *Milvus migrans* on birds between 1-27 years of age. However, this gradual improvement was slower than previously expected, as it took 7 years for kites to become highly repeatable and efficient in their migratory journeys. Additionally, at the population level, this overall improvement was a combination of individuals enhancing their migratory skills and the selective mortality of the birds with worse performance, mainly in the early life stages (Sergio et al., 2014).

Handling environmental conditions in different life stages

On the first post-breeding migration, birds are likely driven by a strong endogenous program (Wynn et al., 2021) which can lead young birds along similar routes as adults (Thorup et al., 2020). However, this is not always the case, and juvenile birds can show a more diverse range of migration orientations than adults (Åkesson et al., 2005). For example, juvenile Honey Buzzards *Pernis apivorus* migrate independently and display a higher variety of routes than adult birds, including in the crossing of water bodies (Hake et al., 2003). Moreover, for juvenile Honey Buzzards, their wintering area is strongly dependent on the winds experienced on migration (Vansteelant et al., 2017), which can be partially explained by the worse ability of juvenile birds to compensate for wind drift (Thorup et al., 2003).

Nonetheless, juvenile birds seem to have an innate ability to cope with the environmental conditions. For instance, juvenile Wandering Albatrosses select the departure dates in relation to the suitable winds (Åkesson & Weimerskirch, 2005). In fact, when faced with suitable environmental conditions, inexperienced birds can perform nearly as well as adults when foraging (e.g., day-light foraging in albatrosses, Pajot et al., 2021) and flying (e.g., Griffon Vultures climbing rates in thermals in low wind shear, Harel et al., 2016). It is only when the environmental conditions are more challenging (e.g., night-time foraging or stronger wind shears) that the differences between these two age groups are exacerbated (Harel et al., 2016; Pajot et al., 2021), which may constrain juvenile's adaptation to new and tougher environments. Studying long-lived species and analysing their age-related and individual responses to diverse environmental conditions, can thus help understand the mechanisms that enable species' adaptation to global environmental change.

1.4 Understanding recent shifts in movement behaviour in response to global environmental change

Human-induced change in climate and distribution and quality of habitats can severely impact the avifauna around the world, culminating in losses of over 500 million of individual birds since the 1980s in the European Union alone (Burns et al., 2021). Long-distance migrants are disproportionally affected by environmental change (Vickery et al., 2014), particularly those species that are not being able to adjust their migratory behaviour (Møller et al., 2008). However, species that can retain some migratory diversity (i.e., within-population diversity in migratory movements and destinations) are less vulnerable to environmental change when compared to full migrants or residents (Gilroy et al., 2016).

Birds have the ability to rapidly adapt to new environmental conditions, and species have been changing their migratory behaviour, phenology, and distance (Gordo, 2007; Wilcove & Wikelski, 2008). Spectacular examples include drastic shifts in breeding grounds (e.g., over 8,000km shift in the range of Cliff Swallows *Petrochelidon pyrrhonota*, Areta et al., 2021), or even the loss of migratory behaviour altogether, with the establishment of resident populations in previously fully migratory species (e.g., White Storks in Iberia Catry et al., 2017).

Species migratory behaviour can constrain their phenological response to environmental change, as long-distance migrants seem to be slower at advancing their migratory and breeding phenology than short-distance migrants or residents (Rubolini et al., 2010; Samplonius et al., 2018). Long-distance migrants are also more vulnerable to the loss of critical stopover sites while on migration, and the disappearance or degradation of these sites can induce population declines in migratory birds (Xu et al., 2019). Nonetheless, environmental changes that improves climate suitability and food availability in the breeding areas during the non-breeding season, allowing for the year-round settlement of individuals in the breeding grounds and creating partial migratory populations, may lead to the increase of population size in otherwise endangered species (Catry et al., 2017).

Predictable anthropogenic food subsidies

Another example of how human activities have been shaping communities and ecosystems is through the provisioning of predictable anthropogenic food subsidies (PAFS) to animals (Oro et al., 2013). These PAFS can take a variety of forms and can be deliberate (e.g., bird feeders or animal feeding in public parks) or incidental (e.g., landfills and fishery discards), but all influence individuals, communities, and ecosystems by changing processes such as competition, predator-prey interactions, and nutrient and disease transfer between biomes (Oro et al., 2013). These food subsidies can also buffer opportunistic species from natural variation in resource availability (Sotillo et al., 2022), allowing these species to increase and/or maintain large population sizes.

Globally, humans waste 30-40% of the produced food (Oro et al., 2013; Parfitt et al., 2010), which may become available for birds and other animals in open air landfills and rubbish dumps. Species are taking advantage of this abundant food resource, leading to changes in species distribution (Tauler-Ametller et al., 2017) as well as in their movement and foraging behaviours (Gilbert et al., 2016). Despite the risks of foraging on landfills (e.g., increased mortality risk by collision with powerlines (Marcelino et al., 2021), there are several advantages in relying on landfills. There, the food is abundant and predictable, thus foraging on landfills can be an energy-saving strategy: White Storks feeding in these areas spend less time foraging and spend less energy overall, even when accounting for the extra distance they must travel to access the landfills (Soriano-Redondo et al., 2021). Consequently, birds relying on landfills have increased body mass (Plaza & Lambertucci, 2018) and experience fewer food shortages (Tauler-ametlller et al., 2019) than birds foraging on natural areas.

However, the regulations on waste management are changing, with the aim of reducing the amount of waste that is being deposited on open air landfills in Europe. In May 2018, the European Commission adopted a new target to reduce landfill deposits to a maximum of 10% of municipal waste by 2030 (EU Directive 2018/851). This change in food availability will surely impact the species that have become reliant on this resource, and species will have to alter their foraging habits (Zorrozua et al., 2020). Although Katzenberger et al., 2019 did not find a negative effect of landfill closure on Egyptian vulture *Neophron percnopterus* breeding success a year after closure, other studies have found that landfill closure decreased the breeding success and adult body mass in Yellow-legged Gulls *Larus michahelis* (Steigerwald et al., 2015) and increased the foraging effort of Lesser Black-backed Gulls (Langley et al., 2021). Therefore, it is critical to understand how individuals and populations are adapting to these rapid changes in environmental conditions.

Mechanisms of adaptation to environmental change

Birds are adapting their migratory behaviour in response to environmental change. At the population level, these adaptations can occur through evolutionary processes, which is generally a slow mechanism as it is driven by the consequences of individual actions, or through phenotypic plasticity, which can be a fast mechanism of adaptation to rapid environmental change (Charmantier et al., 2008; Charmantier & Gienapp, 2014; Winkler et al., 2014).

In general, the mechanisms through which changes in migratory behaviour can occur have been combined in 3 different processes: i) inherited genetic or epigenetic changes that influence migratory behaviour (e.g., Pulido & Berthold, 2010); ii) adult phenotypic flexibility, in which matured individuals can adapt the migratory behaviour to environmental conditions (e.g., Conklin et al., 2021); iii) and developmental plasticity, in which individuals adapt their behaviour irreversibly during the maturation stage (e.g., Gill et al., 2013; Verhoeven et al., 2018).

Quantifying the heritability of migratory traits is not easily accomplished, in the wild or in captivity, but for many nocturnal migratory birds, nocturnal restlessness (*Zugunruhe*) has been used to estimate the heritability of the onset, end, and duration of migratory movements, as well as of migratory propensity (Fudickar et al., 2021; Merlin & Liedvogel, 2019; Pulido & Berthold, 2010). For example, through the selective breeding of Blackcaps *Sylvia atricapilla* in captivity, Pulido & Berthold, 2010 showed a genetic reduction in migratory activity and found that, if the fitness of the residents is high enough, a fully migratory population can thus become fully resident. However, if a resident population retains substantial genetic variation related to the migratory behaviour, subsequent reversals could occur as well (de Zoeten & Pulido, 2020).

When the conditions in the environment change over short periods of time, some species reversibly adapt their migratory behaviour or phenology to the new conditions, which is referred to as phenotypic flexibility (Piersma & Drent, 2003). For example, individual American Redstarts *Setophaga ruticilla* can adjust the timing of spring migration on a year-to-year basis, according to the food availability at the wintering sites, which varies with rainfall (Studds & Marra, 2011). Adult birds can also use previously experienced conditions to adapt their migratory decisions (Sergio et al., 2014), and, for social migratory species, this experience may be passed on to others by social interactions (Mueller et al., 2013). This individual flexibility in the migratory behaviour can be enough to drive long-term and directional changes in population behaviour (Conklin et al., 2021).

Nonetheless, many species seem to be consistent in their migratory behaviour at the individual level (Gill et al., 2014; Gilsenan et al., 2020). In such cases, changes in migratory behaviour at the population level can derive from an inter-generational shift in migratory traits, resulting from the environmental conditions juveniles experience during maturation (Gill et al., 2014). This mechanism may be particularly important for long-lived species with long developmental stages, during which drastic changes in environmental conditions during the maturation process may occur. For example, in two sub-species of Black-tailed godwits *Limosa limosa islandica* and *Limosa limosa limosa*, the staging sites used during migration and the timing of arrival at the breeding grounds have been changing during the past decades, despite individual consistency in migration phenology and route (Gill et al., 2014; Verhoeven et al., 2018, 2021). Instead, these population changes seem to derive from changes in migration timing and staging site used by younger individuals. However, the individual mechanisms or environmental cues that lead juvenile birds to change their migratory behaviour are still unclear.

In summary, different species seem to respond differently to similar environmental challenges, and the role of these three processes in shaping species adaptations is still unclear. Studying how bird movement behaviour varies throughout the lives of individuals during periods of environmental change is fundamental to understand how species are adapting to these new challenges. Recent developments in tracking technology, which allows researchers to follow birds for long periods of time or even throughout their lifetimes, can therefore become an essential tool to help address this challenge.

1.5 Technology to study animal movement

The study of animal movement, and in particular bird migration, has long been a fascinating topic for researchers, yet until the late 19th century, the migration of birds was mostly understood from the perspective of seasonal patterns of appearance and disappearance of bird species (Newton, 2008). Nowadays, field observations in migratory bottlenecks, such as the Strait of Gibraltar, are still used to monitor a large number of soaring bird species and their population trends in a cost-efficient way (Martín et al., 2016). However, some birds migrate during the night or at too high altitudes to be observed from the ground. These can be detected in the network of operational weather radar, which has become an incredibly useful tool to monitor biodiversity (Shamoun-Baranes et al., 2021) and to study bird migration at a continental scale (Dokter et al., 2011).

Whilst field observations can tell us a great deal about bird migration at a larger scale, individual marking of birds is fundamental to truly understand movement. Since 1899, bird ringing has been the most commonly used technique to understand bird migration (Newton, 2008). Independently of the individual mark used to identify the animal, the rule of thumb states that it should not weigh more than 3-5% of the body weight of the animal, thus for small passerines, bird ringing is still the only methodology available today to study their movements. For large-bodied birds, however, the use of tracking technology has remarkably changed how we perceive animal movement and migration.

Since the first radio animal tracking device developed in 1959 (LeMunyan et al., 1959), many other methods have emerged that do not require the recapture of the animal to retrieve the data, all of which have in common a transmitter (that is attached to the bird which collects and sends data) and a receiver (a station that retrieves the data and delivers it to the researcher) (Cooke et al., 2004). This data transmission can occur via satellite (e.g., Berthold et al., 2004), via short-range wireless transceivers (e.g., Bouten et al., 2013) or through the Global System for Mobile communications / General Packet Radio Service (GSM/GPRS) (e.g., Gilbert et al., 2016). Recently, the efforts to miniaturize tracking devices have culminated in the launch of the International Cooperation for Animal Research Using Space (ICARUS) (Wikelski et al., 2007), which promises smaller and highly efficient GPS-tracking devices, increasing the range of species that can be tracked, while also reducing the impact of the loggers on the animals, improving animal well-being and the study results (Kays et al., 2015).

The emerging field of biologging (i.e., a logging device attached to an animal to collect biological data) has revealed incredible feats performed by birds, from the 100,000km migratory journeys of Arctic Terns *Sterna paradisaea* (Egevang et al., 2010) to the 11,000km non-stop migratory flights of Bar-tailed Godwits *Limosa lapponica* (Gill Jr et al., 2009). With higher resolution data, researchers have started asking questions not only about habitat use and large-scale migration patterns, but also on how birds navigate and how they relate to fine-scale environments. Advancements in global atmospheric reanalysis tools (e.g., European Centre for Medium-Range Weather Forecasts ERA5) and in satellite imagery (e.g., Copernicus Sentinel-2) have complemented GPS-tracking technology, and it is now possible to analyse animal habitat suitability in 10 meters spatial scale (Valerio et al., 2020) and how weather phenomena influence bird movement at an hourly resolution (Vansteelant et al., 2015). Moreover, using high-resolution GPS-tracks of soaring birds it is also possible to estimate the wind speed and direction birds were experiencing, both in marine and terrestrial environments (Nagy et al., 2018; Treep et al., 2016; Yonehara et al., 2016).

Using accelerometery to infer behaviour and energy expenditure

Tri-axial accelerometers are commonly used sensors that allow researchers to have an undisturbed view of animal's movement and behaviour. Accelerometers measure acceleration in three directions (surge, sway, and heave), through which is it possible to infer the posture and body movements of the animals to which the tag is attached to (Brown et al., 2013; Shamoun-Baranes et al., 2012). By combining acceleration information with GPS data (such as ground speed and heading), it is possible to identify behaviours such as resting, flight and terrestrial locomotion (Shamoun-Baranes et al., 2012), and even more detailed information such as tending eggs (Gilbert et al., 2016). It is also possible to use accelerometery to detail the type of bird flight, by distinguishing flapping flight through the peaks in acceleration caused by each upstroke and downstroke, and passive flight through the absence of these peaks (Duriez et al., 2014; Nathan et al., 2012; Sur et al., 2017; Williams et al., 2015). Adding magnetometers and barometers, to accurately measure heading and flight altitude, researchers have delved even deeper into the classification of flight behaviour, by distinguishing flapping flight, thermal soaring, slope soaring and gliding (Williams et al., 2015).

With the understanding of how birds behave it is possible to recognise how much energy they use in the different types of locomotion. In 2006, Wilson et al. proposed that, since most of animal activity and energy expenditure is defined in terms of movement, accurate quantification of this movement should correlate with energy expenditure. These authors measured O^2 consumption and CO^2 production in Great Cormorants *Phalacrocorax carbo* during resting and pedestrian exercise in captivity and compared these with Overall Dynamic Body Acceleration (ODBA) measured with an external tri-axial accelerometer. The measurements were validated in free-living Imperial Cormorants *Phalacrocorax atriceps* in this same study. Further exploration of this method by have since then confirmed the utility of this technique to quantify energy expenditure of moving animals, while reinforcing the importance of calibration and animal attachment methods in order to have meaningful and reliable measurements (Gleiss et al., 2011; Halsey et al., 2011).

With the miniaturisation of electronics, it is now possible to attach a myriad of sensors to GPS loggers and remotely collect animal physiological, behavioural, and social information, challenging the limits of bio- and physiologging. With the use of heart rate sensors (e.g., Bishop et al., 2015), by measuring brain waves (e.g., Rattenborg et al., 2016) and by deploying animal-mounted cameras on free-living birds (e.g., Rutz et al., 2007), researchers have attained an undisturbed and detailed look of animal behaviour and physiology in the wild, describing *what* animals do, *where* they go and also *how* and *why* animals undertake the journeys they do (Hawkes et al., 2021).

1.6 Study systems

This thesis investigates the environmental drivers underlying movement decisions of birds, using Shoebills *Balaeniceps rex*, and White Storks as study species. These are two bird species with extraordinarily different movement strategies: Shoebills are thought to be sedentary throughout their range, whereas White Storks are typically a long-distance migrant, although the number of resident individuals in previously wholly migratory populations is increasing (Catry et al., 2017). As long-lived birds, with extensive immature stages (3-4 years), these two species have a long period to improve and potentially adapt their movement strategies. Moreover, due to their large body size, they are able to carry large GPS devices allowing for life-long tracking. Despite being a species of conservation concern (Birdlife International, 2020), the movement ecology of Shoebills is mostly unknown, and the influence of environmental factors on the movement of White Storks with different migratory strategies has not yet been investigated.

The Shoebill

The Shoebill is an iconic, yet enigmatic, wetland specialist. It is irregularly distributed across central-eastern Africa, from South Sudan to Zambia (Figure 1.1) and is classified as *Vulnerable* by the IUCN. The global population estimates vary between 5,000-8,000 individuals (Birdlife International, 2020), but the populations are declining, mostly due to habitat degradation and loss, as well as due to conflicts with humans, such as disturbance and illegal egg-stealing for bird trade markets (Dodman, 2013). The Bangweulu Wetlands, in Zambia, harbours the southernmost population of Shoebills, with estimates of the population size ranging between 200 shoebills, on the first census in 1984 (Howard & Aspinwall, 1984), to 1,296 Shoebills (95% confidence interval: 477–2,372) in a more recent study (Roxburgh & Buchanan, 2010). This large uncertainty in estimating the population size of Shoebills derives from the shy and cryptic nature of this species as well as the remoteness of its habitat.

Figure 1.1 – World distribution of Shoebills. Orange polygons show the areas in which Shoebills are resident. Map adapted from IUCN, 2021a.

Despite being extremely emblematic, the ecology of Shoebills is mostly unknown, and few existing studies focused on deriving population estimates (Roxburgh & Buchanan, 2010) and understanding Shoebill foraging (Mullers & Amar, 2015b) and breeding ecology (Mullers & Amar, 2015a). Shoebills inhabit permanent swampy wetlands, where they prey on fish in shallow waters or in deeper waters using floating vegetation as platforms (Guillet, 1979; Mullers & Amar, 2015b). This species is believed to be sedentary, remaining in the same wetlands all year long (Birdlife International, 2020), however, no study to date has analysed the movement ecology of Shoebills. Between 2011 and 2014, the first ever effort to deploy GPS-tracking devices on Shoebills was performed, and 10 first-year juveniles and 1 breeding adult were fitted with GPS tracking devices. As a species of high conservation concern, it is critical to improve our knowledge of Shoebill ecology and habitat requirements to implement effective conservation measures. These challenges are tackled in Chapter 3.

The White Stork

The White Stork is a large iconic bird and is one of the most well-studied bird species in Europe. The breeding distribution of this species extends throughout the Palearctic, with a small breeding population in South Africa (Figure 1.2). The global conservation status of this species is *Least Concern*, given its abundance and wide distribution (IUCN, 2021b). Although it is currently an abundant species in Europe, White Stork populations suffered a steep decline until the 1980s, as a result of severe draughts in the Sahel and habitat loss in Iberia due to agricultural changes (Carrascal et al., 1993; Catry et al., 2017; Senra & Ales, 1992). Since then, this species has been the target of several reintroduction programs throughout Europe, which helped in the recovery of the European populations (Schaub et al., 2004). Moreover, this species has also profited from newly available foraging resources: the American Crayfish *Procambarus clarkii* was introduced in Iberia in the 1970s and is now a highly abundant prey for the White Stork (Ferreira et al., 2019), and small rubbish dumps spread around Iberia were concentrated in large landfills since the 1980s, providing a stable and abundant food resource for storks all year-round (Gilbert et al., 2016). In Portugal, White Stork populations started increasing in the mid-1980s, and this trend continued as evidenced by increasing number of breeding pairs: 1,533 in 1984, 3,302 in 1994, 7,684 in 2004 and 11,691 in the last census of 2014 (Catry et al., 2017).

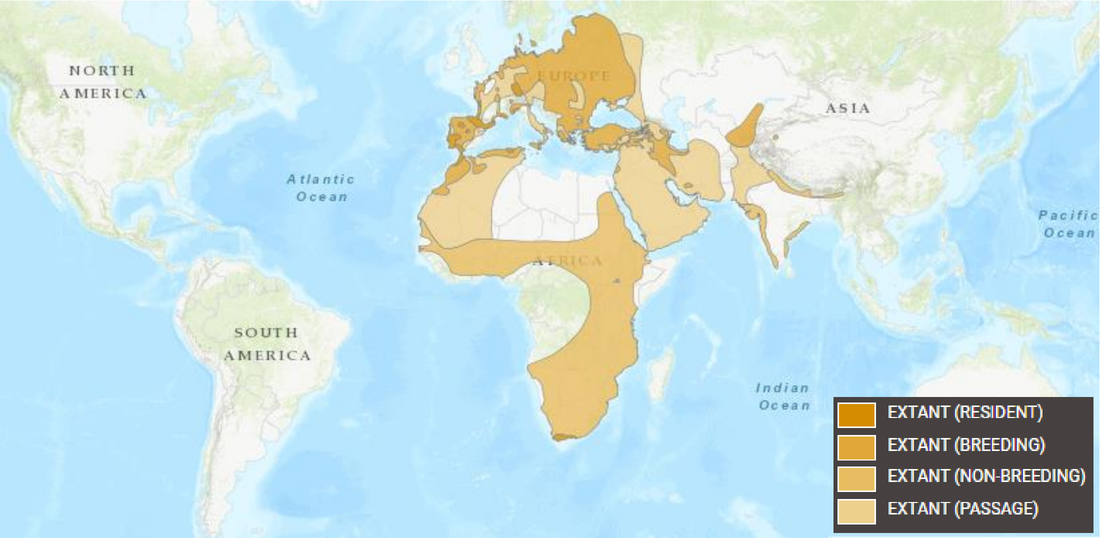

Figure 1.2 - World distribution of White Storks. Shades of yellow to orange show the areas where storks are only present on migration, during the non-breeding period, the breeding period and where storks are resident, respectively. Map adapted from IUCN, 2021b.

The White Stork is a migratory species throughout its distribution range (Figure 1.2). The migratory movements of the populations breeding in the Northern Hemisphere are well known, with the first tracking study with satellite tags going back to 1991 (P. Berthold et al., 2001). The European populations typically overwinter in sub-Saharan Africa, with birds migrating through the Eastern flyway or the Western flyway (Flack et al., 2016). White Storks are social migrants, and juvenile birds require guidance from older individuals to successfully reach their wintering areas (Chernetsov et al., 2004). As a large soaring bird, storks are highly dependent on the weather conditions to fly long-distances (Shamoun-Baranes et al., 2003), particularly the thermal uplifts, and thus avoids sea crossings, concentrating in migratory bottlenecks to cross from Europe to the African continent (Blas et al., 2020; Leshem & Yom-Tov, 1996). White Storks have a large migratory season, both during Autumn and Spring migrations, and storks have been seen crossing the Strait of Gibraltar in large numbers on all months of the year, except June (Onrubia et al., 2019). This high variability in the timing of migration may influence the environmental conditions experienced by storks during their migration, with potential fitness consequences, which is addressed in Chapter 4.

Until recent decades, White Storks were mostly migratory, but numerous individuals have decreased their migratory distance and started wintering in Iberia and Morocco (Cheng et al., 2019; Rotics et al., 2017), while many Iberian individuals have stopped migrating altogether (Catry et al., 2017; Gilbert et al., 2016). For storks migrating from northern European countries, wintering in southern Europe instead of sub-Saharan Africa reduces overall energy expenditure and foraging effort and increases juvenile survival (Cheng et al., 2019; Flack et al., 2016; Rotics et al., 2017). Residency for White Storks also seems to be beneficial, with sedentary birds showing higher breeding performance, laying a larger number of eggs (Massemin-Challet et al., 2006) and defending and maintaining the nest all year long (Gilbert et al., 2016). In Portugal, the number of resident individuals has dramatically increased since the first wintering census in the 1990s. In the last 25 years, the number of resident storks increased from 1,187 in 1995 to 19,295 in 2020, which corresponds to a maximum of 83% of the population becoming non-migratory in only 30 years (Andrade et al., submit.). Warmer winters in Iberia and the use of landfills in Iberia are known to be the main reasons underlying this change of behaviour (Catry et al., 2017), how this change of behaviour is occurring throughout the lives of individuals is only now being explored.

Since 2016, our team has made a vast effort in deploying GPS-GSM tracking devices on White Storks in Southern Portugal to further increase our knowledge on how environmental change is influencing this species. In total, between 2016 and 2020, we deployed GPS devices on 72 adults and 100 juveniles that provided information on their wintering areas. In our most recent work, we analysed three possible mechanisms that could lead this population to become resident: a) inherited genetic differences between resident and migratory individuals; b) individual flexibility in adult stork migratory behaviour, with individuals adapting the wintering area choice to the environmental conditions; and c) developmental plasticity, in which the environmental conditions experienced by juveniles during the maturation stage lead to irreversible changes in migratory behaviour (Andrade et al., submit.). We found that the recent loss of migration in white storks is not explained by genetic differences or by adult phenotypical plasticity, but seems to be driven by developmental plasticity, as some juveniles change their migratory behaviour as they age, progressively becoming resident. However, the mechanisms underlying changes in the migratory behaviour of juvenile storks is still unknown and are addressed in Chapter 5.

Defining the start and end of White Stork migration

Identifying the start and end of migratory movements is the initial step of all studies analysing bird migration. Current GPS tracking technology allows for the estimation of departure and arrival dates at the individual level and at high temporal and spatial resolution. However, such detailed information has presented new analytical challenges, tackled differently by researchers. In Soriano-Redondo et al., 2020, (Appendix 1) we used data from 18 migratory White Storks to compare 5 different methods to estimate the start and end of migration: establishing a spatial threshold (S) or an absolute displacement threshold (AD), combining spatial, temporal and displacement information (SD), calculating the net-squared displacement (NSD) or performing a change-point analysis (CPA) (Figure 1.3). We found significant differences between these methods in estimating the start, end, and duration of White Stork migration, highlighting the need of carefully considering the right methodology to estimate migration phenology.

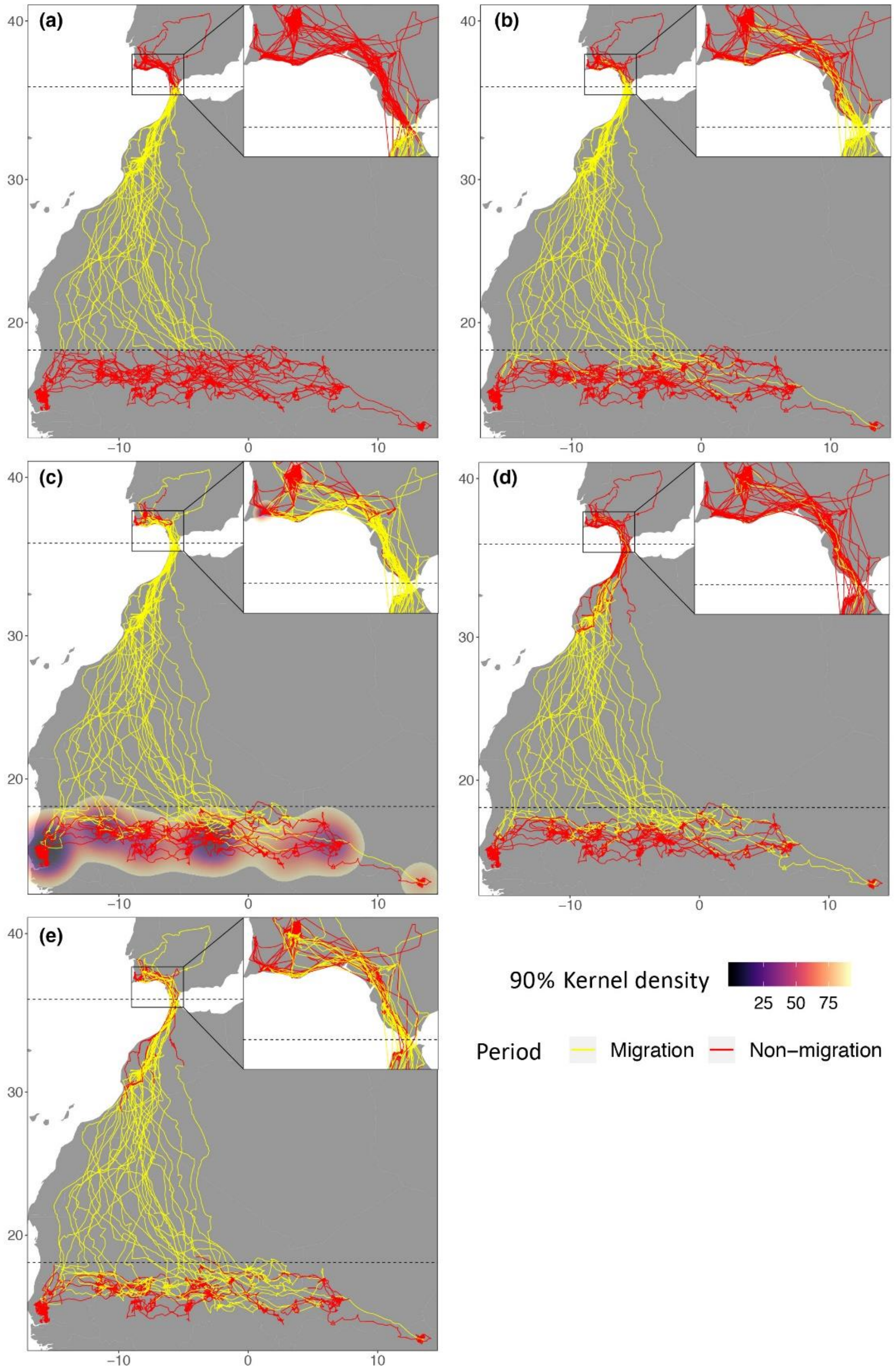

Figure 1.3 – Different methodologies to identify the start of migration of White Storks. Movements of 18 White Storks classified as migratory (yellow) or non-migratory (red), according to a) spatial threshold, b) absolute displacement, c) spatio-temporal displacement, d) net-squared displacement, e) change-point analysis. Dashed lines show spatial thresholds (36ºN – Strait of Gibraltar, and 18ºN – south of the Sahara Desert), used in the spatial threshold and absolute displacement methods. Figure extracted from Soriano-Redondo et al., 2020 (Appendix 1).

In this thesis, I adopted the spatio-temporal displacement method, which requires the establishment of a spatial, displacement and temporal threshold. For the White Stork, I considered the start of autumn (or spring) migration as the first day a stork moved more than 60km between consecutive roosts, which led to leaving the breeding (or wintering) areas. The displacement threshold (60 km) was calculated based on the frequency of distances moved during migration, and the temporal threshold (3 days) was used as it captured the short stops performed before leaving or after arriving at the breeding and wintering areas, without considering that migration had ended. The breeding and wintering areas were calculated using a 90% kernel of June and October GPS locations, respectively.

Determining White Stork behaviour and energy expenditure with the use of accelerometery

In this thesis, I used tri-axial accelerometers to quantify White Stork behaviour and energy expenditure. Due to the use of different models of GPS-ACC tracking devices, I calibrated the accelerometers axis of the different tags by confirming the positions of each axis in different GPS logger positions (Figure 1.4).

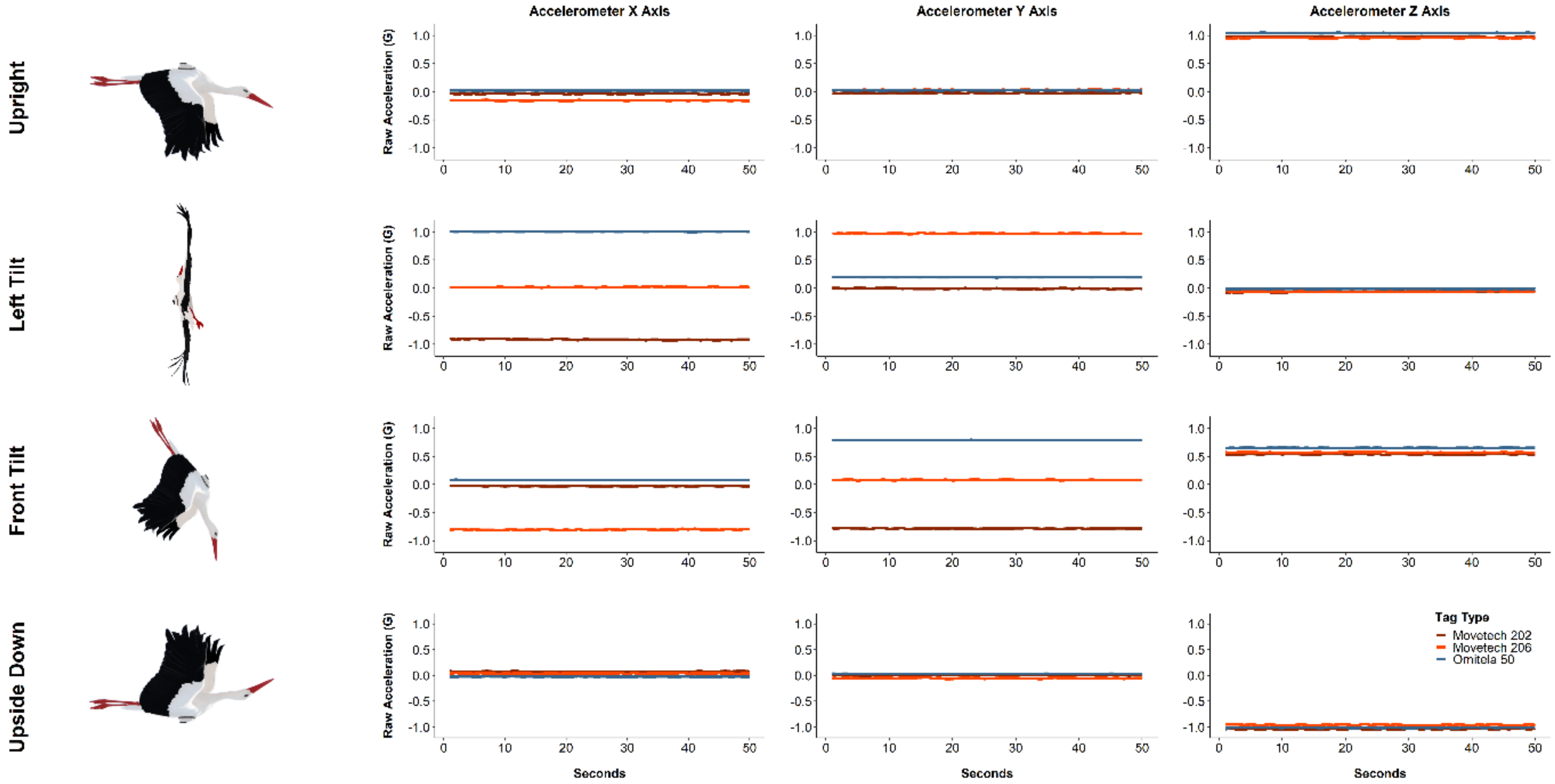

Figure 1.4 - Accelerometer calibration tests for 3 GPS-tracking device models. Raw X, Y and Z acceleration values of Movetech Telemetry V202, Movetech Telemetry TM206-2G and Ornitela Ornitrack-50 devices, in 4 logger positions: upright, left tilt, front tilt and upside down.

In Soriano-Redondo et al., 2021 (Appendix 2), we classified White Stork behaviour using tri-axial accelerometery by manually classifying storks' behaviours and building random forests models. To classify the behaviours, we observed White Storks fitted with GPS devices in different ways. We used video recordings of a captive stork fitted with the GPS logger programmed to take a GPS position and 10 seconds of acceleration at 1Hz every 1 minute. We also deployed cameras in nests where storks had been previously fitted with GPS devices, programmed to take a GPS position and 10 seconds of acceleration at 1Hz every 20 minutes. Moreover, we used data from devices continuously recording GPS and acceleration at 1HZ on wild storks that allowed us to infer the behaviour of the bird (Figure 1.5).

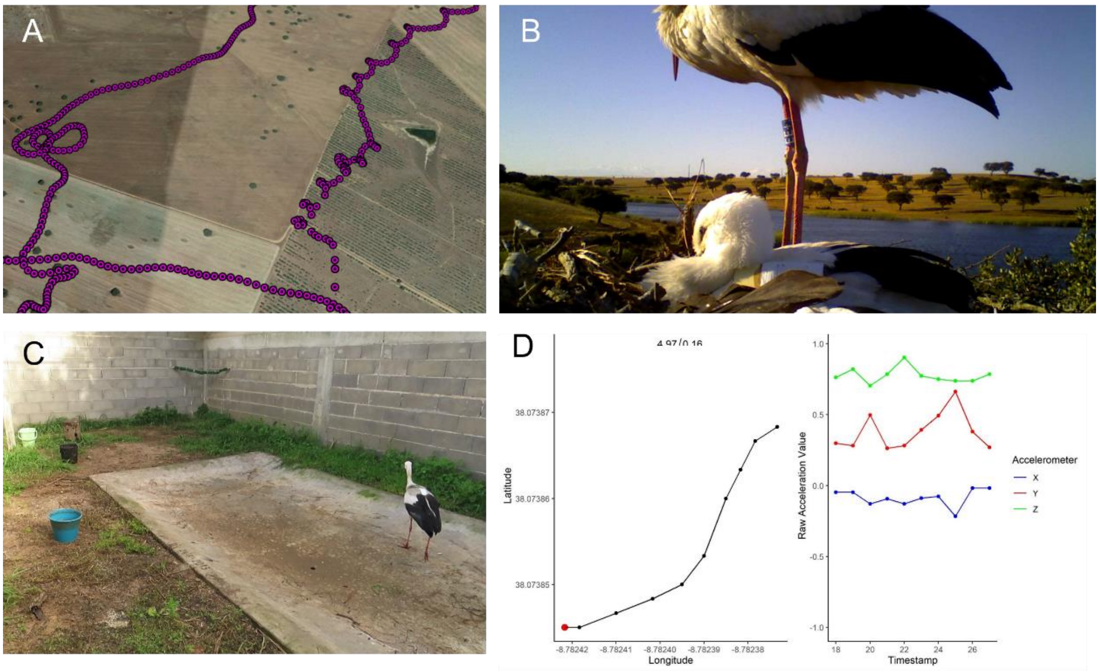

Figure 1.5 – White Stork behaviour observations. A) GPS-tracking device recording continuous GPS and accelerometer data at 1Hz, B) cameras deployed on nests of GPS-tracked White Storks and C) captive White Stork walking while wearing a GPS-tracking device. D) Plots showing the GPS (left) and tri-axial acceleration tracks (right) recorded from the captive White Stork while walking.

Due to logger mal-functioning, approximately 10% of the captive White Stork dataset had acceleration bursts smaller than 10 seconds. We calculated the ODBA of the original 10-second bursts and compared with the ODBA of the same burst sub-sampled to 9 seconds. The subset was performed by removing the last acceleration point of the 10 second burst. To calculate the ODBA, we subtracted each acceleration point from a running-mean of 4 seconds for each axis and summed the resulting values for all three axes (Gleiss et al., 2011; Wilson et al., 2006). We compared the ODBA of bursts of 9 and 10 seconds for all behaviours together and per behaviour using ANOVA's and concluded that there were no significant differences (Figure 1.6).

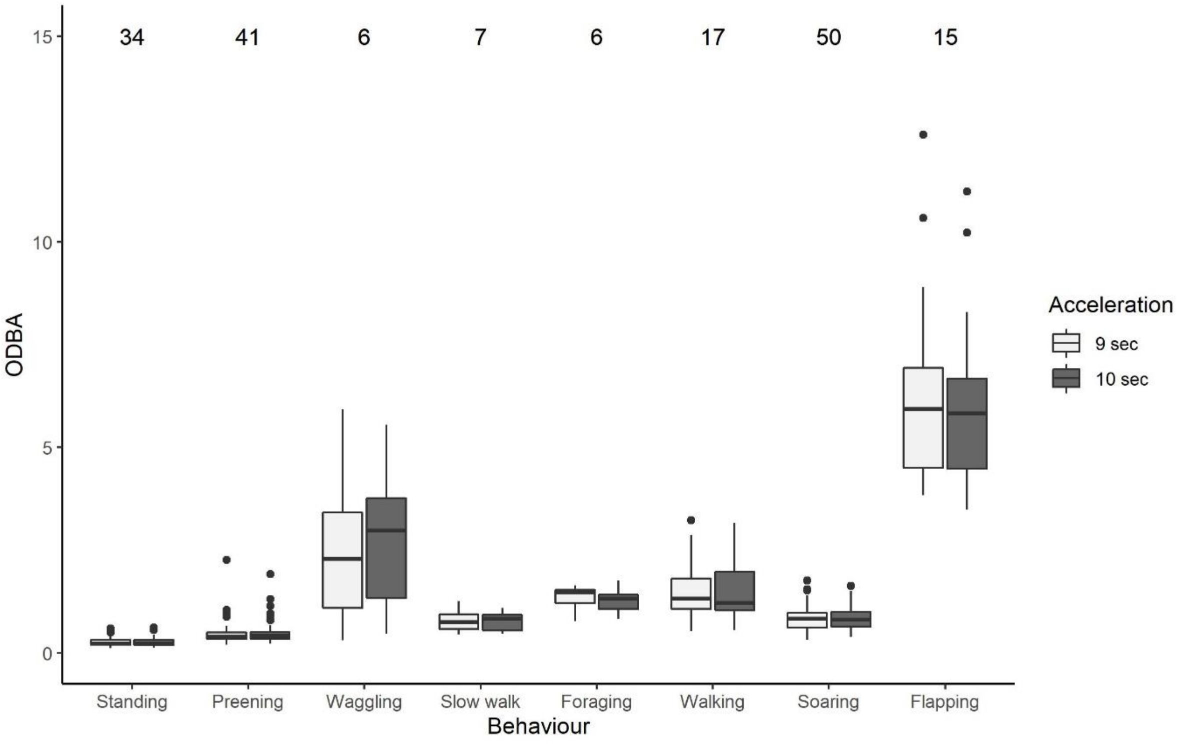

Figure 1.6 – Overall Dynamic Body Acceleration (ODBA) of several White Stork behaviours. ODBA, in G, was calculated using 9 (white) and 10-seconds of acceleration (grey). Boxes show the 25th, 50th and 75th percentiles and whiskers show the 1.5 times the inter-quartile range. Data outside these values are represented as black dots.

Finally, we used the 9-sec acceleration burst at 1Hz for the behaviour classification and defined 2 land behaviours, foraging and resting (which included preening), and 2 flight behaviours, soaring (which included gliding, orographic and thermal soaring) and flapping. We manually classified 1,000 behaviours of each tag type, including juvenile and adult birds in the training dataset. We built two random forests, one for all Movetech Telemetry GPS loggers and one for Ornitela loggers, since these two tags have different accelerometer sensors and housings, which can influence the readings on the birds. In the random forest models, 70% of the data was used to train the algorithm and 30% was used to test it. The final models had 96% accuracy for Movetech Telemetry tags and 97% accuracy for Ornitela tags. These results were published in *Science of Total Environment* (Soriano-Redondo et al., 2021) (Appendix 2).

1.7 Thesis structure

This thesis explores how environmental conditions influence the movement decisions of long-lived birds. I use GPS-tracking technology to study individual movements in different spatial scales, from short-distance dispersal movements to long-distance migratory journeys, and evaluate how habitat changes, weather conditions and use of newly available food resources, influence the movement decisions of birds in several life stages. This research was funded by the Next Generation Unmanned Systems Science Centre for Doctoral Training (NEXUSS CDT), which aims to tackle environmental challenges through the development of technological tools. Therefore, I start this thesis by describing and analysing the accuracy and precision of recently developed GPS-tracking devices in Chapter 2. In Chapter 3, I explore the short-distance movements of immature and adult Shoebills in relation to changes in surface water, whereas in Chapter 4 I expand the spatial scale to study the influence of timing of migration and weather conditions on the long-distance migration of White Storks. In Chapter 5, I investigate the ontogeny of migratory behaviour of White Storks from a population that has recently established non-migratory populations in response to environmental change.

The use of GPS-tracking technologies has revolutionised the study of animal movement providing unprecedentedly detailed information, yet the characterisation of GPS accuracy and precision is essential to correctly identify the spatial and temporal resolution at which studies can be conducted. In Chapter 2, I examine the influence of fix acquisition interval and device deployment on the performance of a GPS/GSM solar powered devices. I conduct stationary tests to describe the horizontal and vertical accuracy and precision of the devices and compare these with the accuracy and precision after deployment on pre-fledgling White Storks. I also assess the performance of GPS-Error, a metric provided by the device, at identifying inaccurate locations. This chapter is currently under review in *PLoS ONE*.

The movement of birds is mainly determined by spatial and temporal changes in resource availability, and, for wetland specialists, the seasonal availability of surface water may be a major determinant of their movement patterns. In Chapter 3, I take advantage of a 5-year GPS tracking dataset to analyse the movements of immature and adult Shoebills. I describe their home ranges and distances moved throughout the year and, by combining the GPS information with remotely sensed imagery, I relate their movements at the start of the rainy season with changes in Normalized Difference Water Index (NDWI, a proxy for surface water). This chapter is published in *Scientific Reports*.

The timing of migratory movements may determine the conditions individuals encounter, and particularly for species with asynchronous migrations (i.e., with individuals migrating at different times over an extended period), the conditions experienced by different individuals during migration may differ dramatically, with potential fitness consequences. In Chapter 4, I combine GPS-tracking with triaxial accelerometery and assess White Stork juvenile and adult migratory performance over a 5-year period. I evaluate the influence of timing of migration on the weather conditions individuals experienced, on their migratory performance and the arrival destination in the wintering areas. This chapter is currently under review in *Movement Ecology*.

Recent human-driven environmental change has significantly altered migratory behaviour, leading to the emergence of non-migratory individuals in previously fully migratory populations. However, the mechanisms enabling these rapid changes in migratory behaviour to occur at the individual level have yet to be explored. In Chapter 5, I hypothesise that the events experienced by juvenile White Storks during one annual cycle can carry over to the following year, modifying the individual migratory program. I use a 5-year GPS and acceleration dataset and evaluate the importance of individual experience and access to highly abundant food resources on the subsequent migratory strategy of storks.

Lastly, in the general conclusions (Chapter 6), I summarise the main findings of this thesis, discuss how it has contributed to understanding the influence of environmental conditions on the movement behaviour and conservation of long-lived birds, and identify potential future research directions.

All chapters have been presented in the style of a standalone publication, with the references and supplementary material at the end of each chapter.

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– Chapter 2 –

Performance of GPS/GPRS tracking devices improves with increased fix interval and is not affected by animal deployment

Performance of GPS/GPRS tracking devices improves with increased fix interval and is not affected by animal deployment

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Author's contributions

All authors developed the concepts and designed the experiment. MA carried out the experiments and the fieldwork, analysed the data and wrote the manuscript. All authors revised and approved the manuscript.

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Abstract

The use of GPS tracking technologies has revolutionised the study of animal movement providing unprecedentedly detailed information. The characterisation of GPS accuracy and precision under different conditions is essential to correctly identify the spatial and temporal resolution at which studies can be conducted. Here, we examine the influence of fix acquisition interval and device deployment on the performance of a new GPS/GSM solar powered device. Horizontal and vertical accuracy and precision of locations were obtained under different GPS fix acquisition intervals (1min, 20 min and 60 min) in a stationary test. The test devices were deployed on pre-fledgling White Storks *Ciconia ciconia* and we quantified accuracy and precision after deployment while controlling for bias caused by variation in habitat, topography, and animal movement. We also assessed the performance of *GPS-Error*, a metric provided by the device, at identifying inaccurate locations (> 10 m). Average horizontal accuracy varied between 3.4 to 6.5 m, and vertical accuracy varied between 4.9 to 9.7 m, in high (1 min) and low frequency (60 min) GPS fix intervals, these values were similar after the deployment on White Storks. Over 84% of GPS horizontal positions and 71% of vertical positions had less than 10m error in accuracy. Removing 3% of data with highest *GPS-Error* eliminated over 99% of inaccurate positions in high GPS frequency intervals, but this metric was not effective in the low frequency intervals. We confirmed the suitability of these devices for studies requiring horizontal and vertical accuracies of 5-10m. For higher accuracy data, intensive GPS fix intervals should be used, but this requires more sophisticated battery management, or larger batteries and devices.

2.1 Introduction

The collection of animal movement data has substantially benefited from rapid technological advances. New tracking technologies enable researchers to unravel novel patterns of animal behaviour and collect detailed spatial and temporal resolution data that can inform species conservation and management (Katzner & Arlettaz, 2020). High accuracy Global Positioning System (GPS) technology devices are now commonly used to track wildlife across taxa and environments and have improved the study of animal movement and habitat use (Bridge et al., 2011; Tomkiewicz et al., 2010), revolutionizing the field of movement ecology (Nathan et al., 2008).

The GPS location data can be archived or remotely transmitted by the tracking devices. The ability to remotely transmit data is particularly convenient and allows researchers to track animals that are difficult to recapture and to collect data at higher fix intervals, since data is recovered regardless of the animals' movements or the device memory (Bridge et al., 2011). There are several transmission protocols, but Global System for Mobile communications / General Packet Radio Service (GSM/GPRS) has become widely used enabling worldwide transmission of large quantities of GPS data with reduced communications costs (Katzner & Arlettaz, 2020). The combination of affordable remote transmission of data with solar power energy led to an improvement in device longevity and an exponential increase in tracking data collection (Bridge et al., 2011).

The spatial resolution of the location data obtained by GPS tracking devices can vary due to environmental and technical reasons. The main environmental sources of variability in GPS device performance are topography (Cain III et al., 2005; D'Eon et al., 2002) and habitat (Augustine et al., 2011; Belant, 2009; Cargnelutti et al., 2007; Forin-Wiart et al., 2015). GPS accuracy tends to decrease in areas with closed canopy forests (Byrne et al., 2017; DeCesare et al., 2005; Hansen & Riggs, 2008; Jiang et al., 2008; Lewis et al., 2007; Recio et al., 2011; Sager-Fradkin et al., 2007) (but see Fischer et al., 2018), where GPS fix acquisition rates are reduced given the attenuation of GPS signal resulting from poor sky availability (Byrne et al., 2017; Cain III et al., 2005; Cargnelutti et al., 2007; Dussault et al., 2011; Adams et al., 2013; Cain III et al., 2005; D'Eon et al., 2002; Hansen & Riggs, 2008; Jiang et al., 2008; Recio et al., 2011; Sager-Fradkin et al., 2007). Moreover, in solar powered devices, fix acquisition rates can be reduced due to poor charging conditions (Byrne et al., 2017). Accuracy variability can also result from technical aspects related with signal acquisition, for example, the number (Moen et al., 1997) and geometry of satellites in the sky (Dussault et al., 2011), which is quantified by the dilution of precision (DOP) metric. Higher DOP values indicate lower accuracy and can be due to poor satellite configuration, low number of satellites available, or increased triangulation errors due to clustering of satellites (Dussault et al., 2011; Moen et al., 1997; Recio et al., 2011). Both the number of satellites (D'Eon et al., 2002; Ironside et al., 2017; Lewis et al., 2007) and DOP (D'Eon & Delparte, 2005; Dussault et al., 2011; Fischer et al., 2018; Lewis et al., 2007) are metrics that can be used to identify and eliminate low accuracy locations, but these methods tend to be poor predictors of fix accuracy (Adams et al., 2013; Byrne et al., 2017; Cargnelutti et al., 2007).

After device deployment, the morphology, movement and behaviour of animals can also influence both accuracy (Bouten et al., 2013; Cargnelutti et al., 2007) and fix acquisition success (D'Eon, 2003; Graves & Waller, 2006; Lewis et al., 2007; Mattisson et al., 2010) (but see (Quaglietta et al., 2012)), hence device accuracy should be quantified before and after deployment. Stationary tests can be used to quantify performance before deployment, by comparing the distance between the estimated location given by the tracking device and the true location obtained by an independent method. These tests can provide realistic assessments of location error and determine device accuracy (Adams et al., 2013; Byrne et al., 2017; D'Eon & Delparte, 2005; Lewis et al., 2007). However, it is difficult to assess device performance after deployment, as it requires knowing the exact positions of the animals after deployment (Frair et al., 2010; Quaglietta et al., 2012), thus accuracy after deployment is normally assessed using pets (Cargnelutti et al., 2007; Forin-Wiart et al., 2015).

It is important to quantify the spatial resolution of data obtained from tracking devices and provide accuracy estimates to the locations used in research applied to conservation and policy making (Katzner & Arlettaz, 2020). Low horizontal GPS accuracy can detrimentally affect habitat selection studies, leading to poor model precision (Frair et al., 2004; Montgomery et al., 2011; Morehouse & Boyce, 2013; Webb et al., 2013), while low vertical accuracy can be critical when determining flight altitude (Poessel et al., 2018; Santos et al., 2020), collision risk with human infrastructures (Khosravifard et al., 2020; Schaub et al., 2020; Sheppard et al., 2015), and for determining 3D habitat utilization distributions of airborne animals (Khosravifard et al., 2020; Tracey et al., 2014). Determining ways to identify low accuracy positions would enable researchers to increase the quality of the location datasets obtained and minimize the constraints caused by low accuracy GPS locations.

With an increasing use of GPS tracking technology, new devices are currently being designed and developed. Differences in hardware and software can influence the performance of tracking devices (Cain III et al., 2005; Frair et al., 2004; Hansen & Riggs, 2008; Poessel et al., 2018), therefore it is critical to assess their accuracy and precision in order to understand their applicability in ecological studies. Here, we describe a novel GPS/GPRS wildlife tracking device and quantify its horizontal and vertical accuracy and precision in stationary tests and after deployment on large birds. We examine device variability and assess if GPS-Error, a metric calculated by the GPS device, can be used to identify low-accuracy locations. We assess the performance of the devices in field conditions and discuss their use in ecological and conservation studies.

2.2 Materials and Methods

GPS/GPRS devices

The Movetech Telemetry Flyways-50 is a compact Quad-band GPS/GPRS unit, a 22% efficiency solar cell, a Lithium-Ion battery, and a nylon plastic 3-D printed housing. The device weight starts at 23g. In this test we used the 50g model suitable for deployment on large birds, such as White Storks *Ciconia ciconia* (Gilbert et al., 2016; Soriano-Redondo et al., 2020, 2021) or Spanish Imperial Eagles *Aquila adalberti* (Ramos et al., 2019). The GPS/GPRS unit contains a GPS module with an on-board chip antenna. The GPS determines the 3D fix coordinates (horizontal and altitude above the ellipsoid) when 4 or more satellites are in view. The device can be programmed to log GPS data from 1 second to 24 hours, allowing for different day and night intervals. The intervals can be updated over the air, permitting an adaptation of the schedule to new environmental conditions.

The GPS unit provides an estimate of the positional error (hereafter *GPS-Error*), which considers the maximum latitude/longitude position displacement in meters with a probability of 67% (i.e., ± 1 standard deviation). This metric is calculated directly by the GPS module and is more reliable than using single metrics of error (e.g. Horizontal Dilution of Precision or number of satellites used to obtain the fix) (Quectel Wireless Solutions Co. Ltd, n.d.). The data can be transferred to Movebank (Wikelski et al., 2020), and then visualized and downloaded for further analysis.

The GSM/GPRS unit, coupled with an agnostic SIM-card, provides global cellular connectivity and there is no external antenna, minimizing drag and interference with animal movements. These are archival devices with a memory for over 60,000 records, reducing the risk of data loss when the animal is in areas without GPRS network.

Accuracy and precision in stationary test

To assess the accuracy and precision of the devices, we performed a stationary test with 11 GPS/GPRS tracking devices, fully sealed within a nylon plastic housing of medium thickness (between 1.5-2 mm) and ready for deployment. The stationary test was completed on a triangulation station located in Southern Portugal. The surrounding landscape is characterized by low altitude, slightly undulating plains, with large areas of non-irrigated agricultural land and low density of Cork *Quercus suber* and Holm-oak Trees *Quercus ilex*. We placed the devices on top of a triangulation station, at about 2 m above the ground, with a clear and uninterrupted view of the sky and programmed the devices over the air at three fix intervals: collecting GPS data every 1 min, 20 min and 60 min.

Horizontal accuracy was calculated as the distance between the coordinates obtained by the devices and the precise coordinates of the triangulation station, provided by the Direcção-Geral do Território (DGT) (Direcção Geral do Território, 2021). Vertical accuracy was calculated as the difference between the altitude above the ellipsoid of the top of the triangulation station, and the altitude obtained by the devices. Negative vertical accuracy values are obtained when the GPS device's altitude value is higher than the true altitude, and positive values result from a reading smaller than the true altitude. Hence, we quantified biases in under or overestimation of vertical locations.

The horizontal precision was determined using the mean and standard deviation of the geodesic distance between all locations obtained by the tracking devices, and the vertical precision as the mean absolute difference between all altitude readings of each device.

We performed a Kruskal-Wallis statistical analysis to assess differences in accuracy and precision between devices. We used data from all devices to compare the accuracy and precision of the positions collected at different fix intervals.

Identification of inaccurate positions

We examined if the *GPS-Error* metric, calculated by the device, could be used to identify horizontal and vertically inaccurate positions (horizontal and vertical locations with more than 10 m error). Location error was classified in three categories: 11-20 m, 21-30 m and larger than 30 m. For each tracking device, we excluded 1%, 3%, 5% and 10% of the positions with highest *GPS-Error* and determined the proportion of locations with above errors remaining in the dataset. We compared the reliability *of GPS-Error* at identifying the locations with the highest vertical and horizontal error for the three device schedules tested.

Accuracy and precision after deployment on birds

To assess the accuracy and precision of GPS devices before deployment, we performed a stationary test on 17 GPS-GPRS devices, programmed with 20 min fix interval, fully sealed within a reinforced housing (between 3-4 mm thickness) and ready for deployment on White Storks. The GPS devices were left in the triangulation station for a minimum of 4 days and a maximum of 15 days. We calculated the horizontal and vertical position of the triangulation station by averaging 3 GPS positions and 3 altitude readings collected with a Ashtech ProMark 220 and an Ashtech 660 external antenna, on differential GPS mode (dGPS). The dGPS provided readings with a horizontal accuracy of 0.98 m (± 0.07 m) and vertical accuracy of 0.57 m (±0.42 m). By using the dGPS coordinates instead of the coordinates provided by DGT, we were able to replicate this protocol to calculate the precise location of the White Stork nests and reliably compare the performance of the GPS devices before and after deployment.

After the stationary test, the 17 devices were deployed on pre-fledging White Stork on nests located in the same region as the stationary test (approximately 50 km radius), in order to control for possible GPS sources error, such as different topography or habitat. The

White Stork chicks tagged were approximately 50 days old, had a minimum wing length of 400 mm and minimum weight 2.9 kg. The device and harness weighted less than 3% of the storks' body weight. The loggers were back-mounted using a Teflon harness, with a weak link consisting of biodegradable cotton stitches below the sternum (Gilbert et al., 2016; Soriano-Redondo et al., 2021). This study was carried out in accordance with the recommendations of Instituto da Conservação da Natureza e das Florestas and the Animal Welfare & Ethical Review Board from the School of Biological Sciences at the University of East Anglia. Licenses to deploy the loggers were granted by the Instituto da Conservação da Natureza e das Florestas (license number 364/2020/CAPT to 368/2020/CAPT).

The nests were located on top of trees providing the devices a clear and uninterrupted view of the sky. To calculate the precise horizontal and vertical position of the nest, we averaged 3 GPS coordinates collected with the dGPS on top of the nest. To calculate the tracking device accuracy and precision after deployment we considered the GPS positions collected during the first 7 days after deployment to guarantee the data was obtained prior to fledgling, as White Stork juveniles do not fledge before 65 days. Horizontal and vertical accuracy, and horizontal and vertical precision of the devices before and after deployment were calculated as described above. We performed a Kruskal-Wallis statistical analysis to assess differences in accuracy and precision before and after deployment. All analysis were performed in R software (R Core Team, 2019), and distances calculated using package *geosphere* (Hijmans, 2019).

2.3 Results

Stationary test

During the stationary test, we collected a variable number of GPS fixes per device using three GPS fix collection intervals (1 min, 20 min and 60 min), with a 100% fix acquisition rate (Table 2.1).

Table 2.1 - Number of devices and locations collected during stationary and deployment tests. Mean and standard deviation of horizontal and vertical accuracy and precision, in meters, in the different fix intervals.

Treatment	Fix interval	Number of devices	Number of locations	Horizontal		Vertical	
				Accuracy Mean (sd)	Precision Mean (sd)	Accuracy Mean (sd)	Precision Mean (sd)
Stationary	**1 min**	1	1929	3.40 (3.10)	4.93 (4.15)	4.95 (4.12)	3.60 (5.94)
	20 min	10	2203	4.23 (4.28)	6.14 (5.46)	6.56 (6.72)	8.79 (9.17)
	60 min	7	1488	6.50 (8.34)	9.15 (9.46)	9.69 (19.28)	14.31 (24.95)
Before Deployment	**20 min**	17	7333	4.21 (18.0)	7.10 (23.4)	7.00 (71.0)	11.00 (85.1)
After Deployment	**20 min**	17	5204	4.10 (15.0)	6.72 (19.7)	6.00 (56.0)	10.00 (66.8)

There was a significant decrease in horizontal ($\chi2 = 508.07$, df = 2, p-value <0.001) and vertical ($\chi2 = 168.23$, df = 2, p-value <0.001) accuracy and horizontal ($\chi2 = 108.41$, df = 2, p-value <0.001) and vertical ($\chi2 = 361.90$, df = 2, p-value <0.001) precision with increasing GPS fix acquisition intervals (Figure 2.1). The horizontal accuracy in the 1 min fix interval was 3.40 m (±3.10 m) and vertical accuracy was 4.95 m (±4.12 m) and decreased to 6.50 m (±8.34 m) and 9.69 m (±19.28 m) horizontal and vertical accuracy, respectively, in the 20 and 60 min fix interval. Vertical location error was approximately symmetric around zero during the longer fix intervals; during short intervals, the vertical errors were always positive, indicating a consistent underestimation of true altitude. Precision was also influenced by the fix collection interval. In the 1 min interval, the horizontal precision was 4.93 m (± 4.15 m) and vertical precision 3.60 m (± 5.90 m). In the 60 min interval, the horizontal precision was 9.15 m (± 9.46 m) and vertical precision 14.31 m (± 24.95 m), with intermediate values in the 20 min interval (horizontal precision = 6.14 m ± 5.46 m, vertical precision = 8.79 m ± 9.17 m) (Table 2.1).

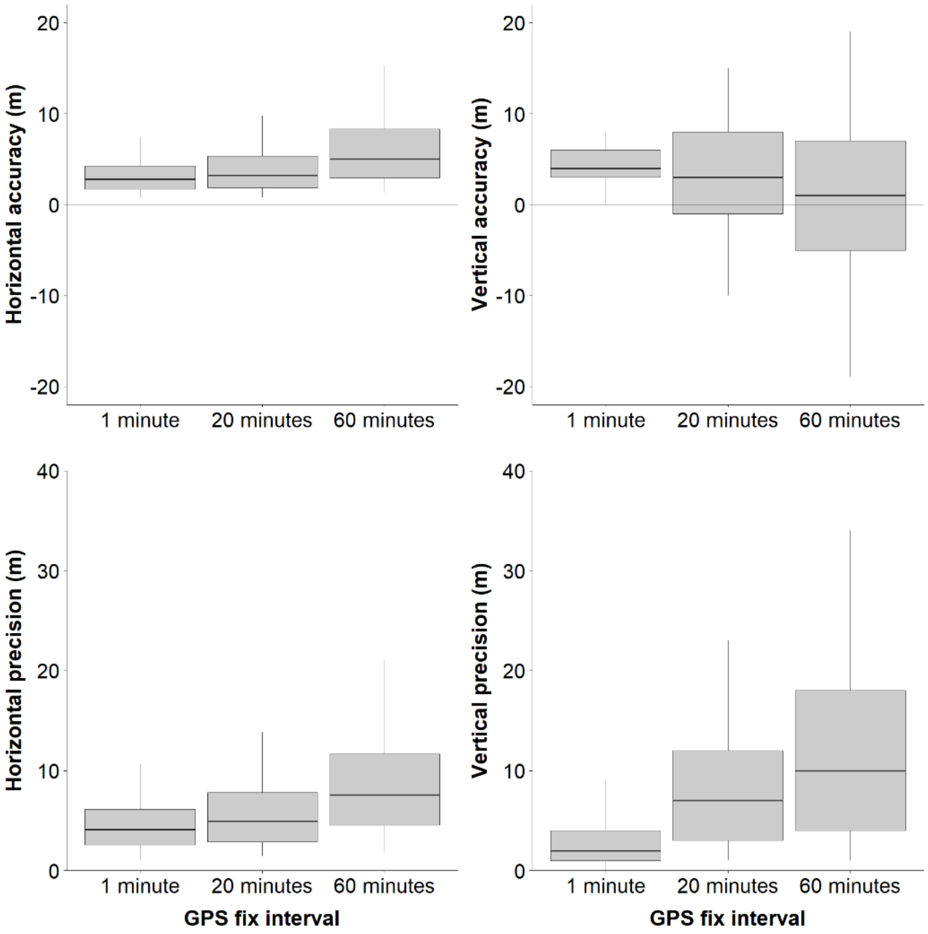

Figure 2.1 – Horizontal and vertical accuracy and precision of devices programmed in different GPS fix intervals. Horizontal (A) and vertical (B) accuracy, and horizontal (C) and vertical (D) precision in meters of devices programmed with fix intervals of 1 minute, 20 minutes and 60 minutes. The box represents 25, 50 and 75% of the data and the error bar represents 5% and 95% of the data.

There was significant variability in accuracy between devices both in the 20 min ($\chi2$ = 82.46, df = 9, p-value <0.001) and 60 min interval ($\chi2$ = 22.62, df = 6, p-value <0.001), however, all devices consistently increased in accuracy in higher frequency GPS fix collection intervals (Figure 2.2).

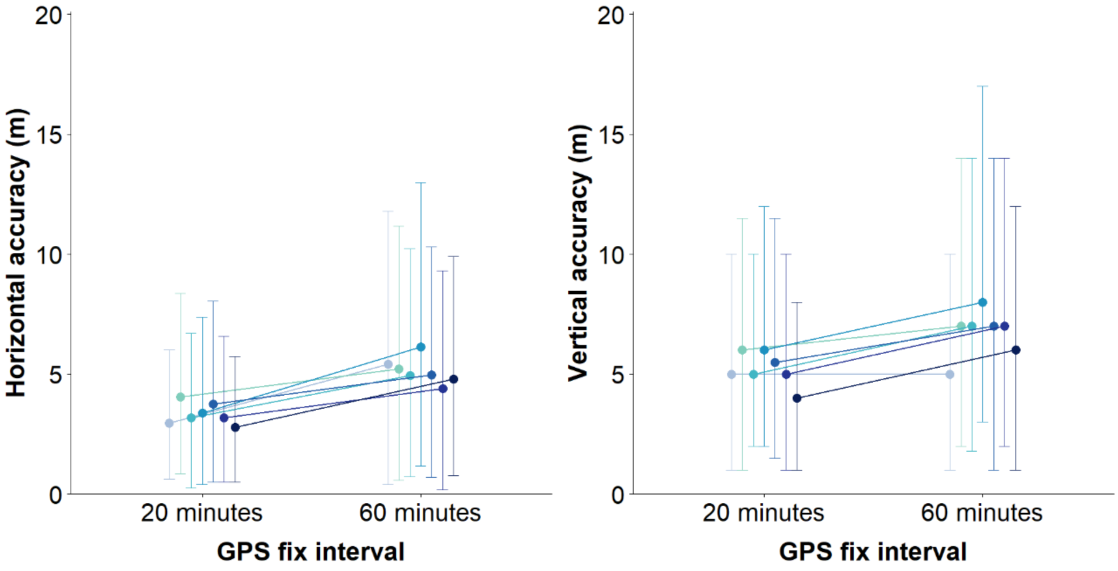

Figure 2.2 – Horizontal and vertical accuracy variability of devices programmed on a 20 and 60 min GPS fix interval. Horizontal (A) and vertical (B) accuracy of tracking devices programmed to collect GPS locations every 20 and 60 minutes. The error bars represent 95% confidence intervals.

Identification of inaccurate positions

The proportion of horizontally accurate positions (location error < 10 m) varied according to the device (Figure 2.3). Approximately 98% and 96% of the positions had a horizontal error below 10 m in the high frequency 1 min and 20 min intervals, respectively. The proportion of accurate locations declined to 83%, in the 60 min fix interval. Vertical accuracy also declined from 98% in the high frequency interval to approximately 71% in the 60 min fix intervals. *GPS-Error* provided a good metric to identify the locations that were less accurate in high intensity fix intervals. Eliminating 3% of the data with the highest *GPS-Error* obtained with the 1min fix interval, reduced 99% of positions with ≥10 m horizontal and vertical errors. *GPS-Error* was not effective at identifying the inaccurate locations in the less intensive schedules (Figure 2.3).

Performance after deployment

In total, across all 16 devices we collected 7,333 positions during the stationary test and 5,204 GPS positions during the deployment test. Horizontal accuracy did not change after deployment of the devices on White Storks ($\chi 2 = 3.80$, df = 1, p-value = 0.051), the mean accuracy was 4.21 m (± 18 m) before and 4.10 m (± 15 m) after deployment (Figure 2.4). Vertical accuracy improved after deployment ($\chi 2 = 43.72$, df = 1, p-value <0.001), from 7 m (± 71 m) to 6 m (±56 m). Both horizontal and vertical precisions improved after deployment. Horizontal precision was 7.10 m (± 23 m) before and 6.72 m (± 19.7 m) after deployment ($\chi 2 = 4543.2$, df = 1, p-value <0.001), and vertical precision improved from 11m (± 85 m) to 10 m (± 67 m) after deployment ($\chi 2 = 6824.0$, df = 1, p-value <0.001) (Table 2.1).

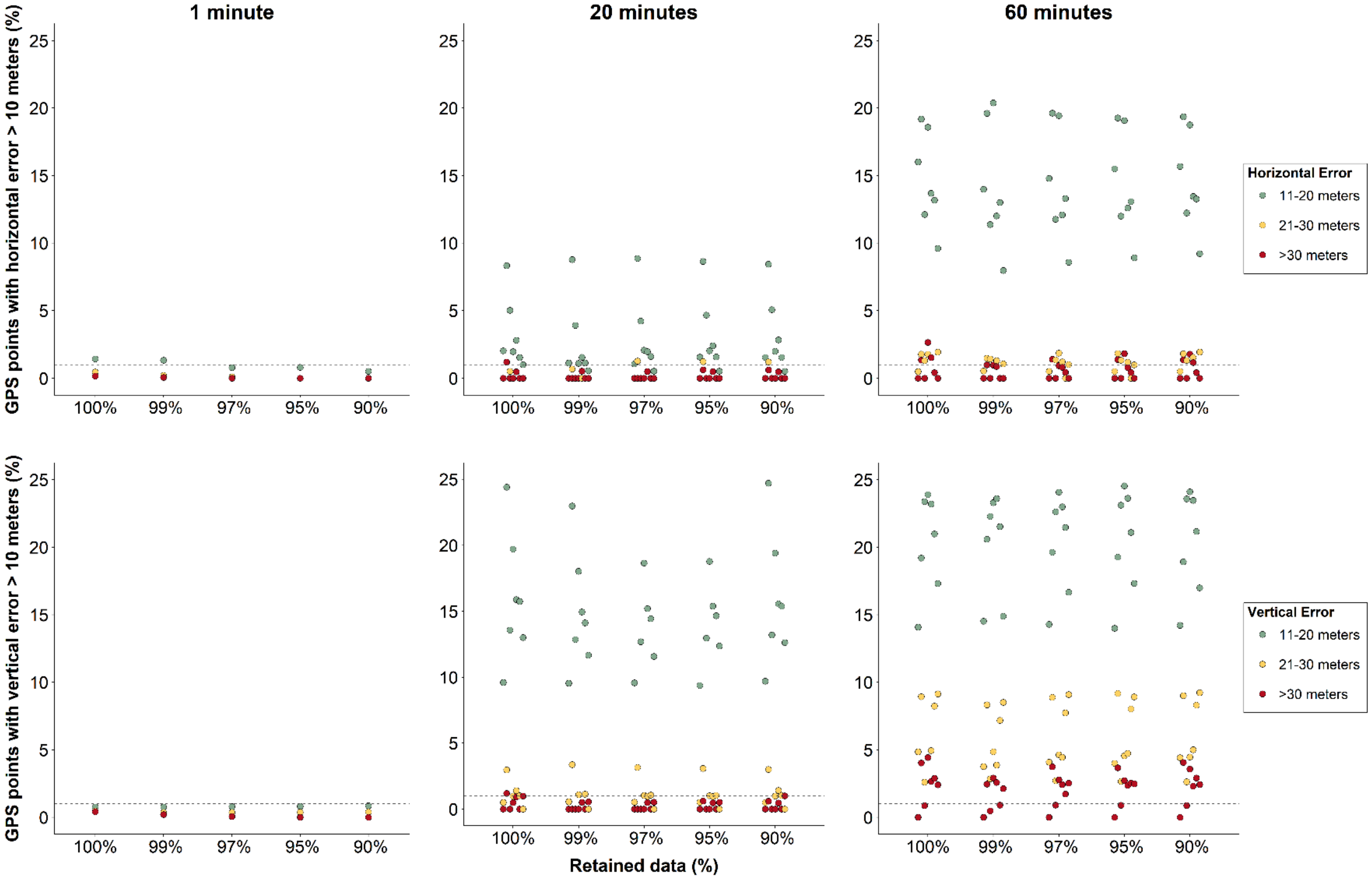

Figure 2.3 – Identification of inaccurate positions in different GPS fix intervals. Percentage of locations with horizontal and vertical error larger than 10 meters for each device, and after removing the points with largest *GPS-Error* and remaining with 99%, 97%, 93%, 95% and 90% of the original data. The dash line indicates 1% of locations with vertical and horizontal errors larger than 10 meters.

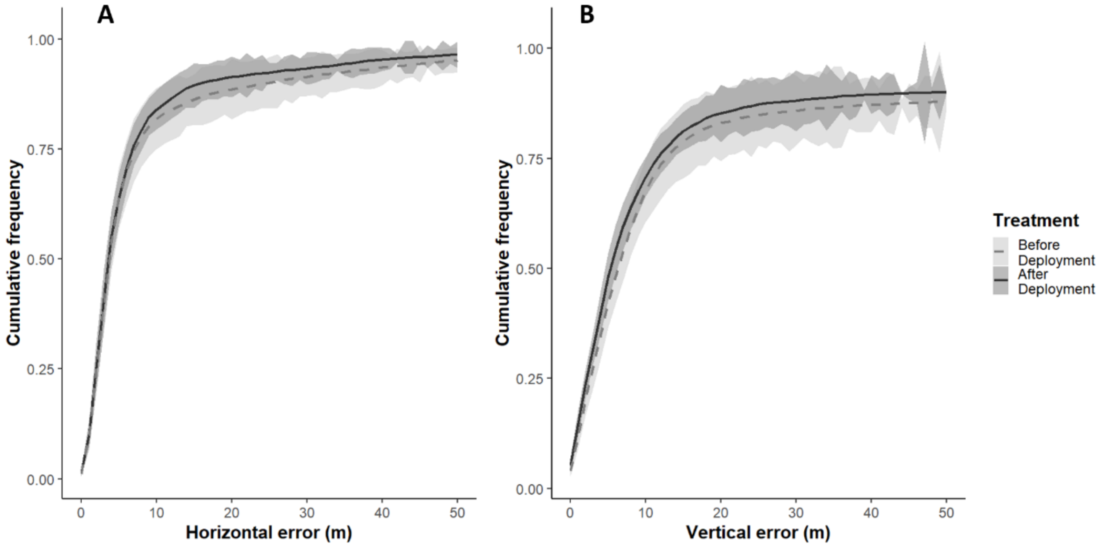

Figure 2.4 – Cumulative frequency of horizontal and vertical accuracy before and after deployment on White Storks. Cumulative frequency of **(A)** horizontal and **(B)** vertical errors (in m) of 16 GPS/GPRS devices before deployment (grey dashed line) and after deployment on White Storks (black line). Shaded areas represent the standard deviation of the errors.

2.4 Discussion

In this study, we quantify the accuracy and precision of Flyway 50 Movetech Telemetry tracking devices and assess its suitability for studies that require high spatial resolution. Horizontal (3.40 m at 1 min fix interval) and vertical (4.95 m at 1 min fix interval) accuracies improved with decreasing fix intervals and were not negatively affected after deployment on birds. This accurate spatial resolution data enables ecological and behavioural studies that require highly accurate and precise information.

GPS fix interval

The fix interval influenced the accuracy and precision of the devices, with a loss of 3.10 m and 4.74 m in horizontal and vertical accuracy, respectively, from the 1 min to 60 min interval (6.50 m horizontal and 9.69 m vertical accuracy at 60 min fix interval). These results support previous findings that longer fix intervals have a negative effect on location accuracy (Augustine et al., 2011; Bouten et al., 2013; Mills et al., 2006). The GPS units store information on the satellite constellation of the previous fix for a period of time (ephemeris retention), which increases the performance of the device when calculating a new location (Augustine et al., 2011), by increasing GPS location acquisition success (Cain III et al., 2005) and providing a fix in a shorter period of time (Jiang et al., 2008), usually designated as a warm start. However, Cain III et al. (Cain III et al., 2005) did not find an effect of fix interval on accuracy and Jiang et al. (Jiang et al., 2008) found that the positions obtained with longer fix intervals (60 min) had lower DOP than in shorter intervals. Forin-Wiart et al. (Forin-Wiart et al., 2015) found higher location errors in the 5 min interval, compared to 15 and 60 min intervals. They proposed that given the high temporal correlation between fixes, a low accuracy location would influence the following GPS position, decreasing the overall accuracy of the device. Our findings do not support this theory, even with similar fix intervals and in similar, open area habitat. This difference in results highlights the importance of testing the GPS units from different manufacturers, as they might produce different results (Cain III et al., 2005; Frair et al., 2004; Hansen & Riggs, 2008). Moreover, with newly developed loggers that collect data in different intervals according to the battery performance (e.g. dynamic fix transmitters (Byrne et al., 2017)), the fix interval should be taken into consideration when accounting for device accuracy.

Performance after deployment

After deployment on White Storks, we did not find a decrease in horizontal accuracy. In fact, the devices performed slightly better after deployment than before (increase in 1 m vertical accuracy and 0.38 m in horizontal precision and 1 m in vertical precision).

The performance of GPS devices can be influenced by environmental factors, such as topography (Cain III et al., 2005) and habitat (Adams et al., 2013; Cargnelutti et al., 2007). Vegetation structure and proximity to buildings might also decrease the sky availability and reflect the GPS signal, which increases location error (Adams et al., 2013). In our study design, we avoided topography and habitat bias by performing the stationary tests geographically close to the deployment locations. However, the stationary test before deployment was performed with our tested devices in close proximity to each other (less than 2cm apart) and on the cement structure the triangulation station, which could have decreased the accuracy of the devices before deployment due to the reflection of the GPS signal.

Moreover, after deployment, the storks were on nests located on top of high trees with uninterrupted view of the sky, which could have slightly increased the accuracy and precision of the devices. Other studies have found that animal movement (Cargnelutti et al., 2007; Graves & Waller, 2006; Recio et al., 2011), behaviour (D'Eon, 2003; Mattisson et al., 2010) morphology of the animal (Graves & Waller, 2006) and tag attachment method (Kölzsch et al., 2016) can restrain the signal reception. The angle of the GPS antenna in relation to the sky has been found to influence the performance of the device, with lower fix acquisition success (Belant, 2009; Quaglietta et al., 2012) and lower accuracy (D'Eon & Delparte, 2005; Forin-Wiart et al., 2015; Weaver et al., 2015) when the antenna is not directly facing the sky. When estimating the post-deployment device accuracy and precision, we prevented animal movement and behaviour bias by deploying the devices on birds before fledging. However, device position varied between 0°, when the bird is lying on the nest, and close to 80° when the bird is standing (Figure 2.5). Despite this large variation in antenna position, White Stork chicks spend a large proportion of the time lying on the nest (pers. obs.), therefore the influence of GPS antenna position on device performance was likely negligible.

Figure 2.5 – Position of the tracking devices on the back of pre-fledging White Storks

Finally, although GPS signal travels through leaves, tree trunks and animal's bodies, there is a reduction of the signal strength and the degree of attenuation depends on the material and distance that the signal has to travel (MacGougan, 2003). Our deployed devices were tested within a reinforced housing, with thicker nylon (between 3-4 mm thickness), which might have increased the number of low accuracy positions when compared to the initial stationary test. Nevertheless, after deployment the tested devices proved to be highly accurate, with over 84% and 71% GPS positions with less than 10 m horizontal and vertical error, respectively.

Elimination of inaccurate positions

Despite slight losses of accuracy with fix interval, the tested devices were still highly accurate. Combining all fix intervals during the stationary test, 95% of the positions were within 11 and 18 m horizontal and vertical error, respectively. Montgomery et al. (Montgomery et al., 2011) found that in small-scale ecological studies (<5 ha size patch), using a 10 m resolution categorical raster, a mean GPS accuracy of <5 m was needed to obtain 90% accurate inferences. An accuracy of <5m could be obtained with the tested devices tested if the fix interval was set between 1 and 20 min intervals.

However, there was a small number of locations with errors above 250 m, both horizontally and vertically. These highly inaccurate positions can lead to a decrease in performance of habitat selection models (Morehouse & Boyce, 2013). For studies requiring very highly accurate GPS locations, such as studies in fragmented landscapes (e.g. urban areas, Adams et al., 2013), or studies of collision with human infrastructures (e.g. wind-farms, Khosravifard et al., 2020; Schaub et al., 2020), it is important to be able to identify and eliminate outlier positions to increase GPS accuracy.

The most commonly used metrics to filter large error in GPS positions are the number of satellites (D'Eon et al., 2002; Ironside et al., 2017; Lewis et al., 2007) and DOP (Adams et al., 2013; D'Eon & Delparte, 2005; Dussault et al., 2011; Fischer et al., 2018; Jiang et al., 2008; Lewis et al., 2007). However, these can result in the elimination of a large proportion of the dataset, including accurate positions, while not eliminating all inaccurate positions (Bjørneraas et al., 2010; Ironside et al., 2017; Lewis et al., 2007; Recio et al., 2011). Estimating the true altitude error and relate it to the horizontal error, produces acceptable results in eliminating poor quality fixes in comparison with single metric models (Laver et al., 2015). This method however is only suitable for broad-scale habitat analysis, and since it relies on knowing the exact altitude of the animal, it is not appropriate for arboreal or flying species.

The devices tested in this study provide a *GPS-Error* estimate that proved to be effective at identifying low accuracy positions in short fix intervals (1 min), but it was not possible to replicate the results with longer fix intervals. Moreover, since the performance of the device is related to the habitat, by excluding locations with large positional errors there can be a bias in excluding data related to a single habitat (Frair et al., 2004, 2010; Ironside et al., 2017; Laver et al., 2015; Lewis et al., 2007; Webb et al., 2013). Using species-specific GPS metadata, such as unrealistic speed, turning angles or distances travelled between consecutive fixes is effective in eliminating large positional errors (Bjørneraas et al., 2010). However, this method is dependent on the mobility of the species, as well as the fix interval (Laver et al., 2015). Other modelling techniques, such as using sensors (accelerometers and magnetometers) and GPS drift-corrected dead reckoning, have successfully increased the accuracy of animal movement estimates in low intensity GPS schedules (Dewhirst et al., 2016). This is particularly important in non-solar tags in which, in order to maximize the lifespan of the battery, longer fix intervals are used.

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– Chapter 3 –

Changes in surface water drive the movements of Shoebills

© Adapted from Frank J. Willems original photograph

Changes in surface water drive the movements of Shoebills

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AA, RHEM, FJW and MA conceptualised the study. AA, RHEM, MA, AMAF and FJW designed the methodology. RHEM conducted the fieldwork and data collection. MA analysed the data and wrote the manuscript. All authors read, edited, and approved the final manuscript.

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Abstract

Animal movement is mainly determined by spatial and temporal changes in resource availability. For wetland specialists, the seasonal availability of surface water may be a major determinant of their movement patterns. This study is the first to examine the movements of Shoebills *Balaeniceps rex*, an iconic and vulnerable bird species. Using GPS transmitters deployed on 6 immature and 1 adult Shoebills over a 5-year period, during which 4 immatures matured into adults, we analyse their home ranges and distances moved in the Bangweulu Wetlands, Zambia. We relate their movements at the start of the rainy season (October to December) to changes in Normalised Difference Water Index (NDWI), a proxy for surface water. We show that Shoebills stay in the Bangweulu Wetlands all year round, moving less than 3 km per day on 81% of days. However, average annual home ranges were large, with high individual variability, but were similar between age classes. Immature and adult Shoebills responded differently to changes in surface water; sites that adults abandoned became drier, while sites abandoned by immatures became wetter. However, there were no differences in NDWI of areas used by Shoebills before abandonment and newly selected sites, suggesting that Shoebills select areas with similar surface water. We hypothesise that the different responses to changes in surface water by immature and adult Shoebills are related to age-specific optimal foraging conditions and fishing techniques. Our study highlights the need to understand the movements of Shoebills throughout their life cycle to design successful conservation actions for this emblematic, yet poorly known, species.

3.1 Introduction

One of the key challenges in ecology is to understand how environmental fluctuations drive animal movements. Changes in the environment can alter resource distribution, which consequently determines animal migratory (Shariatinajafabadi et al., 2014; Somveille et al., 2015; Van Der Graaf et al., 2006) and, local, movements (Bennetts & Kitchens, 2000; Trierweiler et al., 2013). In wetlands, the distribution of surface water is one of the main determinants of species' spatial distribution (Donnelly et al., 2019; Ma et al., 2010; Smit, 2011) and individual movements (Bennitt et al., 2014; Kleyheeg et al., 2017). In tropical systems with strongly seasonal environments, prolonged periods of drought followed by extreme floods can lead to striking changes in habitat suitability (Bennitt et al., 2014; Roshier et al., 2008) and drive the large-scale movements of waterfowl (Henry et al., 2016), due to fluctuations in the abundance and availability of foraging resources (Cook et al., 2014).

The way individuals explore the environment can change as they age (Krüger et al., 2014; Weimerskirch et al., 2014), and recent advances in GPS tracking technology and increases in device longevity, have enabled the detailed study of individual movements for several years or even throughout lifetimes. This has unravelled differences between adults and juveniles in space use (Krüger et al., 2014; Wolfson et al., 2019), habitat selection (Péron & Grémillet, 2013; Weimerskirch et al., 2014), and timing (Gschweng et al., 2008; Hake et al., 2003; Miller et al., 2016) and efficiency of movements (Miller et al., 2016; Rotics et al., 2016; Sergio et al., 2014). Understanding the drivers of movement of long-lived birds relies on information on the spatial and temporal dynamics of movement at different ages in relation to environmental variables. Such information has only been available relatively recently, through the integration of data from GPS trackers with remotely sensed environmental data (Howison et al., 2018; Thorup et al., 2017; Wang et al., 2019). Indices based on satellite imagery have been increasingly used to interpret environmental conditions and infer ecological processes (Thorup et al., 2017; Wang et al., 2019). The Normalised Difference Water Index (NDWI) proposed by McFeeters (McFeeters, 1996) is an index that uses remotely sensed imagery to map surface water. The NDWI delineates and highlights open water by distinguishing it from vegetation and bare soil, and has mostly been used to map waterscapes in urban settings (Mcfeeters, 2013; Yang et al., 2017). More recently, this index has been used to map surface water for animal movement studies (Henry et al., 2016), and to identify suitable habitat and inform area protection for shorebird species (Choi et al., 2019).

The Shoebill *Balaeniceps rex* is an iconic wetland specialist, with a patchy distribution in central-eastern Africa, from South Sudan to Zambia (Birdlife International, 2020; Guillet, 1978). The Shoebill is a large long-lived species, categorised as *Vulnerable* by the IUCN. Shoebills have a declining population trend, due to habitat degradation and loss, illegal bird trade and disturbance by humans (Birdlife International, 2020; Dodman, 2013). The global population estimate for the species is 5,000-8,000 individuals, although large uncertainty around this estimate exists, given that this species is cryptic and found in inaccessible areas (Birdlife International, 2020). Shoebills inhabit permanent swampy wetlands with seasonal flooded grasslands, where they prey on fish in shallow waters or use floating vegetation as fishing sites (Guillet, 1979; Mullers & Amar, 2015b). Despite being a highly emblematic species, there are very few studies on Shoebill ecology, and existing studies have focused on deriving local population estimates (Guillet, 1978; Roxburgh & Buchanan, 2010), and better understanding their foraging (Guillet, 1979; Mullers & Amar, 2015b) and breeding ecology (John et al., 2013; Mullers & Amar, 2015a). This species is believed to be sedentary, staying in the same region all year long (Dodman, 2013; Elliott et al., 2020); however, to date, the movement ecology of the Shoebill is completely unknown, which is unsurprising given that very few birds have ever been ringed and no previous tracking studies have occurred on this species. Being a species of high conservation concern, as well as an important source of tourism revenue (African Parks, 2018), it is critical to improve our knowledge of Shoebill ecology and habitat requirements to implement effective conservation measures (Dodman, 2013).

Using GPS tracking data collected over 5 years, we characterise the movements of immature and adult Shoebills in the Bangweulu Wetlands, Zambia. In common with many other areas occupied by Shoebills, the Bangweulu Wetlands undergoes dramatic changes in water levels between the dry (breeding season) and the wet season. We therefore hypothesise that changes in surface water drive the movements of Shoebills, and that their selected areas have similar surface water. Using the NDWI as a proxy for surface water, we compare 1) the NDWI of areas while Shoebills were present with the NDWI of the same areas the week after the birds left (to examine how these abandoned areas change), and 2) the NDWI of areas used by Shoebills the last week before abandonment with the NDWI of areas the first week after Shoebill arrival (to examine whether they select for similar habitats in relation to surface water). We explore these questions for both adult and immature birds. By analysing the movements of Shoebills in different life stages, and how these movements relate to available surface water, a key environmental factor for wetlands, our goal is to improve our ecological understanding of Shoebills, to ultimately inform the conservation of this mostly unknown and emblematic species.

3.2 Methods

Study area and data collection

This study was conducted in the Bangweulu Wetlands, a Game Management Area (GMA) located in the Muchinga province in north-eastern Zambia (approximately between 11°40' to 12°34'S and 29°78' to 30°87'E). The Bangweulu Wetlands consist of miombo *Brachystegia* sp.

woodlands, grasslands, floodplains, seasonal swamps, and permanent wetlands (Kamweneshe, 2000). This reserve is classified as an Important Bird Area and the area of Chikuni is classified as a Ramsar Site (BirdLife International, 2020). The climate is characterised by a heavy rainfall season from November to April, with a total annual precipitation of 1,200 mm to 1,400 mm (Ng'onga et al., 2019; Thurlow et al., 2009). The lowest water levels occurs in November, and the mean annual water level difference is 1.4 m (Evans, 1978; Kolding & van Zwieten, 2012). This area harbours the southernmost population of Shoebills (Birdlife International, 2020; Elliott et al., 2020), however the size of this population is largely unknown. In 1984, the first Shoebill census in the Bangweulu Wetlands estimated the population at 200-300 individuals (Howard & Aspinwall, 1984). Nevertheless, a large area of the wetland remained un-surveyed (Kamweneshe, 2000) and, in a more recent survey, Roxburgh and Buchanan (Roxburgh & Buchanan, 2010) provided an estimated population size of 1,296 individuals, although this estimate was based on very few sightings, and there was considerable uncertainty around this estimate (95% confidence interval: 477–2,372).

Between August and September of 2011 to 2014, 10 juvenile and 1 adult Shoebills were fitted with 70g satellite-based GPS-trackers (Solar Argos/GPS PTTs, Microwave Telemetry) (Table 3.1). The transmitters were fitted using the body-loop attachment method, with a Teflon-tube harness. Eight pre-fledging juveniles were tagged on their nests when they were on average 84 days old (range 80 - 89 days). Shoebills fledge at approximately 95-105 days (Elliott et al., 2020). Two juveniles (511 and 521) were raised in a recovery centre after being confiscated from the illegal bird trade, and fitted with the GPS transmitter before being released at unknown ages, but likely older than 80-89 days of the other birds. Only one Shoebill (517) was tagged as an adult, which was caught at its nest site. Tracking devices, including harness, weighted 80g, representing 1.3-1.6% of the body mass of birds at the time of deployment (4,900-6,300g). Licences to catch and deploy the tracking devices were provided by the Zambia Wildlife Authority (now Department of National Parks and Wildlife

(DNPW)), and the work was approved by the University of Cape Town Science Faculty Animal Ethics Committee.

Table 3.1 – Information of the tracked Shoebills. Age of the individual at the time of logger deployment, start and end dates of tracking, total number of valid GPS positions, excluding outliers, and total number of tracking days as immature and adult.

Bird ID	Age	Start of tracking	End of tracking	Number of GPS positions	Immature tracking days	Adult tracking days
521	Juvenile	03/12/2011	28/10/2014	10,763	617	-
514		09/09/2012	26/11/2013	2,187	-	-
518		15/09/2012	21/04/2013	2,537	-	-
520		03/08/2013	02/05/2018	19,335	725	623
509		26/08/2013	05/03/2018	18,998	724	634
510		30/08/2013	14/11/2013	962	-	-
515		02/09/2013	15/05/2017	16,138	728	347
512		10/09/2013	29/10/2018	21,224	724	863
516		15/11/2013	05/01/2015	3,480	-	-
511		28/10/2014	08/06/2016	6,769	366	-
517	Adult	29/07/2013	15/08/2017	16,928	-	1,444

Data processing and spatial analysis

The trackers provided a GPS fix every 1-hour between 6 A.M. and 6 P.M., GMT+2, which corresponds to the activity period of Shoebills. The transmitters provided location (latitude and longitude) with a mean error of 18 m (Microwave Telemetry, 2020). We considered all valid GPS locations until the transmitter failed or when there was no movement for several days, indicating death or loss of the GPS transmitter. GPS data was filtered for outliers based on unrealistic movements or speed (more than 150 km/h between two consecutive hourly locations) and visually inspecting the tracks.

Birds were classified as juveniles until the start of the following breeding season (1st of May), as immatures during the second and third year and as adults from the fourth year onwards, since Shoebills start to breed after three years (Elliott et al., 2020). For this study, we only considered the movements of immature and adult birds, since first year juveniles remained near the nest for a long period after fledging (Mullers & Amar, 2015a). Six individuals provided more than 1 year of data, maturing from juvenile to immature birds, and four immature birds provided more than 3 years of data, becoming adults (Table 3.1).

We estimated the annual home range area of individual immature and adult birds using Kernel Density Estimation, with *h-ref* algorithm and grid size of 500 m, using R package a*dehabitatHR* (Calenge, 2006). The year was defined from the start of the breeding season (May) until the following April. We also calculated cumulative home ranges of immature and adults, across all years and individuals, to visualise the area used by this species in the Bangweulu Wetlands.

We quantified the maximum range of Shoebill individual daily movements by calculating the distance between all GPS locations each day and selecting the maximum value (hereafter maximum daily distance). All distances were calculated using R package *geosphere* (Hijmans, 2019a). To understand how movements changed throughout the year for immature and adult birds, we calculated the mean maximum daily distance per month of each individual. All data processing and analysis were performed in R 3.6.1. (R Core Team, 2019).

Influence of NDWI on Shoebill movements

We analysed Shoebill movements between 2013 and 2017, in relation to changes in surface water from October to December each year. During this period, the levels of surface water change dramatically in the Bangweulu Wetlands, as the rainy season typically starts in November. This period also encompasses the end of the Shoebill breeding season and birds are less constrained by the location of the nests. We compared the NDWI of areas used by

Shoebills prior to and after they abandoned them, and compared the NDWI of used areas the last week before abandonment with the NDWI of the newly selected areas, the first week after arrival.

To understand when Shoebills performed large movements, we analysed the frequency of the maximum daily distances. We defined a size threshold (in km's) which captured 80% of smaller scale movements and considered the remaining 20% as '*Moving Days'*. Here we also accounted for movements performed during the night, by calculating the distance between the first GPS location of the day and the last GPS location of the previous day. Movements performed during the night were allocated to the previous day. We classified as '*Areas'*, the regions where birds stayed for a minimum of two days between Moving Days. We computed the 95% minimum convex polygons (MCPs) of these Areas and, to understand if birds moved to a different geographical area or remained in a similar location after a Moving Day, we overlayed the MCPs of two consecutive Areas. If the two MCPs overlapped, we considered the individual to have remained in the same Area; if they did not overlap, we considered that the individual moved to a different Area. MCPs were calculated using R packages *sp* (Bivand et al., 2013; Pebesma & Bivand, 2005) and *adehabitatHR* (Calenge, 2006).

We used the NDWI as a proxy for surface water and calculated this index for the Bangweulu Wetlands for all weeks of October until January. When using satellite imagery there is a trade-off between temporal and spatial resolution. In this study, we favoured imagery with higher temporal resolution, using satellite imagery from MODIS Terra Surface Reflectance with 8-days and 500 m resolution (NASA Goddard Space Flight Center, 2018), since the pixel size of 500 m was still smaller than the analysed range of movements. All images had a minimum of 92% of pixels with good quality and a maximum of 2% of pixels not classified due to cloud cover or other reasons. To calculate the NDWI, we used McFeeters (McFeeters, 1996) formula:

$$NDWI = \frac{(Green - NIR)}{(Green + NIR)}$$

where *Green* is MODIS Band 4 (545-565 nm wavelength) and *NIR* (near infrared) is MODIS Band 2 (841-876 nm). The NDWI varies between 1, indicating open water features, and -1, indicating a dry area, on a gradient of surface water. This index was interpreted comparatively, e.g. an area of NDWI of -0.6 is drier than an area of NDWI -0.5 (Figure 3.1). All satellite imagery manipulation was performed using R packages *raster* (Hijmans, 2019b) and *rgdal* (Bivand et al., 2019) and *rgeos* (Bivand & Rundel, 2019).

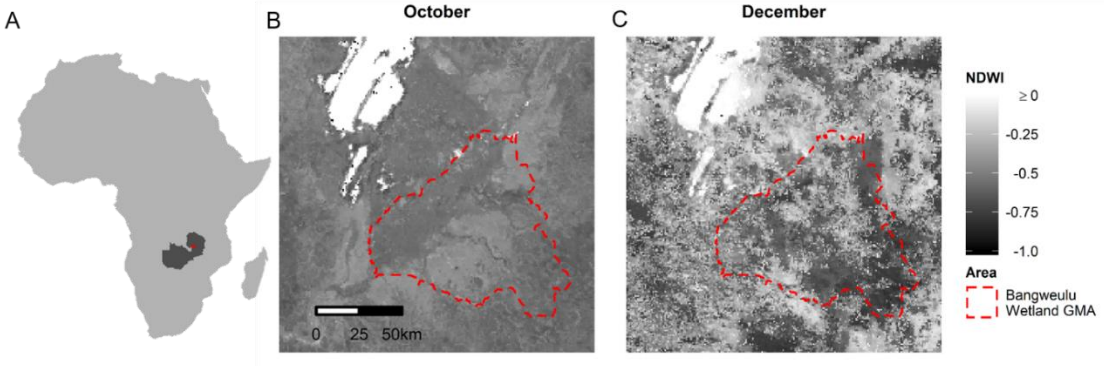

Figure 3.1 – Description of the study area. A) Location of the Bangweulu Wetlands Game Management Area (in red) within Africa (light grey) and Zambia (dark grey); B) Changes in NDWI between the start of October (week between 30/09/2015 and 07/10/2015), just prior to the start of the rainy season and C) the end of December (week between 19/12/2015 and 26/12/2015), which is during the rainy season. The red dashed line indicates the border of the Bangweulu Wetlands Game Management Area. Satellite imagery obtained from MODIS Terra Surface Reflectance (doi: 10.5067/MODIS/MOD09A1.006).

To test if Shoebills move due to changes in surface water, we extracted the daily mean NDWI of the GPS positions of Shoebills while they were in a particular Area. We then compared the locations where birds were present, with the locations one week after the birds abandoned the Area. We used binomials Generalised Linear Mixed Models (binomials

GLMMs), with presence (0) / abandonment (1) of Shoebills as the response variable, daily mean NDWI as the fixed effect, and year and Area nested within bird ID as random effects, to account for lack of independence of measures within years and within the Areas used by different Shoebills. Due to the non-linearity of the relationship between Shoebill presence/abandonment and NDWI (as areas Shoebills abandoned could have become drier or wetter, *i.e.*, with lower or larger NDWI values), we introduced the NDWI as a second-degree polynomial term in the GLMM. We calculated the marginal and conditional R-squared, to assess the variance explained by the fixed effect of the model (mean daily NDWI), and the fixed and random effects of the model, respectively. We built two models, one for adults and another for immatures, to evaluate if the two age groups responded differently to changes in surface water.

To understand if Shoebills select areas of similar surface water when they move, we compared the Shoebill locations the first week after arrival (1) with the locations the last week before they abandoned an Area (0). We tested this hypothesis for immatures and adults. We used binomials GLMMs, with newly selected area (1) / previously occupied area (0) as the response variable, mean daily NDWI as a fixed effect, and year and Area nested within bird ID as random factors. We assessed the variance explained by the model using marginal and conditional R-squared. GLMMs were computed using R package *lme4* (Bates et al., 2015), and R-squared values computed using the package *MuMIn* (Barton, 2019).

3.3 Results

We tracked 11 Shoebills in the Bangweulu Wetlands, Zambia, between December 2011 and October 2018 and collected 119,321 valid GPS positions (Table 3.1). We obtained 47,134 GPS positions for 6 Shoebills tracked as immatures and 44,985 GPS positions of 5 Shoebills tracked as adults. All other GPS positions were from juveniles (n=4), which died or disappeared before they became immatures and were thus excluded from this research, also because they remained near the nest for a long period after fledging. From the adult GPS positions, 28,057 locations were from 4 immature Shoebills that matured into adults during the tracking period, and 16,928 GPS locations from the one individual tagged as a breeding adult.

Spatial analysis

Shoebill annual home range was similar in size for adults and immatures (mean 95% kernel = 1,514 km^2 (± 1,172) and 1,547 km^2 (± 1.296) for adults and immatures, respectively; Figure 3.2, Table 3.2). There was large individual variation in home range size, both for immatures (range 95% kernel: 233 km^2 and 2,628 km^2) and adults (range 95% kernel: 304 km^2 and 3,375 km^2) (Table 3.2).

Table 3.2 – Description of Shoebill home ranges. Individual average annual home range area (in km^2 ± standard deviation) and total average home range of immature and adult Shoebills, estimated as the 95% and 50% kernel, based on the GPS tracking periods indicated in Table 3.1.

ID	Immature		Adult	
	95% kernel (km^2)	**50% kernel (km^2)**	**95% kernel (km^2)**	**50% kernel (km^2)**
521	233 (± 318)	46 (± 63)	-	-
520	1,094 (± 585)	212 (± 129)	1,039 (± 866)	145 (± 124)
509	2,458 (± 617)	431 (± 59)	2,167 (± 241)	389 (± 85)
515	2,628 (± 2,309)	403 (± 359)	3,375	652
512	1,585 (± 360)	257 (± 56)	2,167 (± 474)	343 (± 133)
511	981	200	-	-
517	-	-	304 (± 108)	54 (± 15)
All individuals	**1,547 (± 1,296)**	**263 (± 204)**	**1,514 (± 1,172)**	**247 (± 204)**

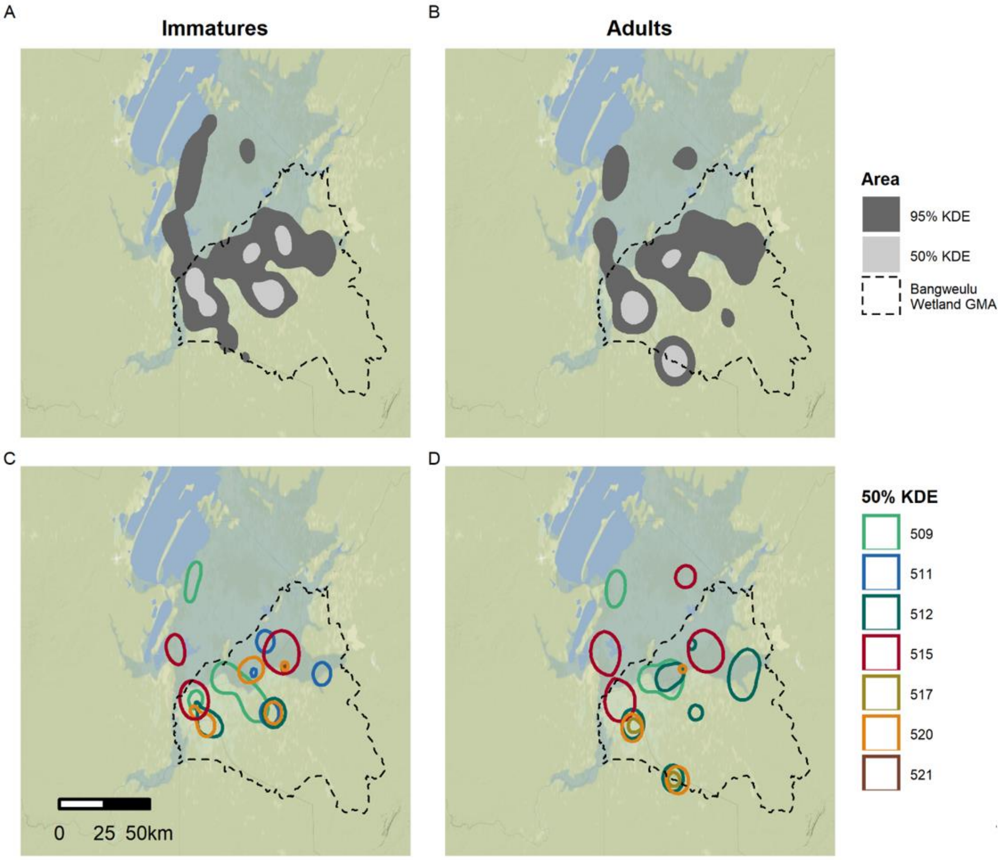

Figure 3.2 – Map of Shoebill home ranges. Cumulative 95% and 50% kernel density estimations for all tracked (A) immature and (B) adult Shoebills, and cumulative 50% kernel density estimation for each (C) immature and (D) adult individual, based on the GPS tracking periods indicated in Table 3.1. The dashed line indicates the border of the Bangweulu Wetlands Game Management Area. Map tiles by Stamen Design (https://stamen.com/), data by OpenStreetMap (https://www.openstreetmap.org/).

For both adults and immatures, the distribution of the maximum daily distance moved was highly skewed (Figure 3.3). On most days both age classes moved relatively short distances (median values; adults: 0.84 km/day, immatures: 0.73 km/day). For both age classes, on 81% of days, birds moved less than 3 km (Figure 3.3).

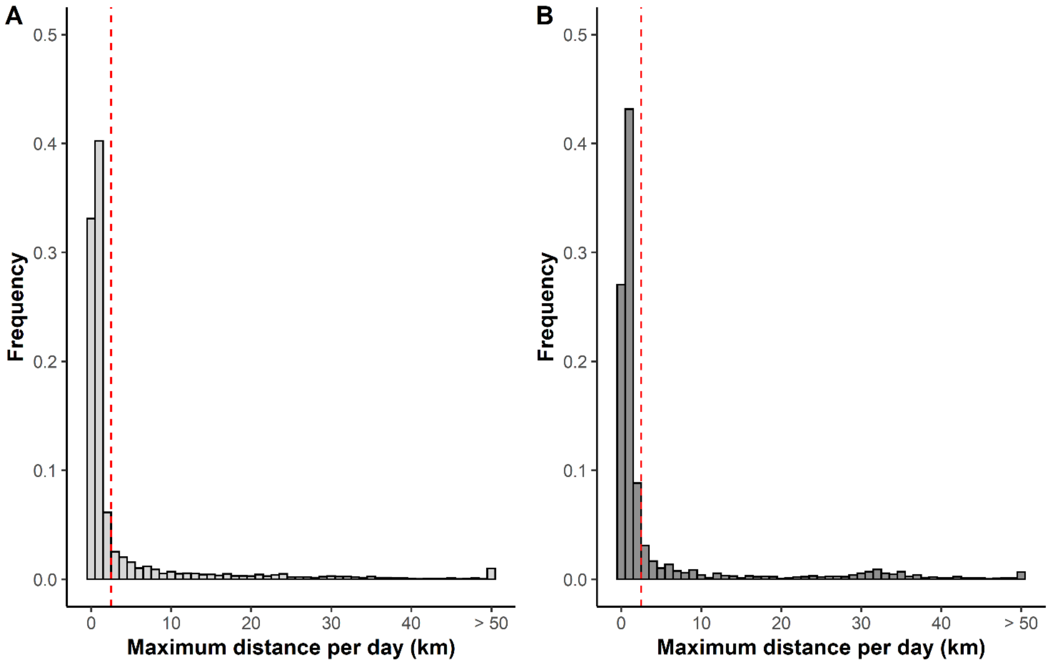

Figure 3.3 – Frequency of the maximum daily distance moved by Shoebills. Histograms show the frequency of distances moved (in Km's) of (A) immature and (B) adult Shoebills. The dashed red line indicates the threshold that captures 80% of movements, used to define Shoebills' Moving Days.

The mean maximum daily distances moved varied throughout the year, particularly for adult Shoebills. During the breeding season, from June until October, adults performed shorter movements, with the mean maximum daily distance moved being the lowest in August (1.1 km per day). In October, towards the end of the breeding season, adult mean maximum daily distance started to increase, peaking in December (10.5 km per day). Immature Shoebills show less variation in movement distances over the year. Birds moved least in September (1.9 km per day), while movement distances peaked in May to 5.5 km per day (Figure 3.4).

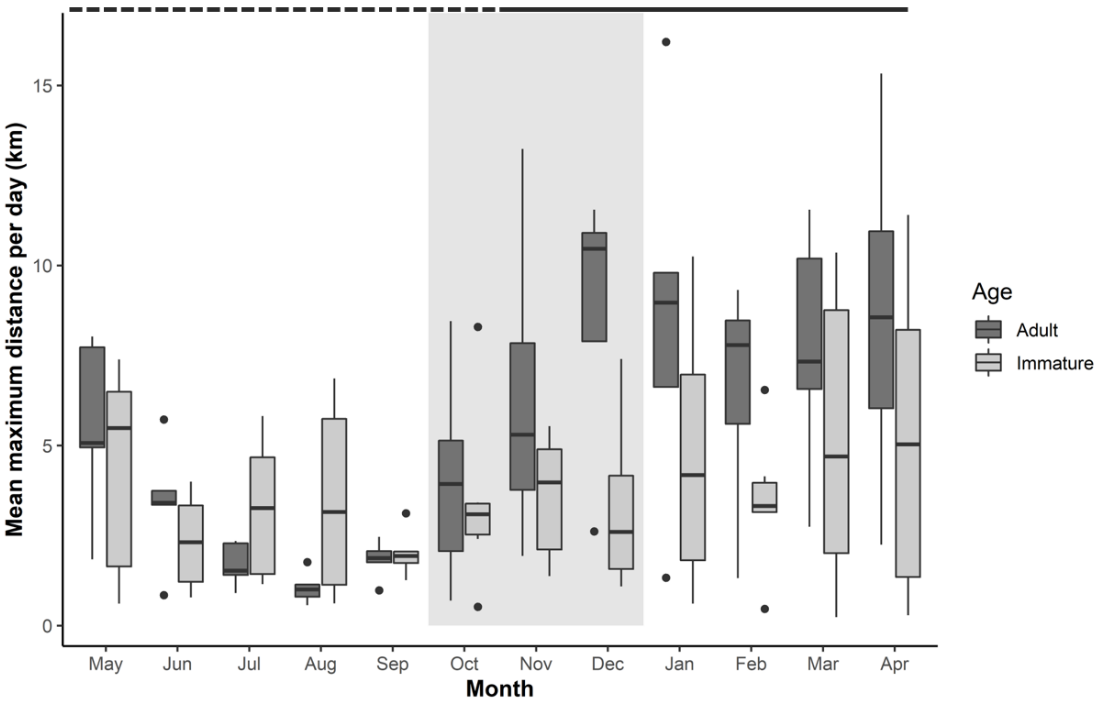

Figure 3.4 – Boxplots of the mean maximum daily distance per month, for individual immature and adult Shoebills, between 2011 and 2018. Data is organised to start at the beginning of the breeding season (May). The boxes represent the 25th, 50th and 75th percentiles of the mean maximum daily distance. Whiskers the 1.5 times the value of inter-quantile range, with values outside this range plotted as black dots. The dashed line above the plot indicates the dry season (May to October) and the wet season (November to April). The shaded area highlights the period between October and December, with an increase of adult mean maximum daily distances.

Influence of NDWI on Shoebill movements

On over 80% of the days, Shoebills moved less than 3 km, thus ‘Moving Days’ were defined as days when Shoebills moved more than 3 km (Figure 3.3) and the regions where birds stayed for a minimum of two days between Moving Days were classified as ‘Areas’ (further details in the Methods section). Between October and December of 2013-2017, across the 5 adults we located 39 different Areas, and, in 2014 and 2015, across the 6 immatures, we identified 33 Areas. Immature birds stayed on average 14±19 days in Areas, whereas adult birds spent 17±24 days in Areas before moving to another location. These locations always had negative daily mean NDWI values, indicating that Shoebills were not in open water areas and selected relatively dry regions.

We found that the NDWI of the Areas used by Shoebills between October and December was statistically different from the NDWI of the same Areas the week after the birds abandoned (Table 3.3), both for immature and adult Shoebills. However, these relationships differed between the age classes. Adult Shoebills used Areas with an average NDWI value of -0.52, varying from -0.68 to -0.10. The week after adults left the Area, it became drier with the NDWI decreasing to an average of -0.57 (range -0.79 to -0.18). In contrast, for immatures, the mean NDWI of Areas used was -0.53, with a minimum NDWI value of -0.76 and maximum of -0.10.After abandonment, the average NDWI of these Areas increased to -0.43 (range -0.66 to -0.07), indicating that the Areas became wetter (Figure 3.5 A and B). The variance explained by the immature model was higher (marginal R-squared 0.27) than by the adult model (marginal R-squared 0.14), and in both cases the random factors slightly increased the R-squared (immature conditional R-squared 0.32; adult conditional R-squared 0.15) (Table 3.3).

We did not find a statistical difference between the NDWI of Areas used by Shoebills the week before abandonment, and the NDWI of the newly colonised Areas the first week after Shoebill arrival; this was the case for both adults and immatures (Table 3.3). The mean NDWI of Areas used by adult Shoebills the week before abandonment and the week after arrival was -0.54 (ranging from -0.76 to -0.16). For immatures, the NDWI of Areas before abandonment was -0.49 (varying from -0.76 to -0.07), compared to -0.50 (from -0.66 to -0.09) the week after arrival (Figure 3.5 C and D).

Table 3.3 – Results of the GLMM models. The models compared the values of: a) daily mean NDWI of Areas before Shoebill abandonment, with the values of NDWI after the birds abandoned the Area, using year and Area nested within bird ID as random effects. Daily mean NDWI was transformed as a second-degree polynomial (poly 1 and poly 2); b) daily mean NDWI of used Areas the last week before abandonment, with the daily mean NDWI of used Areas the first week after arrival, using year and Area nested within bird ID as random effects.

Model	Age	Parameter	Estimate (SE)	Z-value	P-value	Marginal R^2	Conditional R^2
a) Comparison of NDWI of Areas before and after Shoebill abandonment	Immature	Intercept	0.17 (0.19)	0.87	0.384	0.270	0.320
		NDWI (poly1)	33.87 (3.38)	10.02	<0.001		
		NDWI (poly2)	-7.35 (2.70)	-2.72	0.007		
	Adult	Intercept	0.06 (0.08)	0.76	0.445	0.144	0.151
		NDWI (poly1)	-23.12 (2.65)	-8.72	<0.001		
		NDWI (poly2)	15.03 (2.73)	5.50	<0.001		
b) Comparison of NDWI of used Areas the last week before abandonment and the first week after arrival	Immature	Intercept	-0.03 (0.54)	-0.05	0.963	<0.001	<0.001
		NDWI	-0.05 (1.01)	-0.05	0.957		
	Adult	Intercept	-0.50 (0.46)	-1.10	0.272	<0.001	<0.001
		NDWI	-0.95 (0.85)	-1.11	0.268		

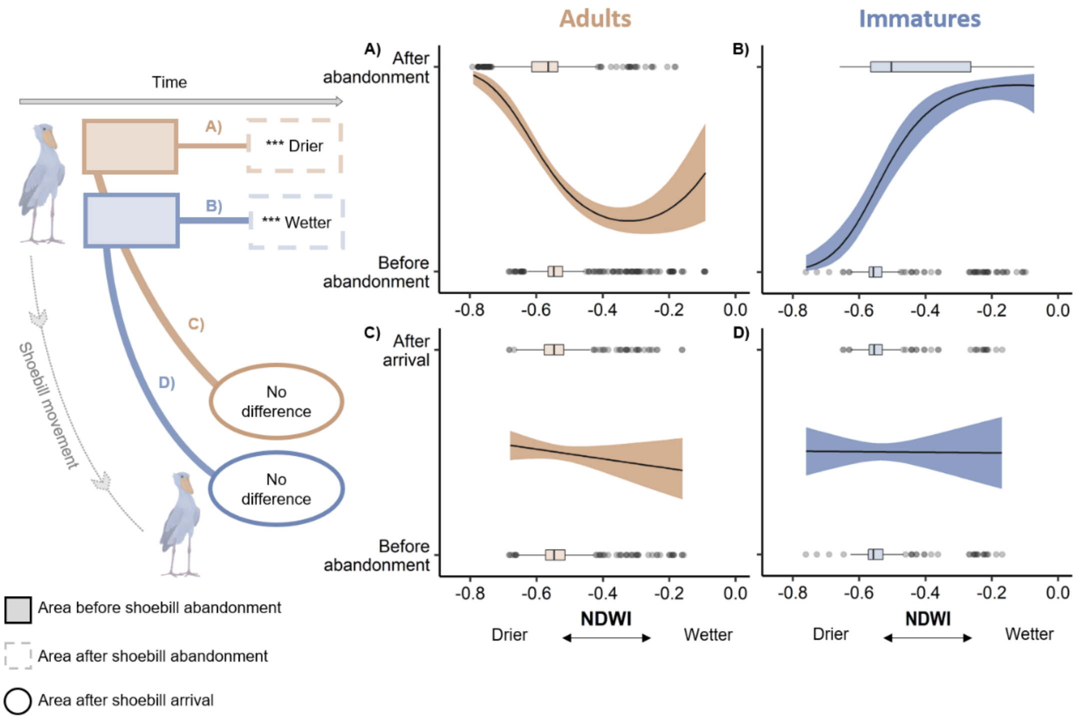

Figure 3.5 – **Diagram describing the analysed spatial and temporal relationships of Shoebill movements.** The plots show the predicted mean daily NDWI values (solid line) and 95% confidence interval (shaded areas) for (A) adults and (B) immatures of 'Areas' before and after Shoebill abandonment, and for (C) adults and (D) immatures before Shoebill abandonment and after Shoebill arrival in a new 'Area'. The boxplots display the observed values of daily mean NDWI, with the boxes representing the 25th, 50th and 75th percentiles and the whiskers the 1.5 times the value of inter-quantile range. Values outside this range are plotted as grey dots. Brown colours indicate adult data and blue colours indicate immature data.

3.4 Discussion

We described for the first time the annual home range sizes and variation in distances moved over the year for adult and immature Shoebills, providing evidence of age-related differences in their movement ecology. Furthermore, we show that movement patterns of Shoebills were associated with changes in surface water, but these changes contrasted between age classes, with adult abandoning sites that became drier, whereas immatures abandoned sites that became wetter. Despite the small number of tracked Shoebills, which can make the generalisation of our results to other Shoebill populations challenging, this species inhabits similar habitats throughout their narrow distribution range (Birdlife International, 2020), and thus their movement ecology is likely influenced by analogous environmental drivers.

Shoebills in the Bangweulu Wetlands were largely sedentary, moving less than 3km on over 80% of days. The main prey of Shoebills in the Bangweulu Wetlands are catfish, which they catch mainly through the tactics of stand and wait on top of floating vegetation (Guillet, 1979; Möller, 1982; Mullers & Amar, 2015b). Indeed, field studies in the Bangweulu Wetlands found that they spent 85% of the time performing low-energy activities, such as standing, sitting and preening (Mullers & Amar, 2015b). Walking and flying behaviours may also be associated with foraging, given that a Shoebill strike may disturb the prey and require a move to a different location (Möller, 1982). Therefore, much of these Shoebill's daily movements were likely related to foraging events or searching for suitable foraging habitat.

The average annual home range of Shoebills was around 1,500 km^2 which is larger than for similar species, such as Abdim's Storks *Ciconia abdimii* in Niger (10–120 km^2 (Christensen et al., 2008)). However, there was large individual variation in home range size, both for adult (304 – 3,375 km^2) and immature Shoebills (233 – 2,628 km^2). Other studies have shown large individual variation in home range size of similar wetland species, such as Wattled Cranes *Bugeranus carunculatus*, with 95% kernel density estimates varying between 0.4 and 110.4 km^2 (McCann & Benn, 2006), Mauritanian Spoonbills *Platalea leucorodia balsaci*, with home ranges varying from 23 to 101 km^2 (El-Hacen et al., 2013), or American White Pelicans *Pelecanus erythrorhynchos* summer home range varying between 177 and 4,710 km^2 (King et al., 2016). These variations in individual home range size in the same habitat and within the same species show that animal movement is more complex than a simple reflection of underlying resource distribution (Roshier et al., 2008; Shaw, 2016), and other factors (e.g.

social attraction/repulsion) may also influence individual distribution (Folmer et al., 2012; Folmer & Piersma, 2012).

Several factors can influence the home range size in birds, such as age (King et al., 2016; Krüger et al., 2014; Mendez & Weimerskirch, 2017; Weimerskirch et al., 2014), sex (King et al., 2016; Patrick & Weimerskirch, 2014b; Weimerskirch et al., 2014) and degree of individual specialisation in particular foraging areas (Patrick & Weimerskirch, 2014a). Shoebills do not exhibit strong sexual dimorphism, and the birds in this study were not genetically sexed, thus it was not possible to investigate possible sex differences in home range size. We did not find age-related differences in annual home range size, and although 2 individuals slightly decreased their home range size by an average of 173 km^2 as they aged from immatures to adults, 2 other individuals increased their home range size by an average of 665 km^2 as they matured. However, there is a suggestion of individual consistency, since the individuals with smallest and largest home ranges as immatures maintained smaller and larger home ranges as adults (Table 3.2). In many situations, breeding adults have smaller home ranges than non-breeders during part of the year because their movements are constrained by the location of their nest site (Krüger et al., 2014; Wolfson et al., 2019). Although animals in areas of higher productivity tend to have smaller home ranges (Doherty & Driscoll, 2018; Roshier et al., 2008), this might not be the case in swampy areas. In the wet season, with an increase in water levels, Shoebill prey species occupy larger areas of the swamps, forcing birds to increase their home ranges. Adult birds, with more experience, may build up knowledge of the landscape, occupying the most suitable foraging locations and outcompeting less experienced birds (Riotte-lambert & Weimerskirch, 2013). Consequently, a possible increase in adult home range size during the wet period may be counterbalanced by the seasonal constraint of the nest site location, resulting in approximately the same average home range size for adult and immatures.

Indeed, immature Shoebills moved consistent distances throughout the year, while adults moved smaller distances during the breeding season (May-October), particularly during the incubation and chick-rearing period (June-September). During the breeding season, adults forage close to the nest, moving smaller distances and occupying smaller home ranges (Krüger et al., 2014; Wolfson et al., 2019). Shoebills chicks hatch in June-July, and until the chicks are about 40 days old, at least one adult is constantly on the nest (Mullers & Amar, 2015a). Later in the breeding season (September and October), adult daily distances moved started to increase. Shoebills build their nests on top of floating vegetation (Buxton et al., 1978; John et al., 2013), but as the breeding season progresses, the water levels recede to the point that by the end of the breeding season, the nests are resting on solid ground (Mullers & Amar, 2015a). This might also decrease the suitability of the foraging areas surrounding the nest, forcing adult birds to increase their daily moved distances as the breeding season progresses to find suitable foraging sites.

Environmental factors can also determine movement and home range size in birds, and, for water-dependent species, the spatial and temporal distribution of surface water is one of the main drivers of movement (Bennitt et al., 2014; Henry et al., 2016; Kleyheeg et al., 2017). Bird species respond differently to changes in water availability, with some functional groups responding to sequences of flooding and drying patterns, while others respond immediately to changes in flooded area (Roshier et al., 2002). For example, Black Storks *Ciconia nigra* wintering in West Africa move as the rivers begin to dry (Chevallier et al., 2010), Mallard *Anas platyrhynchos* movements are highly predictable and strongly linked to the presence of surface water (Kleyheeg et al., 2017) and Grey Teal *Anas gracilis* fly hundreds of kilometres directly towards temporary water sources (Roshier et al., 2002). In Southern Africa, the patterns of rainfall and primary productivity are the main drivers of large-scale movements of Egyptian Geese *Alopochen aegyptiaca* and Red-billed Teal *Anas erythrorhyncha*

(Henry et al., 2016). Here, we show that drying and flooding patterns of the Bangweulu Wetlands at the start of the rainy season are important drivers in the movement of Shoebills.

In the Bangweulu Wetlands, November marks the start of the rainy season, being the month with lowest water levels in this region (Ng'onga et al., 2019). Our results show that between October and December, Shoebills occupied areas of low surface water availability (low NDWI values), which is likely the most available habitat. There were, however, differences in how adult and immature birds responded to changes in surface water. While adults seemed to abandon areas that became drier, immatures abandoned areas that became wetter, suggesting age-related differences in habitat use or foraging strategies. Moreover, the areas selected by Shoebills had the same surface water as the areas they were previously occupying, which suggests a selection for an optimal surface water level by this species. Water-depth limits non-diving waterbirds foraging ranges, by directly restricting the accessibility of the habitats due to birds morphology (e.g. neck and metatarsus) (Ma et al., 2010). Consequently, Shoebills foraging locations are also restricted to the water-depths suitable for foraging.

We hypothesise that the different movements in response to surface water between age-classes might be related to prey availability and optimal foraging conditions. Immature birds tend to be less efficient foragers (Grissac et al., 2017; Rotics et al., 2016) and occupy less optimal foraging locations (Riotte-lambert & Weimerskirch, 2013). Distributions of waterbirds are greatly influenced by the hydrology of the wetlands and distribution of food resources (Bolduc & Afton, 2004), since different species have different foraging methods and depend on particular water depths and prey vulnerability (Ma et al., 2010). Shoebills are typically solitary birds, but they occasionally concentrate in drying pools of water, where fish may become highly abundant (Guillet, 1979). Immature Shoebills may take advantage of this recession of the water level, which promotes the availability of prey (Cook et al., 2014) and thus would be suitable areas for immatures to gain experience in capturing prey. Shoebills also forage in deep water, using floating vegetation as fishing sites and then diving forward, described by Guillet, 1979 as a "peculiar and complicated technique called collapsing". Although birds using this technique have lower foraging success than on flooded grassland, the catfish caught in deeper waters are on average larger than on flooded grasslands (Mullers & Amar, 2015b), as larger catfish prefer deeper waters (Mullers & Amar, 2015b; Ratcliffe, 1972). Therefore, immature birds might prefer drier areas with higher abundance of relatively smaller prey, whereas adults having already mastered the highly specialised deep-water foraging technique, might prefer flooded areas with larger prey, and thus greater rewards per capture. Nonetheless, our interpretations are based on, as yet, unverified validation of the NDWI in swampy areas, particularly the areas used by Shoebills that are typically densely vegetated and have water with low oxygen content (Guillet, 1979), which can pose constraints on the identification of water features using satellite imagery (Xu, 2006). In future research, newly available satellite imagery (e.g. Sentinel-2, launched in 2015) and recently created indexes (e.g. Xu, 2006) may provide further detail on how surface water influences the movements of wetland species. However, these indexes need to be validated in swampy wetlands, which may have their own unique characteristics (Tian et al., 2016).

Moreover, changes in water surface may not be the only environmental variable driving the movement of Shoebills. Henry et al., 2016 explored the main environmental variables influencing the movement decisions of Egyptian Geese and Red-billed Teal in Southern Africa, and although changes in surface water appeared in several of their models, suggesting that the flooding and drying patterns of wetlands have some predictive power, rainfall and primary productivity were found to be more important in explaining movement patterns in these species. The relatively small variance explained by our models also suggest that other non-measured variables likely play a role in driving the movements of Shoebills; we therefore suggest for future research to complement the use of NDWI with high temporal and spatial records of rainfall and NDVI to further explore the drivers of movement patterns and spatial distribution of Shoebills in the Bangweulu Wetlands.

Approval for animal experiments

Licences to catch and deploy the tracking devices were provided by the Zambia Wildlife Authority (now Department of National Parks and Wildlife (DNPW)). The work was carried out with approval from the University of Cape Town Science Faculty Animal Ethics Committee (permit number: 2011/V14/AA). Capture, handling and tagging procedures were carried out by RHEM, qualified in 2007 under the Article 9 of the Experiments on Animals Act in The Netherlands. No bird was injured by the capturing/handling procedure.

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– Chapter 4 –

Timing of migration influences the performance and destination of a long-distance migrant

Timing of migration influences the performance and destination of a long-distance migrant

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Author’s contributions

MA, IC, and AF conceived the idea. IC, JPS, PWA and AMAF coordinated the study. MA and IC performed fieldwork for logger deployment. MA, IC and ASR collected behavioural data and built the tracking dataset. MA analysed the data and wrote an initial version of the manuscript, which was critically edited and revised by all authors. All authors gave final approval for publication.

Abstract

Migration phenology is shifting for many long-distance migrants due to global climate change. The timing and duration of migration may determine the environmental conditions individuals encounter, with potential fitness consequences. In species with asynchronous migrations, i.e., when individuals of a population migrate over a broad time-window, the conditions individuals experience during migration can differ and affect their migratory performance, route, and destination. Here, we examine if timing of autumn migration influences the migratory performance (duration, distance, route straightness, energy expenditure) and migration destinations of a long-distance, asynchronous, migrant, the White Stork *Ciconia ciconia*. We also compare the weather conditions (wind speed, wind direction, and boundary layer height) encountered on migration and examine the influence of wind direction on storks' flight directions. From 2016 to 2020, we GPS-tracked 172 White Storks and obtained 75 complete migrations from their breeding grounds in Southern Europe to the sub-Saharan wintering areas. Autumn migration season spanned over a 3-month period (July-October) and arrival destinations covered a broad area of the Sahel, 2450 km apart, from Senegal to Niger. We found that timing of migration was highly influential: later storks spent fewer days on migration, adopted shorter and more direct routes in the Sahara and consumed more energy when flying, as they were exposed to less supportive weather conditions. In the Sahara Desert, storks' flight directions were significantly influenced by wind direction, with later individuals facing stronger easterly winds (i.e., winds blowing to the west), hence being more likely to end their migration in western areas of the Sahel region. Contrastingly, early storks encountered more supportive weather conditions, spent less energy on migration and were exposed to westerly winds, thus being more likely to end migration in eastern Sahel. Our results show that the timing of migration influences the environmental conditions individuals face, the energetic costs of migration, and the wintering destinations, where birds may be

exposed to different environmental conditions and distinct threats. These findings highlight that ongoing changes in migration phenology, due to environmental change, may have critical fitness consequences for long-distance soaring migrants.

4.1 Introduction

Every year, billions of birds travel from their breeding grounds to the wintering areas and the phenology and routes of those migrants have been shaped to take advantage of predictable weather events (Alerstam et al., 2003; Shamoun-Baranes et al., 2017). For instance, birds facing long trans-oceanic flights wait for greatest wind assistance before starting their migratory endeavour (Gill et al., 2014a), whereas birds crossing large land barriers, such as the Sahara Desert, may adopt different routes in autumn and spring migration to exploit seasonal tailwinds (Vansteelant et al., 2017).

In species with asynchronous migrations, in which individuals of a population migrate at significantly different times, the timing and duration of those movements strongly determine the conditions birds experience during migration (e.g., social cues and weather conditions) (Bauer et al., 2016) which can affect their fitness and survival. Many studies have investigated the consequences of changes in the timing of spring migration, generally concluding that spring arrival dates are advancing (Gill et al., 2014b; Saino et al., 2011) and that birds arriving earlier at the nesting grounds have higher breeding success (Smith & Moore, 2005; Vergara et al., 2007). However, earlier spring migrants may experience worse weather conditions during migration, increasing their energy expenditure (Rotics et al., 2018). The consequences of variability in timing of the autumn migration are less well understood (Kanerva et al., 2020; La Sorte et al., 2015) and may be species specific (Jenni & Kéry, 2003; Scholer et al., 2016), thus more challenging to determine. Nevertheless, autumn migration is marked by high mortality of juveniles on their first migration (Cheng et al., 2019), as well as by the choice of wintering location (Vansteelant et al., 2017) that may have carry over effects to the remaining annual cycle (Schlaich et al., 2016).

Selecting the timing and route that maximizes exposure to favourable weather conditions is particularly important for soaring birds, which rely on supporting winds and strong thermal updrafts to fly (Vansteelant et al., 2015). These allow them to soar more efficiently (Bohrer et al., 2012) and to minimise energy expenditure (Duriez et al., 2014; Harel et al., 2016; Sapir et al., 2010). Simultaneously, many bird species are highly vulnerable to weather conditions, which can be extremely dynamic and change throughout the migratory season (Shamoun-Baranes et al., 2017); the weather can enhance bird's migratory performance by increasing daily speeds and displacements (e.g., Mellone et al., 2014; Vansteelant et al., 2015), but it can also hinder migratory progression (Pastorino et al., 2017), interrupt migration (Klaassen et al., 2017), or lead to mortality (Loonstra et al., 2019). Wind conditions are highly influential, shaping the migratory routes by promoting unintended detours (Vansteelant et al., 2017) and even determining bird's wintering areas (Vansteelant et al., 2017), ultimately influencing population migratory connectivity (Norevik et al., 2020). Using high spatial and temporal resolution tracking data of long-distance migrants can thus help unravel the effects of exposure to variable weather conditions due to variability in the timing of migration.

In this study, we use GPS tracking data to examine if timing of autumn migration influences the migratory performance and destination, as well as the weather conditions birds experience *en route*, and how these influence bird's flight directions. Our study focuses on White Storks *Ciconia ciconia* from a partial migratory population, where some individuals remain in the breeding area all year round, while others still undertake a long-distance migration to the original Sub-Saharan wintering grounds (Soriano-Redondo et al., 2020). White storks are large soaring birds exhibiting high variability in the timing of migration (Onrubia et al., 2019). Moreover, the range of the migration period has been increasing over the last few decades (Scholer et al., 2016). This species has been observed crossing the Strait of Gibraltar all months of the year except in June (Fernández-Cruz, 2004; Onrubia et al., 2019), thus making it an ideal study species to investigate the influence of timing of migration on individual performance.

We use a 5-year GPS tracking dataset with tri-axial acceleration, enabling us to identify bird behaviour and energy expenditure, to understand the consequences of variability in the timing of migration. Specifically, our goal is to examine if timing of migration influences (i) migratory performance i.e., migration duration, distance travelled, route straightness and flight energy expenditure, and (ii) the autumn migration destination in the Sahel. Finally, we examine storks' exposure to the weather conditions (wind speed, wind direction, and boundary layer height) during migration, and assess the influence of wind direction on bird's flight direction. This work can provide a mechanistic understanding of the influence of timing of migration on migratory performance and wintering site selection, with potential consequences for migratory connectivity and exposure to anthropogenic threats.

4.2 Methods

Tracking data and behavioural classification

Between 2016 and 2020, we GPS-tracked 100 first-year juveniles and 72 adult white storks. Among the 72 tracked adults, 10 were long-distance migrants (14%) while the remaining 62 were either residents in Iberia or short-distance migrants to Morocco. This study included 16 adult bird/years (5 adults tracked for 1 migration, 4 adults tracked for 2 migrations, and 1 adult tracked for 3 migrations), and 59 first-year juveniles with completed sub-Saharan autumn migrations, from southern Portugal to the Sahel wintering areas. Adults were trapped at landfill sites, using nylon leg nooses, and at their nests with a remotely activated clap trap. Pre-fledging juveniles were retrieved from their nests for tag deployment and returned afterwards. Storks were equipped with GPS/GSM loggers with tri-axial acceleration ("Flyway-50" from Movetech Telemetry, with 4 different models, and "Ornitrack-50" loggers from Ornitela), weighing between 50-80g. The devices were attached as backpacks using a Teflon ribbon thoracic full harness, in total weighing between 1.1-2.9% of the bird's body mass (more details on tag deployment and harnesses in (Gilbert et al., 2016; Soriano-Redondo et al., 2020, 2021)). This study was carried out in agreement with the recommendations of Instituto da Conservação da Natureza e das Florestas and the Animal Welfare & Ethical Review Board from the School of Biological Sciences at the University of East Anglia. Licenses to deploy the loggers were granted by the Instituto da Conservação da Natureza e das Florestas (2016: 493/2016/CAPT; 2017: 661/2017/CAPT to 663/2017/CAPT; 2018: 549/2018/CAPT; 2019: 247/2019/CAPT to 250/2019/CAPT; 2020: 364/2020/CAPT to 368/2020/CAPT).

The loggers provided 9 consecutive GPS and acceleration fixes at 1Hz every 20 minutes during daylight, thus acceleration and location matched in space and time. These acceleration bursts allowed the calculation of Overall Dynamic Body Acceleration (ODBA) and bird behaviour. ODBA is a valid proxy for energy expenditure (Gleiss et al., 2011) and it was calculated by subtracting each acceleration point from a running-mean of 4 seconds for each axis and summing the resulting values for all three axes. To infer bird behaviour, we trained a random forest machine-learning algorithm using 1,000 manually labelled acceleration bursts of 4 different behaviours: foraging, resting, soaring and flapping flight (see Soriano-Redondo et al., 2021 for a full description of ODBA and behaviour classifications). To account for disparities in accelerometery sensors of different logger manufacturers, we built separate random forest models for Movetech Telemetry and Ornitela loggers, with 96% and 97% accuracies, respectively. In this study, we combined soaring and flapping flight behaviours into one single *flight* category. If acceleration information was not available, we classified a GPS fix as *flight* if the GPS recorded ground speed was over 5km/h.

Influence of timing on White Stork migration performance and destination

White Storks travelling to the sub-Saharan wintering locations must cross three major ecological barriers, the Strait of Gibraltar, the Atlas Mountains, and the Sahara Desert. This species can take long stopovers during migration, hence the timing of crossing each ecological barrier is not necessarily correlated for all individuals, as early birds may perform long stopovers and end migration later. Therefore, we divided migration into three legs corresponding to the crossing of ecological barriers (Figure 4.1A) and classified the timing of migration as the date storks start each leg: *Leg 1*, from the start of migration in Portugal until the day the stork crosses the Strait of Gibraltar (defined as 36° latitude); *Leg* 2, from the day after crossing the Strait of Gibraltar until the day the stork crosses the Atlas Mountains (defined by the equation $y = 0.58x + 36.12$); *Leg 3*, from the day after crossing the Atlas Mountains until the end of migration, south of the Sahara Desert.

The start and end of autumn migration (i.e., start of leg 1 and end of leg 3) was classified using the spatio-temporal displacement method described in Soriano-Redondo et al., 2020. This method combines movement displacement and spatial and temporal thresholds to define the start and end of migratory movements. Thus, we defined the start of migration as the first of three consecutive days a stork moved more than 60km between roosts after having left the breeding area (calculated as the 90% kernel of June GPS locations), and the start of wintering period as the first of three consecutive days a stork displaces less than 60km between roosts after having arrived at the wintering area (calculated as the 90% kernel of October GPS locations). The end of autumn migration was defined as the last day before the start of the wintering period, and the destination of the autumn migration was the location where birds ended autumn migration. All analysis were performed using R package *geosphere* (Hijmans, 2019) for distance calculations and *adehabitatHR* for kernel estimations (Calenge, 2006).

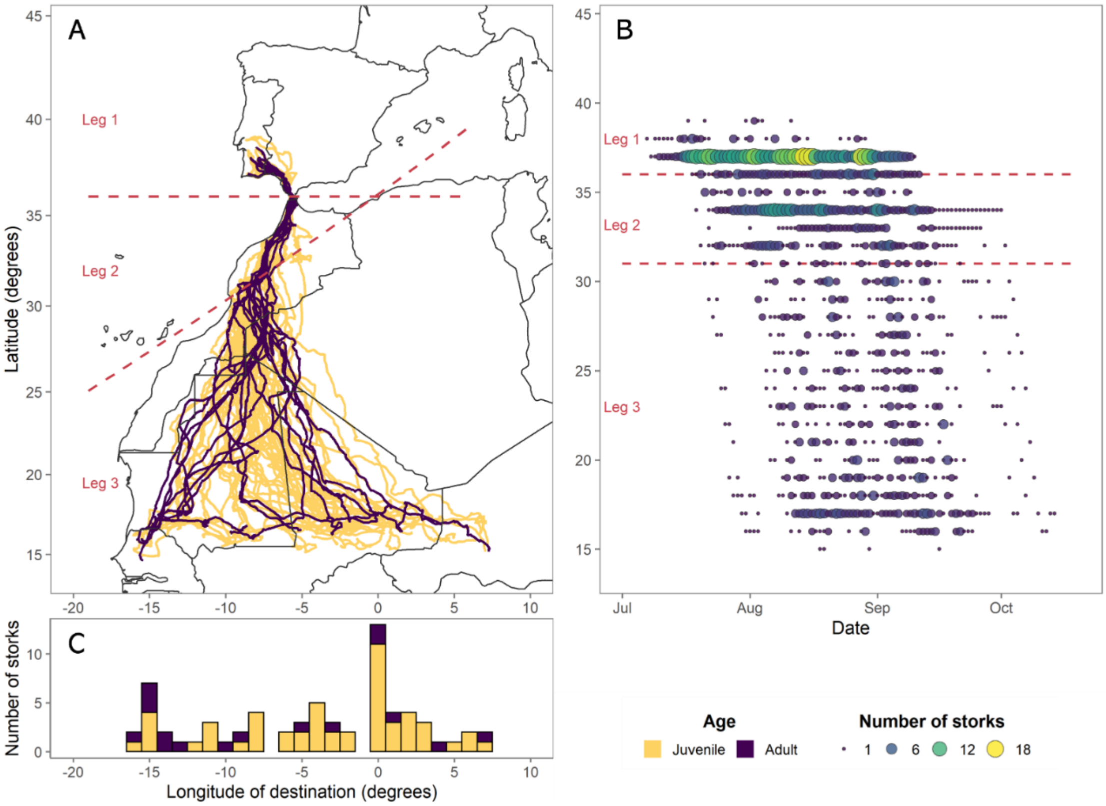

Figure 4.1 – White Stork autumn migration routes, timing, and migration destination. (A) Autumn migration routes of adult (purple, n=16) and juvenile (yellow, n=59) White Storks tracked between 2016 and 2020. Dashed lines indicate the migratory legs: Leg 1 - from Portugal until the Strait of Gibraltar; Leg 2 - from the Strait of Gibraltar until the Atlas Mountains; Leg 3 - from the Atlas Mountains until south of the Sahara Desert. Map was plotted using Mercator projection. (B) Temporal pattern of latitudinal progression of White Storks during Autumn migration. Larger and lighter circles indicate a greater number of storks. Leg 2 was represented as 32º latitude, as over 50% of the GPS tracked White Storks crossed the Atlas Mountains at that latitude. Latitude was plotted using Cartesian coordinates. (C) Longitude of autumn migration destination, plotted using Cartesian coordinates.

We assessed migratory performance of individual White Storks using several metrics: migration duration (in days), total number of migratory and stopover days, total migration distance (in kms), straightness of the migratory route (index between 0-1) and mean flight energy expenditure (in G). These metrics were calculated for the overall migration and for each leg, and we only included individuals for which we had daily data for the entire period.

Migration duration and leg duration were determined as the difference in days between the start and end of migration, and between the start and end of each migration leg. Stopover and migratory days corresponded to days when birds moved less or more than 37km between consecutive night roosts, respectively (see Appendix S4.1 for a description of the calculation of stopover and migratory days' threshold).

Total migration distance (hereafter, beeline distance) is the shortest great-circle (i.e., orthodromic) route between the start and end locations of autumn migration. White Storks from the Portuguese population must cross the Strait of Gibraltar on their way to Africa, hence we calculated the migration beeline distance as the distance between the first autumn migration GPS location and the location at the Strait of Gibraltar and summed it to the migration distance from the Strait of Gibraltar to the arrival location in the Sahel. The beeline distance of each migratory leg was calculated as the shortest orthodromic route between the GPS location at the start of the leg and the first GPS position of the subsequent leg, or, for leg 3, the last GPS position of autumn migration.

We calculated the cumulative travelled distance as the sum of the distances between all daylight GPS fixes on migratory days. Route straightness was defined as the ratio between the beeline distance and the cumulative distance travelled, for the whole migration and for each migratory leg. Finally, we summarised White Storks' flight energy expenditure as the mean ODBA of all accelerometer bursts classified as *flight*.

The influence of timing of migration on migratory performance was examined using separate models for each performance metric and migratory leg. Using the R package *lme4* (Bates et al., 2015), we built linear mixed models (LMMs), with migration duration, number of stopover and migratory days, beeline distance and mean flight energy expenditure as response variables, with timing of start of leg (in Julian day) and age as fixed effects (to account for possible age differences in performance), and bird ID and year as random effects. For mean flight energy expenditure, we also added logger type as a random effect, to control for differences in ODBA estimates between loggers with different accelerometer sensors. To analyse the influence of timing of migration on route straightness, we built a generalised linear mixed model (GLMM) with beta distribution using *glmmTMB* package (Brooks et al., 2017), with route straightness as the response variable, and timing of start of leg and age as fixed effects, and bird ID and year as random factors.

We built two LMMs with latitude and longitude of the destination of autumn migration as response variables to examine the influence of timing on the location where birds finish autumn migration. Timing of start of leg (in Julian day) and age were included as fixed effects, and bird ID and year as random effects. For all LMMs we estimated *p-values* using *car* package (Fox & Weisberg, 2019), and pseudo-R^2 using *MuMIn* package (Barton, 2019), and multicollinearity was analysed by verifying the variance inflation factor (VIF < 2, Zuur et al., 2010).

Influence of timing on the weather conditions experienced by White Storks

To examine the weather conditions individual birds experienced, we firstly annotated the White Stork GPS locations on migratory days with hourly weather data from ERA-5 (Copernicus Climate Change Service (C3S), 2017; Hersbach et al., 2020), with 30 km spatial resolution, using the *GAMT* R package (Bird et al., in prep.) and bilinear interpolation. Similarly to other studies of migratory soaring birds (Mellone et al., 2012; Shamoun-Baranes et al., 2003; Vansteelant et al., 2015), we selected boundary layer height (a proxy for of thermal convection, Vansteelant et al., 2015) and wind zonal (i.e. westward(-)/eastward(+)) and meridional (i.e. southward(-)/northward (+)) components at 925 mB (corresponding to approximately 700m, which is the mean flight altitude for soaring birds on migration, Vansteelant et al., 2017)). Using wind zonal and meridional components, we calculated for each GPS location the wind speed and direction, as well as the wind support each bird experienced (Krietsch et al., 2020; Safi et al., 2013).

We summarised the weather conditions experienced by White Storks on each leg as the mean boundary layer height, mean wind support, and mean zonal wind speed. We then fitted LMMs with the summarised weather variables as response variables, with timing of start of leg (in Julian day) and age as fixed effects, and bird ID and year as random effects.

Influence of timing and wind direction on White Stork flight direction

The crossing of the Sahara Desert (leg 3) is a critical stage of migration, as the high temperatures and the almost complete absence of food and water (Newton, 2008) make it a mortality hotspot for many bird species (Strandberg et al., 2010). Moreover, this is the final stage of migration before White Storks reach the sub-Saharan wintering grounds. To determine if the timing of crossing leg 3 and the direction of the winds influence stork's flight direction, we examined the daily movements of White Storks during the crossing of the Sahara Desert in more detail. First, we determined bird's ground speed and bearing on GPS *flight* fixes, by calculating the time, distance, and direction between two consecutive locations. We then derived stork's flight direction as the longitudinal speed (i.e. westward(-)/eastward(+))

at each GPS location (Vansteelant et al., 2017) and calculated the mean daily longitudinal speed. Using the weather data, we calculated the mean daily zonal wind speed experienced by the storks when flying. Finally, using a LMM we assessed if the start date of leg 3, daily mean zonal wind speed, and their interaction affected the mean stork longitudinal speed. Bird ID and year were included as random effects.

4.3 Results

Between 2016 and 2020 we GPS-tracked 172 White Storks and recorded 75 complete sub-Saharan autumn migration tracks (adults = 16, juveniles = 59), consisting of 1,235 migratory days and 900 stopover days. In total, the dataset comprised 96,630 GPS fixes (adults = 17,638, juveniles = 78,992), with an average of 1,288 GPS fixes per track (sd = 809). Storks began their autumn migration over a two-month period, between the 7th of July and 4th of September (median date = 5th of August ± 17 days) and arrived at the wintering grounds between the 31st of July and 14th of October (median date = 6th of September ± 15 days), displacing more than 2500 km (adults = 2563 ± 38.4 km, juveniles = 2525 ± 15.3 km), and taking on average 25 (adults, sd = 12) and 31 (juveniles, sd = 17) days (Table 4.1). Both age groups finished their migration over a large area in the Sahel region, spanning 2450 km, from Senegal to Niger (Figure 4.1).

Table 4.1 – Summary of adult and juvenile White Stork migration characteristics for the whole migration and for the three different migration legs. Leg 1 – from Portugal until the Strait of Gibraltar; Leg 2 – from the Strait of Gibraltar until the Atlas Mountains; Leg 3 – from the Atlas Mountains until south of the Sahara Desert.

Migratory Leg	Age	Mean start date (range)	Mean migration duration, in days (SE)	Mean number of migration days (SE)	Mean number of stopover days (SE)	Mean beeline distance, in km (SE)	Mean route straightness index (SE)	Mean latitude of destination, in degrees (range)	Mean longitude of destination, in degrees (range)
All migration	**Adult**	-	25 (3.1)	16 (0.5)	10 (3.0)	2563 (38.4)	0.73 (0.02)	16.68 (14.65 – 17.94)	-7.28 (-15.51 – 7.27)
	Juvenile	-	31 (2.2)	18 (0.3)	14 (2.1)	2525 (15.3)	0.67 (0.01)	16.67 (15.25 – 17.98)	-3.24 (-15.53 – 7.03)
Leg 1	**Adult**	10.Aug (09.Jul – 03.Sep)	9 (2.2)	4 (0.3)	6 (2.1)	376 (11.2)	0.71 (0.03)	-	-
	Juvenile	04. Aug (07.Jul – 04.Sep)	10 (1.4)	4 (0.1)	6 (1.4)	374 (7.6)	0.63 (0.01)	-	-
Leg 2	**Adult**	20. Aug (21.Jul – 12.Sep)	6 (1.4)	3 (0.1)	3 (1.4)	562 (21.0)	0.85 (0.02)	-	-
	Juvenile	14.Aug (19.Jul – 10. Sep)	9 (1.5)	3 (0.2)	6 (1.4)	504 (17.2)	0.78 (0.02)	-	-
Leg 3	**Adult**	26.Aug (06.Aug – 15.Sep)	11 (1.1)	9 (0.6)	2 (0.6)	1679 (53.0)	0.74 (0.02)	-	-
	Juvenile	24.Aug (22.Jul – 03.Oct)	12 (0.4)	11 (0.3)	1 (0.3)	1723 (21.9)	0.69 (0.01)	-	-

Influence of timing on White Stork migratory performance and arrival at the wintering grounds

Timing of migration significantly influenced migratory performance for all metrics analysed, but at different stages of the migration (Figure 4.2). Storks starting leg 1 and leg 3 earlier took longer to complete the respective legs, spending more days on stopovers on leg 1, and adopting longer and less direct routes on leg 3. Early storks also spent less energy when flying on leg 1 and leg 3. When comparing the migratory performance of adults and juveniles, we found that adults adopted significantly straighter routes than juveniles when crossing leg 1 and leg 3, but found no differences in flight energy expenditure (Figure 4.2, Tables 4.2 - 4.3).

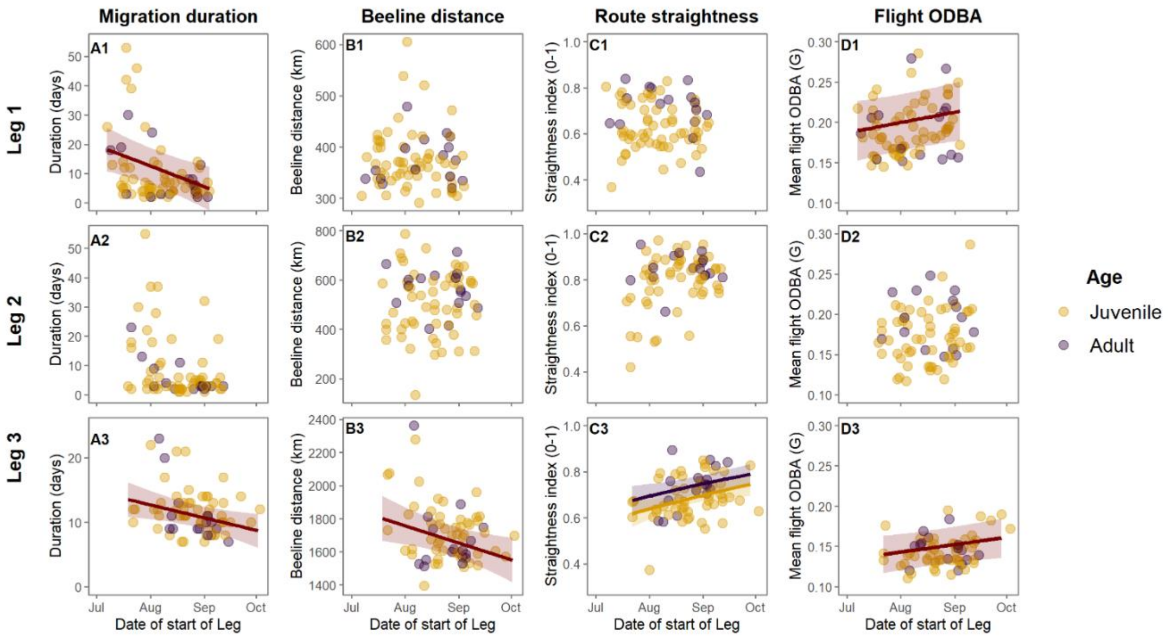

Figure 4.2 – Influence of timing of start of leg 1, leg 2 and leg 3 on White Stork migratory performance. Model predictions of the relationship between the starting date of migratory legs and (A1-A3) migration duration (days), (B1-B3) beeline migratory distance (km), (C1-C3) route straightness (0-1), and (D1-D3) mean flight energy expenditure (ODBA, G). Data was modelled using LMMs and GLMMs, with gaussian (models A, B and D) and beta distributions (models C), using bird id and year, and (models D) logger model, as random factors. Red lines show the statistically significant relationships, and purple and yellow lines highlight the statistically significant differences between adult and juvenile performance, respectively. Shading represents 95% confidence intervals and points show the raw data for adults (purple) and juveniles (yellow).

Table 4.2 – Results of the LMMs, testing the influence of timing of White Stork migration and age on migration duration and on the number of migratory and stopover days. Models used bird ID and year as random factors. The variable "Date" has been scaled by subtracting the mean date and dividing by the standard deviation.

Response	Leg	Predictor	Estimate (SE)	t-value	p-value	R^2 marginal	R^2 conditional
Migration duration	1	Intercept	11.51 (3.15)	3.66	-	0.12	0.88
		Date	-3.92 (1.24)	-3.17	0.002 **		
		Age (juv.)	-1.86 (3.38)	-0.55	0.582		
	2	Intercept	7.26 (3.44)	2.11	-	0.01	0.88
		Date	0.07 (0.55)	0.14	0.893		
		Age (juv.)	1.79 (3.73)	0.48	0.632		
	3	Intercept	11.10 (0.88)	12.68	-	0.09	0.09
		Date	-1.10 (0.47)	-2.34	0.019 *		
		Age (juv.)	0.78 (1.00)	0.77	0.439		
Migratory days	1	Intercept	3.73 (0.31)	11.95	-	0.01	0.12
		Date	-0.07 (0.13)	-0.58	0.565		
		Age (juv.)	0.19 (0.31)	0.62	0.534		
	2	Intercept	2.69 (0.41)	6.54	-	0.05	0.75
		Date	-0.11 (0.15)	-0.70	0.483		
		Age (juv.)	0.62 (0.41)	1.49	0.136		
	3	Intercept	9.40 (0.56)	16.88	-	0.13	0.13
		Date	-0.78 (0.30)	-2.61	0.009 **		
		Age (juv.)	1.10 (0.64)	1.72	0.085 .		
Stopover days	1	Intercept	8.08 (3.10)	2.61	-	0.11	0.95
		Date	-3.65 (1.18)	-3.09	0.002 **		
		Age (juv.)	-2.39 (3.35)	-0.71	0.475		
	2	Intercept	1.70 (0.51)	3.32	-	0.02	0.02
		Date	-0.32 (0.27)	-1.16	0.244		
		Age (juv.)	-0.32 (0.59)	-0.55	0.581		
	3	Intercept	1.87 (0.62)	3.02	-	0.03	0.62
		Date	-0.29 (0.28)	-1.04	0.296		
		Age (juv.)	-0.49 (0.68)	-0.72	0.472		

Table 4.3 - Results of the LMMs (and GLMM, for route straightness), testing the influence of timing of White Stork migration and age on migration beeline distance, route straightness and flight ODBA. Models used bird ID and year as random factors, and on the flight ODBA model, logger model was a random factor. For the route straightness and flight ODBA models, the variable "Date" has been scaled by subtracting the mean date and dividing by the standard deviation. Pseudo-R^2 values are not available for GLMMs with beta distributions.

Response	Leg	Predictor	Estimate (SE)	t/z-value	p-value	R^2 marginal	R^2 conditional
Beeline distance	**1**	Intercept	449.4 (88.0)	5.11	-	0.01	0.80
		Date	-0.32 (0.39)	-0.82	0.412		
		Age (juv.)	-6.59 (18.5)	-0.36	0.722		
	2	Intercept	499.3 (230.5)	2.17	-	0.04	0.59
		Date	0.27 (0.99)	0.27	0.787		
		Age (juv.)	-55.92 (41.07)	-1.36	0.173		
	3	Intercept	2470.4 (328.2)	7.53	-	0.10	0.23
		Date	-3.35 (1.37)	-2.45	0.014 *		
		Age (juv.)	47.00 (51.84)	0.91	0.365		
Route straightness	**1**	Intercept	0.91 (0.12)	7.89	<0.001 ***	-	-
		Date	-0.06 (0.05)	-1.10	0.270		
		Age (juv.)	-0.39 (0.13)	-3.06	0.002 **		
	2	Intercept	1.79 (0.25)	7.24	<0.001 ***	-	-
		Date	0.18 (0.10)	1.77	0.077 .		
		Age (juv.)	-0.40 (0.26)	-1.58	0.115		
	3	Intercept	1.03 (0.10)	9.90	<0.001 ***	-	-
		Date	0.15 (0.05)	2.70	0.007 **		
		Age (juv.)	-0.25 (0.12)	-2.13	0.034 *		
Flight ODBA	**1**	Intercept	0.202 (0.018)	11.32	-	0.04	0.59
		Date	0.007 (0.003)	2.08	0.038 *		
		Age (juv.)	0.014 (0.008)	1.62	0.104		
	2	Intercept	0.200 (0.019)	10.30	-	0.01	0.81
		Date	0.003 (0.004)	0.96	0.340		
		Age (juv.)	-0.005 (0.010)	-0.53	0.594		
	3	Intercept	0.150 (0.011)	13.39	-	0.04	0.89
		Date	0.005 (0.002)	2.23	0.026 *		
		Age (juv.)	0.002 (0.006)	0.44	0.661		

The latitude of autumn migration destinations did not differ between early and late migrants, but longitude was significantly influenced by the timing of migration: storks migrating earlier were more likely to arrive to Eastern Sahel, while later migrants were more likely to arrive to Western Sahel (Figure 4.3). Adults and juveniles finished their migration in similar areas (Table 4.4).

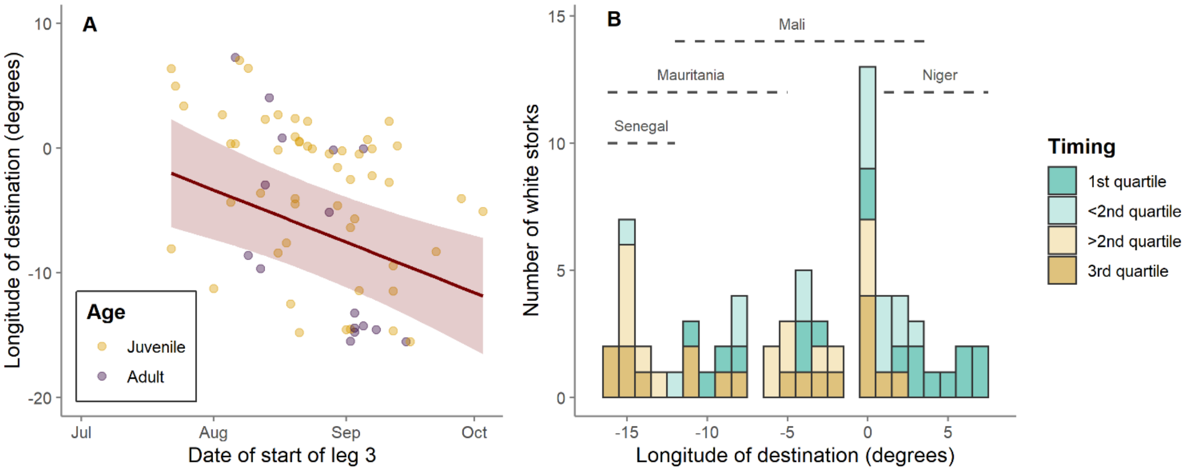

Figure 4.3 – Influence of timing of start leg 3 (crossing the Sahara Desert) on the destination of autumn migration. (A) Model predictions of the relationship between the start date of leg 3 and the longitude of autumn migration. Data was fitted with linear mixed models with gaussian distribution, using bird id and year as random factors. Red lines show the statistically significant relationship, shading represents 95% confidence interval and points show the raw data for adults (purple) and juveniles (yellow). (B) Longitude of the autumn migration destination in the Sahel for early and late migrant White Storks. Early birds starting leg 3 on the 1st and 2nd quartile of the migration dates are represented as dark blue and dark brown, respectively, while late birds (later than the median) are represented as light blue and light brown, respectively.

Table 4.4 – Results of LMMs, testing the relationship between the latitude and longitude of the migration destination of White Storks, and the date of start each leg and age of the bird. Models used bird id and year as random factors.

Response	Leg	Predictor	Estimate (SE)	t-value	p-value	R^2 marginal	R^2 conditional
Latitude of autumn migration destination	**1**	Intercept	17.04 (1.20)	14.17	-	<0.01	0.08
		Date	0.00 (0.01)	-0.27	0.791		
		Age (juv.)	-0.03 (0.22)	-0.14	0.893		
	2	Intercept	17.28 (1.31)	13.14	-	<0.01	0.08
		Date	0.00 (0.01)	-0.43	0.668		
		Age (juv.)	-0.03 (0.22)	-0.15	0.884		
	3	Intercept	17.78 (1.34)	13.29	-	<0.01	0.09
		Date	0.00 (0.01)	-0.80	0.423		
		Age (juv.)	-0.02 (0.21)	-0.12	0.908		
Longitude of autumn migration destination	**1**	Intercept	12.57 (9.25)	1.36	-	0.11	0.97
		Date	-0.09 (0.04)	-2.10	0.036 *		
		Age (juv.)	3.25 (2.11)	1.54	0.124		
	2	Intercept	25.03 (9.19)	2.73	-	0.18	0.97
		Date	-0.14 (0.04)	-3.50	<0.001 ***		
		Age (juv.)	3.07 (1.99)	1.55	0.122		
	3	Intercept	25.36 (9.20)	2.76	-	0.17	0.97
		Date	-0.13 (0.04)	-3.53	<0.001 ***		
		Age (juv.)	3.28 (1.99)	1.65	0.099 .		

Influence of timing on the weather conditions experienced by White Storks

The weather conditions varied along the season (Figures 4.4 – 4.5, Table 4.5): early birds encountered higher boundary layers (i.e., stronger thermals) on leg 2 and leg 3 and more supportive wind conditions on leg 1 (Figure 4.4). Earlier migrants also experienced significantly stronger westerly winds (i.e., winds blowing to the east) on leg 3 (Figure 4.5). We only found age related differences in leg 2, juveniles travelled on days with less supportive winds, compared to adults (Table 4.5).

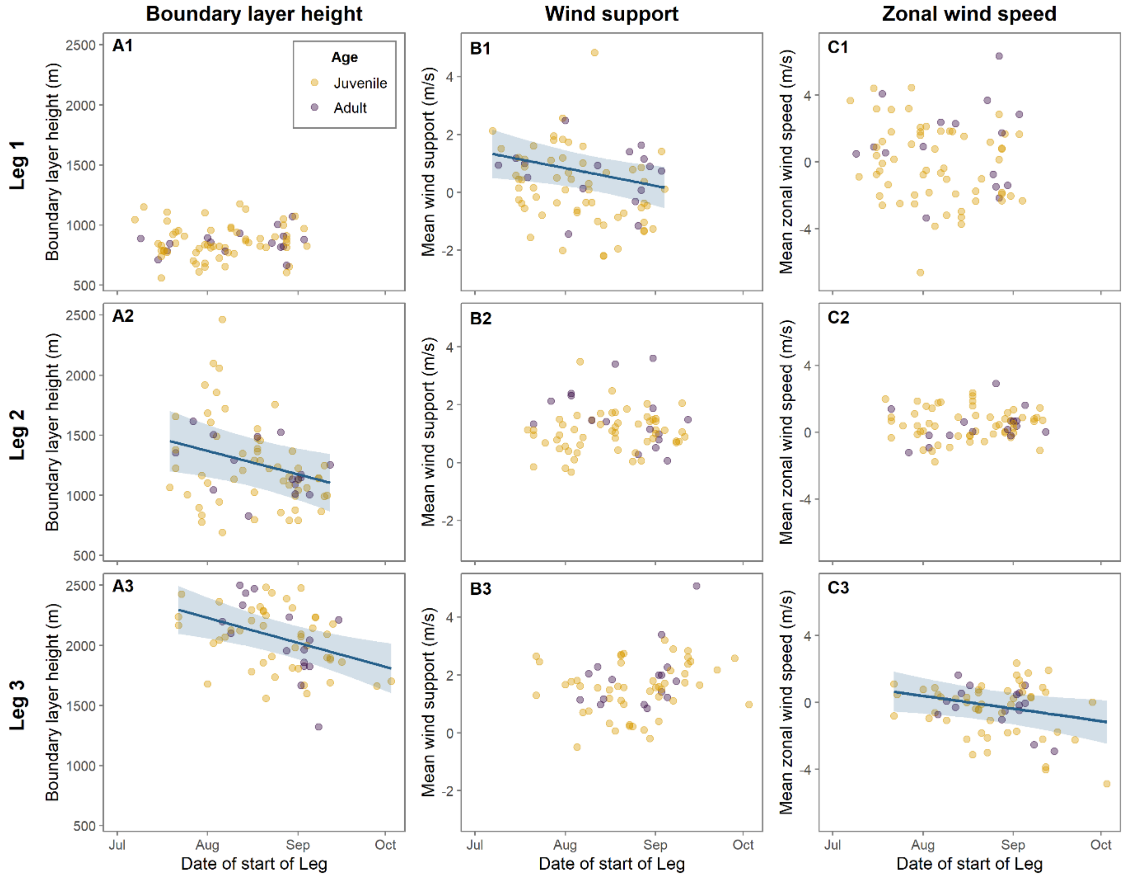

Figure 4.4 – Influence of timing of starting leg 1, leg 2 and leg 3 on the weather conditions experienced by White Storks. Model predictions (blue line) of the relationship between White Stork timing of migration and (A1-A3) boundary layer height (m) and (B1-B3) mean wind support (m/s), and (C1-C3) mean zonal wind speed (m/s). Data was modelled using linear mixed models, with gaussian distributions, using bird id and year as random factors. Blue lines show the statistically significant relationships, shading represents 95% confidence intervals and points show the raw data for adults (purple) and juveniles (yellow).

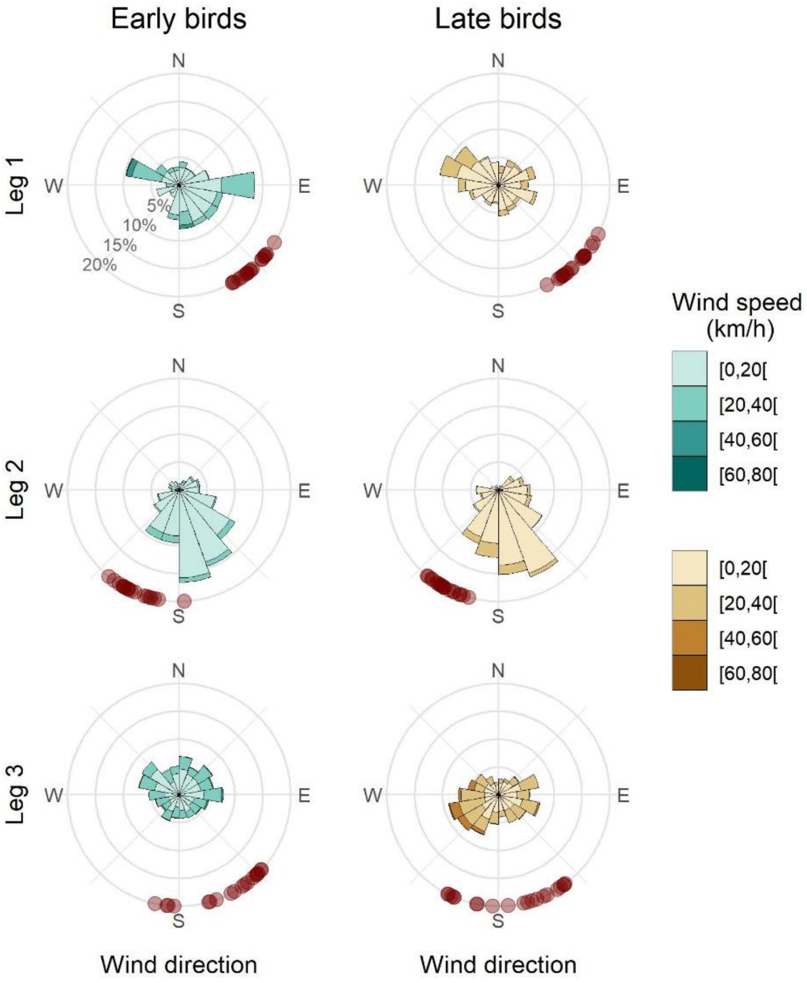

Figure 4.5 – Wind conditions experienced by White Storks crossing each migratory leg on the 1st (early birds) and 3rd (late birds) quartile of the migration period. Wind direction and wind speed (both in % of GPS flight fixes) are represented by the length and colour of the bars. Red points show the directions taken by the birds when crossing the migratory leg, calculated as the bearing between the first and last GPS location of the leg.

Table 4.5 – Results of LMMs, testing the relationship between weather conditions White Stork's experienced (mean boundary layer height, mean wind support, and mean zonal wind speed) and timing of migration and age. Models used bird ID and year as random effects.

Response	Leg	Predictor	Estimate (SE)	t-value	p-value	R^2 marginal	R^2 conditional
Boundary layer height	1	Intercept	649.8 (208.9)	3.11	-	0.01	0.56
		Date	0.92 (0.93)	1.00	0.379		
		Age (juv.)	3.37 (43.35)	0.08	0.937		
	2	Intercept	2710.2 (612.6)	4.42	-	0.08	0.73
		Date	-6.29 (2.63)	-2.39	0.017 *		
		Age (juv.)	-17.64 (111.8)	-0.16	0.875		
	3	Intercept	3648.9 (507.9)	7.18	-	0.13	0.15
		Date	-6.67 (2.11)	-3.16	0.002 **		
		Age (juv.)	15.26 (77.52)	0.20	0.844		
Wind support	1	Intercept	5.020 (1.92)	2.61	-	0.09	0.09
		Date	-0.020 (0.01)	-2.31	0.021 *		
		Age (juv.)	-0.557 (0.35)	-1.61	0.107		
	2	Intercept	1.315 (1.37)	0.96	-	0.06	0.15
		Date	0.001 (0.01)	0.18	0.860		
		Age (juv.)	-0.449 (0.22)	-2.02	0.043 *		
	3	Intercept	-1.152 (1.71)	-0.67	-	0.06	0.31
		Date	0.013 (0.01)	1.78	0.074 .		
		Age (juv.)	-0.334 (0.28)	-1.21	0.228		
Zonal wind speed	1	Intercept	5.677 (3.66)	1.55	-	0.05	0.12
		Date	-0.020 (0.02)	-1.29	0.197		
		Age (juv.)	-1.201 (0.67)	-1.79	0.073 .		
	2	Intercept	-0.368 (1.61)	-0.23	-	<0.01	0.19
		Date	0.003 (0.01)	0.54	0.590		
		Age (juv.)	-0.019 (0.26)	-0.07	0.942		
	3	Intercept	5.673 (2.78)	2.04	-	0.06	0.87
		Date	-0.025 (0.01)	-2.13	0.033 *		
		Age (juv.)	-0.207 (0.51)	-0.40	0.688		

Influence of timing and wind direction on White Stork flight direction

White Stork's longitudinal speed varied significantly with the wind's zonal speed, with significant differences between adults and juveniles in longitudinal speed (statistics in Table 4.6). A significant interaction between wind zonal speed and timing of migration indicated that earlier migrating storks were more influenced by wind direction than later birds (Figure 4.6, Table 4.6).

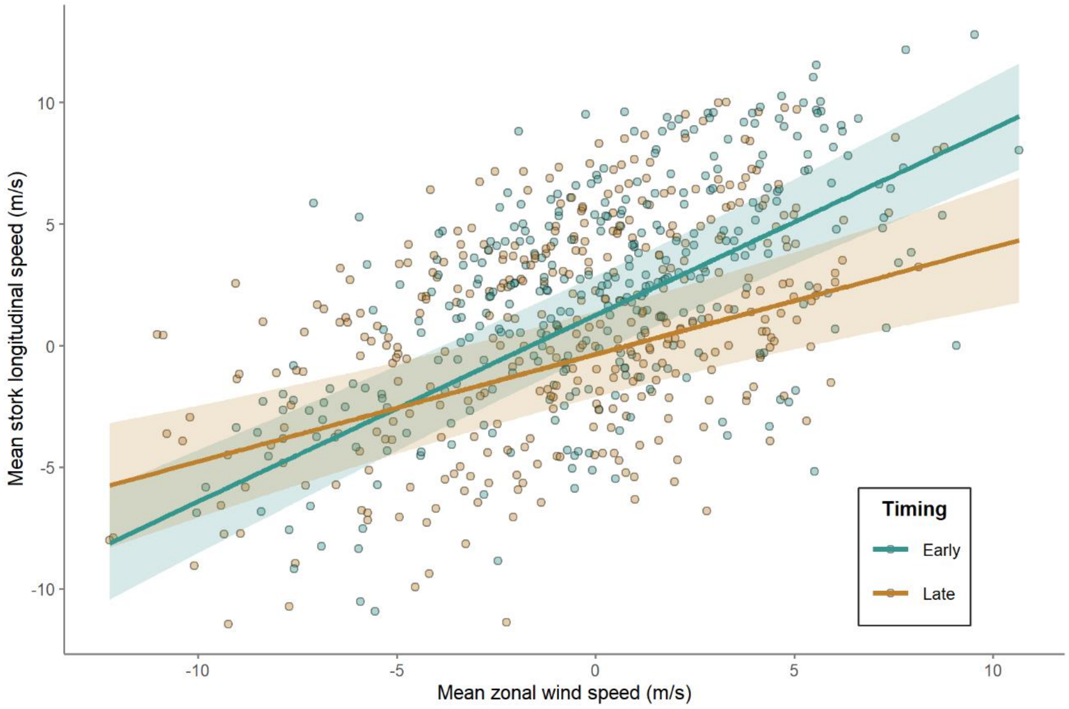

Figure 4.6 – Influence of zonal wind speed (m/s) on White Stork longitudinal speed (m/s) when crossing migratory leg 3 (from the Atlas Mountains until south of the Sahara Desert), with a significant interaction with timing of start migratory leg 3. Data was modelled using a linear mixed model, with bird id and year as random factors. Blue and brown lines indicate the model prediction for the earliest (22nd July) and latest (3rd October) bird, respectively, and shading represents 95% confidence intervals. Points show the raw data, with individuals starting leg 3 on a date earlier or later than the median date (2nd quartile) coloured as light blue and light brown, respectively.

Table 4.6 - Results of LMM, testing the relationship between White Stork longitudinal speed and age, timing of migration, zonal wind speed, and an interaction between these two fixed effects. The model used with bird ID and year as random effects.

Response	Predictor	Estimate (SE)	t-value	p-value	R^2 marginal	R^2 conditional
Bird longitudinal speed	(Intercept)	5.740 (3.72)	1.55	-	0.33	0.49
	Date	-0.022 (0.02)	-1.42	0.198		
	Age (juv.)	1.506 (0.69)	2.19	0.028 *		
	Zonal wind speed	1.674 (0.45)	3.73	< 0.001 ***		
	Date : zonal wind speed	-0.004 (0.002)	-2.36	0.019 *		

4.4 Discussion

Successful migration is highly dependent on the weather conditions individuals face (Newton, 2008) and, in asynchronous migratory populations, individuals may experience different environmental conditions throughout their migration, with potential consequences for individual fitness and population connectivity (Bauer et al., 2016). We studied a soaring bird species, with highly asynchronous migratory movements: counts in the Strait of Gibraltar show that White Storks migrating through the western flyway cross the Strait between July and October (median in 11th August) (Onrubia et al., 2019), corroborating our results obtained with the Portuguese population. This large variability in the timing of migration determines the environmental conditions individuals encounter *en route* and influences the migratory performance and arrival destination in the Sahel. White Storks crossing Iberia and the Sahara Desert earlier in the season encounter more supportive wind and better thermal conditions, spend less energy when flying, and face stronger westerly winds in the Sahara (i.e., winds blowing to the east), leading to increased probability of finishing migration in eastern Sahel, whereas later storks are exposed to winds blowing west and more likely to go to western Sahel.

Influence of timing on weather conditions and migratory performance

Weather conditions experienced by travelling birds play a critical role in determining flight energy expenditure (Amélineau et al., 2014) and migratory performance (Mellone et al., 2014; Vansteelant et al., 2015). Late departing storks were confronted with poorer weather conditions, facing less wind support and weaker thermals, hence spent more energy when flying. Despite the additional energy expenditure in Iberia and in the Sahara, late migrants adopted shorter and straighter routes and spent fewer days on stopovers, possibly as a response to progressively deteriorating weather conditions in autumn. These results suggest that earlier birds stop more often to minimize energy expenditure, whilst later birds tend to minimize migration time (Sergio et al., 2014).

Winds are particularly important in shaping the migratory journeys of soaring birds (Mellone et al., 2012; Shamoun-Baranes et al., 2003, 2017; Vidal-Mateo et al., 2016). We found that the zonal wind direction explained 33% of the variation in White Stork longitudinal movements when crossing the Sahara, a lower variance when compared with lone-migrant juvenile Honey Buzzards *Pernis apivorus* (44% of variation explained, Vansteelant et al., 2017), suggesting that White Stork movements are determined by a combination of environmental variables and other (e.g. social) cues (Chernetsov et al., 2004). However, wind conditions are highly dynamic and change throughout the migration season. In the Sahara Desert, the easterly winds, known as the ‘Harmattan winds’ (Vansteelant et al., 2017), are particularly strong towards the end of the migration season (September – November), hence later birds finishing their migration in central Sahel had to challenge the dominant winds to successfully reach the wintering sites.

When crossing the Sahara Desert, adult storks adopted straighter routes compared to juveniles. Birds improve their migratory performance as they age (Sergio et al., 2014) and, since adult White Storks are consistent in their migration timing and wintering areas (Appendix S4.2), they likely optimise their migration route in consecutive years (Mueller et al., 2013). Unlike results from other studies (Rotics et al., 2016), we did not find significant differences in flight energy expenditure (i.e., ODBA) between adults and juveniles. Firstly, we only included in the analysis birds that successfully completed the autumn migration. As juveniles with higher energy costs are more likely to perish on migration (Rotics et al., 2016), this could have minimised the differences between age groups. Moreover, it is possible that juveniles from southern populations have more time to improve their flight performance before and during migration, when compared to central-European juveniles: they have more time between fledging and start of migration (median German = 32 days (Cheng et al., 2019), median Portugal = 37 days), and they stop more often while on migration (71% of German storks migrate non-stop (Rotics et al., 2016), compared to 14% of the Portuguese storks). These extra learning periods could thus minimise the differences between juveniles and adults.

Influence of migration timing on destination

The wintering area of White Storks migrating through the western flyway covers a large area of the Sahel (Cheng et al. 2019; Flack et al. 2016; Soriano-Redondo et al., 2020) and we found that the weather conditions experienced during migration influenced where storks finished their autumn migration in the Sahel: late migrants, exposed to stronger easterly winds, were more likely to end migration in western Sahel, while earlier migrants had a higher probability of ending migration in eastern areas. As expected for this social migratory species, this pattern is true for both adults and juveniles. Adult White Storks, as other soaring species, show high repeatability in the timing of migration (López-López et al., 2014), which possibly exposes storks to similar environmental conditions during migration, directing them to similar wintering areas in successive years (Appendix S4.2). Conversely, the population asynchronous migration timing, exposes individuals to different weather conditions, conducting them to distinct areas in the Sahel, which can promote low population migratory connectivity within this flyway (Vansteelant et al., 2017).

The choice of wintering grounds can influence individual energy expenditure (Flack et al., 2016; Rotics et al., 2017) and can also determine annual survival (Buechley et al., 2021; Cheng et al., 2019; Rotics et al., 2017). In fact, severe droughts in the Sahel have been associated with increased over-winter mortality and White Stork European population declines in the 70s (Schaub et al., 2005). The Sahel region comprises several different habitats (Atkinson et al., 2014), which have been subjected to a variety of human-induced changes (from habitat conversion to increased hunting activity, Vickery et al., 2014), thus individuals wintering in distinct areas might be exposed to different threats (Atkinson et al., 2014; Oppel et al., 2021). While there is strong evidence that White Stork's spring migratory phenology has been changing, with an advancement of the dates of arrival at the Iberian breeding grounds (Gordo et al., 2007; Gordo & Sanz, 2006), the spatial and temporal patterns of autumn departure are still unclear (Gordo et al., 2007): some studies report an advancement on the timing of autumn migration (Martín et al., 2016), while others describe a delay in the crossing of the Strait of Gibraltar (Scholer et al., 2016) or no significant change in the last decade (Panuccio et al., 2016). An advancement of the autumn migration might lead more storks to winter in eastern longitudes, where there is likely increased hunting pressure (e.g., White Storks are hunted in Niger and Nigeria, Zwarts et al., 2009). Conversely, for White Storks delaying their autumn migration, exposure to poor weather conditions *en route* will lead to higher energy expenditure, which can increase mortality during migration (Rotics et al., 2016). Current climate predictions show that wind strength and storm frequency will increase in the Sahara region (Taylor et al., 2017), but the effects of these changes on migratory birds crossing the Sahara are still unknown (Loonstra et al., 2019). It is therefore important to continue to assess the mortality risks associated with travelling at different times during the migratory season, and to understand the threats birds face in their wintering ranges, to have a full understanding of how on-going autumn phenology and climate change will impact sub-Saharan migrants.

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Chapter 4 Supplementary Materials

Appendix S4.1 - Definition of migratory days and stopover days

Appendix S4.2 - Consistency in the timing and destination of autumn migration of adult White Storks

Appendix S4.1

Definition of migratory days and stopover days

To distinguish between migratory and stopover days, we used receiver operating characteristics (ROC) curves as a binary classifier for the daily latitudinal displacement. We assumed birds displace on a southerly direction on migratory days and then determined a daily displacement threshold to classify if birds were migrating or on a stopover. This threshold was computed as the optimal value maximizing sensitivity and specificity, using Youden's J statistic. ROC curves, threshold and the Area Under the Curve (AUC) were computed using functions "roc" and "coords" and "auc" from package "pROC" (Robin et al., 2011), respectively. The ROC optimal threshold was 36.9km (which was then rounded to 37km), with specificity = 0.84, sensitivity = 0.64, and AUC = 0.769. The 37km threshold was then confirmed by visually inspecting the GPS tracks.

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Appendix S4.2

Consistency in the timing and destination of autumn migration of adult White Storks

We analysed the individual consistency in the timing and destination of autumn migration of 5 adult White Storks that were tracked for 2 (n=3) or 3 consecutive years (n=2). To do so, we first calculated the start and end of autumn migration using the spatio-temporal displacement method described in Soriano-Redondo *et al*. (2020) and extracted the longitude of the location where stork's finished autumn migration. We then calculated the repeatability of the dates of start of autumn migration (in julian days) and using the "rpt" function of the R package "rptR" (Stoffel et al., 2017), which indicated that individuals were consistent in the timing of start of autumn migration (R = 0.79, SE = 0.22, *p-value* = 0.004). Using the same protocol, we calculated the repeatability of the longitudes of the location where individuals ended the autumn migration, which showed that White Storks were highly consistent in the destination of autumn migration (R = 0.99, SE = 0.04, *p-value* < 0.001).

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– Chapter 5 –

Individual experience facilitates changes in migratory behaviour and adaptation to environmental change

Individual experience facilitates changes in migratory behaviour and adaptation to environmental change

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Author's contributions

MA, IC, and AF conceived the idea. IC, JPS, PWA and AMAF coordinated the study. MA and IC performed fieldwork for logger deployment. MA, IC and ASR collected behavioural data and built the tracking dataset. MA analysed the data and wrote an initial version of the manuscript, which was critically edited and revised by all authors. All authors gave final approval for publication.

Abstract

Recent human-driven environmental change has significantly altered migratory behaviour, leading to the emergence of non-migratory individuals in previously fully migratory populations. Developmental plasticity, in which the traits of individuals irreversibly change during ontogeny due to variations in the environment, has been shown to be a mechanism that enables these rapid changes in migratory strategies to occur. However, the processes causing individual variability in migratory strategies within populations remain to be explored and could be associated with individual experience during development. Using GPS-tracking data from 93 immature White Storks tracked for up to 5 years, we investigate the ontogeny of migratory behaviour in this long-distance migratory species with increasing numbers of non-migratory individuals in Southern Europe. We hypothesise that individual flight efficiency, migratory performance, and access to abundant food resources at landfill sites, during the first years of life can influence the migratory strategy adopted in subsequent years. We show that during development and prior to maturation, immature White Storks can decrease their migration distance by up to 2500 km and that this radical shift in migratory behaviour is explained by individual experience (migratory performance and flight efficiency), rather than the use of abundant and predictable food resources. Individuals with later and slower autumn migrations, and those with lower flight efficiency (i.e., with higher energetic costs associated with flying) are more likely to decrease migratory distance and become residents. The rapid increase of the resident White Stork population in Iberia is therefore likely to be occurring through a generational shift in the proportion of migratory and non-migratory individuals, with immatures with poorer individual performance decreasing migratory distance, exacerbated by the increased survival of resident individuals, associated with access to anthropogenic food sources.

5.1. Introduction

Bird migration is a highly adaptive behaviour that allows migrants to take advantage of peaks in resource abundance and move to wintering areas once resources in the breeding areas decline (Newton, 2008). Yet if environmental conditions change, resource availability might also shift. In recent decades, human-induced climate and land use changes have significantly altered the environmental conditions and habitats, and migratory birds have rapidly adjusted the phenology (Conklin et al., 2021; Gordo, 2007) and distance (Visser et al., 2009) of migratory movements. Recently, even more dramatic changes have been reported in response to environmental change, with the emergence of non-migratory individuals in previously fully migratory populations (Catry et al., 2017; Wilcove & Wikelski, 2008).

Shifts in migratory behaviour can occur through inherited mechanisms (Pulido & Berthold, 2010) as well as through phenotypic flexibility, with individuals adapting their migratory strategy to the environmental conditions (Conklin et al., 2021; Fraser et al., 2019; Piersma & Drent, 2003). For species displaying high individual consistency in behaviour, changes in migratory behaviour can occur through developmental plasticity, in which environmental cues experienced by immature individuals lead to irreversible changes in their phenotype (Piersma & Drent, 2003). At the population level, changes in migratory phenology and route can thus derive from an inter-generational shift in the frequency of individuals with differing migratory strategies that are defined during ontogeny (Gill et al., 2014; Verhoeven et al., 2018, 2021). This mechanism may be particularly relevant for long-lived species, as drastic changes in environmental conditions may occur during the slow maturation period. Furthermore, during this critical phase, immature birds develop their flight (Rotics et al., 2016) and foraging skills (Grecian et al., 2018; Riotte-lambert & Weimerskirch, 2013) and enhance their migratory performance (Sergio et al., 2014). However, to the best of our knowledge, the influence of individual experience during ontogeny on subsequent migratory decisions has yet to be studied, with implications for changes in population migratory behaviour.

White Storks were once a typical example of a long-distance migrant but are now becoming a classic case study of a widely distributed species in Europe that is changing their migratory behaviour in response to human-induced environmental change. Until the last three decades, White Storks in Europe were exclusively migratory, but new wintering sites have emerged in the Iberian Peninsula (Flack et al., 2016), and growing numbers of Iberian storks have since then become non-migratory (Catry et al., 2017). In Portugal, the number of resident (i.e., non-migratory) White Storks have dramatically increased from 1187 individuals in 1990 to 19,295 storks in 2020, which corresponds to a maximum of 83% of the population becoming non-migratory in only 30 years (Andrade et al., submit.). While the warmer winters and the use of newly available and predictable food resources, such as open landfills, undoubtedly play a role in the establishment of this resident population (Catry et al., 2017; Gilbert et al., 2016; Tortosa et al., 1995), the processes underlying this rapid shift in migratory behaviour are only now starting to be explored. Recent evidence shows that the recent loss of migration in White Storks is not likely to be explained by genetic differences between migrants and residents, nor by adult flexibility in changing migratory behaviour (Andrade et al., submit.). Alternatively, this dramatic change in migratory behaviour seems to be driven by developmental plasticity, as some juveniles change their migratory behaviour during the 3-4 years maturation period, progressively becoming resident (Figure 5.1). However, what factors influence juvenile storks to become residents, while others maintain their original migratory behaviour, is still unknown.

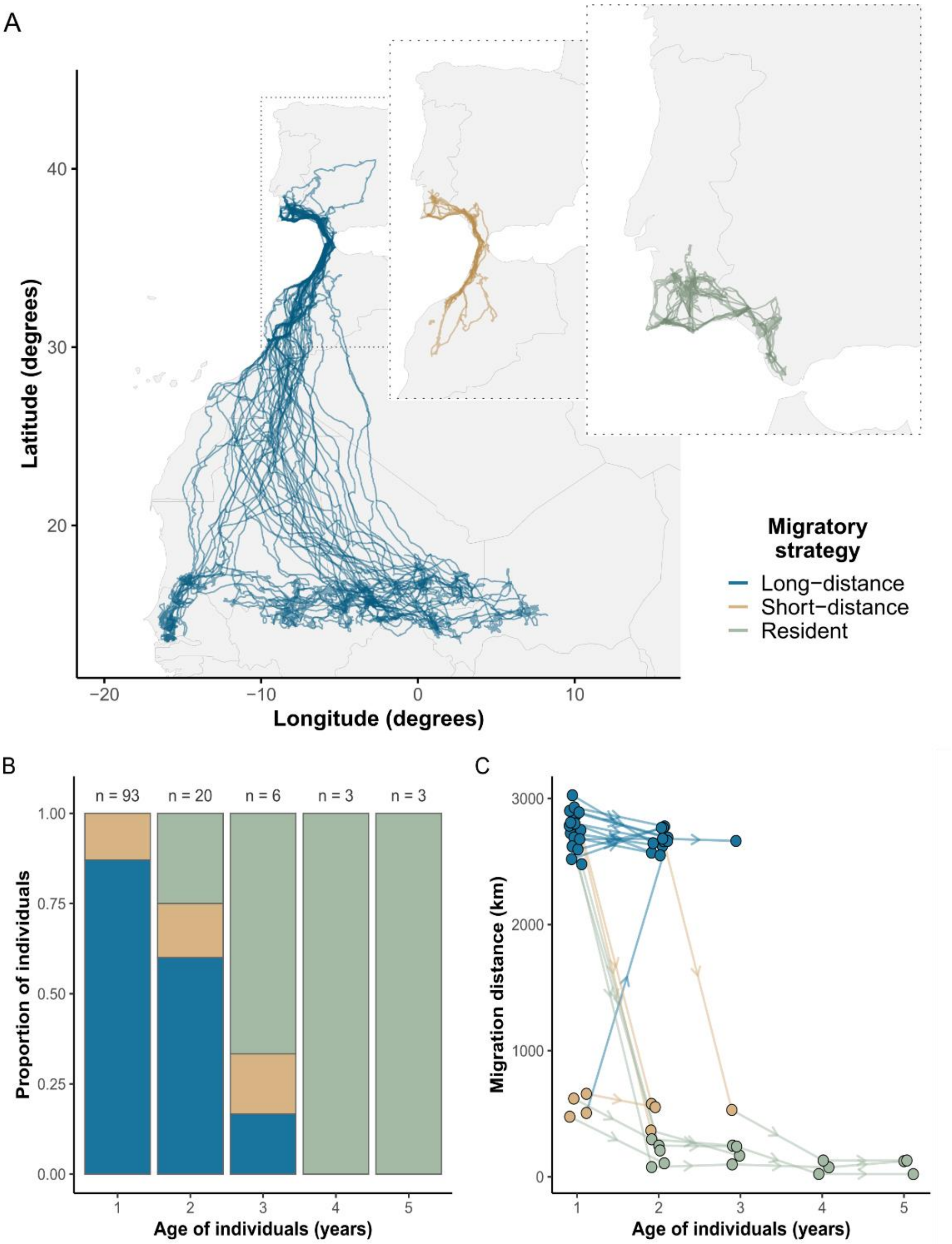

Figure 5.1 – Plasticity of migratory behaviour during White Stork development. (A) GPS tracks of juvenile White Storks collected between 2016-2020, highlighting the different migratory strategies: in blue the long-distance migrants, in yellow the short-distance migrants and in green, the residents in Iberia. (B) Proportion of first-year White Stork individuals employing the different migratory strategies as they age. Sample sizes are indicated on top of each age bar. (C) Migratory distance of first-year individual White Storks as they age. Circles represent GPS-tracked individuals and lines connect the same individual in consecutive years. Colours of the circles indicate the migratory strategy and colour of the lines indicate the migratory strategy of the following year. Long- (blue) and short-distance (yellow) migrants wintered in the Sahel and in Morocco, respectively, and residents (green) wintered in Iberia.

Here, we hypothesise that events experienced by immature storks during one annual cycle can carry-over to the following year, modifying their migration program. To test this hypothesis, we use GPS-tracking of juvenile White Storks and evaluate the importance of individual experience (previous migratory performance and flight efficiency) and access to highly abundant and predictable food resources on the subsequent migratory strategy of juvenile birds. Specifically, we tested: 1) if the timing of autumn migration, migration duration, flight efficiency and landfill use during autumn migration influence the following year's migratory strategy; 2) if individual flight efficiency and landfill use during spring and on the pre-migratory period influence the subsequent migratory strategy. Understanding how migratory performance, flight efficiency and use of highly competitive foraging areas influence the migratory decisions will provide crucial information on the mechanisms underlying dramatic changes in migratory behaviour in long-lived birds.

5.2. Methods

GPS tracking data, behavioural classification, and energy expenditure

Between 2016 and 2020, we GPS-tracked 93 first-year White Storks between the breeding grounds in Portugal – Southern Europe population – and their wintering areas in Iberia, Morocco, and the Sahel region in Africa. Storks were tracked for up to 5 years after fledging. The GPS devices ("Flyway-50" from Movetech Telemetry and "Ornitrack-50" loggers from Ornitela), transmitted data remotely over the GSM network and had built-in accelerometers. To deploy the loggers, we retrieved the pre-fledging juveniles from their nests and attached the devices as backpacks, using a Teflon ribbon thoracic full harness. The loggers weighted between 50-80g, corresponding to 1.1-2.9% of the bird's body weight (more details on tag deployment and harnesses on Soriano-Redondo et al., 2021). This study was carried out in agreement with the recommendations of Instituto da Conservação da Natureza e das Florestas and the Animal Welfare & Ethical Review Board from the School of Biological Sciences at the University of East Anglia. Licenses to deploy the loggers were granted by the Instituto da Conservação da Natureza e das Florestas (2016: 493/2016/CAPT; 2017: 661/2017/CAPT to 663/2017/CAPT; 2018: 549/2018/CAPT; 2019: 247/2019/CAPT to 250/2019/CAPT; 2020: 364/2020/CAPT to 368/2020/CAPT; 2021: 198/2021/CAPT to 202/2021/CAPT).

The loggers provided 9 seconds of GPS and acceleration fixes at 1Hz every 20 minutes, thus acceleration and location matched in space and time. Using the accelerometer data, we calculated the Overall Dynamic Body Acceleration (ODBA) and applied a supervised learning algorithm to classify White Stork behaviour. ODBA is a proxy for energy expenditure (Gleiss et al., 2011) and was calculated by subtracting each acceleration point from a running-mean of 4 seconds for each axis and summing the resulting values for all three axes. To classify bird's behaviour, we built a random forest using 1,000 manually labelled acceleration bursts of 4 distinct behaviours: foraging, resting, soaring flight, and flapping flight (see Soriano-Redondo et al., 2021 for a full description of behaviour classification). To account for differences in sensors due to logger type, we created two random forest models, one for Movetech Telemetry and one for Ornitela loggers, with 96% and 97% accuracies, respectively. In this study, we combined soaring and flapping flight behaviours into one single *flight* category and resting and foraging behaviours as a *ground* category. If acceleration information was not available, we classified the GPS fix as *flight* or *ground* if the ground speed was over or under 5 km/h, respectively.

Definition of White Stork's migration strategy and distance

White Storks from the Portuguese population were originally long-distance migrants, migrating to the Sahel, but in the last decades two other migratory strategies emerged: a short-distance migration to Morocco, or remaining in Iberia all year long (becoming residents) (Figure 5.1). All juveniles migrated on their first year, but once they become resident the subsequent years were not included in the analysis, as juveniles that wintered in Iberia became consistent in their behaviour and did not migrate to Africa in the following years.

We used migratory distance as a proxy for migratory strategy and defined stork's annual migration distance as the maximum distance a stork moved from their nest during one year (April to March). As all storks were tagged before fledging, we could assess the migration distance as individuals aged.

Defining White Stork's annual cycle

We divided White Stork's annual cycle into two major seasons: autumn migration, and spring. We did not assess spring migration separately as juvenile White Storks perform extraordinarily long spring migrations (they can take up to 5 months to reach the breeding areas after leaving the wintering grounds) and often do not return to the breeding areas. Moreover, the comparison between Moroccan and Sahelian migrants would not be feasible, as the duration of spring migration is remarkably different for these two strategies (mean spring migration duration for Sahelian migrants = 106 days, SD = 38; mean spring migration duration for Moroccan migrants = 39 days, SD = 27), which is not the case for autumn migration (mean autumn migration duration for Sahelian migrants = 26 days, SD = 13; mean autumn migration duration for Moroccan migrants = 17 days, SD = 11).

To classify the start of autumn migration for storks wintering in the Sahel and in Morocco, we used the spatio-temporal displacement method described in Soriano-Redondo et al., 2020, which defines spatial and temporal thresholds to identify the start and end of migratory movements. Thus, we identified the start of autumn migration as the first of three consecutive days a stork moved more than 60 km between roosts after having left the breeding area. The breeding area was calculated as the 90% kernel of June GPS locations. We then identified the start of the wintering season as the first of three consecutive days a stork displaced less than 60 km between roosts after having arrived at the wintering area (calculated as the 90% kernel of October GPS locations).

Finally, the start of the spring season was defined as the day storks abandoned the wintering area and started the spring migration; this was calculated as the first of three consecutive days a stork moved more than 60 km between roosts after having left the wintering area. As individuals wintering in Iberia often do not perform an autumn migration, and often do not even leave their spring areas all year long, we defined the end of spring season as the median date of start of autumn migration for all storks tracked in that same year. All tracks were visually inspected to correct possible miscalculations in the dates of start and end of each season. Analyses were performed using R package geosphere (Hijmans, 2019) for distances calculation and adehabitatHR (Calenge, 2006) for kernel estimations.

Determining the influence of individual experience on White Stork migratory strategy

To assess if events experienced by immature storks during one annual cycle can influence the following year's migratory strategy, we tested two hypotheses: (1) the previous autumn migration performance influences the following year's migratory strategy and (2) the events experienced during the previous spring and during the 15-day period that preceded autumn migration (hereafter *pre-migratory period*) determined the subsequent year's migratory strategy.

To assess the influence of the previous migratory performance on White Stork's migratory strategy in the following year, we used several metrics: date of start of autumn migration (in Julian day), date of arrival at the wintering area (in Julian day), migration speed (in km/day), flight efficiency (i.e., flight ODBA, in G) and landfill use during autumn migration (0-1). We calculated migration speed as the total migration distance divided by the difference in days between the start and end of migration. Flight efficiency as calculated as the mean ODBA of all accelerometer bursts classified as *flight* during autumn migration.

To calculate the use of landfills, we started by identifying all landfills and rubbish dumps used by the GPS-tracked White Storks in our study through the visual inspection of satellite images (Google Earth and Bing Maps). Landfills were located in Portugal, Spain and Morocco (Figure S5.1). Then, each GPS location was classified as either inside or outside a landfill if they were within a 1km buffer from the centre of the landfill. We classified *landfill days* when there were more than 5 GPS locations obtained during the daylight hours, considered representative of bird's activity, and at least 1 *ground* GPS location was located inside the landfill buffer. Finally, we calculated the frequency of *landfill days* during autumn migration and spring by dividing the number of landfill days by the number of non-landfill days in each season.

To test if the previous spring and pre-migratory period can determine the subsequent year's migratory strategy, we examined White Stork flight efficiency and landfill use during these periods. We calculated flight efficiency as the mean ODBA of all accelerometer bursts classified as *flight* during spring and the pre-migratory period. During the pre-migratory period, all individuals had at least 9 days with GPS and accelerometer data (median = 15 days), but we excluded from the analysis individuals with less than 10 flight observations during the pre-migratory period (median = 30 flight observations).

Statistical analysis

The timing of start of migration and arrival at the wintering area were correlated, and migration speed, flight efficiency and landfill use were also correlated with each other (Table S5.1), therefore we only included in the models two uncorrelated metrics: timing of arrival at the wintering areas and flight efficiency. A linear mixed model (LMM) was built, using R package *lme4* (Bates et al., 2015), with migration distance of the following year as the response variable (log transformed) and arrival date at the wintering area and flight efficiency of the previous autumn migration as fixed effects; bird ID was included as a random effect.

We fitted LMMs separately for the spring period and for the pre-migratory period, with migration distance of the following year as the response variable, flight efficiency and landfill use of the previous spring and pre-migratory period as fixed effects and bird ID as a random effect. Due to the small sample size, we modelled separately the influence of flight efficiency and landfill use on migration distance, for the pre-migratory period. For all LMMs, we estimated p-values using *car* R package (Fox & Weisberg, 2019) and pseudo-R^2 using *MuMIn* package (Barton, 2019). Multicollinearity was analysed by verifying the variance inflation factor (VIF < 2, Zuur et al., 2010).

5.3. Results

Between 2016 and 2020, we followed 93 juvenile White Storks on their first autumn migration, but the number of tracked storks decreased over the years, due to logger failure and/or bird mortality: 20 storks were tracked for two years, 6 storks for three years and 3 storks for four and five years. In total, the dataset consisted of 1,138,278 GPS positions, spanned over the 5 years.

White Storks adopted three distinct migratory strategies: long-distance migration to the Sahel (mean distance = 2674 km, SD = 73 km), short-distance migration to Morocco (mean distance = 507 km, SD = 95 km) or remained in Iberia all year long (mean distance = 176 km, SD = 79 km). The percentage of immatures adopting each migratory strategy changed as storks aged, with the proportion of migrants decreasing and the proportion of residents increasing (Figure 1). On their first year, 87% of storks migrated to the Sahel and no bird remained in Iberia during the winter, whereas on their second and third year, the percentage of Sahelian migrants decreased to 60% and 17%, respectively, and the percentage of residents in Iberia progressively increased to 25% and 67%. The percentage of individuals wintering in Morocco was similar across years (Figure 5.1). These differences in proportion of migrants and residents were explained by individual storks shifting their migratory strategy as they aged, from migrants to residents (Figure 5.1).

We assessed the influence of previous autumn migration performance on following year migratory strategy for 19 individuals, in a total of 23 migrations. Autumn migration started between the 9th of July and 9th of September, and birds arrived at the wintering areas between 26th of July and 4th of October, on an average speed of 109 km/day (SD = 63 km). During autumn migration, storks spent an average of 41% of days using landfills, but landfill use differed according to the individuals (range = 0 - 95%). There was also large variation in flight efficiency (flight ODBA range = 0.12 – 0.26 G). We found that storks that arrived later at the wintering grounds and storks that spent more energy during flight were more likely to decrease migratory distance (i.e., change migratory strategy) in the following year (Figure 5.2, Table 5.1).

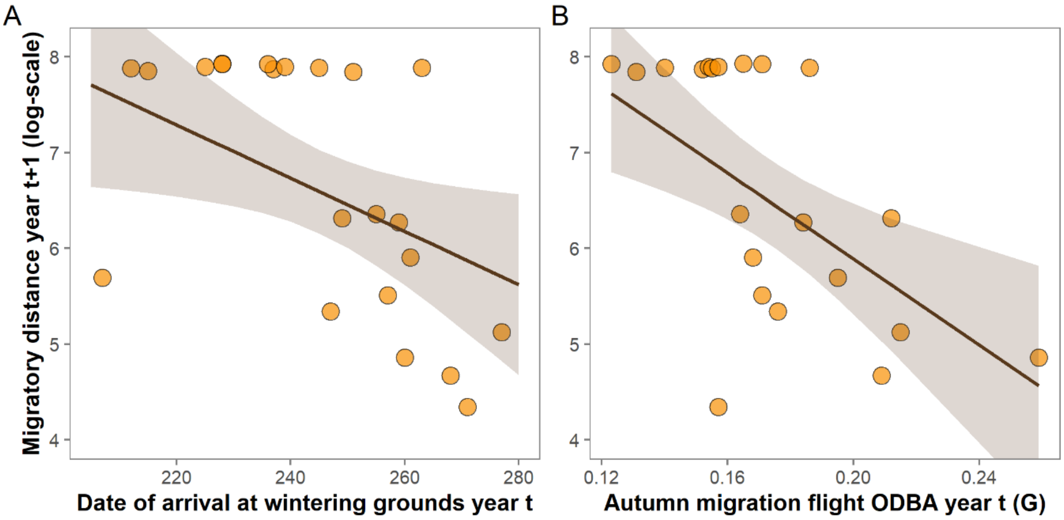

Figure 5.2 – Influence of autumn migration timing and flight efficiency on subsequent year's migratory distance. The probability of juvenile White Storks undertaking a long-distance migration decreases with (A) later arrival at the wintering grounds and (B) increased flight ODBA during previous autumn migration. Lines represent predictions from a linear mixed model, shading represents 95% confidence intervals, and orange circles show the raw data.

Table 5.1 – Results of the LMM, testing the influence of White Stork's previous year arrival date at the wintering area and flight efficiency (flight ODBA) during autumn migration, on the following year's migration distance. Model used bird ID as random factors.

	Estimate (SE)	t-value	p-value	Marginal R-squared	Conditional R-squared
Intercept	17.30 (2.88)	6.00	-	0.54	0.72
Date of arrival at wintering area	-22.40 (6.97)	-3.22	0.001 **		
Autumn migration flight ODBA	-0.03 (0.01)	-2.26	0.024 *		

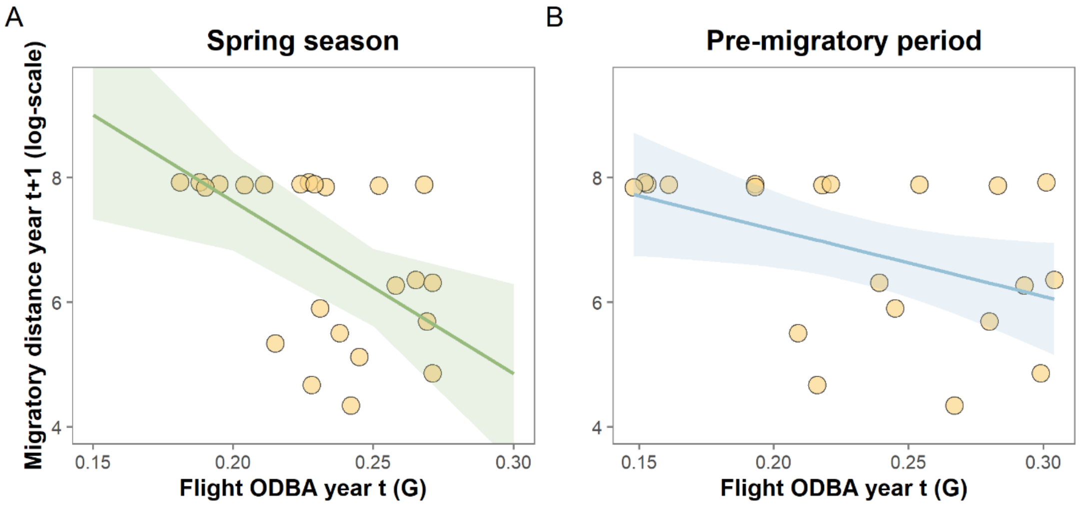

Figure 5.3 – Influence of White Stork flight efficiency during spring and pre-migratory period on subsequent year's migration distance. The probability of juvenile White Storks undertaking a long-distance migration decreases with higher flight ODBA during (A) spring and (B) the pre-migratory period. Lines represent predictions from a linear mixed model, shading represents 95% confidence intervals, and yellow circles show the raw data.

Table 5.2 - Results of the LMM, testing the influence of White Stork's previous spring flight efficiency (flight ODBA) and landfill use, on the following year's migration distance. The model used bird ID as random factors.

	Estimate (SE)	t-value	p-value	Marginal R-squared	Conditional R-squared
Intercept	12.24 (2.13)	5.74		0.27	0.40
Spring flight ODBA	-27.67 (10.04)	-2.76	0.006 **		
Spring landfill use	1.90 (1.49)	1.28	0.200		

Table 5.3 - Results of the LMM, testing the influence of White Stork's previous pre-migratory period flight efficiency (flight ODBA), on the following year's migration distance. Model used bird ID as random factors.

	Estimate (SE)	t-value	p-value	Marginal R-squared	Conditional R-squared
Intercept	9.33 (1.27)	7.67		0.19	0.19
Pre-migratory period flight ODBA	-10.77 (5.13)	-2.10	0.036 *		

Table 5.4 - Results of the LMM, testing the influence of White Stork's previous pre-migratory period landfill use, on the following year's migration distance. The model used bird ID as random factors.

	Estimate (SE)	t-value	p-value	Marginal R-squared	Conditional R-squared
Intercept	7.49 (0.56)	13.34		0.09	0.32
Pre-migratory period landfill use	-1.04 (0.70)	-1.48	0.14		

5.4. Discussion

In this study, we showed that lower individual performance can act as a mechanism leading juveniles to lose the innate migratory behaviour during maturation. We tracked White Stork immatures during their developmental years, in which the migratory strategy changed before becoming permanent as birds reach sexual maturity. We found clear evidence that individual flight efficiency and migratory performance can influence the migratory decisions individuals adopt on subsequent years.

In their first year of life, White Storks, as several other species (Åkesson & Helm, 2020), are mostly driven by an innate and inherited migratory program (Chernetsov et al., 2004), as shown by the fact that all 93 GPS-tracked juveniles migrated to Africa on their first year, even though up to 83% of the White Stork adult population is resident (Andrade et al. *in prep*). However, in subsequent years, learning and experience may override this endogenous migratory program. During maturation, long-lived bird species have the chance to enhance their foraging (Grecian et al., 2018; Riotte-lambert & Weimerskirch, 2013), flight (Rotics et al., 2016) and migratory performance (Sergio et al., 2014). Yet, at the population level, this refinement in performance during ontogeny is a combination of both individual improvement and selective mortality, as migrants that do not improve their migratory performance progressively disappear from the population (Sergio et al., 2014). In the case of Iberian White

Storks, however, juveniles with weaker flight and migratory performances have the possibility of stop migrating altogether and become residents, increasing their survival probability (Cheng et al., 2019).

The use of predictable and abundant food resources on landfills has been pointed as the main driver of change of migratory behaviour in White Storks (Catry et al., 2017; Gilbert et al., 2016). However, in our study, individual experience during autumn migration and spring, and not landfill use, were the key factors determining stork's migratory strategy in subsequent years. Whilst we did not find significant differences on landfill use during spring on the following year migratory strategy, other specific aspects of landfill use for these immatures should be assessed, such as the time they spend using landfills per day and their ability forage efficiently in these areas (e.g., quantifying foraging ODBA). Still, the importance of landfills for White Storks should not be diminished; we found that storks with worse flight efficiency migrated at a slower pace, taking advantage of landfills to perform stopovers, and likely increasing their survival probabilities, as poorer fliers have a higher probability of perishing on migration (Rotics et al., 2016). Additionally, these storks with worse flight efficiency, were more likely to become residents in Iberia, strongly relying on the existence of year-round food resources on landfills. During the winter, storks are particularly dependent on this food source (Soriano-Redondo et al., 2021), which provides a nutritious (Pineda-Pampliega et al., 2021) and energy-efficient resource, due to decreased travelling and foraging energy costs when compared to natural habitats (Soriano-Redondo et al., 2021). Furthermore, despite the evident role of individual experience on the loss of migratory behaviour, we cannot discard other un-tested factors, such as the individual genetic propensity for migration, body and health conditions at the time of migration, or even learning and other social components.

Whereas in other species differential survival is not likely to be involved in changes in population migratory behaviour (Verhoeven et al., 2018), this is not the case for the white stork. Resident or short-distance migrant White Storks have lower energy costs (Flack et al., 2016), and storks wintering in Iberia have higher survival than long-distance migrants (Cheng et al., 2019). Although we cannot attest to these results within our population, as for most of the individuals wintering in the Sahel we cannot confirm the cause of disappearance (death or logger failure), we found that 8 of 11 juveniles disappeared in the Sahel on their second migration, whereas no resident juvenile disappeared in Iberia before reaching sexual maturity and recruitment, at 3 or 4 years old. Whilst we show that the resident immatures are the birds with worse flight performance, they benefit from access to highly abundant food resources all year round and probably have higher annual survival, thus replacing the migratory individuals in the population. Therefore, it is likely that the rapid increase of the resident White Stork population in Iberia is occurring through a generational shift in the proportion of migratory and non-migratory individuals, with immatures as the agents of change, exacerbated by the increased survival of resident individuals.

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Chapter 5 Supplementary Materials

Figure S5.1 – Location of landfills and rubbish dumps in Portugal, Spain, and Morocco.

Table S5.1 – Correlation between autumn migration performance metrics.

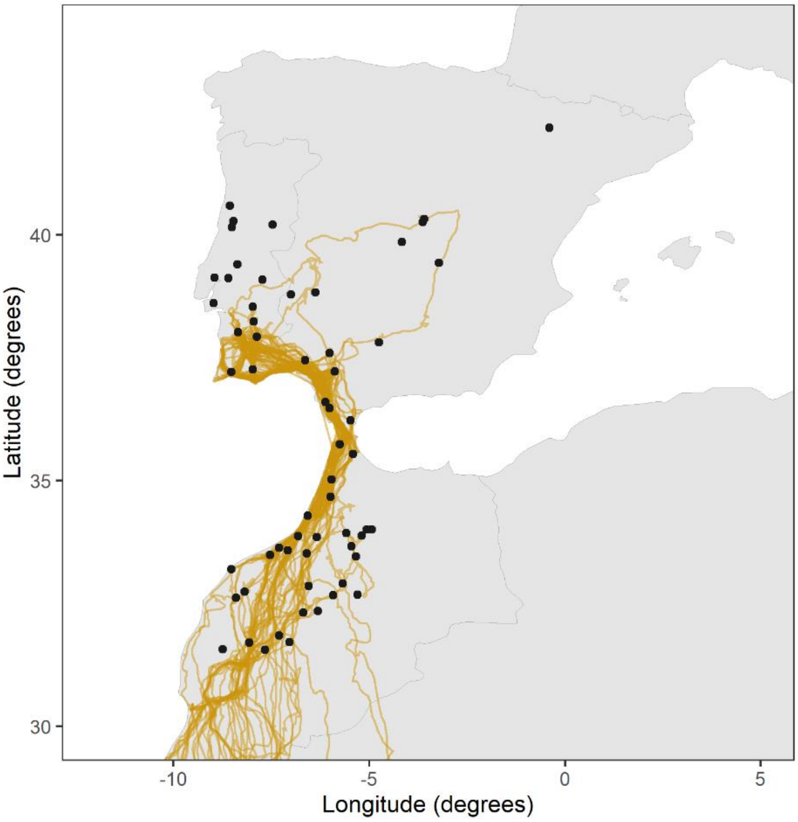

Figure S5.1 – Location of landfills and rubbish dumps in Portugal, Spain, and Morocco. Location (dark circles) was determined based the inspection of satellite imagery of areas used by 93 White Storks between 2016 and 2020 (yellow lines) and, in all possible cases, were confirmed by visits or contact with local authorities.

Table S5.1 – Correlation between autumn migration performance metrics. Correlation matrix, showing the Pearson correlation coefficients (r-values) and p-values, calculated using the R package "*Hmisc*" (Harrel Jr, 2021). Blue colours highlight statistically significant positive correlations with r > 0.60, and orange colours highlight statistically significant negative correlations with r < -0.60.

	Date of start of migration	Date of arrival at wintering area	Autumn migration Flight ODBA	Migration speed	Autumn migration landfill use
Date of start of migration	-	-	-	-	-
Date of arrival at wintering area	$r = 0.79$ $p < 0.001$	-	-	-	-
Autumn migration Flight ODBA	$r = 0.35$ $p = 0.115$	$r = 0.38$ $p = 0.090$	-	-	-
Migration speed	$r = -0.14$ $p = 0.547$	$r = -0.47$ $p = 0.027$	$r = -0.62$ $p = 0.003$	-	-
Autumn migration landfill use	$r = 0.12$ $p = 0.595$	$r = 0.36$ $p = 0.111$	$r = 0.76$ $p < 0.001$	$r = -0.77$ $p < 0.001$	-

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– Chapter 6 –

General conclusion

Even if we could turn back,

we'd probably never end up where we started

- Haruki Murakami -

General Conclusion

6.1 Summary of main findings

Wildlife GPS tracking devices are commonly used by the scientific community, but standardised tests to assess their accuracy and precision are rarely performed. In Chapter 2, we found that the GPS devices used in Chapter 4 and Chapter 5 were highly accurate, with location and altitude errors varying between 3-7m and 5-10m. Moreover, this accuracy did not considerably change after deployment on White Storks. However, reducing the GPS fix acquisition intervals did significantly decrease the accuracy and precision of the devices, and the *GPS-Error* metric provided by the devices was only successful at identifying outlier locations in high GPS fix acquisition intervals. Our results confirm that researchers should carefully consider the GPS fix acquisition intervals taking into account the study objectives, the accuracy required for the study and the longevity of the devices.

GPS-tracking and remote sensing are invaluable tools to study species that inhabit remote locations. In Chapter 3, we explored the movement ecology of Shoebills, described their home ranges, and demonstrated that their movements are influenced by changes in surface water. Moreover, we showed that immature and adult birds did not respond to these changes in the same way: adults abandoned areas as they became drier, whilst juveniles abandoned areas as they flooded. These findings suggest different habitat use between adults and immatures, likely driven by the intricate foraging strategy of this species, and highlight the importance of studying animal movement in various life stages.

In Chapter 4, we combined GPS-tracking data of adult and juvenile White Storks with tri-axial accelerometery and weather information we found that the timing of autumn migration determined the migratory performance, the weather conditions *en route*, and the destination of both juvenile and adult White Storks. Late migrants spent fewer days on migration and adopted a shorter and more direct route when crossing the Sahara Desert. They spent more energy in flight when traversing Iberia and the Sahara, as they experienced worse weather conditions in these areas (weaker thermal uplifts and stronger headwinds). Interestingly, we found that timing of migration determined the wind direction storks faced and the wintering destination of storks. Our results show that the recent and ongoing changes in migration phenology due to environmental change may have important fitness consequences for long-distance migrants.

Developmental plasticity is one mechanism through which individuals can adapt their migratory behaviour as a response to human-driven environmental change. In Chapter 5, we analysed the mechanisms leading to White Stork loss of migratory behaviour, becoming residents in Iberia, and showed that during the developmental years, White Storks may decrease their migration distance by up to 2500 km. We provided the first evidence that individual characteristics (migratory performance and flight efficiency), rather than the use of landfills, can explain this radical shift in migratory behaviour. The rapid increase in the resident White Stork population in Iberia may therefore be the result of juveniles with poorer individual performance decreasing the migratory distance during their developmental years, exacerbated by the increased survival rates of resident storks compared to migrants, associated with access to anthropogenic food sources.

Overall, this research contributes to the understanding of how environmental conditions determine and influence the short and long-distance movements of long-lived birds in different life stages. Moreover, it provides new insights on the mechanisms through which species are adapting to ongoing environmental change.

6.2 Broader context of this PhD research

Using GPS tracking for conservation

Animal GPS tracking technology has come to be a commonly used tool by researchers, as shown by the growing number of users and GPS data points on regularly used archival websites, such as Movebank (Kays et al., 2021; Wikelski et al., 2020): as of October 2021, this website hosted 3.2 billion animal locations of over 1,139 taxa! The value of this data is unquestionable, but despite many ecology studies stating a conservation implication of their studies, until 2014 only 35% of the studies made explicit conservation and management guidelines (Fraser et al., 2018). Nevertheless, this same study found that on average 60% of government conservation planning documents were informed by movement data, corroborating its importance for conservation. In fact, recent studies have used GPS tracking data for applied conservation: researchers have used GPS tracking data to build tools for identifying potential locations for Key Biodiversity Areas (Beal et al., 2021), to inform on protected area design (Choi et al., 2019) and to reveal connections between countries, quantifying their political responsibility in the conservation of migratory species (Beal et al., 2021). Yet, despite the increase of studies incorporating movement data, there are still large knowledge gaps for species of conservation concern (Fraser et al., 2018, Chapter 3).

Preserving the endangered Shoebill

In Chapter 3, we used GPS tracking technology to study the movements of Shoebills in the Bangweulu Wetlands, Zambia. Despite being some of the most biodiverse biomes, tropical wetlands are amongst the most threatened habitats across the globe (Kingsford et al., 2016), and are currently under extreme pressure, due to the influence of human activities and climate change (Junk, 2002; Schneider et al., 2017). In the Bangweulu Wetlands, the local communities have been critical for the conservation of Shoebills, and recently guards have been hired to protect Shoebill chicks from disturbance, illegal trafficking, and fires (Mullers & Amar, 2015a). However, climate models for 2010-2070, project an increase in the mean temperatures in Zambia and a decrease in annual rainfall by 8-30% (Ng'onga et al., 2019). The effects of climate change are already visible in the Bangweulu region, with a decrease in rainfall and water levels in the Lake Bangweulu, negatively affecting human fisheries (Ng'onga et al., 2019). The Bangweulu Wetlands support a large community of people that are mainly dependent on fishing (Mullers & Amar, 2015b; Roxburgh & Buchanan, 2010), which is regulated by the Bangweulu Wetland Management Board. Human disturbance can pose a constraint for birds tracking suitable resources (Chevallier et al., 2010; Wang et al., 2019), and humans in this area are the main competitors of Shoebills for catfish (Mullers & Amar, 2015b). With climate change already threatening fish abundance in this region, it is possible that human-wildlife conflicts could increase in the future due to changes in water levels, particularly for fish-dependent species, such as the Shoebill.

Throughout its range, most Shoebill populations reside in Ramsar sites, national protected areas and Important Bird Areas, however this does not ensure this species protection as the resources and capacity to manage these areas are quite limited (Dodman, 2013). Yet, the conservation of Shoebills can highly benefit local populations, both through the maintenance of habitat integrity and fish stocks, and through the promotion of ecotourism and generation of alternative income sources for locals, as highlighted by the Shoebill Single Species Action Plan (Dodman, 2013). This action plan also underlines the significant knowledge gaps about Shoebill population sizes, breeding ecology, foraging requirements and movement behaviour. Consequently, our work in understanding Shoebill movements throughout the year, particularly the geographic range of movement, was a fundamental first step to identify the spatial extent necessary to successfully preserve this emblematic species.

The determinants of movement

Bird movement can be driven and influenced by environmental conditions individuals experience: changes in temperature can drive the start of migratory movements (Burnside et al., 2021) and wind direction may shape the migratory routes of species (Kranstauber et al., 2015). Our results in Chapter 3 go in line with previous findings, showing that the movement of wetland specialists is influenced by changes in surface water (Henry et al., 2016; Kleyheeg et al., 2017). In Chapter 4, we provided evidence that weather conditions influence the movement direction, energy expenditure and migration destination of soaring birds (Amélineau et al., 2014; Vansteelant et al., 2015, 2017), but more importantly, we show that the timing of migration is the main determinant of these weather conditions. As bird species are shifting the migration phenology as a response to global climate change (Gordo, 2007), our results show that advancing or delaying the timing of migration may determine bird's energy expenditure on migration and their wintering destination, both of which with important consequences for individual survival (Buechley et al., 2021; Loonstra et al., 2019; Rotics et al., 2016).

Changes in movement behaviour during ontogeny

For long-lived birds, the developmental period, before birds become breeding adults, can be rather long. During this period, immatures and adults may have different habitat requirements (Grecian et al., 2018, Chapter 3) and different migratory (Sergio et al., 2014) and flight performances (e.g., White Storks from northern European populations, Rotics et al., 2016). Surprisingly, we could not find differences in flight energy expenditure between adults and first year juveniles in the Portuguese White Stork population, which shows the importance of studying several populations under different conditions and with distinct migratory strategies.

Recent studies have also concluded that plasticity in behaviour in early life can be an important mechanism that enables bird species to change migratory phenology or routes (Gill et al., 2014; Verhoeven et al., 2018, 2021). A recent study with White Storks confirm these findings, showing that the loss of migration in this species is likely driven by developmental plasticity, not genetics or flexibility in adult migratory behaviour (Andrade et al., submit.). In Chapter 5, we showed that this plasticity in migratory behaviour may be driven by individual experience: birds with worse migratory performance and flight efficiency were more likely to change migratory strategy, decreasing migration distance and becoming residents. Our results revealed that individual experiences during the developmental period may act as a mechanism enabling species to adapt to environmental change. Nevertheless, further studies are necessary to elucidate if these processes may be similar for other long-lived species.

6.3. Future studies and implications

Integrating GPS movement data and environmental conditions

Identifying the environmental drivers of movements is fundamental to anticipate the influence of environmental change on movement patterns and behaviour (Shaw, 2016). Remotely sensed data is particularly important for species that inhabit remote and difficult to access locations, however, field validations of these data sources are required and are often missing (e.g., NDWI in Chapter 3).

Moreover, the scale mismatch between the GPS tracking data and environmental data must be acknowledged (Katzner & Arlettaz, 2020). Notwithstanding the importance of removing outlier positions to improve the accuracy of animal positions (Chapter 2), GPS devices are usually accurate to a spatial scale of only a few meters and at the temporal scale of a second. This accuracy by far exceeds the highest resolution of present land cover or weather data: Sentinel-2 land cover data has 10 meters spatial resolution is only available every 5-day, and ECWMF weather data is available at 1-h temporal resolution but at 30km spatial resolution. Animal-borne sensors can tackle this issue, as they can sample environmental conditions the animals are experiencing (Wilmers et al., 2015). This technology has been widely used in oceanic environments and data has now been compiled in the Animal Borne Ocean Sensors network (AniBOS). Marine animals, such as seals and sharks, can be equipped with biological and physical sensors and collect environmental, biological, and hydrographic conditions in a wider range of areas and at different depths than the static network of sensors (McMahon et al., 2021). Extending these tools to the terrestrial environment will allow a higher resolution weather information in areas of the globe where there are few weather stations with which to validate the weather forecast models (e.g., Sahara Desert).

Non-environmental determinants of movement

The movement of birds may be driven by factors other than the environmental conditions that surround them. For example, studies have analysed the movement of birds in relation to human disturbance, by quantifying the distance of the animal to human settlements (Chevallier et al., 2010) or to sanctuaries and areas of high hunting pressure (McDuie et al., 2021). For species that perform small-scale movements in areas inhabited by humans (such as the Shoebills in the Bangweulu Wetlands), it is harder to remotely quantify the influence of human disturbance on the movement of birds, and field work should be performed.

Disentangling the influence of sociality and environmental variables on the movement behaviour of migratory birds is also a tricky task, and it has been accomplished mostly for species in which it is possible to know how many younger and older individuals were in the same flock (Teitelbaum et al., 2016). For the White Stork, this is nearly impossible to do, since there are thousands of individuals migrating throughout Europe and Africa every year. In some instances, GPS-tracked individuals may travel together, which makes it possible to compare individuals within the same flock (e.g., Flack et al., 2018), but these are generally short periods in time and space and not throughout the whole migratory route. Using more advanced modelling tools, such as novel step selection functions that explicitly integrate energy and weather landscapes (e.g., Eisaguirre et al., 2020) may help to understand if birds select routes with highest weather assistance (e.g., tailwinds and thermals), or if they are following a particular route possibly defined by older individuals flying in the same flock.

Fitness and survival consequences

Identifying the fitness and survival consequences of different movement strategies is fundamental to understand how these may influence population dynamics. GPS-tracking data is extremely useful to understand when and where mortality occurs during the bird’s annual cycle (Buechley et al., 2021; Strandberg et al., 2010), however many GPS-tracking devices still lack the reliability to accurately assess mortality.

In Chapter 4, we quantified the energy expenditure of storks to assess the fitness consequences of travelling at different times of the migration season. Nevertheless, and due to difficulty in assigning a fate to the individuals whose transmitter stopped with no confirmation of mortality (or in areas without GSM coverage), we only used data from storks that were successful on their journeys. Moreover, as it was not possible to assess the cause of disappearance for most of the storks wintering in different parts of the Sahel, we could not evaluate the mortality rates associated with timing of migration or wintering area. Improving the reliability of GPS-GSM tracking devices or using more expensive satellite transmitters, is one way of tackling this issue in future studies. Additionally, by using more sophisticated modelling techniques, such as Bayesian frameworks, it would be possible to include the uncertainty in the classification of bird fate in the models (e.g., Buechley et al., 2021), and assess how the timing of migration (Chapter 4), overall changes in autumn migration phenology, or even the drastic shifts in migratory strategy (Chapter 5) influence individual survival and White Stork population dynamics.

Understanding how long-lived birds adapt to environmental change

Life-long tracking of birds is critical to understand individual interactions with their environments and adaptation mechanisms to environmental change. From long-term tracking of individuals, it is possible to discern different responses to environmental conditions as individuals mature (Chapter 3), changes in migratory performance and behaviour (Chapter 4 – 5) and even that early life experiences may determine adult movement strategies (Chapter 5). However, to study individuals for such long periods, it is necessary to increase the longevity of tracking devices or, as an alternative, to be able to replace old devices with new ones. Tracking birds from their first year of age proved to be an even tougher challenge, due to the low survival rates of first-year juveniles. Targeting and deploying tracking devices on immatures, with have higher survival probability, would surely maximize the number of GPS-tracked years per individual, increasing the overall sample size to unravel the mechanisms that lead to changes in movement behaviour during the developmental stage.

The White Stork is an excellent case study to understand how species adapt to changes in the environment. Adults can live for up to 39 years (EURING) and this species is currently losing its migratory behaviour as a response to the high food availability and climate change in the breeding range (Catry et al., 2017). There is now considerable evidence that juvenile storks from the Portuguese population migrate to Africa during their first year of life (Chapter 5), yet adult storks exhibit several migratory phenotypes (long- and short-distance migrants, dispersive- and local residents, Figure 6.1). Thus, by continuing to study the movements of White Storks as they age, we can compare the different migratory strategies (e.g., Brown et al., 2021) and understand how changes in migratory behaviour emerge (Chapter 5).

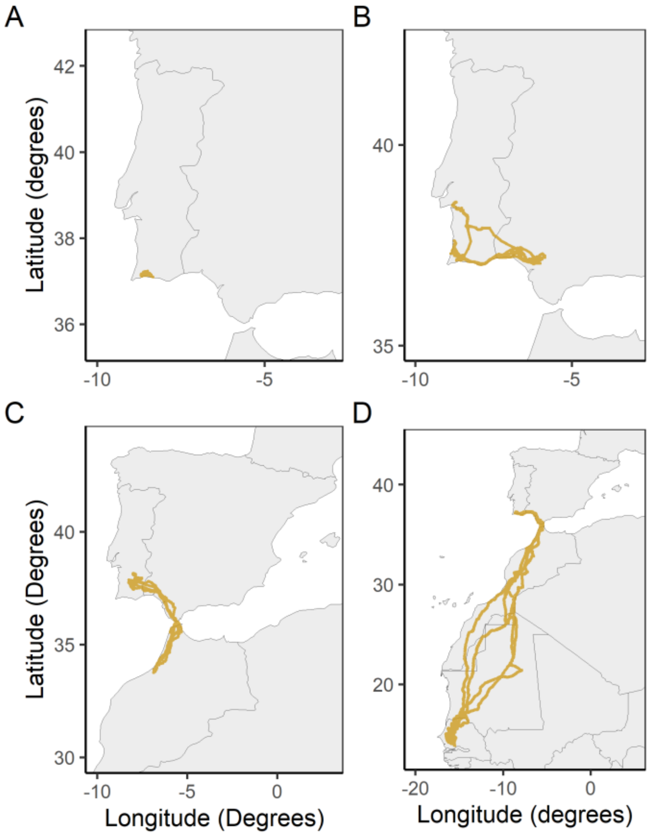

Figure 6.1 – Different migratory phenotypes of adult White Storks from the Portuguese population. A) local resident, B) dispersive resident, C) short-distance migrant and D) long-distance migrant. Each map shows 2 GPS-tracking years of 4 different adult White Storks.

Understanding how species adapt their migratory behaviour is particularly relevant now, as critical changes in the environment are occurring. High food availability in landfills has drastically changed the movement and migratory behaviour of White Storks (Gilbert et al., 2016) and many other landfill-reliant species (e.g., Lesser Black-backed Gulls *Larus fuscus* Sotillo et al., 2022), but this resource will soon disappear. Recent changes in European Directives dictate that in 8 years' time (by 2030), only 10% of human waste should be deposited on open air landfills (European Union, 2018). It is unclear what will happen to landfill-reliant species during this period of adaptation and after landfill closure, particularly White Storks, that have lost their original migratory behaviour.

Adult White Storks studied between 2016 and 2021 seemed to be highly consistent in their migratory strategy (Andrade et al., submit., Chapter 4), however, during the years of this study, the food availability in the breeding grounds remained unchanged. After landfill closure, and subsequent drastic decrease in food availability, we may find that adults still maintain some phenotypic flexibility and resume their original migratory behaviour. On the other hand, even if most adults remain consistent in their migratory strategies, immatures may again be the driver of populational changes in migratory behaviour, with better performing immatures migrating to areas of higher food availability in Africa and increasing their survival likelihoods when compared to poorer performant juveniles that remain in Iberia.

In all cases, after landfill closure it is likely that White Storks will shift their foraging strategies, increase their use of agricultural lands (Langley et al., 2021; Zorrozua et al., 2020) and become reliant on the invasive crayfish on rice fields to survive the winter. This will probably increase human-wildlife conflicts, as storks are already seen as pests by farmers, particularly on rice fields. On the other hand, landfills and rubbish dumps in Morocco will not be affected by the European laws, therefore this resource will still be available for birds. Notwithstanding, after landfill closure , White Stork breeding success may decrease

(Steigerwald et al., 2015) and we might witness a decrease in population size in European storks. Thus, to avoid local collapse of populations, regional governments and non-governmental organizations could provide supplementary feeding resources for storks, as recently seen in Madrid after landfill closure (GREFA, 2021). Reducing food waste and having more effective waste treatment options is enormously important for human food security and public health, however we will need to closely monitor the populations of birds and other animals that have become reliant on this abundant food supply to understand how these drastic changes will impact their populations.

Overall, this thesis provided evidence on the importance of environmental conditions and individual traits to determine bird movement. Hopefully, this research will stimulate researchers to further investigate and disentangle the influence of weather and other environmental conditions, individual experience, social learning, and genetics on species adaptation to ongoing environmental change.

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– Appendix 1 –

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

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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

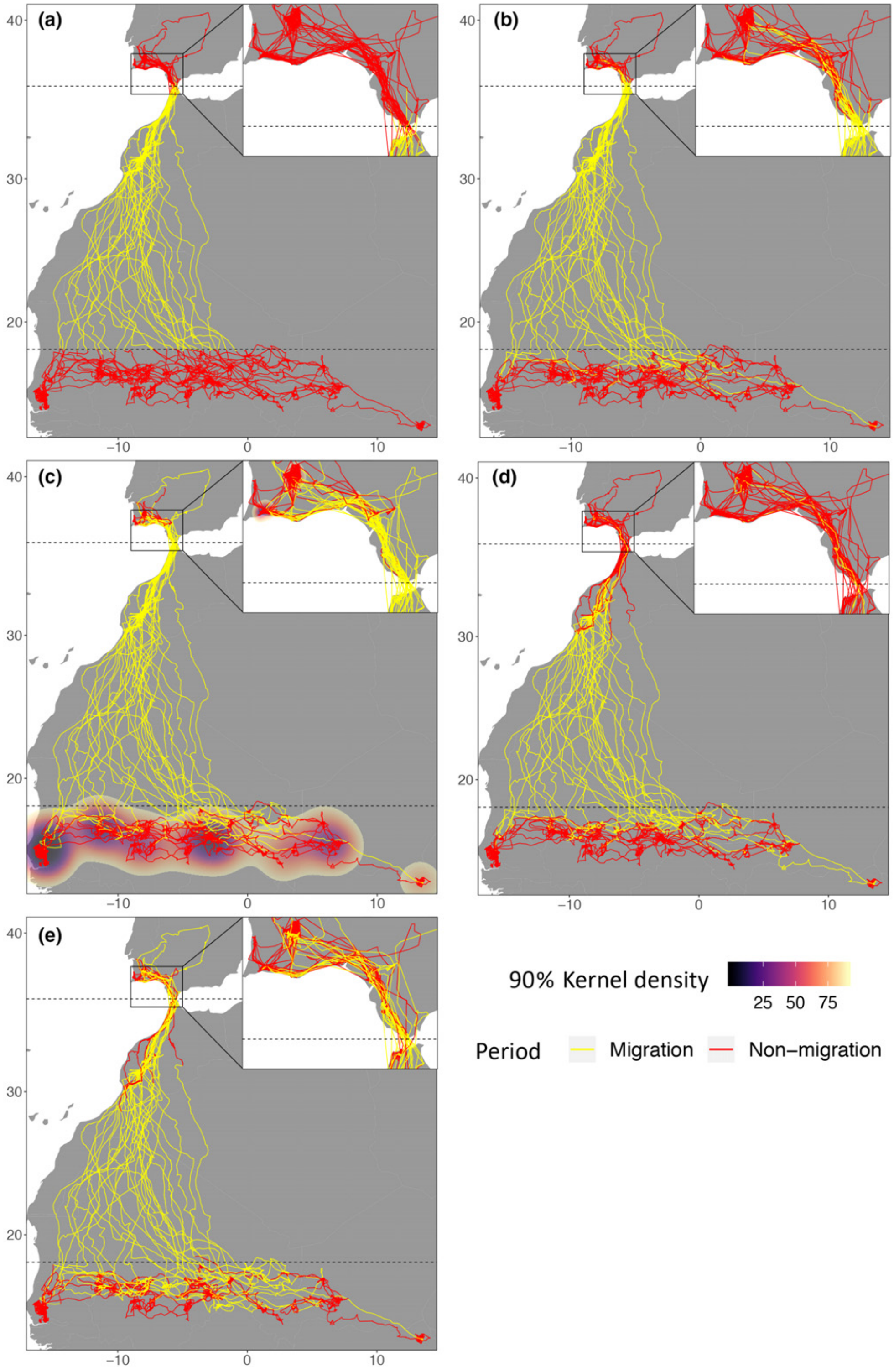


Figure 1. Annual movements of 18 White Storks classified as migratory or non-migratory according to the (a) spatial threshold (S), (b) absolute displacement (AD), (c) spatio-temporal displacement (SD), (d) net squared displacement (NSD) and (e) change point analysis (CPA) methods. Dashed lines represent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

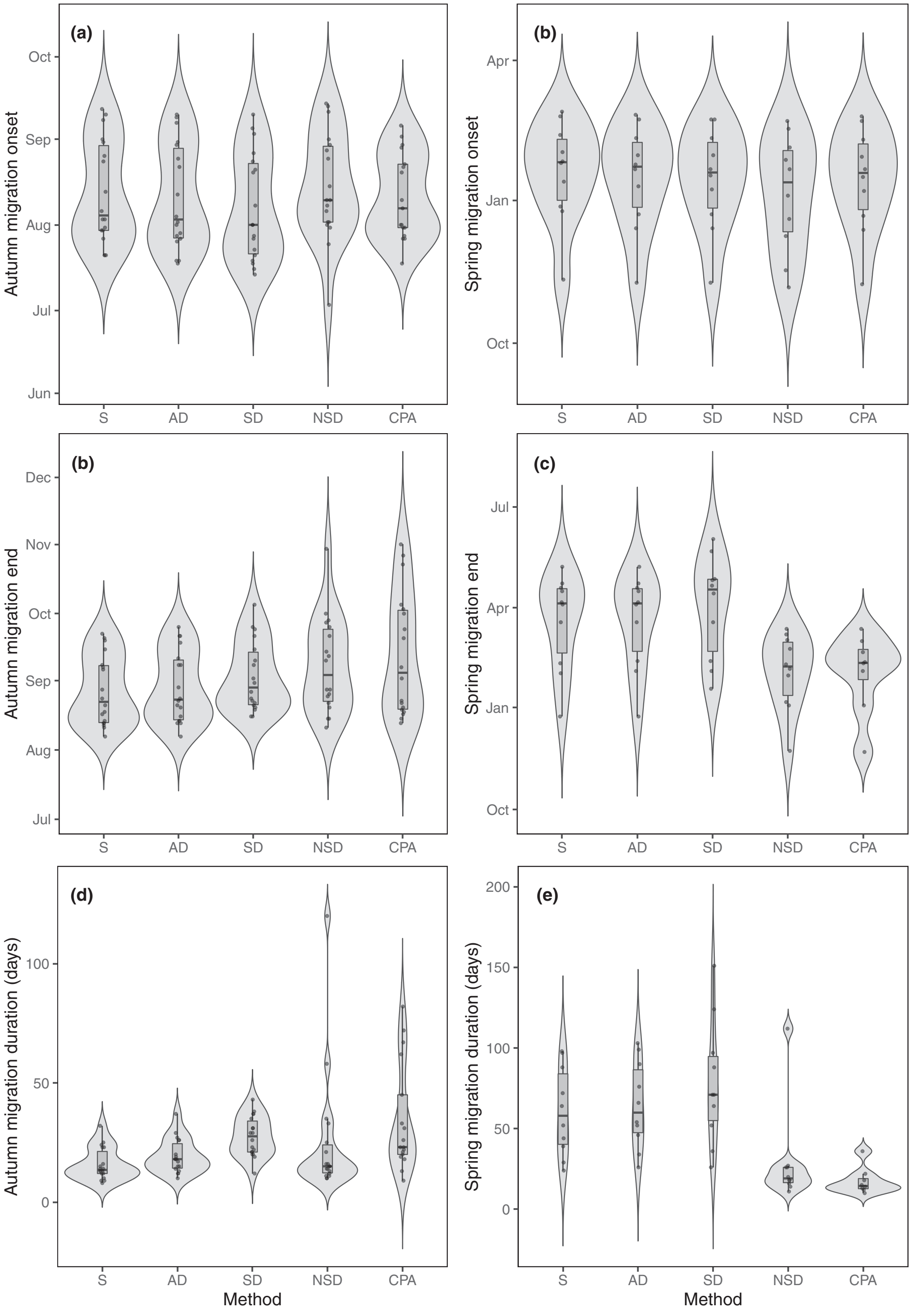


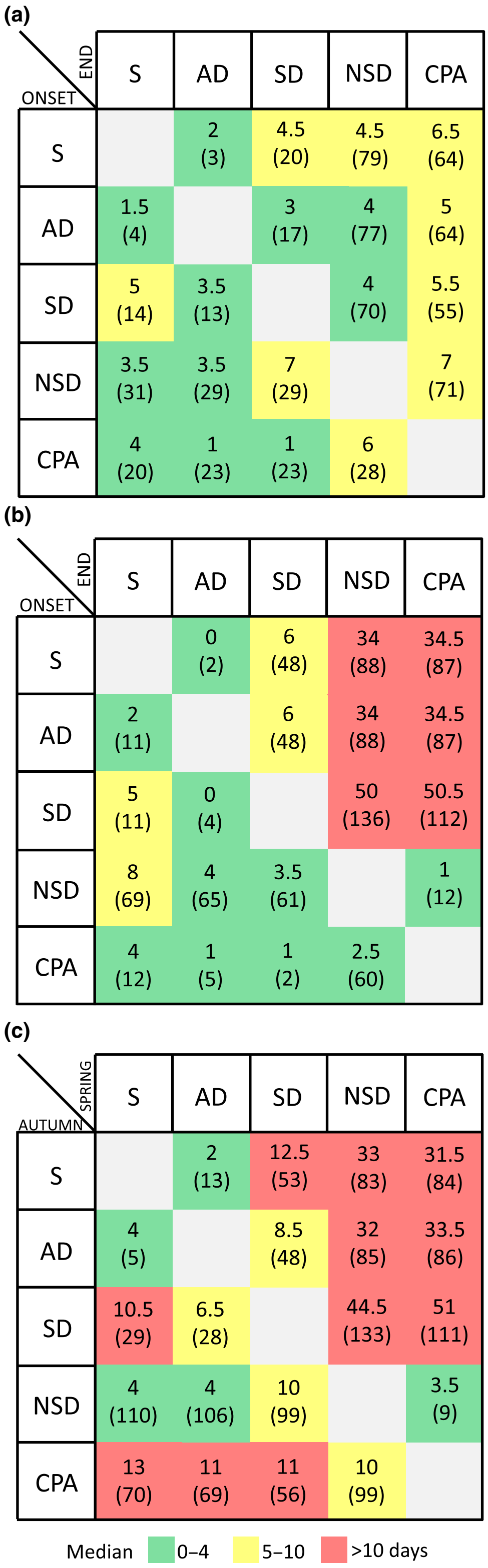
Figure 2. Violin plots of the distribution density of the start of (a) autumn and (b) spring migration; end of (c) autumn and (d) spring migration; and duration in days of (e) autumn and (f) spring migration obtained using different methods. Middle, lower and upper hinges of the boxplot correspond to 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)

ONSET / END	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)

ONSET / END	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)

AUTUMN / SPRING	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

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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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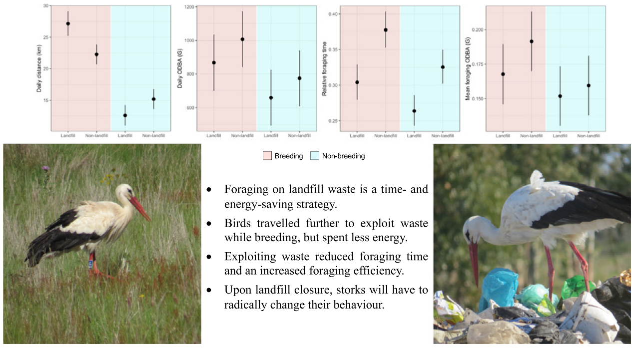
HIGHLIGHTS

- 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

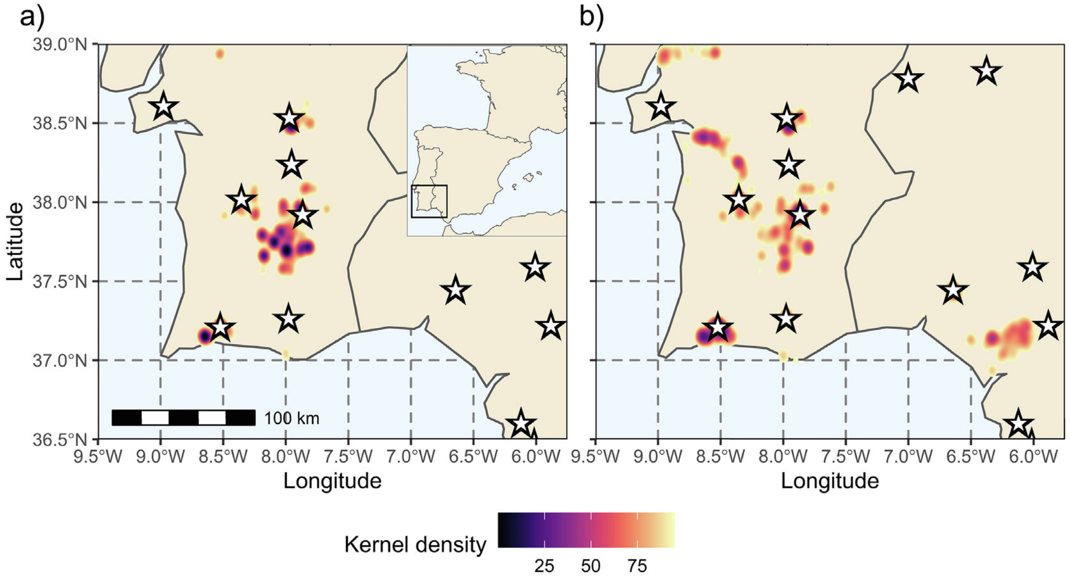

Fig. 1. Foraging areas of tracked white storks in southern Iberia (Portugal and Spain) between 2016 and 2019 during a) the breeding and b) the non-breeding periods. Stars indicate landfill sites.

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.

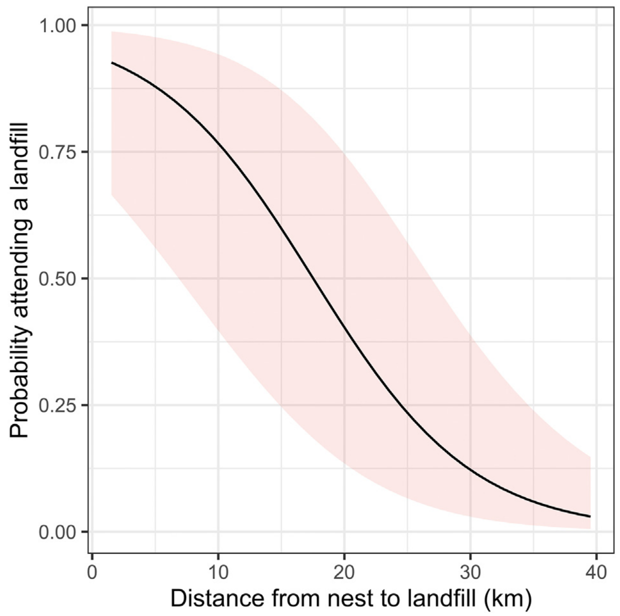

Fig. 2. Estimates from GLMMs explaining the probability of white storks attending a landfill during the breeding season as a function of the distance from the nesting site to the closest landfill.

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; $\chi 2 = 2.882$; $p = 0.09$), with individuals nesting closer to a landfill site foraging there more often (Fig. 2).

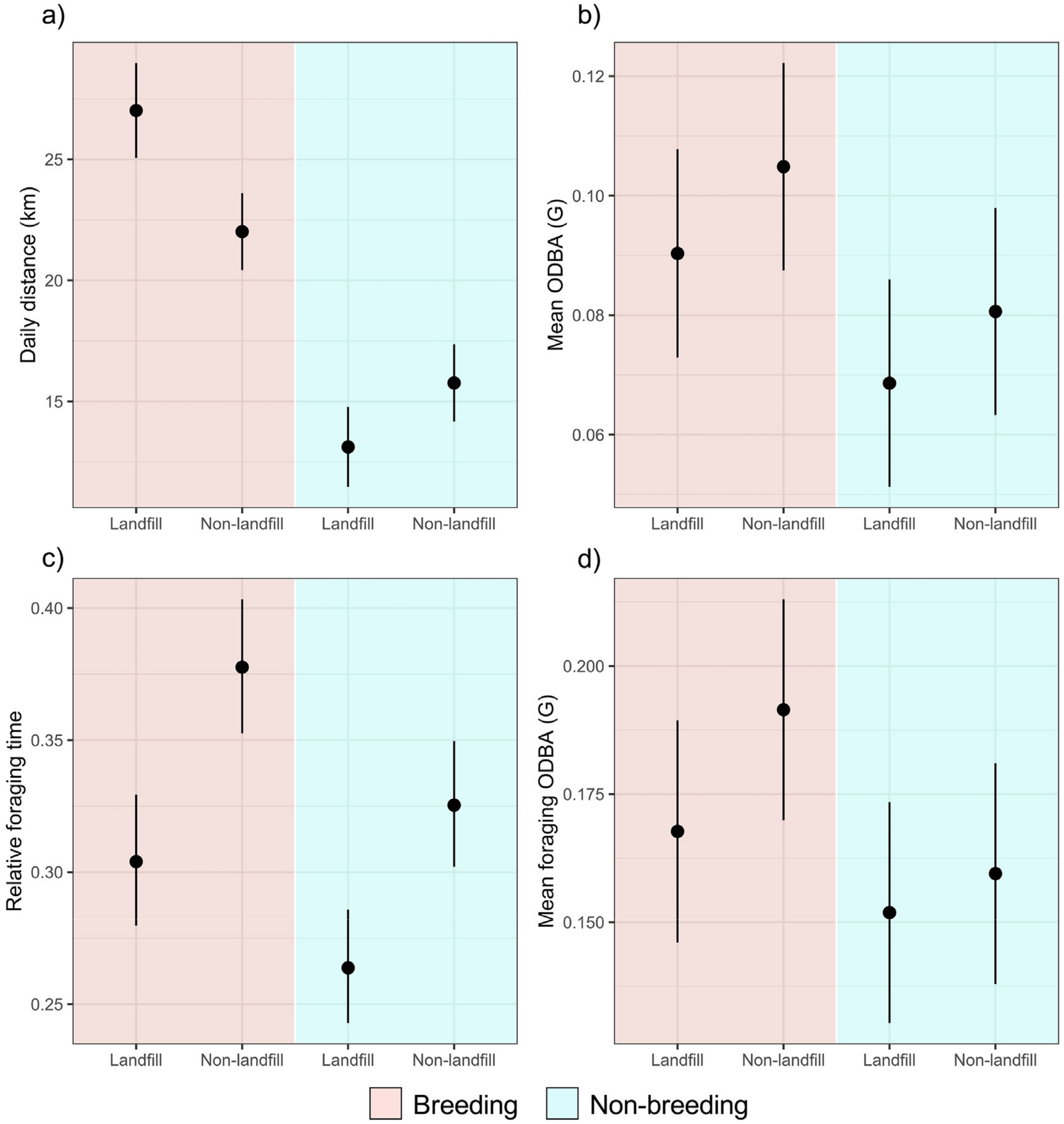

Fig. 3. Predicted values and 95% confidence intervals from GLMMs explaining (a) daily distance travelled, (b) mean overall dynamic body acceleration (ODBA), (c) relative foraging time, and (d) mean foraging ODBA of foraging white storks, as a function of season (breeding or non-breeding) and foraging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

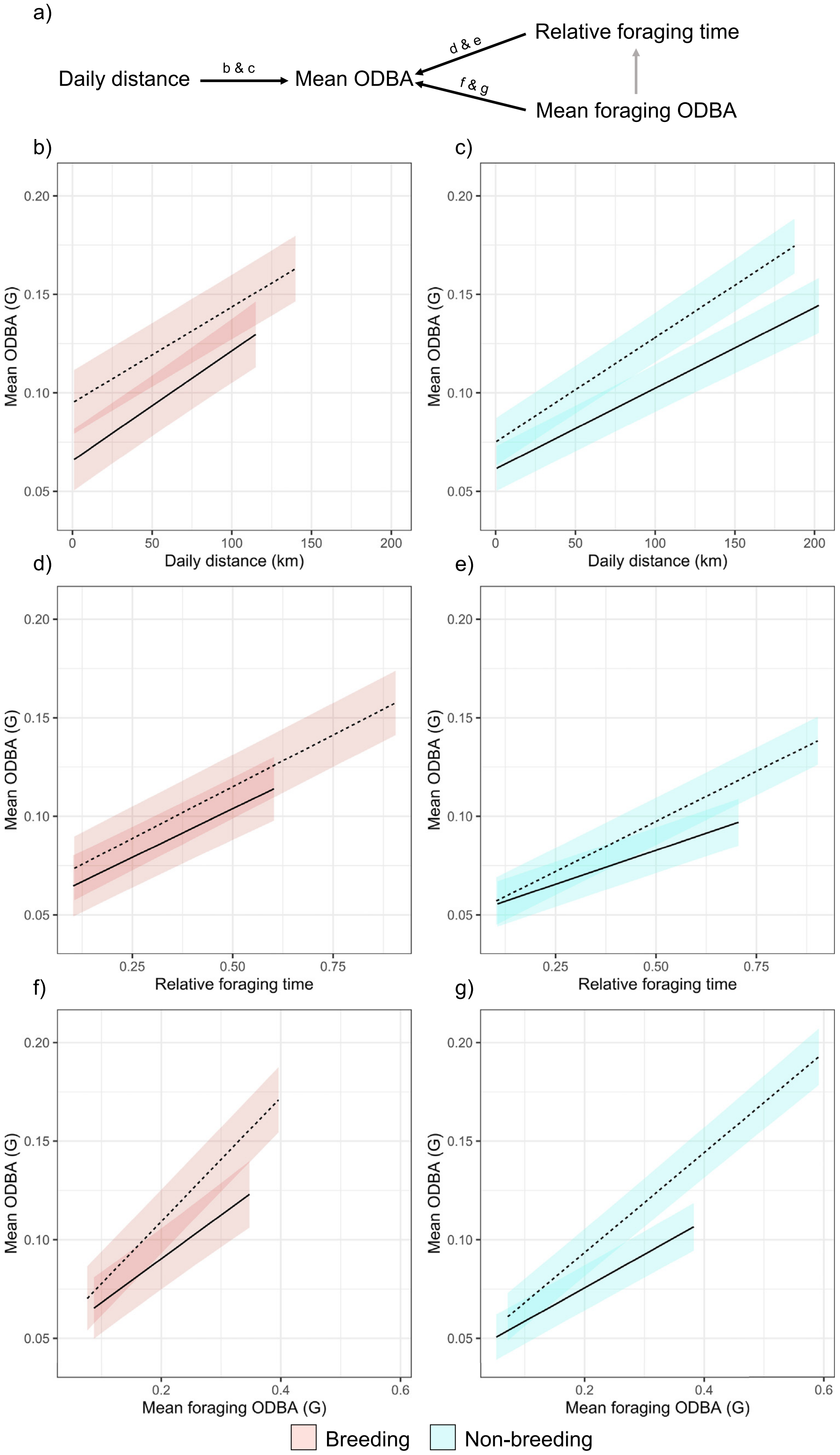

Fig. 4. (a) Graphical explanation of the structural equation model (SEM) showing the relative contribution of white storks' foraging decisions into the mean overall dynamic body acceleration (ODBA). Black arrows indicate relationships represented in the figure and the grey arrow relationship not represented 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.

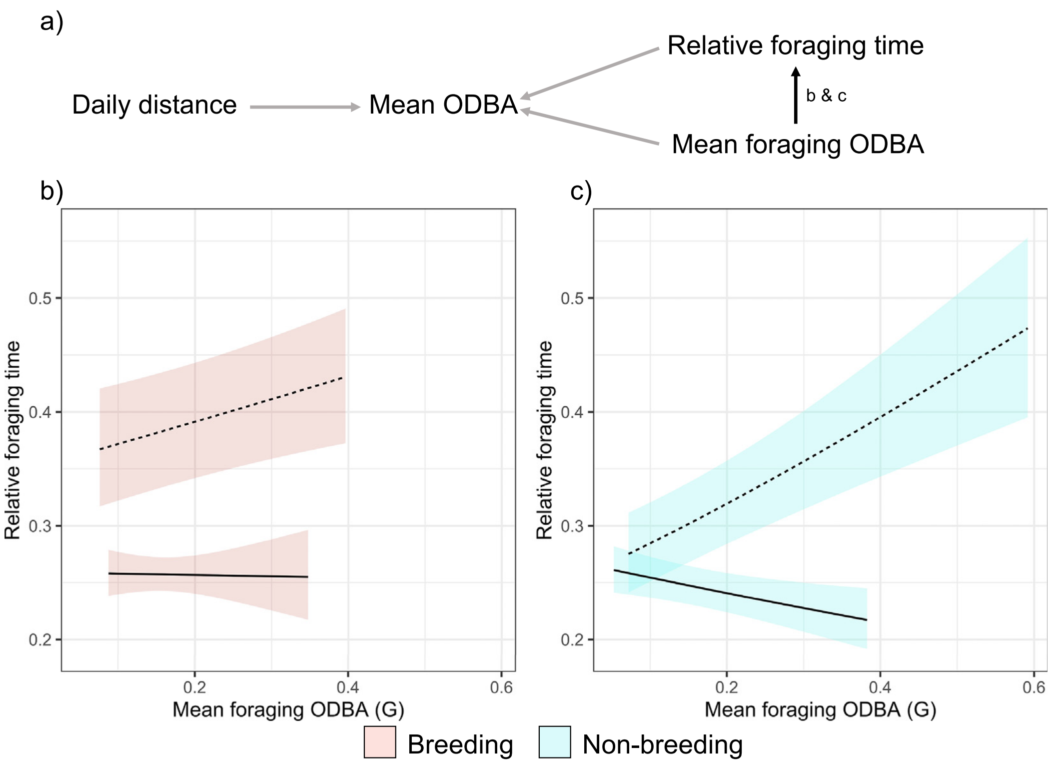

Fig. 5. (a) Graphical explanation of the structural equation model (SEM) showing the relative contribution of white storks' foraging decisions into the mean overall dynamic body acceleration (ODBA). Black arrows indicate relationships represented in the figure and the grey arrow relationship not represented 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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