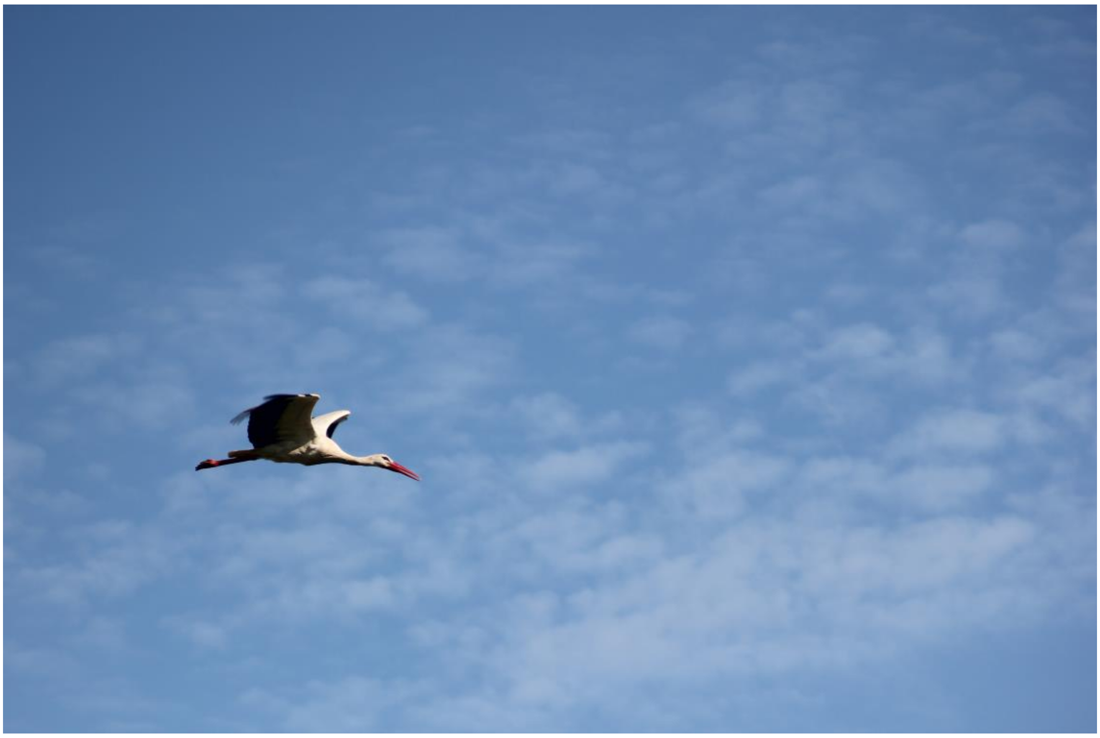
Storks on the move:
The influence of anthropogenic food subsidies on the migration and movement behaviour of white storks, *Ciconia ciconia*.



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Abstract

Migratory bird populations often comprise individuals that undertake a range of differing migratory journeys; environmental conditions and social cues can cause variation in migratory behaviour. The mortality risks for migratory birds also vary depending on their journeys, access to social cues and resources that are encountered. Over millennia human activities have influenced resource availability at the landscape level, for example farming practices, organic waste and, in recent decades, garden bird feeders, all provide predictable food subsidies that can affect the demography, survival and movement behaviour of the wildlife species that feed on them, including migratory birds.

This thesis investigates how use of anthropogenic food subsidies influences migratory behaviour and mortality of white storks (*Ciconia ciconia*). White storks have recently become partially migratory in Southern Europe and this has been associated with their year-round use of landfill sites for foraging. I will also explore if associations and social cues from family members influence juvenile migratory behaviour and use of new anthropogenic food subsidies. Recent advances in tracking technology allowed me to track storks with GPS/GSM devices and to study in-depth their daily movements in order to understand use of anthropogenic food subsidies and associations between individuals, as well as their large-scale movements such as trans-continent migration.

The study findings indicate that greater use of landfill sites is associated with lower mortality rates for juvenile white storks. In addition juveniles that spend more time at landfill sites prior to migration delay the onset of migration, while juveniles that visit landfill sites more on migration have slower migrations, taking more days with slower speeds. Juvenile use of landfill sites and their migratory behaviour is independent of their family members. The impending closure of landfill sites across the EU may therefore have negative implications for white stork demography and may alter migratory behaviour for migratory populations.

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This work is dedicated to my family and future family, Alex.

Chapter 1

Introduction

Photo of adult white stork in nest in Portugal, taken by K Rogerson

1.1 The phenomenon of animal migration

Animal migration is a spectacular form of animal movement and is a diverse phenomenon (Chapman, Bronmark, *et al.*, 2011). It is undertaken by organisms of all taxa and at all scales, from short distances and changes in altitude undertaken by mammalian herbivores to cross-continental movements by insects (Alerstam and Bäckman, 2018). Migration differs from other types of movement, such as dispersal, because it requires two journeys in specified directions, one away from the breeding area and one returning to it (Newton, 2008; Winger *et al.*, 2019).

The study of animal migration is important as the behaviour influences the fate of individuals and populations as well as influencing the ecosystems they are a part of (Nathan *et al.*, 2008; Chapman, Bonmark, *et al.*, 2011). Migratory behaviour is flexible, with partial migratory species and populations containing both individuals that migrate and individuals that remain resident in breeding areas all year-round (Newton, 2008). Differences and changes in migratory behaviour are studied to understand the processes and patterns behind the movement behaviour, such as how it evolved, why migratory behaviours change and how migratory species can be conserved (Wilcove and Wikelski, 2008; Chapman, Bonmark, *et al.*, 2011).

Animal migration has been studied extensively. In this first section of my introduction, I will explore the literature on bird migration, focusing on processes behind the evolution of the behaviour, variation seen in migratory bird species and what variables influence migratory birds' behaviour and survival. Over 19% of extant bird species are migratory (Kirby *et al.*, 2008) and birds undertake some of the longest migrations of any taxa (Alerstam and Bäckman, 2018). Bird migration is integral to ecosystems across the globe as it results in the seasonal redistribution of millions of migratory birds (Somveille, Rodrigues and Manica, 2018).

1.1.1 Evolution of migratory behaviour

The term "evolution of migratory behaviour" is defined by Winger *et al.* (2019) as "*the appearance or intensification of migratory behaviour in a population/lineage that was previously sedentary or less migratory*"; migration is a plastic trait seen across animal groups and the behaviour can be lost and regained in species and populations (Alerstam and Bäckman, 2018; Winger *et al.*, 2019). The theories of the evolution of migration are diverse and concentrate on migratory behaviour being an adaptation to enhance fitness in seasonal environments (Cox, 1968; Alerstam, Hedenstro and Susanne, 2003; Salewski and Bruderer, 2007). Winger *et al.* (2019) adds to these theories by hypothesising migration is an adaptation to seasonality for organisms that have breeding site fidelity. Breeding site fidelity would drive the regular round trip to and from breeding grounds, which is maintained by potentially enhanced reproductive success by returning to successful breeding sites. In addition, Somveille *et al.* (2018) suggests that migration evolved as a resource-tracking strategy, so that animals can optimise their energy budget when living in seasonal environments and dealing with competition (Somveille, Rodrigues and Manica, 2018).

Migration is an adaptive behaviour and the birds that undertake migration require adaptations to migrate successfully. Firstly, in order to be able to return to the same breeding area they must be able to orientate and navigate (Newton, 2008; Alerstam and Bäckman, 2018). Animals use a range of different compasses, employing celestial (sun and star), geomagnetic or odour cues to orientate themselves (Gould, 1998; Cochran, Mouritsen and Wikelski, 2004). Secondly, there are physiological adaptations, such as the ability to store fat reserves prior to long distance migrations (McWilliams *et al.*, 2004). Thirdly, Shaw & Couzin (2013) propose that migratory birds need to be able to use non-resource information to direct movements, for example information from their history, or social information to be able to travel large distances (Shaw and Couzin, 2013). Finally, migrants need the ability to start the movement at the appropriate time to enhance resource availability at breeding and non-breeding areas (Gordo *et al.*, 2005; Helm, Piersma and van der Jeugd, 2006). This could be directed by an innate endogenous system that controls migration round trips (Winger *et al.*, 2019) and complements the other adaptations and processes that have evolved to facilitate migratory journeys.

1.1.2 Variability in migratory behaviour

Individuals are often faithful to their migratory strategy, completing similar migratory distances and using the same non-breeding grounds in consecutive migrations (Grist *et al.*, 2014; Chambon *et al.*, 2019; Gill, Alves and Gunnarsson, 2019). Migration diversity within a population, variability in migratory movements and destinations between individuals, can improve the resilience of the population to environmental change. Diversity buffers partially migratory populations from extinction by making them less likely to decline compared to fully migratory or resident populations (Gilroy *et al.*, 2016).

Variability in migratory strategy in the same species or population, partial migration, can be controlled by genetic variation or conditional cues (Chapman, Bonmark, *et al.*, 2011). Genetically inherited information can influence migration routes and destinations, for example there are genetic differences in black caps (*Sylvia atricapilla*) that migrate to the UK and Mediterranean (Berthold *et al.*, 1992; Pulido, 2011). Individual condition can be associated with differences in migratory behaviour, such as the outcomes of dominance and competitive interactions influencing whether individuals are resident or migrants (Alerstam, Hedenstro and Susanne, 2003). Dominant individuals, such as adults and males, may not undertake migration as they can access limited resources in the breeding grounds, while subordinate individuals, such as juveniles and females migrate to areas with better or more accessible resources (for example, Smith and Nilsson, 1987). In addition, larger individuals may be more likely to be resident than smaller individuals either because they are dominant or because they can survive harsh winter conditions in the non-breeding season (Ketterson and Nolan, 1976; Perez-Tris and Telleria, 2002; Jahn *et al.*, 2010; Chapman, Bonmark, *et al.*, 2011).

1.1.3 Factors influencing the establishment and maintenance of migratory behaviour

‘How do birds know where to go on migration?’ is a question constantly being asked by researchers studying migratory birds. The answer is that there are different mechanisms underlying migratory behaviour which vary from species to species.

1.1.3.1 Innate or endogenous control of migration

Migratory juveniles may rely on an innate program or endogenously controlled schedule that prompts them to undertake migratory movements in certain directions and at certain times (Perdeck, 1958; Thorup *et al.*, 2007; Wiltschko and Wiltschko, 2012).This may mean that juveniles from the same breeding area can be displaced by weather conditions while on migration which may lead them to have varied non-breeding areas due to the innate controls on their migratory direction (Thorup *et al.*, 2007; Cresswell, 2014). Experienced migratory birds on the other hand may be able to supplement the innate program with prior knowledge of migration to be able to use the same routes and same destinations every year (Gwinner, 2003; Thorup *et al.*, 2003, 2007; Blackburn and Cresswell, 2016; Chambon *et al.*, 2019). They can also use prior experience to improve route accuracy between their breeding and non-breeding areas (Mueller *et al.*, 2013). Flexibility in finding non-breeding areas between generations - juveniles use different cues to their predecessors, locating different non-breeding grounds and then remaining faithful to those areas (Gill, Alves and Gunnarsson, 2019) - may result in greater resilience of the population to environmental change as the entire population is not fixed to certain non-breeding areas (Cresswell, 2014).

1.1.3.2 Social/cultural learning

Social interactions and social learning may be important to maintain migratory behaviour as well as to help reduce risk and uncertainties during migration (Helm, Piersma and van der Jeugd, 2006; Fagan *et al.*, 2012; Nemeth and Moore, 2014). Species within the Anatidae (for example, pink-footed geese, *Anser brachyrhynchus*) and Gruidae families (for example, common crane*, Grus grus*) have strong family associations and juveniles stay with parents from fledging to the non-breeding locations (Lazarus and Inglis, 1978; Alonso, Bautista and Alonso, 2004) . The parents actively influence migratory timings; consequently routes and timings are culturally transmitted and maintained in the population (Rees, 1989; Helm, Piersma and van der Jeugd, 2006). Other species learn migratory behaviour, such as timing, routes and destinations, from other conspecifics (Chernetsov, Berthold and Querner, 2004; Palacin *et al.*, 2011).

Bird species are often sociable during migration even if normally solitary, although relying on social cues is also costly as cognitive abilities need to be high (van Noordwijk *et al.*, 2006; Shaw and Couzin, 2013). Those that are gregarious on migration, responding to social cues to be recruited to large flocks, may benefit from finding favourable conditions, thermals (Loon, Bouten and Davis, 2011), and stopover sites and destinations (van Noordwijk *et al.*, 2006).

The cultural transmission of migratory behaviour between individuals can be important for the maintenance of migration. Migration behaviour may be lost if there is a reduction in the number of experienced individuals, resulting in a possible switch from a partially or wholly migratory population to a purely resident one (Fagan *et al.*, 2012). This can arise from factors changing the environment, survival rates, breeding success or social learning (Fagan *et al.*, 2012). The migration routes of whooping cranes (*Grus americana*) and Canada geese (*Branta canadensis*) are culturally transmitted and could die out if populations become extinct in the wild (Ellis *et al.*, 2003; Fagan *et al.*, 2012; Mueller *et al.*, 2013). Endangered juvenile Egyptian vultures (*Neophron percnopterus*) from Italy have high mortality during their first autumn migration if they cross the Mediterranean Sea to Africa instead of going via Turkey, this error in navigation has been linked to the small and declining population and the low likelihood of following experienced migrants (Oppel *et al.*, 2015).

1.1.3.3 Changes in environmental conditions

Migratory birds can enhance their fitness and respond to the environmental conditions in their breeding and non-breeding areas to adjust timings and directions of movements with resource availability (Thorup *et al.*, 2017). Migratory birds often respond to external cues, such as weather and climatic conditions, to know when to start and end migration and these conditions can also influence other parameters of migration such as timing, duration and speed of migration. Temperature can influence start dates of migration, this includes cues like frost days (Xu and Si, 2019). Weather conditions at the breeding grounds, for example an increase in bad weather and conditions leading to poor flight conditions, can trigger the start of migration (Shamoun-Baranes *et al.*, 2006) and while on migration crosswinds can lead to soaring birds being slower and moving shorter distances per day (Vansteelant *et al.*, 2015).

In our current rapidly changing climate, the external cues for migration phenology are changing. Earlier arrival dates at the breeding grounds in Europe can be associated with weather at wintering and stopover areas, for example, high levels of precipitation and high temperatures in North Africa (Saino *et al.*, 2007; Haest, Hüppop and Bairlein, 2018). Future climate predictions suggest prevailing wind conditions could change, potentially altering the wind assistance available to birds migrating over the USA, which could alter the time and energy expended on migration (La Sorte *et al.*, 2019). Changes in migration phenology due to climate change can become a problem for migratory birds when there are phenological mismatches between their arrival and abundance of their prey at breeding and non-breeding grounds (Saalfeld *et al.*, 2019).

Our changing climate may also influence the resources available to migratory birds across their annual cycle which in turn will influence migratory behaviour (Gordo, 2007). Food availability can influence timing and duration of migration, for example, when food availability is low at stopover locations the duration is increased (Russell *et al.*, 1994). In addition, resource availability can be influenced by body condition which may then alter migratory behaviour. Redstarts (*Setophaga ruticilla*) that wintered in areas with better resources, mangrove habitats, had better body condition and departed earlier on spring migration than those that wintered in dry scrub areas (Studds and Marra, 2007). Condition of feathers post-moult, effected by food availability, could influence the flying performance of birds (Gordo, 2007).

1.1.4 Mortality in migratory populations

Understanding the survival rates of migratory birds requires knowledge of mortality over the whole migration cycle and this information can be difficult to acquire. The study of survival rates for migratory species requires long term ringing studies or studies relying on advanced tracking technology (Leyrer, Lok and Brugge, 2013).

Mortality of juveniles is high post-fledging in migratory and resident species (Grüebler, Korner-Nievergelt and Naef-Daenzer, 2014), but migratory juveniles are also at risk on their first migration. Dangers can include lack of social cues from experienced adults (Oppel *et al.*, 2015) and displacement by bad weather leading to routes to sub-optimal non-breeding areas (Thorup *et al.*, 2007).

Survival of migratory adults is commonly high all year round (Grüebler, Korner-Nievergelt and Naef-Daenzer, 2014) but they are influenced by changes in conditions across their annual cycle and geographical range. Conditions in the non-breeding area, weather and habitat conditions can impact on survival in the non-breeding area (Kanyamibwa *et al.*, 1990; Kanyamibwa, Bairlein and Schierer, 1993) as well as having carry over effects on the return migration (Lok, 2013) and subsequent breeding period (Alves *et al.*, 2013).

In our changing world, with threats to wildlife from urbanisation, habitat destruction and climate change, migratory bird species are threatened by multiple variables across their annual geographical range (Culp *et al.*, 2017; Zurell *et al.*, 2018). The current rapid changes to the environment, changes in temperature, wind conditions and frequency of weather extremes, will influence survival of migratory birds at all parts of their annual cycle (Culp *et al.*, 2017). In addition, anthropogenic structures, for example, buildings and energy infrastructure – which are increasing in number as urban areas increase in size and number – can result in mortality for migratory birds on land and at sea (Cleasby *et al.*, 2015; Martín *et al.*, 2018; Nichols *et al.*, 2018). The multiple risks faced by migratory birds throughout their annual cycle need to be considered when planning their conservation and protection. Currently, only 9% of migratory birds have their annual geographical range adequately covered by protected areas compared to 45% of non-migratory birds (Runge *et al.*, 2015). The whole annual cycle of a migratory species and changes to environmental conditions in the areas they use need to be considered when studying their survival rates.

1.2 Impacts of human activities on resource availability for migratory species

Human activities impact upon a wide range of aspects of animal biology. Infrastructure (Holderegger and Di Giulio, 2010), artificial light (Russart and Nelson, 2018) and human produced noise (acute or chronic; Shannon *et al.*, 2016) can influence survival rates, breeding success and movement behaviour of species across all taxa.

Predictable anthropogenic food subsidies, PAFS (Oro *et al.*, 2013), are food resources produced by human activities across the world and which are accessible to wildlife. The resources can be predictable in time and space; however not all anthropogenic food resources are completely predictable due to the human activities that produce them. In this section, I will consider the human activities that produce food subsidies for a range of vertebrate species, which species use these resources, how it influences their ecology and how policies around the provision of certain subsidies are changing.

1.2.1 Where do anthropogenic food resources come from?

Humans have produced food subsidies for wildlife for millennia. The subsidies can come from deliberate human activities providing food for wildlife while others are produced incidentally and often occur across large scales (Oro *et al.*, 2013). Examples of these activities and subsidies are summarised in Table 1.

Table 1. Examples of human activities that provide food subsidies for vertebrate species, split between deliberate and incidental activities.

Human activity	Description	References
Deliberate		
Garden feeders	Feeders for garden birds and sometimes mammals in private gardens. For all or part of the year.	(Reynolds *et al.*, 2017; Thabethe and Downs, 2018)
Feeding wild animals as a tourist attraction.	Regular feeding of wild animals for tourists. E.g. commonly seen with primate populations (Burman *et al.,* 2017) and the shark diving industry (Hammerschlag *et al.,* 2012).	(Orams, 2002; Berman *et al.*, 2007; Hammerschlag *et al.*, 2012)
Ritualised feeding due to religious or cultural views	Regular food offerings for certain species due to religious views. E.g. feeding of black kites (*Milvus migrans*) by Muslims in Delhi (Kumar *et al.*, 2018; Kumar, Gupta, *et al.*, 2019), deer (*Cervus nippon*) in Japan (Usui and Funck, 2017) and rhesus macaques (*Macaca mulatta*) in South-East Asia (Sengupta, McConkey and Radhakrishna, 2015).	(Sengupta, McConkey and Radhakrishna, 2015; Usui and Funck, 2017; Kumar *et al.*, 2018; Kumar, Gupta, *et al.*, 2019)
Supplementary food as a conservation tool	Food provided at regular times and locations for reintroduced or declining populations. E.g. vulture “restaurants”.	(Ewen *et al.*, 2015; Schabo *et al.*, 2017)
Incidental		
Litter	Poor waste management by private individuals leading to waste and rubbish across urban areas. E.g. American white ibises (*Eudocimus albus*) feed on litter in urban areas (Murray *et al.*, 2018); raptors feed on the scavenger bird species that	(Saj, Sicotte and Paterson, 1999; Kettel *et al.*, 2018; Murray *et al.*, 2018; Vallino *et al.*, 2019)

	thrive in urban areas on human litter (Kettel *et al.*, 2018).	
Fishery discards	Fish rejected by fisheries. Fish offal and non-target species thrown back into the sea.	(Phillips *et al.*, 1999; Patrick *et al.*, 2015; Real *et al.*, 2018)
Agricultural discards	Edible matter left over from harvesting crops. Can be at the farm/field or discarded as they are transported.	(Smart and Gill, 2003; Galle *et al.*, 2009)
Landfill sites and rubbish dumps	Open areas where rubbish from homes and businesses is collected together. Organic waste is foraged for by vertebrates.	(Duhem *et al.*, 2003; Plaza and Lambertucci, 2017; Spelt *et al.*, 2019)

Deliberate food subsidies provided by humans often stem from the enjoyment and satisfaction we get from seeing the animals and providing food for them (Reynolds *et al.*, 2017). PAFS that are commonly provided by private individuals across the globe are garden feeders for birds (Thabethe and Downs, 2018). In the UK, feeding garden birds is thought to be able to fully support a minimum of 31 million birds with an approximate daily cost of £0.35 per household for provisioning (Orros and Fellowes, 2015b). After the re-introduction of red kites (*Milvus milvus*) in the south of England, it became popular for individuals to feed them in gardens, and this non-official feeding could potentially support large numbers of kites although the food could have potential issues as it has low nutritional value (Orros and Fellowes, 2015a).

The types of human activities that lead to PAFS for wildlife can overlap. In Japan, deer are considered sacred and have cultural values (Usui and Funck, 2017), they are protected and fed. However, the human-deer relationship has intensified as feeding deer has become a very popular tourist attraction resulting in more human-wildlife conflicts (Usui and Funck, 2018).

The incidental food resources humans create for wildlife is through our waste and rubbish (Table 1). Opportunistic and scavenger species take advantage of the organic matter that humans discard, however at the same time they also come into contact with other waste products such as flame retardants (Tongue *et al.,*2019) and plastic (Peris 2003). When human rubbish is discussed it is difficult not to talk about the problem with human reliance on single-use plastics. Although plastic waste is not a direct food resource, it is often considered as food by many organisms and consumed as such, potentially influencing their health and survival (Bond *et al.*, 2014; Schuyler *et al.*, 2014).

1.2.2 Who uses anthropogenic food subsidies?

Deliberate anthropogenic food subsidies (Table 1) have a target species or set of species, for example, when used as a conservation tool or for human enjoyment. The target species for garden feeders is for species that people like to see or hear while the non-target species are thought of as noisy or aggressive (Cox and Gaston, 2018). Bird feeders can result in more garden visits by mammals that also eat the seeds (Reed & Bonter 2018);some of these would be considered beneficial and “nice” to view while others like grey squirrels may be regarded as pests (Hanmer, Thomas and Fellowes, 2018). Unintentional anthropogenic food subsidies do not have a target species and the species that use them are the scavengers or opportunistic species in the local ecosystem, which are often thought of as “pests”: gulls (*Larus* spp., Spelt *et al.*, 2019), storks (*Ciconia* spp., Arizaga *et al.*, 2017) or primate species (baboons, *Papio hamadryas*, (Boug *et al.*, 1994) and vervet monkeys, *Chlorocebus pygerythrus*,(Saj, Sicotte and Paterson, 1999)).

1.2.3 How do anthropogenic food subsidies influence wildlife ecology?

The provision of food resources by a range of human activities (Table 1) influences the demography and ecology of the species that use them. A review by Plaza and Lambertucci (2017) showed that research into the effects of anthropogenic waste on vertebrates is mostly positive (72.6% of 159 articles). The food subsidies can positively or negatively influence survival rates and breeding success, alter movement behaviour and have carry over effects into the local ecosystems and community structure (Plaza and Lambertucci, 2017). For example, at areas with anthropogenic food subsidies there can be increased predation pressures (Robb *et al.*, 2008), changes to disease transmission (Murray *et al.*, 2016) and increased human-wildlife conflicts (Newsome and van Eeden, 2017).

Survival rates of the individuals that use anthropogenic food resources can be improved and result in increased populations, for example populations of UK garden birds (Plummer *et al.*, 2019), Cape griffon vultures (*Gyps coprotheres*, Piper, Boshoff and Scott, 2009) and lynx (*Lynx lynx*, Lopez-Bao, Rodrıguez and Palomares, 2008) have been increased or strengthened by supplementary food. However increased predation around landfill sites or bird feeders can lead to increased mortality (Otali and Gilchrist, 2005; Hanmer, Thomas and Fellowes, 2017). In addition, changes to disease transmission when individuals forage on anthropogenic food can negatively influence survival rates. There is a risk of greater disease transmission due to the higher than usual densities of individuals and diversity of species that would not normally associate together in close proximity (Murray *et al.*, 2016; Lawson *et al.*, 2018).

Breeding success is regularly shown to be improved by the use of anthropogenic food subsidies (for example, Massemin-Challet *et al.*, 2006; Gilbert, 2016; Kettel *et al.*, 2018). In addition, the removal of anthropogenic food subsidies from the landscape, for example, closure of landfill sites and removal of carcasses, have resulted in reduced breeding successes for the populations that were using them (Margalida, Colomer and Oro, 2014; Steigerwald *et al.*, 2015).

Movement behaviours have also been shown to be altered by the presence of anthropogenic food subsidies in the environment. This can be on a small scale, such as longer and costly foraging trips (van Donk *et al.*, 2019) or smaller home range sizes (Bino *et al.*, 2010). However, it can also influence large scale behaviours. The non-breeding distribution of Anna’s hummingbirds (*Calypte anna*) increased and colder and urban areas were colonised where people provided nectar for them (Greig, Wood and Bonter, 2017).

The use of supplementary food for garden birds was the main driver in a change of migratory route of black caps; new non-breeding areas in the UK were used instead of traditional areas in the Mediterranean (Plummer *et al.*, 2015).

1.2.4 Policy changes to anthropogenic food subsidies

The resources that are provided to wildlife unintentionally by humans centre on poor food waste management. Gordon *et al.* (2016) and Newsome and van Eeden (2017) discuss how the increasing human population has a growing demand for food and with the rapidly changing environment, food security is a priority for governing bodies. Reducing food waste at all parts of the supply chain is crucial for achieving this. The removal of food waste has the potential to impact all taxa across the ecosystems that interact with each step of food production, from agricultural practises to the food sent to landfill sites (Gordon *et al.*, 2016). A key message is that species need to be monitored to understand their response to the reduction in food from anthropogenic sources (Newsome and van Eeden, 2017).

There are plans and policies currently in place in the European Union to ban discards to create sustainable fisheries (Real *et al.*, 2018) and to reduce food waste at landfill sites (*EU Directive 2018/851*, 2018). The impacts of the removal of these anthropogenic subsidies can be varied and may be negative or positive depending on the relationship between the wildlife and the subsidy (Figure 1; Newsome & van Eeden 2017). Studies when food subsidies have been removed showed varying changes in the studied population, one showed no short term negative effects on breeding success for Egyptian vultures (*Neophron percnopterus*) a year after a landfill site closed (Katzenberger *et al.*, 2019), although there was a reduction in breeding success and a decline in adult body mass for yellow-legged gulls three years after landfill closure (Steigerwald *et al.*, 2015).

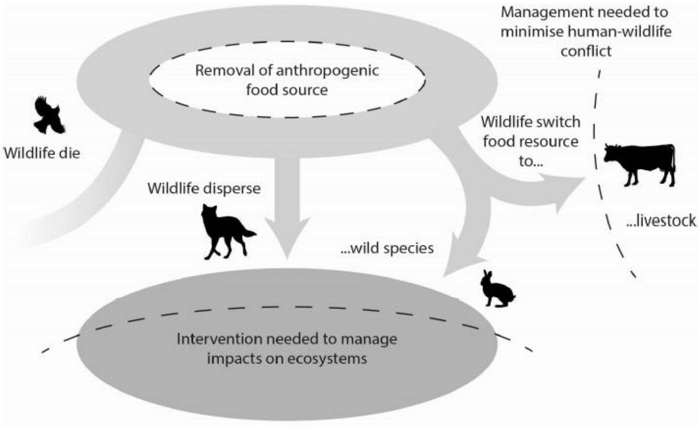

Figure 1. Conceptual diagram showing how the removal of anthropogenic food resources may impact wildlife and ecosystems. E.g. wildlife may die of starvation, disperse or switch dietary preferences to wild prey or livestock. Taken from Figure 3 by Newsome and Eeden (2017).

1.3 Tracking wild migratory birds

The study of birds and their migratory behaviour has been of interest for scientists since Aristotle in the fourth century BC (Winger *et al.*, 2019). Before the 1890s, the study of birds and their behaviour relied on collecting specimens but then bird ringing started in the Netherlands. Since the 1950s the technology to study bird movement has rapidly advanced with the use of weather radars, biologging and molecular techniques (Alerstam and Bäckman, 2018).

1.3.1 Examples of different techniques to study and track migratory birds

There are several approaches available to researchers that want to study and track migratory birds. In Table 2 I have outlined some examples of the technology that is currently being used to study the movements of migratory individuals.

Table 2. Examples of techniques to study and track movements of migratory birds. I highlight the resolution of movements and locations gathered from the techniques, number of individuals that researchers can track with the technique, the benefits and limitations of the techniques, examples of study questions that can be answered with the data gathered and examples of relevant studies.

Techniques	Resolution of movements and locations	Number of individuals	Benefits	Limitations	Examples of study questions	Examples	References
Stable isotope analysis	Low (approximate geographical area is known).	Many individuals (limited by time and laboratory access).	Nothing is carried by the bird (unless rings are needed for ID and repeat measurements).	Usefulness depends on timing of moult (if using feather samples)	Identifying migrants and residents in the same population. Location of wintering or breeding areas and migratory connectivity.	Feather samples for 90 individuals of Amur Falcon (Symes and Woodborne, 2010). Claw samples of 130 Common Eiders (Steenweg *et al.*, 2019).	(Newton, 2008)
Radar	High (for movements around the radar station) but individuals can only be tracked while in that precise area.	Thousands (but can only ID them while they are in the area of the radar).	Study orientation and reaction to different weather conditions. Ability to have continental-scale radar monitoring networks.	Individuals tracked for short time. Cannot identify species.	Study causes and consequences of movement. Interactions between movement and weather conditions.	Quantify and predict timing and intensity of migratory movements (Horton *et al.*, 2019).	(Newton, 2008; Shamoun-baranes *et al.*, 2014; Doren and Horton, 2018)

Techniques	Resolution of movements and locations	Number of individuals	Benefits	Limitations	Examples of study questions	Examples	References
Ringing (metal bands and colour rings)	High accuracy in location of re-sighting but low number of re-sightings (depends on re-sighting effort and bird species)	Thousands (depends on number of ringers and frequency of ringing sessions, which varies from country to country)	Ringing is undertaken by many private individuals across the world (under licenses), re-captures are reported by 1000s of ringers and, if colour-banded, re-sightings can be reported by birders and citizen scientists. This results in continual data collection and is not costly to the scientist. Colour banding allows birds to be ID'd without handling.	Questions often only answered with long term studies. Only using metal rings requires the birds to be caught before identification is known.	Survival rates of populations. Life expectancy of bird species. Locations of wintering areas. Monitoring individual migration phenology.	Migratory Icelandic black-tailed godwits (*Limosa limonsa islandica*) studied from 1999 to 2018. 1 – 2% of population colour banded. (Gill *et al.*, 2014; Gill, Alves and Gunnarsson, 2019). Studied migration routes of Mediterranean gulls (*Larus melanocephalus*) with 472 colour ringed individuals plus over 19,000 ringed birds from 18 countries (1990 - 2009; Carboneras, Tavecchia and Oro, 2013).	(Newton, 2008; Alves *et al.*, 2013; Allen *et al.*, 2019)

Techniques	Resolution of movements and locations	Number of individuals	Benefits	Limitations	Examples of study questions	Examples	References
						Survival rate of great skuas (*Catharacta skua*), 551 monitored (1989 to 1999; Ratcliffe *et al.*, 2002).	
Geolocators	Medium (knowledge of approximate area but daily movements not known)	Few (dependent on return rates)	Perfect for movements of small birds (< 50 g). Allow year-round tracking.	Birds have to be recaptured to collect the data. Processing data is time consuming and needs expert knowledge. Geolocators can cause drag (greater if attached between wings rather than on a leg loop)	Individual migration phenology, route and geographic range.	Revealed two distinct migration routes and wintering areas *Phalaropes lobatus* (Bemmelen *et al.*, 2019). Longest animal migration by Arctic tern (*Sterna paradisaea*) was revealed by tracking 11 individuals with geolocators (Egevang *et al.*, 2010).	(Bachler *et al.*, 2010; Bowlin *et al.*, 2010; Mckinnon *et al.*, 2014; Pancerasa *et al.*, 2019)

Techniques	Resolution of movements and locations	Number of individuals	Benefits	Limitations	Examples of study questions	Examples	References
Very High Frequency (VHF) radio telemetry	Low (exact location is known for a certain time).	Many.	Low cost devices and devices can be carried by small – medium sized birds.	Birds have to be located to get information which can be time and labour intensive.	Individual migration phenology and geographic range.	Southward migration of 77 western sandpipers (*Calidris mauri*, Iverson *et al.*, 1996).	(Newton, 2008)
Automated radio telemetry system (development on VHF manual technique above)	Low.	Many.	Devices can be carried by birds too small for GPS tags. Collaborative research network of receivers has been created across America. Birds can be detected across their geographical range without intensive fieldwork.	Limited by number of receivers. Need to be placed at strategic locations.	Individual migration phenology and geographic range.	Motus Wildlife Tracking system started in 2012 and in 2017 had 9000 individuals carrying devices with 25 million detections, receivers across North and South America (Taylor *et al.*, 2017).	(Newton, 2008; Taylor *et al.*, 2017)

Techniques	Resolution of movements and locations	Number of individuals	Benefits	Limitations	Examples of study questions	Examples	References
Satellite tags (Argos Platform Transmitter Terminals, PTTs)	High (depending on frequency of locations recorded).	Few (high cost of devices).	Independent tracking of birds anywhere in the world	Only large birds can be tracked (device should be at maximum 3 – 4% of body weight). Small negative effects of tagging on survival and reproduction, while positive effects on foraging duration. Different attachment types have differing effects.	Individual migration phenology, route and geographic range. Daily movements to understand energy budgets and home range sizes Interaction between movements and weather conditions, vegetation, and other environmental variables.	Migration routes of three juvenile Egyptian vultures (*Neophron percnopterus;* Meyburg *et al.*, 2004) Discovered breeding and non-breeding locations for 48 tagged Gyrfalcons (*Falco rusticolus;* Burnham and Newton, 2011)	(Webster *et al.*, 2002; Newton, 2008; Bodey *et al.*, 2017)
GPS tags	Same as Satellite tags. Underlying satellite technology is different (GPS calculates geographical position from the signal from multiple satellites)			If devices transmit data over a GSM network, Usefulness	Same as Satellite tags.	Breeding movements of 12 gulls (*Larsus fuscus*) with GPS devices, data	(Newton, 2008; Bouten

Techniques	Resolution of movements and locations	Number of individuals	Benefits	Limitations	Examples of study questions	Examples	References
	and GPS tags require a radio transmitter or use of Global System for Mobile Communications (GSM) networks for location data to be retrieved from tags remotely.			will be limited in areas with no or patchy GSM coverage.		retrieved with radio transmitters (Spelt *et al.*, 2019)	and Baaij, 2013)
						17 non-migratory white storks (*Ciconia ciconia*) tracked during non-breeding season with GPS devices using GSM technology (Gilbert *et al.*, 2016)	

1.3.2 Biologging – beyond just tracking

Researchers can use tracking devices to study more than just the locations of birds (Figure 2). Large tracking devices can carry sensors that measure many aspects of movement behaviour. Tracking devices can include an accelerometer to record the tri-axial position of the device (for example, Gilbert *et al.*, 2016; Flack *et al.*, 2018; Spelt *et al.*, 2019). This can provide information on the posture, flight type and behaviour of the bird which in turn allows the energy expenditure of the birds to be calculated (Shamoun-baranes *et al.*, 2012). Magnetometers in devices can reveal even more information about the movements of birds as they reveal directional change when altitude is constant (Williams *et al.*, 2017) allowing for more in depth study of flight behaviour (Williams *et al.*, 2015). In addition, including a barometer to measure air pressure and calculate altitude allows further study of flight behaviour and their risk of collisions with structures to be quantified, for example, wind turbines (Cleasby *et al.*, 2015).

There have been moves to record the internal activity of birds while tracking their movements (Yoda, 2019). To study how bar-headed geese undertake high altitude flights over the Himalayas, researchers use implanted loggers to measure abdominal temperature, abdominal pressure and electrocardiography (Bishop *et al.*, 2015).

Bird-borne video cameras can be can be used to understand the social interactions between individuals within and between species or populations (Yoda 2019) as well as providing detailed information about foraging techniques and learning between individuals (Troscianko, Rutz and Rutz, 2015). Information on sociality can also be recorded with proximity loggers, which record interactions between animals that carry the devices (Drewe *et al.*, 2012). Proximity loggers have the potential to be used for birds that are gregarious on migration, a limited number can carry tracking devices while others carry the smaller proximity loggers. If enough proximity loggers were deployed, it would reveal information about flocking behaviour and reduce costs for scientists wishing to track large numbers of birds.

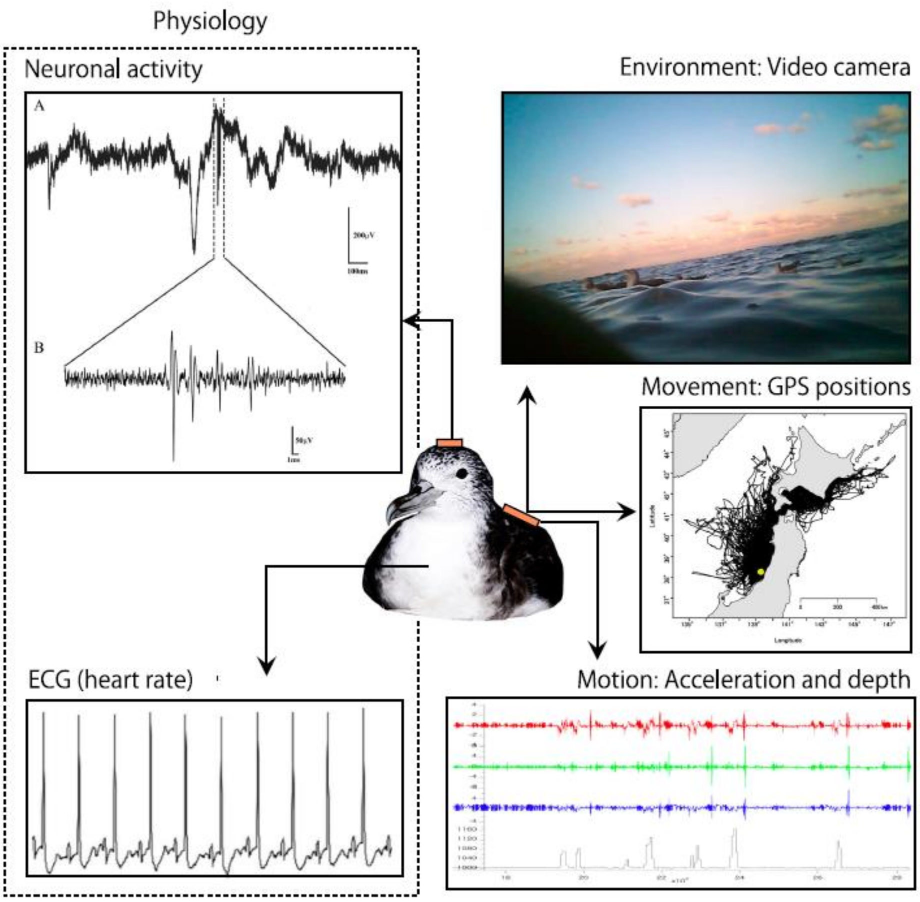

Figure 2. Bio-logging allows biologists to study behaviour, physiology and the environment of wild animals. This figure shows examples of bio-logging data obtained from streaked shearwaters and is taken from Figure 2 by Yoda (2019).

1.3.3 Future of tracking

The future of tracking is for smaller and better devices (Figure 3, Kays *et al.*, 2015). This, coupled with lower costs, will allow more bird species to be tracked, more individuals to be tracked and greater resolution of movement data. This will provide greater knowledge of movements, such as migratory routes, non-breeding period locations, and habitat preferences for birds that cannot currently be tracked with today's devices. The larger numbers of individuals that can be tracked will also result in greater understanding of individual variability and species/populations ability to adjust to our rapidly changing climate.

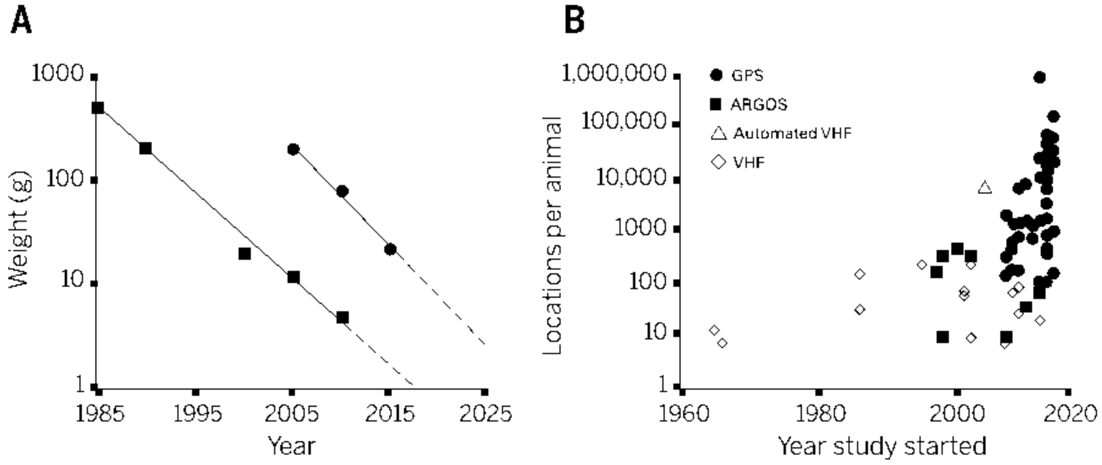

Figure 3. Rapid technological developments have led (A) to decreased size of transmitters over time and (B) an increase in the amount of data retrieved from each tracked animal (split by type of device). Adapted from Figure 3 by Kays *et al.* (2015).

The International Cooperation for Animal Research Using Space (ICARUS) Initiative, led by the Max Plank Society, has the aim of tracking small wild organisms from vertebrates to insects across the globe (Wikelski *et al.*, 2007). The Initiative uses transmitters that weigh only 5g and transmit to a satellite on the International Space Station (https://www.icarus.mpg.de/en). Instead of piggy-backing on technologies developed for other purposes (most tracking technologies were developed for defence agencies, although radar stations are now used to measure weather conditions) this technology is purpose built specifically for animal tracking.

Drone technology is advancing and regularly being used in a variety of areas of scientific research, from mapping to atmospheric studies (Marris, 2013) and it could be useful for improving the ability of track migratory birds. Unmanned aerial vehicles (UAVs) could be used in conjunction with low cost, light weight VHF transmitters to independently track radio tagged birds (Van Nguyen *et al.*, 2019). In addition, UAVs could help retrieve data from tracking devices at locations that are difficult for humans to access regularly, for example, seabird colonies (Rees *et al.*, 2018). The use of drones could help minimise disruption from humans, however the potential disturbance by drones to the study organism should be assessed (Vas *et al.*, 2015).

There is a plethora of techniques and technologies available to researchers tracking migratory birds, keen to understand their movement behaviour. However it is crucial that the techniques, devices and sensors used fit the biological questions being asked (Williams *et al.*, 2019). Their use has ethical implications as birds are affected during implementation of all techniques (except radar, Newton, 2008) deployed to study movement behaviour.

1.4 Research Objectives

Bird migration is an evolutionarily adapted behaviour (Winger et al., 2019) and as environmental conditions change migratory birds have to be able to adapt to new situations. Studying the causes and consequences of changes in migratory behaviour is important to fully understand the drivers of migration behaviour. I aim to understand how the use of an anthropogenic waste subsidy can influence the survival rates and behaviour of a migratory bird (Figure 4). It is of particular interest to understand how the use of anthropogenic food subsidies influences survival and behaviour in the face of changing regulations around waste management in the EU.

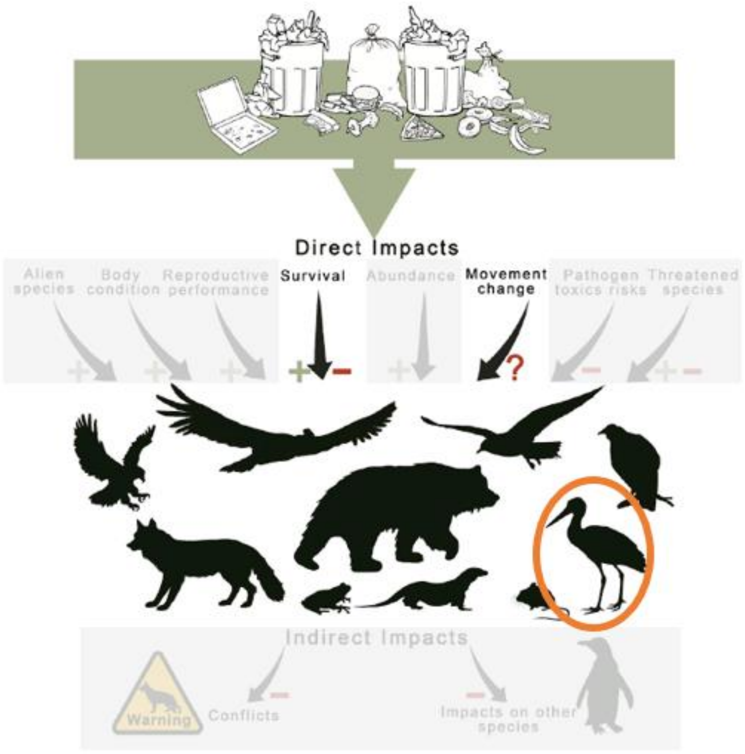

Figure 4. The direct and indirect impacts of anthropogenic waste on vertebrate species. E.g. landfill sites, rubbish dumps and litter, adapted from Plaza and Lambertucci (2017). I have highlighted the aspects of impacts of anthropogenic subsidies that will be addressed in subsequent chapters and the study species.

I aim to understand causes and consequences of changing environmental conditions on a migratory species (Figure 5). (a) I will explore how mortality varies with use of an anthropogenic food resource; (b) how the use of anthropogenic food resources influences parameters of migration and (c) if behaviour, migratory behaviour and use of novel foraging areas (for example, anthropogenic food resources), is transmitted between family members, and if social interactions with family members influences mortality.

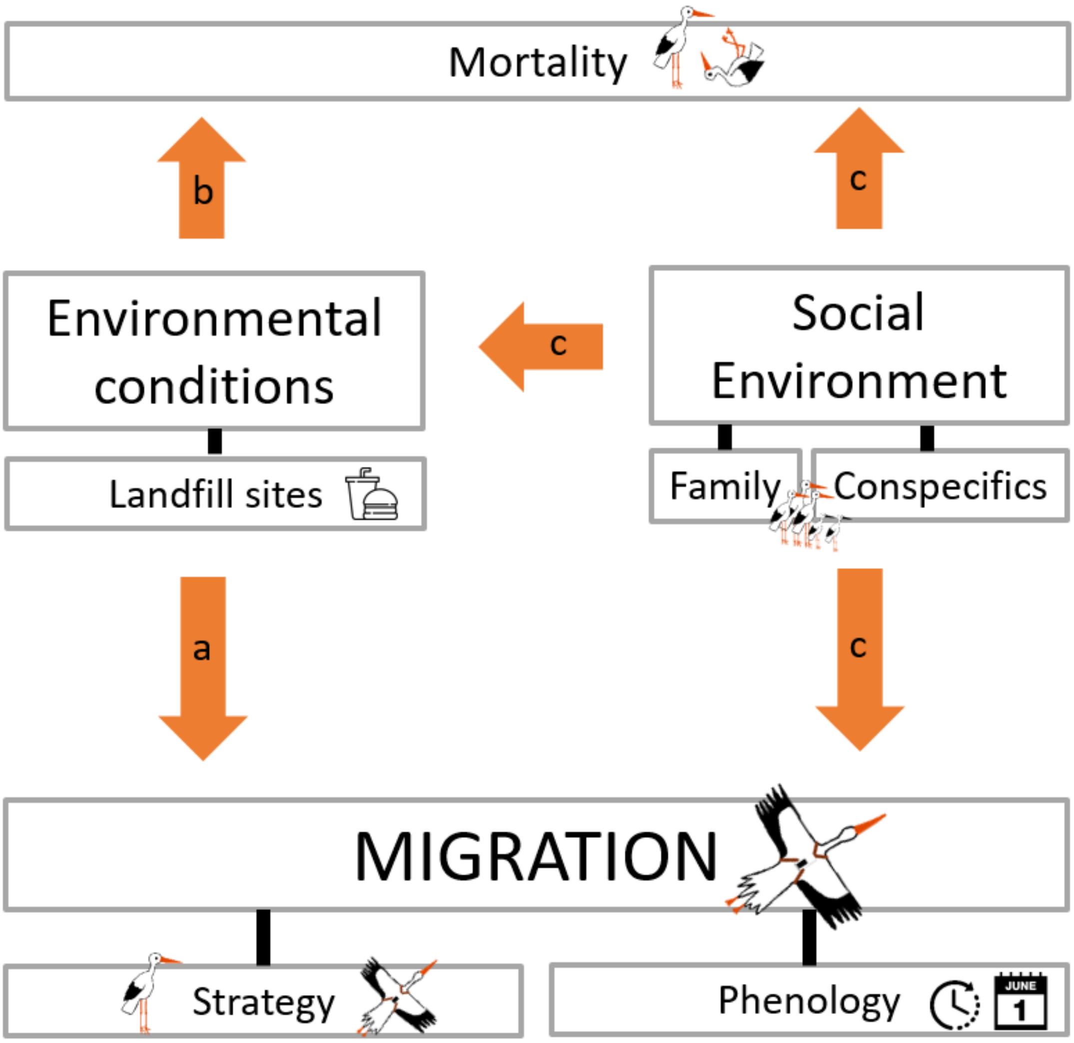

Figure 5. Conceptual diagram indicating objectives of my research. To understand how environmental conditions (anthropogenic waste food resources) influence (a) migratory behaviour (migratory strategy or phenology) and (b) mortality, as well as (c) understanding if social cues influences use of resources in the landscape, migration behaviour and mortality.

1.5 Study system and technology

1.5.1 Study species and population

The species that I studied to achieve my research objectives is the European white stork (*Ciconia ciconia*). White storks breed across Europe and are known for their annual long distance migration from Europe to sub-Saharan Africa (Figure 6, Birdlife International, 2019). They have two main migratory routes to Africa, the Western and Eastern Europe flyways, via Iberia and Turkey respectively (Figure 6). White storks were classified Vulnerable in the 1980s after a large decline in numbers across Europe (Tucker and Heath, 1994) and over the last three decades there has been increases in western Europe thanks to reintroduction programmes and improvements in natural foraging habitats. The species is now classified as Least Concern (Birdlife International, 2019). In addition, there have been changes in the numbers of individuals undertaking the long standing migration to sub-Saharan Africa with higher frequencies of individuals undertaking shorter migrations or no longer undertaking migration (Flack *et al.*, 2016).

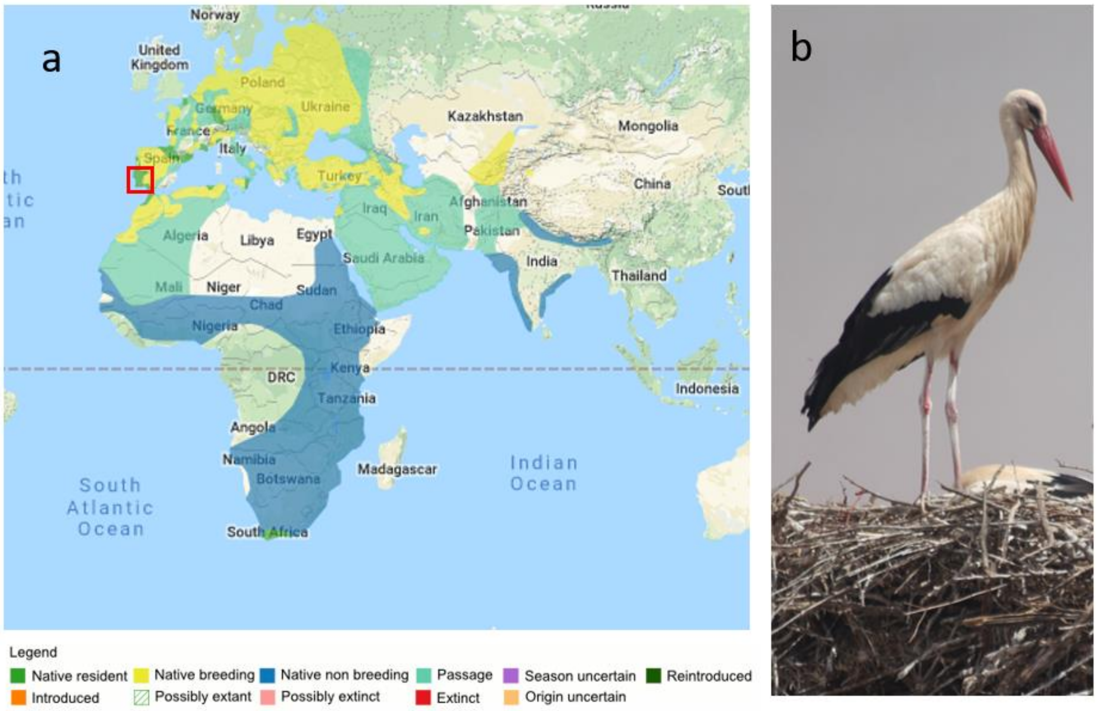

Figure 6. (a) European white stork geographical distribution showing breeding and non-breeding areas along with areas of passage for migratory birds and areas with resident individuals, red square indicates the partially migratory population in Portugal. Map adapted from Birdlife International (2019). (b) Adult white stork in nest in an urban area in Portugal (photo by K Rogerson).

White storks forage at landfill sites across their geographical range and on migration (Robert Kruszyk and Ciach, 2010; Gilbert, 2016; Arizaga *et al.*, 2017; Rotics *et al.*, 2017). For many populations across Europe the provision of organic waste at landfill sites has also been associated with increases in numbers (Schaub, Pradel and Lebreton, 2004; Saether *et al.*, 2006). In addition the use of landfill sites has been linked to changes in frequencies of migratory strategy (migrant or resident) seen across the European population (Tortosa, Caballero and Reyes-Lopez, 2002; Nevoux, Barbraud and Barbraud, 2008; Shephard *et al.*, 2015).

For my research I tracked Portuguese white storks. In line with the European white stork population, the Portuguese population has increased over the last three decades, simultaneously the number of individuals that remain in Iberia all year round has increased (Figure 7, Encarnação, 2015; Catry *et al.*, 2017). The population is now considered partially migratory, with over 60% of the breeding population (23,000 individuals in 2015, Encarnação, 2015) no longer undertaking the traditional annual migrations to sub-Saharan Africa (Figure 7, Catry *et al.*, 2017). The switch from migratory to partially migratory behaviour is thought to be facilitated by the use of anthropogenic food subsidies at landfill sites (Tortosa, Caballero and Reyes-Lopez, 2002; Catry *et al.*, 2017) as well as the abundance of invasive American crayfish (*Procambarus clarkii*) in waterways and rice fields (Tablado *et al.*, 2010; Sanz-Aguilar *et al.*, 2015; Gilbert, 2016) which provide a constant food resource throughout the year.

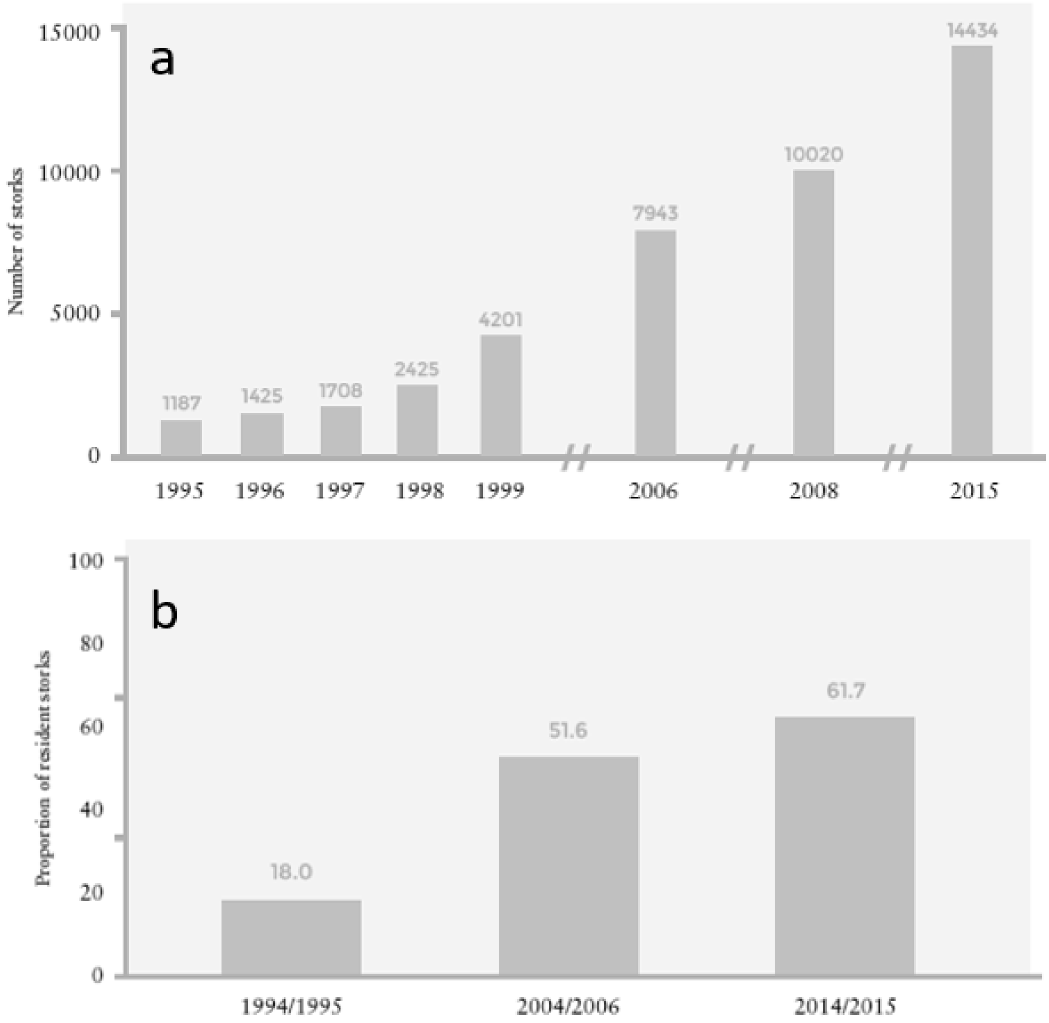

Figure 7. (a) Population trend of wintering white storks in Portugal between 1995 and 2015, (b) resident population in Portugal since 1995 as estimated proportion of wintering individuals of the breeding population. Adapted from figures 2 and 3 by Catry *et al*. (2017).

Individuals from this population, adults and juveniles, have been tracked as part of a wider study on the migratory strategy of white storks since 2012. A previous PhD student studied the behaviour of resident adult white storks (Gilbert, 2016). She studied the landfill site use of 17 resident adults in the breeding and non-breeding periods (Figure 8, Gilbert *et al.*, 2016).

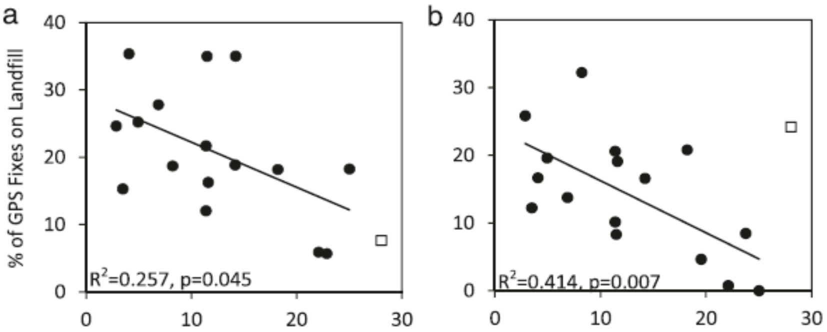

Figure 8. Landfill site use by 17 resident adult white storks from Portugal (Gilbert et al., 2016). Percentage of fixes on landfill sites in relation to distance from nest to the landfill site during (a) non-breeding and (b) breeding seasons. Adapted from Figure 4 by Gilbert *et al*. (2016).

1.5.2 Technology to answer my questions

My research greatly benefits from the use of advanced tracking technologies. I was able to use state-of-the-art GPS transmitters developed by © Movetech Telemetry (http://movetech-telemetry.com/) through a partnership between the University of East Anglia (UEA), British Trust for Ornithology (BTO), University of Lisbon and University of Porto. The technology helped me delve into juvenile white stork social interactions, migration behaviour and use of landfill sites.

- The GPS transmitters use GSM networks to transmit data to Movebank (an online repository for animal movement data, Wikelski and Kays, 2019). This is a cheaper way of retrieving data than using satellite transmitters. While using radio telemetry (Bouten and Baaij, 2013) would require the birds to return to a known location, which is unpredictable for juvenile white storks, and would not allow me to study mortality outside of the breeding areas.
- The transmitters can have additional sensors as white storks can carry an ~ 90g transmitter (< 3% of bird weight, Geen, Robinson and Baillie, 2019). Sensors in the devices I deployed on juveniles were tri-axial accelerometers and thermometers. Although I did not use these sensors for my research, they have subsequently enabled the data from the transmitters I deployed to be used for other projects, including

studying white stork movements around energy infrastructure and how weather conditions influence flight behaviour on migration.

- The transmitters have high spatial and temporal resolution for the location data (depending on fix schedule), allowing me to calculate a proxy for time at landfill sites and social associations between tracked birds. This level of detail would not have been possible with other approaches such as data from geolocators or stable isotopes.
- The use of solar-powered batteries meant the transmitters would last at least a year, allowing me to capture the first migration of juveniles in detail.
- The use of stable isotopes to understand migratory behaviour and locations for white storks is not feasible. This is because white storks do not moult feathers simultaneously or every year (Hall, Gwinner and Bloesch, 1987); knowing which feathers to analyse to understand location in the non-breeding period is impossible. In addition, their use of food from landfill sites means the isotope analysis would not show the isotopic structure of the local diet or hydrology (Gilbert, 2016)
- Due to my connection with © Movetech Telemetry through my supervisors, I was able to use loggers that were in development, resulting in lower costs per device and then greater sample sizes for my studies. Large studies are crucial to understand variation in movements and foraging behaviour that cannot be resolved by tagging a few individuals.
- Geolocators or non-GSM GPS devices would not have been suitable for this study. Re-capturing white storks is extremely difficult as they are intelligent birds; capturing adults at the nest and landfill sites requires lots of time and labour. The use of bird-borne cameras might have benefitted my understanding of social interactions and foraging at landfill sites, however the cost and difficulty of recapture meant that it was not suitable for this study species.

1.5.3 Monitoring white storks

I undertook two field seasons during the white stork breeding season in Portugal (2016 and 2017). I concentrated on recording laying dates, numbers of eggs, chicks and fledglings of nests across colonies in southern Portugal (Figure 9, Figure 10) as well as deploying GPS transmitters on juveniles, approximately a week before they fledged, and breeding adults.

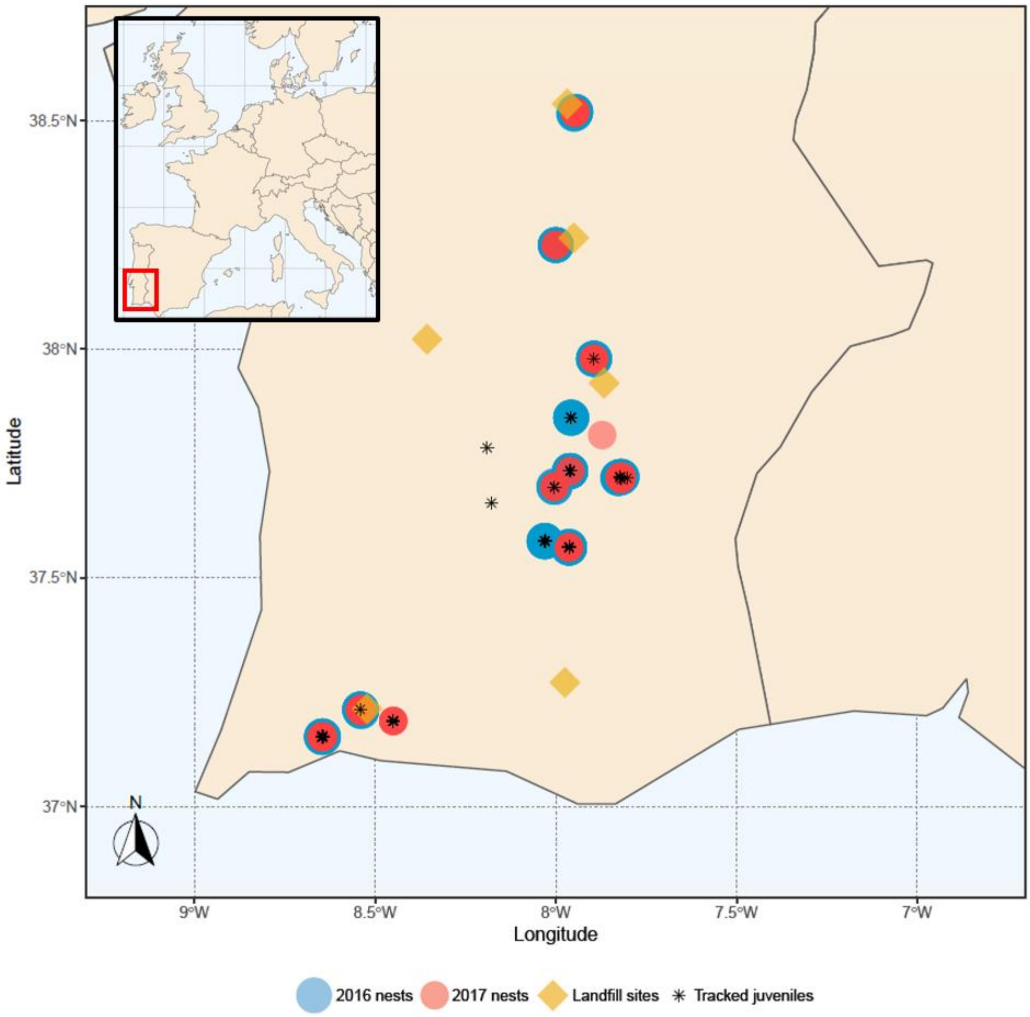

Figure 9. Locations of colonies where nests were monitored during the breeding seasons of 2016 (135 nests across 11 colonies) and 2017 (84 nests across 10 colonies) across southern Portugal, locations of natal nests of juveniles deployed with GPS transmitters (n = 73) and locations of all landfill sites in Portugal.

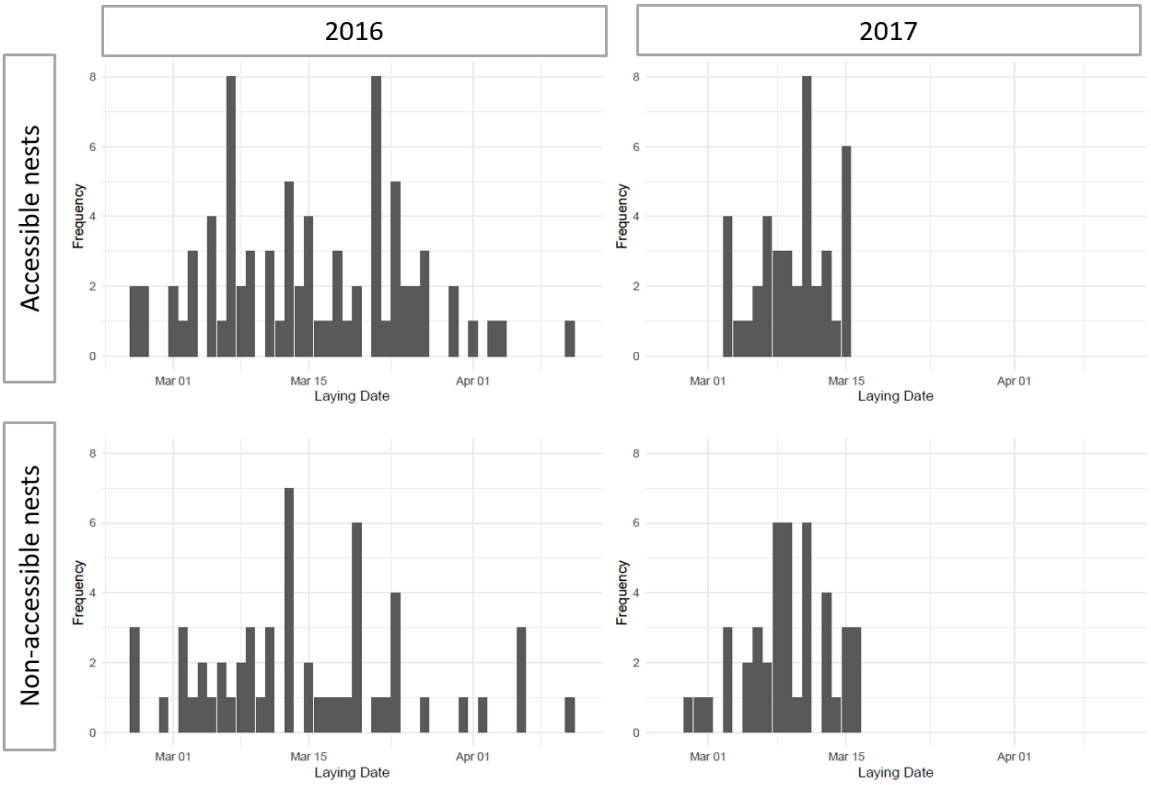

Figure 10. Laying dates in nests from across southern Portugal in 2016 (n = 135) and 2017 (n = 84) split across ladder accessible and non-accessible nests.

I focused on colonies that were a range of distances from landfill sites (Figure 9). In 2016, detailed information was recorded for each observed nest from March to July. In 2017, I observed the beginning of the breeding season (1 – 22 March) and the end of the breeding season (25 May – 15 July, defined by first predicted fledging dates from first laid nests, and last fledged individuals). Exact laying dates are known for the earliest nests and fledging numbers were known for all nests. If chicks were present later in nests empty in March, the eggs were laid in the second half of the laying season (Figure 10).

I was able to observe nests up to 10m from the ground in a range of structures, for example, trees, buildings, ruined buildings, telegraph poles and the bottom of electricity pylons. I used a self-created camera pole with a small sports camera, with WiFi connectivity, on top of a 10m flag pole; I observed nests via a WiFi link to my smart phone (Figure 11). In addition, I had the use of a drone (dependent on weather and surrounding environment) to observe nests over 10m high, although for colonies in trees not all nests could be seen with the drone.

Figure 11. Photos of nests taken with camera pole (a - d) with eggs and chicks of varying ages. (e) A ladder accessible nest and (f) deploying a logger on an adult white stork.

Permits to capture and deploy GPS transmitters on juvenile and adult white storks were granted by the Instituto da Conservação da Natureza e das Florestas (ICNF) in Portugal. In addition, the University of East Anglia Ethical Committee approved the research activities. Adult white storks were captured at the nest with a remote-controlled clap trap and at landfill sites using leg lassoes (Gilbert *et al.*, 2016). Juveniles that were tracked with GPS transmitters were from nests accessible with a 6m ladder. Nests were on a range of natural and artificial structures (Figure 11). In 2016, chicks in ladder accessible nests were monitored every week and wing, weight, bill and tarsus measurements were taken (Figure 12). Fledging dates were approximately 55-60 days after hatching (33 days after laying) and this was known for all observed nests in 2016. If laying date was not known, age was approximated from observations with the camera pole as well as targeted weighing sessions to ensure the birds were large enough in mass and wing length to have a transmitter deployed on them.

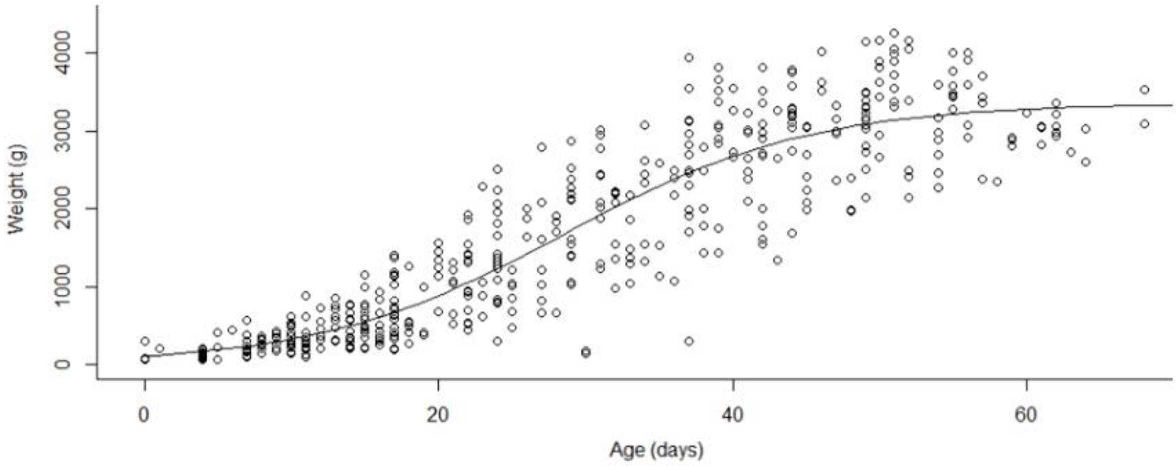

Figure 12. Weight and age (days since hatching date) of chicks monitored weekly during the nest growing season of 2016.

The morphometric measurements of each bird were used to calculate an index of body size. The index takes into account the skeletal size and mass of each bird and is the standardised residuals from the linear relationship between mass (g) and tarsus length (mm). The index indicates whether each individual is larger or smaller than the size that would be predicted by the linear relationship, for example individuals with positive body size index are larger than the linear model predicts. Throughout my research I have used the body size indices of individual birds in order to include a proxy for body size and body condition in my statistical analysis.

I wanted to track birds from nests at a range of distances from landfill sites, and with laying dates across the range seen in the breeding population (Figure 13, Figure 10). This study set up allowed me to understand the influence of landfill site proximity on juveniles' behaviour as well as being able to control for birds that fledged early and late in the breeding season.

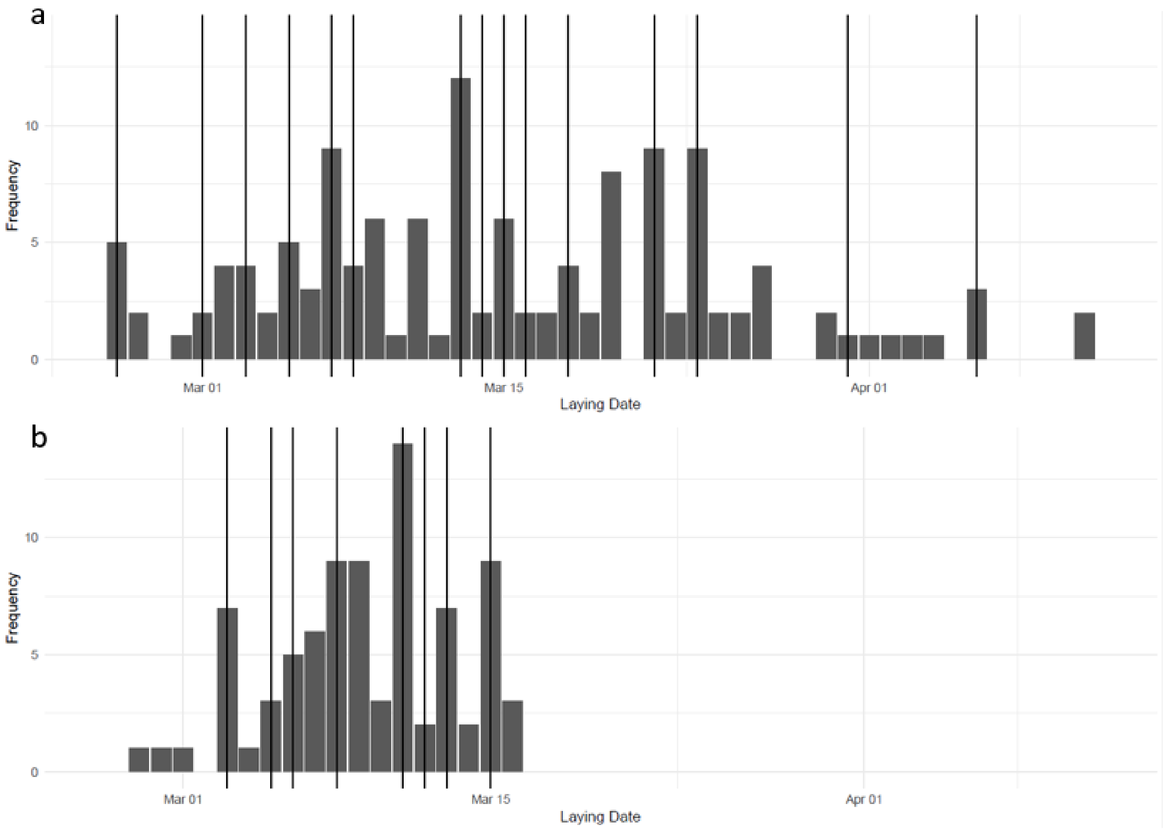

Figure 13. Variation of laying dates for nests across the study area in (a) 2016 and (b) 2017. Vertical lines indicate known laying dates for birds deployed with transmitters in 2016 and 2017.

In 2016, an extremely wet spring resulted in high chick death across the nests that I was studying (n = 135). Therefore I tagged birds of the right size in accessible nests for which I had not observed laying or hatching dates (Figure 9). Significantly more chicks reached fledging age in 2017 then 2016 (W = 2750.5, p < 0.0001, Figure 14).

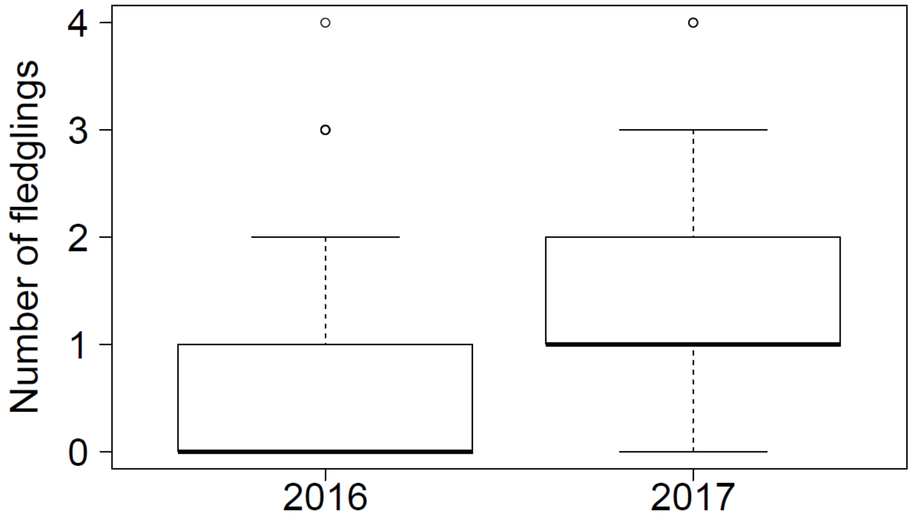

Figure 14. Number of chicks to reach fledging age in nests observed across the study area in 2016 and 2017.

A considerable amount of data was collected by the devices that were deployed on juvenile white storks in 2016, 2017 and 2018 (Figure 15). In 2016 and 2017 devices recorded locations every 20 minutes during the day, with one night location, and in 2018 the devices recorded locations every 10 minute during the day with a night fix. This high resolution data enabled me to explore the local daily movements of the storks, such as associations between individuals during the day and use of landfill sites, as well as large scale movements such as their first-year migrations (Figure 15).

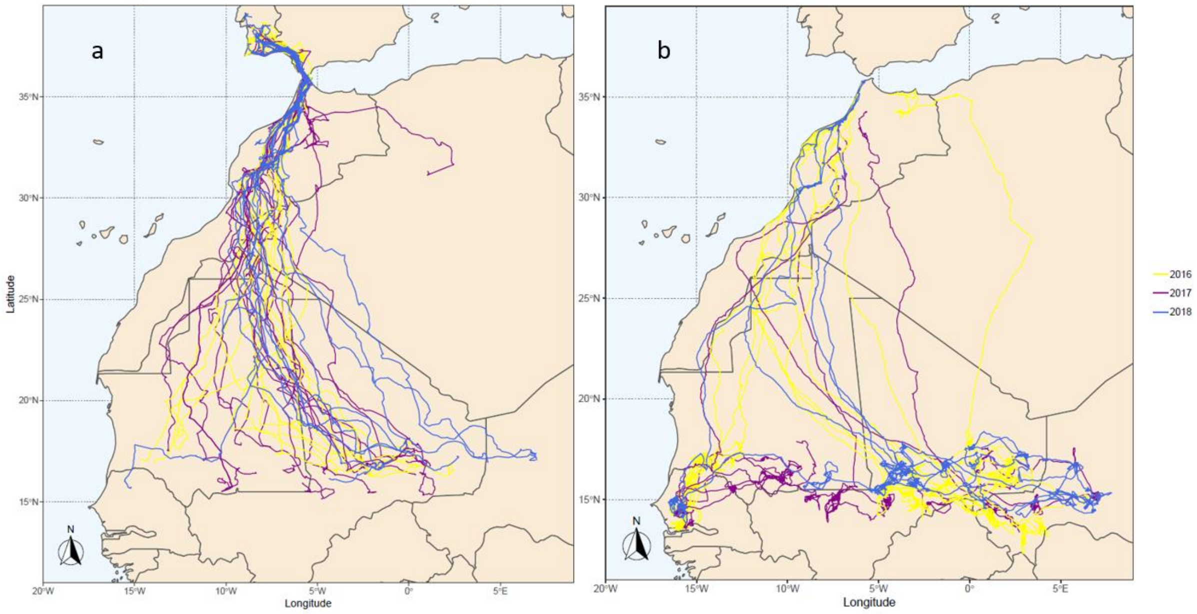

Figure 15. Maps showing tracks from tracking devices deployed on juveniles (2016-2018): (a) tracks for their first southward migration (from fledging to arriving in the Sahel region) and (b) tracks from their first northward migration (from arriving in the Sahel to returning to North Africa).

1.6 Chapter descriptions

I will present my research in this thesis for each of my objectives (Figure 5) over the next three chapters. The chapters have been written as papers and will be submitted for publication in peer-reviewed journals in the near future.

Chapter 2 aims to understand how mortality rates of adult and juvenile white storks vary with use of anthropogenic waste subsidies. This provides further understanding of the impacts of anthropogenic food resources on the demography of the species that use it (Figure 4, Plaza and Lambertucci, 2017). The analysis benefits from previous tracking of the Portuguese white stork population from 2012 to 2015, plus the devices deployed on adults and juveniles in 2016 and 2017. This chapter will be submitted as a research article to the Journal of Applied Ecology in the very near future.

Chapter 3 assesses the influence of use of anthropogenic food subsidies on the migration parameters of first-year juvenile white storks. This research highlights the first-year migration of European white storks and is the first study to quantify the use of landfill sites in North Africa. Tracking data from juveniles in 2016, 2017 and 2018 was used for this analysis. The first half of this chapter concentrates on the first southward migration of the juveniles from Portugal to sub-Saharan Africa and will be submitted to Movement Ecology. The second half of the chapter examines the parameters of migration of the return/northward migration of first year juveniles, and how they are influenced by timing and use of landfill sites.

Chapter 4 investigates the family associations of white storks, and whether these influence juvenile migratory behaviour, use of novel foraging sites (anthropogenic waste subsidies) or post-fledging mortality. This work indicates whether changes in migratory behaviour are transmitted by family members and this is important for the Portuguese population of white storks which has seen a dramatic increase in the frequency of resident individuals over the last decades. The high resolution tracking data from parents, offspring and siblings in 2016, 2017 and 2018 were used for this analysis. This chapter will be submitted to Animal Behaviour as a research paper.

The general conclusions, Chapter 5, will tie together the results of Chapters 2 - 4 and highlight how this research has contributed to understanding mechanisms underlying migratory behaviour and the influence of anthropogenic waste resources on migratory behaviour and mortality. I will also examine issues that came up during the research as well as future research questions that have emerged from this body of work.

Chapter 2

Effect of anthropogenic food sources on year-round mortality rates of white storks

Photo of white storks at a landfill sites in Beja, Portugal, photo taken by K Rogerson

2.1 Abstract

Human activities can generate foraging opportunities for wildlife by providing predictable anthropogenic food subsidies (PAFS) and changes in these activities can rapidly alter availability of key resources. The impact of such changes depends on their contribution to fitness of the individuals exploiting the resources. Recent EU directives require the reduction of organic waste at landfill sites leading to dramatic decreases in resource availability for species using landfills for food, but the consequent fitness impacts are not yet known. White storks (*Ciconia ciconia*) use landfill sites across Europe and this, previously wholly migratory, population now has large numbers of storks remaining in Europe and using landfill resources year-round. Drastic reductions in food availability at landfill sites could have potentially severe impacts on this population. Using GPS-tracks of 43 adults and 75 juvenile storks that vary in use of landfill sites and use nests between 1.7 and 75.7 km from landfill sites, I quantified timing of mortality in relation to landfill use. Mortality rates were very low for adults nesting within 30 km of landfill but increased for individuals nesting further away. In the post-fledging period, juveniles that used landfill more had the lowest mortality rates, mortality decreased by 9% with increased use of landfill sites from 5% to 40%. These findings suggest that the removal of organic waste through landfill closure could potentially lead to increased mortality rates among white storks that breed in Iberia. Higher mortality among individuals that make little use of landfill suggests that current alternative resources may not be sufficient to offset the loss of these organic waste resources. A range of other bird species also use resources at landfill sites and will also be influenced by future reductions.

2.2 Introduction

Human activities can alter the seasonal and spatial distribution of key resources for wildlife (Oro *et al.,* 2013), in particular through provision of predictable anthropogenic food subsidies (PAFS), which can dominate many species' diets. The provision of these PAFS include resources from intentional activities such as supplementary food provided in gardens (Plummer *et al.,* 2015) or release of large numbers of gamebirds into the environment (Pringle *et al.,* 2019) as well as from waste, such as discards from fisheries (Granadeiro, Brickle and Catry, 2014) and organic waste at landfill sites (Weiser and Powell, 2010).

The use of PAFS can influence population demography, through positive and negative contributions to individual fitness (Weiser and Powell, 2010; Oro *et al.,* 2013). PAFS can be of low nutritional value, which can lead to reduced breeding success (Pierotti and Annett, 2001), and can increase toxin exposure (Tongue *et al.,* 2019), pathogen infection risk (Murray *et al.,* 2016) and attract predators, leading to reduced survival (Otali and Gilchrist, 2005; Hanmer, Thomas and Fellowes, 2017). However, in a recent review Plaza and Lambertucci (2017) found positive impacts of PAFS at landfill sites and rubbish dumps on vertebrates in 73% of studies reviewed, and several studies have shown that abundant and easy to access PAFS resources can be associated with enhanced breeding success or survival (for examaple Bino *et al*., 2010; Steigerwald *et al*., 2015).

Organic waste deposited at rubbish dumps and landfill sites is a major source of PAFS widely used by predator and scavenger bird species, for example gulls (*Larus* spp.) and kites (*Milvus* spp.). Understanding the influence of such resources on species' demography is especially important when there are changes to policies controlling the anthropogenic activities which provide the food (Margalida, Colomer and Oro, 2014; Gordon *et al*., 2016). Regulations are requiring dramatic reductions in food waste in open-air landfill sites across Europe (EU Directive 2018/85, 2018). Understanding the implications of the loss of the organic landfill waste for the species that use these resources is therefore of great urgency.

Landfills are used extensively by white storks (*Ciconia ciconia*) across Europe (Massemin-Challet *et al*., 2006; R Kruszyk and Ciach, 2010; Arizaga *et al*., 2017; Catry *et al*., 2017), and this has been linked to recent increases in the breeding population (Tortosa, Caballero and Reyes-Lopez, 2002; Encarnação, 2015) and in the number of individuals that no longer migrate to Africa for the non-breeding period (Shephard *et al*., 2015; Catry *et al*., 2017; Rotics *et al*., 2017; Cheng *et al*., 2019). White storks breeding close to landfill sites have been shown to have larger clutches (Tortosa, Perez and Hillstrom, 2003), with larger eggs (Djerdali *et al*., 2016) and higher breeding success (Tortosa, Caballero and Reyes-Lopez, 2002; Massemin-Challet *et al*., 2006; Gilbert, 2016). However, storks using landfill sites have also been recorded ingesting plastic (Henry, Wey and Balanca, 2011) and high concentrations of toxic metals have been found in blood samples of chicks close to landfill sites (de la Casa-Resino *et al*., 2014). Use of landfill resources could therefore potentially enhance or reduce survival rates of storks, depending on the benefits and costs of the resources that are foraged.

GPS-tracking technology enabled me to accurately quantify use of landfill sites and mortality, across different periods of white stork life cycles. In this study, adult and first-year juvenile storks were tracked to estimate variation in mortality rates in relation to (1) extent of use of landfill sites during the breeding period (for adults) and post-fledging period (for juveniles), (2) the distance between nest sites and the nearest landfill site (a proxy for adult use of landfill sites during chick rearing), and (3) an index of body size (to control for body condition). As mortality risk can vary throughout the annual cycle, and use of landfill might enhance or reduce these seasonal patterns, total survival rates were quantified for stationary and migratory periods (breeding/post-fledging, southward/northward migrations and non-breeding) for adults and juveniles to explore the influence of landfill use on the timing of mortality across the annual cycle.

2.3 Methods

2.3.1 Data collection

One hundred and eighteen individual white storks were tracked from colonies in Portugal that varied in distance from landfill sites (1.7 – 75.7 km; appendix 2.1). GPS/GSM transmitters (Flyway 50, © Movetech Telemetry, British Trust for Ornithology, Norwich, UK), weighing less than 3% of each birds mass, were deployed on 43 adults and 75 juveniles between 2013 and 2017 (Table 3). Adults (age unknown) were captured at landfill sites with leg lassoes, or at the nest with a remotely activated clap trap (Gilbert *et al*., 2016). Transmitters were deployed on juveniles one week before fledging (~55-60 days old), using backpacks with a Teflon harness sewn together with cotton thread as a weak link, following Gilbert *et al*. (2016). At deployment, morphometric (weight, wing and tarsus) measurements were taken for each individual. Body size indices for each tagged individual were calculated as the standardised residual from linear models of the relationships between mass (g) and tarsus length (mm) for adults and juveniles separately (appendix 2.2 and 2.3). From 2013 to 2015 the transmitters recorded locations every three hours between 5 am and 5 pm GMT (Gilbert *et al*., 2016) and, in 2016 and 2017, locations were recorded every 20 minutes from 5 am to 9 pm GMT, with an additional fix at 1 am GMT.

Table 3. Numbers and periods of tracking of GPS-tagged adult and juvenile white storks. *One adult previously caught in 2013 had a new transmitter deployed in 2017.

	Adults (n = 43)		Juveniles (n = 75)	
		Mean months tracked (range)		Mean months tracked (range)
2013	24	6.9 (2 – 17.8)	6	2.6 (1.9 – 3.2)
2014	0		6	3.1 (0.5 – 11.2)
2016	4	22.5 (21.9 – 23.6)	37	7.2 (0.7 – 22.5)
2017	16*	10.3 (1.4 – 15.1)	26	5.4 (0.6 – 10.2)

2.3.2 Time periods for survival estimates

I examined total survival rates in different periods of the white stork annual cycle, across four time periods: breeding/post-fledging period, southward migration, northward migration and non-breeding period (Figure 16). The periods are defined by the start and end date of the two migration periods. Five of the 43 adults (all tagged in 2017) migrated to Africa for the non-breeding season and all juveniles migrated in their first year. For migrants, each period was defined from the dates on which northward and southward migration began and ended for each individual, using the net square displacement (NSD) method (R package migrateR; Spitz, Hebblewhite and Stephenson, 2017; Figure 16) to calculate start and end dates of migration (Bunnefeld *et al*., 2011). The resulting dates were then visually inspected on graphs of displacement from deployment location to ensure they matched the beginning and ending of periods of large (> 100 km/day) displacements during migration, as storks can also undertake large movements within Africa during the non-breeding season. In 34% (20/64) cases the NSD method failed to correctly identify dates of migration and included movements in the non-breeding area as being part of migration. I reclassified these dates using geographical cut-offs (crossing Sahara at latitude 20° N), daily displacements (> or < 70 km), and allowed stopovers of less than 13 days (mean number of days with displacement < 70 km), in order to calculate start and end dates of migration. For resident adults, the four time periods were defined by the mean dates of northward (4 – 8 Jan) and southward migrations (13 Aug – 4 Sept) by migrants.

Northward migration start dates were highly variable (range = 28 Sept – 2 Apr) and birds with unknown status in the non-breeding period in the Sahel did not have a northward migration start date calculated for them. This could have resulted from the fact that there were only two daily transmissions of data from loggers; individuals could have started their return, northward, migration before dying or transmitter failing, while others could have entered an area with no GSM coverage in the Sahel before dying or transmitter failing. Therefore, for birds that had an unknown status in the non-breeding period located in the Sahel, I assumed they had started their return migration to Europe if they were in the Sahel after the mean northward migration start date. These individuals (n = 2) then had alive status for the non-breeding period and unknown status for their return migration. I wanted to accurately estimate mortality on northward migration while not underestimating mortality in the non-breeding period, from hunting, disease or predation (Leyrer, Lok and Brugge, 2013).

The survival analysis was re-run for adults to understand if there was any difference in survival rates within the breeding period, while offspring were on the nests and after offspring had fledged. The mean fledging date, 30th June, was taken as the changing point between nest period and post-breeding period.

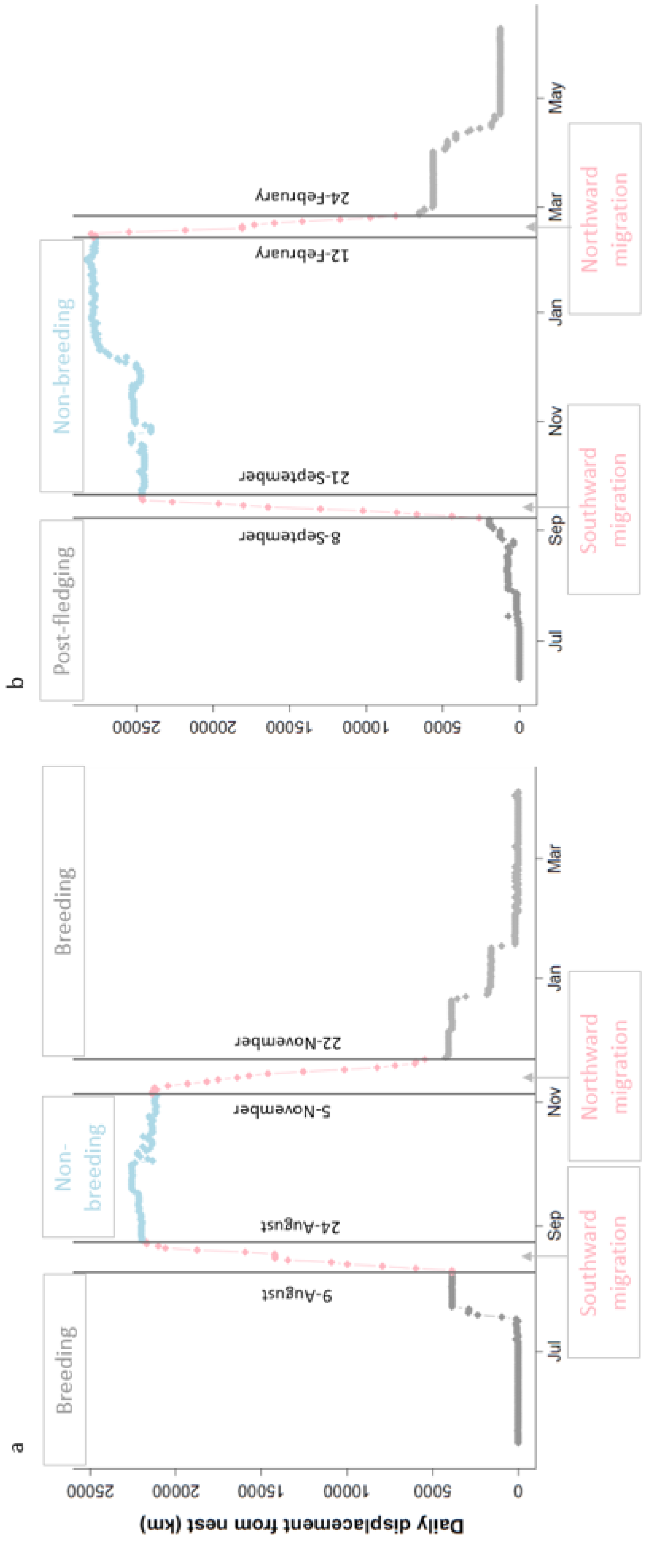

Figure 16. Daily displacement from nest (km) for one annual cycle for (a) an adult (2017-18) and (b) a juvenile (2016-17) split into different time periods by vertical lines indicating start and end date of southward (mean for all birds = 13-Aug and 4-Sept) and northward migrations (mean for all birds = 4-Jan and 8-Jan).

2.3.3 Influence of landfill use on survival rates

I used two metrics of variation in landfill site use in Iberia by tagged storks: (1) the distance between the nest of each tagged individual (identified from field observations or clusters of night GPS fixes during the breeding period) and the centre of the nearest landfill site (km), and (2) the proportion of fixes on landfill sites, calculated for each individual as the number of ground fixes (excluding fixes with speeds > 5 km/hr indicating birds in flight) during the day (05:00 – 19:00) on landfill sites (within a 1000 m radius of the centre coordinates), during the breeding (for adults) or post-fledging (for juvenile) period, divided by the total number of ground day fixes. Only fixes during the breeding/post-fledging were used because not all landfill sites outside Iberia were known. For 19 adults tracked for more than one breeding season the mean proportion of fixes on landfill sites during the breeding period was used (appendix 2.4).

2.3.4 Estimating survival probabilities with seasonal and spatial variation

I used known-fate analysis (Program MARK; Cooch and White, 2018) to determine total survival probabilities in each period (breeding/post-fledging, southward migration, non-breeding and northward migration) and quantified the contribution of landfill site use and body size indices on these probabilities. Known-fate analysis incorporates staggered deployments and uncertainties of transmitter failure and bird death (Cooch and White, 2018). Twenty-three periods were used in this analysis, one for each period between December 2012 and April 2018 and the status of each individual for period was defined as alive (10), dead (11) or unknown (00; appendix 2.5). Unknown outcomes occurred when birds headed into an area of no GSM coverage in the Sahara (Rotics *et al*., 2017), death could not be confirmed or a logger failed (appendix 2.5). Time periods in which the status was defined as unknown are excluded in known fate analysis, providing a minimum estimate of survival rates. To explore the influence of defining status as unknown in this area on the survival estimates, I re-categorised unknown periods which occurred in Africa up to a year after deployment as deaths (n = 34). My justification is that the number of loggers that stopped in the Sahel was far greater than would be expected from logger failure rates (appendix 2.6) and these re-categorised unknowns were likely to be true deaths. In addition, there is high site fidelity in this species (Vergara *et al*., 2006, Itonaga *et* *al*.,2011); two migrant adults that stopped transmitting in Africa were not subsequently observed at their nests or colony the following breeding season, while three that continued to transmit were all observed. Univariate statistics were undertaken to see if birds which were re-categorised from unknown to dead status were significantly different from the other individuals across three variables: landfill site use, distance between nest and closest landfill sites and body size indices.

To determine variation in total survival rates between time periods, four models with different temporal structures were created, from simple to complex: (1) constant survival across all periods (Φc), (2) survival varying between stationary (breeding/post-fledging and non-breeding) periods and migration (southward and northward) periods (Φstationary + Φmigration), (3) survival varying among breeding/post-fledging, non-breeding and migration (southward and northward) periods (Φbreeding + Φmigration + Φnon-breeding) and (4) survival varying among the four periods separately (Φpostfledging + ΦSmigration + Φnon-breeding + ΦNmigration). The most parsimonious model was selected using AIC adjusted for small sample sizes (AICc; Burnham and Anderson, 2002; Inselman *et al*., 2016). If models were within Δ2 AICc the models were averaged. Separate survival analyses were conducted for adults and juveniles. Due to uncertainties in determining the cause of mortality outside Europe the survival analysis was repeated re-categorising unknown outcomes in Africa up to a year after deployment as deaths. A high proportion of adults were resident in Portugal (88% of 43, in this study), and a separate analysis of survival rates of only resident storks was conducted to understand if the inclusion of migrant individuals influenced the survival estimates. In addition, when a post-breeding period was included for adult survival rates in 28 encounter histories and a fifth temporal structure was investigated Φbreeding + Φpost-breeding + ΦSmigration + Φnon-breeding + ΦNmigration.

The model that best explained the temporal structure of survival (i.e. most parsimonious) was next used to explore the contribution of landfill site and body size indices on survival rates. Three covariates were tested in three separate models: distance from nest to landfill sites, frequency of use of landfill site during the breeding period and body size. Models with single covariates (i.e. a simple additive effect across all time periods) and covariate-period interactions (i.e. separate additive effects for each of the four types of time period) were created. Models were removed from consideration if the upper 95% confidence interval of the survival estimate exceeded 1 or if a covariate in the model had 95% confidence intervals that contained zero (Barber-Meyer, Mech and White, 2008; Smith *et al.*, 2015). The most parsimonious model had the lowest AICc. If models were within 2 ΔAICc the models were averaged.

2.4 Results

2.4.1 Influence of land fill use and seasonal variation on adult survival

There was no seasonal variation in adult white stork survival rates, the four periods had similar survival probability for each of the three analyses undertaken (Table 1, (a) adult survival rates = 0.99 (SE = 0.003), (b) adult survival rates with unknowns re-categorised as deaths = 0.97 (SE = 0.01), (c) adult survival rates with only resident birds = 0.98 (SE = 0.01) and (d) adult survival rates including a separate post-breeding period = 0.99 (SE = 0.003). Tagged storks varied in their distance between nests and landfill sites (mean 19.4 km, range: 3.87 – 48.2 km, SE: 1.79, n: 43), and those breeding close to landfill sites had higher survival probability than those further away, with survival declining from 0.99 (95% CI = 0.95 - 1) for birds nesting within 5 km of landfill sites to 0.82 (95% CI = 0.45 - 0.96) for birds nesting 45 km away (Figure 17, Table 4a - d). I could find no effect of the body size indices and use of landfill sites on adult survival.

Table 4. Top models of white stork survival across four seasonal time periods and in relation to distances between nests and landfill sites, proportion of time spent on landfill sites during the breeding period and body size. Models are ranked according to Akaike Information Criterion, corrected for small sample sizes (AICc). K is the number of parameters in each model, the ΔAIC indicates the differences in AICc between each model and the best fitting model and Deviance is the total amount of deviance explained by each model. * indicates that models were averaged for the period survival.

	Model	AICc	ΔAIC	K	Deviance
(a)	Adult survival rates				
1	Φc + landfilldistance	17.21	0	2	13.13
2	Φc	23.24	6.03	1	21.22
(b)	Adult survival rates with unknowns re-categorised as deaths				
1	Φc + landfilldistance	34.98	0	2	30.90
2	Φc	38.97	3.99	1	36.94
(c)	Adult survival rates with only resident birds				
1	Φc + landfilldistance	17.04	0	2	12.95
2	Φc	22.70	5.66	1	20.67
(d)	Adult survival rates including post-breeding period				
1	Φc + landfilldistance	17.37	0	2	13.30
2	Φc	23.89	6.52	1	21.86
(e)	Juvenile survival rates				
1	Φpostfledging + Φmigration + Φnon-breeding + landfilluse	108.80	0	4	100.54
2	Φpostfledging + Φmigration + Φnon-breeding	116.98	8.18	3	110.83
3	Φstationary + Φmigration	121.69	12.89	2	117.62
4	Φc	130.15	21.35	1	128.13
(f)	Juvenile survival rates with unknowns re-categorised as deaths				
1	Φc *	274.00	0	1	271.99
2	Φstationary + Φmigration *	275.02	1.02	2	270.98
3	Φpostfledging + Φmigration + Φnon-breeding	276.06	2.06	4	267.91

4	Φpostfledging + ΦSmigration + Φnon-breeding + ΦNmigration	276.49	2.49	3	270.40

Model notation: Φ = survival (across each life history period), Φc = survival constant across life history periods, Φstationary + Φmigration = temporal variation in survival between stationary (breeding/post-fledging and non-breeding) and migration periods (southward and northward migrations), Φbreeding + Φmigration + Φnon-breeding = temporal variation in survival across three periods: breeding/post-fledging, migration and non-breeding, Φpostfledging + ΦSmigration + Φnon-breeding + ΦNmigration = temporal variation in survival across four periods: post-fledging, southward migration, non-breeding and northward migration. Covariates: landfilldistance = distance between nest and landfill site (km), landfilluse = proportion of fixes at landfill sites during breeding/post-fledging periods.

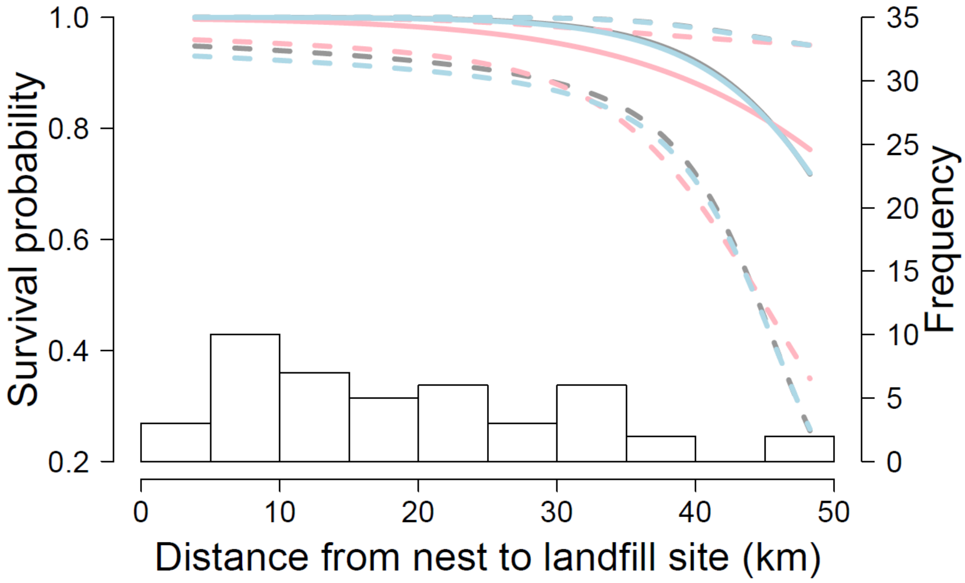

Figure 17. Variation in survival rates of adult white storks across the range of distances between nests and closest landfill sites for all top models: grey = survival, pink = survival with unknowns re-categorised as deaths and blue = survival with only resident individuals (Table 4). Dashed lines show 95% confidence intervals of predictions. Bars show numbers of tagged individuals breeding at different distances from landfill sites.

2.4.2 Influence of landfill use and seasonal variation on juvenile survival

First year juvenile survival rates varied between the post-fledging, migration (southward and northward combined) and non-breeding periods (Table 4e). Survival rates were low in the post-fledging period, with migration and non-breeding periods having similar high survival probabilities, 0.97 and 0.96 respectively. However, when juveniles with unknowns in Africa were re-categorised as deaths, the most parsimonious model showed survival rates only varied between stationary and migratory periods. Averaged parameters for the two top models (Table 4f) showed survival rates of stationary periods to be 0.79 (SE = 0.03) and migratory periods were 0.81 (SE = 0.03).

Use of landfill sites was associated with increased juvenile survival in each period (3.86, 95% CI = 0.19 - 7.52; Figure 18). Survival rates during the post-fledging period increased from 0.72 (95% CI = 0.54 - 0.85) for birds with 5% of fixes on landfill sites to 0.80 (95% CI = 0.60 and 0.92) for birds with 40% of fixes on landfill sites (Figure 18). Models including the body size indices and distance between nests and landfill sites were not included in the final models. When unknown outcomes on migration in Africa were re-categorised as deaths none of the covariates tested influenced survival (Table 4f). The individuals that were re-categorised from unknown to dead status were not significantly different from the birds with known deaths across the three variables studied ($p > 0.05$).

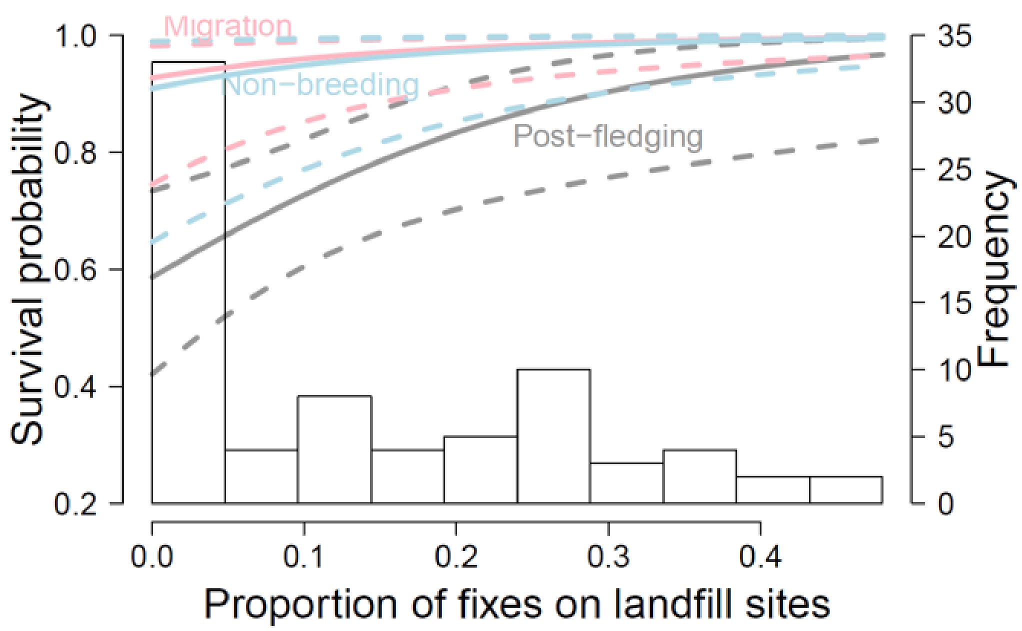

Figure 18. Survival probabilities (± 95% CIs) of juvenile white storks in relation to landfill site use across three time periods. Predictions from top model estimating survival rates (Table 2d); solid lines denote survival predictions for each period, post-fledging (grey), migration (pink) and non-breeding (blue) and dashed lines 95% CIs. Bars show frequency of individuals using landfill sites in the post-fledging period.

2.5 Discussion

This study demonstrates that white storks that use landfill sites have lower mortality across their annual life cycle. Adults nesting close to landfill sites and juveniles that use landfill sites the most in the post-fledging period have lower total mortality rates. There are 12 landfill sites in Portugal and six in Spain available for the tracked storks. Over 72,000 storks cross the strait of Gibraltar every year (Miller *et al*., 2016) and have access to the southern Spanish landfill sites as well as sites in central and northern Spain and France (Arizaga *et al*., 2017). The reduction of organic waste at landfill sites that will occur across Europe in the near future is likely to impact upon a large number of white storks that use the western flyway (Tortosa, Caballero and Reyes-Lopez, 2002) and could increase total mortality rates.

Low mortality rates, due to shorter distances between nest and landfill site and high landfill site use, may reflect the high energy and high protein food provided at landfill sites

(Pierotti and Annett, 1987; Weiser and Powell, 2010) which can result in improved body condition for adults and juveniles. In addition, food at landfill sites is easily obtained and can reduce energy expenditure. For adults, distance between nest and closest landfill site correlates with landfill site use (Gilbert *et al*., 2016) and these birds can reduce their energy expenditure during chick rearing, a costly period of the year (Golet, Irons and Estes, 1998). Conversely landfill site use could have an indirect influence on mortality, the distance between nest and closest landfill site could correlate with adult age and nest location. White storks have strong nest-site fidelity (Vergara *et al*., 2006, Itonaga *et al*.,2011) and young adults may create their nests close to landfill sites while older adults remain nesting further away. For juveniles, the use of landfill sites could benefit them by providing them with small areas with large numbers of adult white storks (Arizaga *et al*., 2017) leading to more social learning opportunities for foraging and flight behaviour, as well as more potential experienced leaders to wintering areas (Flack *et al*., 2018).

My results show adult mortality was low and constant across stationary (breeding and non-breeding) and migration time periods. Adult white storks were tracked for a very short time (< 2 years) compared to their life expectancy (16-year generation time) and the study (2013 - 2018) captured four mortality events for adults and two re-categorised deaths in Africa in the non-breeding period. Conclusions of survival benefits for nesting close to landfill sites are therefore limited and longer term studies are needed to assess overall benefits to long term mortality rates. In addition longer studies could also tease apart the mechanism by which landfill sites improve adult survival rates.

My results show that landfill site use and body size were not predictive of adult white stork survival. It was surprising that landfill site use was not a significant predictor while distance from nest to closest landfill site is a proxy for landfill site use by adults (Gilbert *et al*., 2016). However, Gilbert *et al*. (2016) only looked at landfill site use during the period adults were tending eggs and rearing chicks whereas this study calculated landfill use for a longer period from the end of northward migration to start of the southward migration, including time before and after chick rearing. Body size indices were calculated from body measurements at logger deployment and deployments occurred throughout the year, in European winter and throughout the breeding season. White stork body mass varies seasonally (Hall, Gwinner and Bloesch, 1987); no link between body size and survival could be picked up.

Juvenile survival rates varied across time periods; mortality rates were high in the post-fledging period which is expected as juveniles are still learning to fly and forage and many fail to find enough resources to survive (Grüebler, Korner-Nievergelt and Naef-Daenzer, 2014; Tobolka 2014). Mortality on migration was low, similar to the non-breeding period. This result contrasts with Cheng *et al*. (2019), who found birds from central Europe had highest mortality on autumn migration. The differences in the survival rates may result from the different post-fledging environments, for example different availability of landfill sites, as well as the differences in migratory distances in the two populations. Juveniles from central Europe travel significantly longer to reach the Sahel and have more barriers to cross such as the Alps and Pyrenees.

Re-categorising birds that stopped transmitting in Africa as dead provided a maximum survival rate estimate and showed that mortality in the post-fledging period was similar to the mortality on migration and there was no influence of the covariates studied. This suggests that juvenile mortality is extremely stochastic and influences from the breeding ground, pre-fledging body size and post-fledging use of landfill sites, do not affect survival on migration. Mortality on migration is influenced by energy infrastructure (Garrido and Fernandez-Cruz, 2003), wind conditions (Lok, 2013) and poor fuelling in the Sahel at the end of the non-breeding season (Klaassen *et al*., 2014). These impacts could be exacerbated in juveniles that are learning flight optimization and migration routes (Oppel *et al*., 2015). My study did not contain resident first-year juveniles and I was unable to corroborate that juveniles have improved survival if they have remain in Europe (Rotics *et al*., 2017; Cheng *et al*., 2019).

Regulations are changing around PAFS such as fishery discards (Bicknell *et al*., 2013) and landfill sites; EU directives are reducing organic waste at landfill sites. The wildlife that currently rely on these resources may be negatively impacted (Plaza and Lambertucci, 2017; Gordon *et al*., 2016) as they are forced elsewhere in search of food resources. This has the potential to negatively affect the wider ecosystems as large numbers of individuals change their diet and forage on other prey species (Osterback *et al.*, 2015). Alternatively, if food from the natural environment cannot sustain the populations that fed on landfill sites, populations of species that feed on PAFS will reduce. This study suggests that the removal of anthropogenic organic waste from the landscape will cause an increase in mortality which could lead to declining population trends if all other variables remain equal.

There are other considerations that need to be considered when predicting potential future mortality. Weather conditions, in Europe or Africa, have influenced survival rates in the past (Saether *et al.*, 2006; Nevoux, Barbraud and Barbraud, 2008) and current climate change could reduce or increase mortality (Gunnersson *et al.*, 2012; Morrison *et al.*,2010). In addition, the possible decline in numbers of white storks due to landfill site closures may be exacerbated if migratory strategy is not flexible. Many adult white storks no longer migrate to sub-Saharan Africa but remain in Europe during the non-breeding period (Shephard *et al.*, 2015; Catry *et al.*, 2017; Rotics *et al.*, 2017). In 2015 the Portuguese white stork wintering population was over 60% of the breeding population (Encarnação, 2015). If residents cannot return to migratory behaviour there may be too little natural food available during the non-breeding period to maintain the large resident population. Future studies should concentrate on understanding the population size that can be supported by the natural environment in the absence of landfill sites.

The positive association between use of landfill sites and reduced mortality suggests that if migratory strategy is not flexible and natural environments cannot support the current population then food subsidies could be used to counterbalance increased mortality. Supplementary food has been shown to sustain populations of Iberian lynx (*Lynx pardinus*; López-Bao, Rodríguez and Palomares, 2008), enhance number of breeding pairs in Cape Vulture (*Gyps coprotheres*; Schabo *et al.*, 2017) and improve breeding success for a reintroduced population of white storks (Hilgartner, Stahl and Zinner, 2014). It is beyond the sphere of this study to discuss the ethical implications of providing a subsidy. However white storks were classified by the IUCN Red List as Vulnerable in 1980s (Tucker and Heath, 1994) and over the last three decades the numbers have steadily increased in Western Europe thanks to significant funds and conservation efforts, such as reintroduction programmes and improvements in natural foraging habitats, as well as the organic waste at landfill sites (Schaub, Pradel and Lebreton, 2004; Saether *et al.*, 2006; Hilgartner, Stahl and

Zinner, 2014). In 2004 the species was re-classified as Least Concern. Food subsidies in Iberia may just be one extra step to ensure the population does not decline again.

Chapter 3

Investigations into factors influencing phenology and parameters of first-year migrations.

Photo of K Rogerson deploying tracking device on juvenile white stork in Portugal, 2016.

3.1 Abstract

Seasonality in abundance of foraging resources that occur at higher latitudes underlies migratory behaviour of millions of birds worldwide. However, during the last century anthropogenic activities have led to dramatic changes in the spatial and temporal distribution of resources across the globe, providing an opportunity to understand their influence on demography and migration phenology. The use of anthropogenic food resources may influence phenology and parameters of migration and could contribute to observed changes in migratory timings and ranges; however, these links are poorly understood. I studied the phenology and parameters of migration of juvenile white storks (*Ciconia ciconia*) from a partially migratory breeding population that forages on landfill sites in Iberia. I tracked 99 juveniles during their first year of life to understand how the use of anthropogenic food resources influences timing (start date and duration), flight speed, route efficiency and likelihood of completing their first migration. In addition, I studied whether body size indices, location of nest in relation to landfill sites or timing of the start of migration was associated with the use of landfill sites on migration. Tracked birds varied in use of landfill sites prior to starting migration from 0 to 50% and on their southward migration use ranged from 0 to 80%. Greater use of landfill sites throughout southward migration in Iberia and Africa was associated with longer migration durations and slower flight speeds. Individuals that made more use of landfill sites before migration departed later on their southward migration than birds that did not use them as much. All surviving birds migrated to Africa for their first non-breeding period. Higher frequency of landfill use by juvenile birds did not influence the likelihood of successfully migrating to Africa. Greater use of landfill sites on migration was associated with birds with larger body size indices and those that started migration earlier in the season. During their first northward migration, use of landfill sites by juveniles was low and did not influence the parameters of migration. Northward migration was longer and slower than the southward migration, and the duration of northward migration was significantly influenced by the start date, which varied from November to March. Regulations for disposal of organic waste are changing, in line with EU directives, resulting in less food being available for wild birds at landfill sites which could reduce foraging opportunities before and during migration. These changes are likely to influence the parameters of southward migration for white storks but are not likely to influence the northward migration parameters.

This chapter is divided into two sections.

The first investigates how use of landfill sites affects the parameters of southward migration of first year individuals. This section has been written as a paper and will be submitted to Movement Ecology in the near future.

The second section describes the parameters of northward migration and investigates whether migration parameters are influenced by: movement behaviour during the non-breeding period, use of landfill sites or start date of northward migration.

Section 1: Use of anthropogenic food resources influences duration and timing of migration of first year birds of a partially migratory species.

3.2.1 Introduction

Resource availability influences species distributions as well as year-round movements of bird species (Thorup *et al.*, 2017; Clausen *et al.*, 2018). Migration is a response to seasonal variations in resources and enhances the energy budgets of migratory individuals across the annual cycle (Somveille, Rodrigues and Manica, 2018). Parameters of migration, such as timing and duration, may be influenced by climate and resource availability. It is well documented that the phenology of migration is changing with climate change: with increasing spring temperatures spring migration dates of many species have advanced since the 1970s (Gienapp, Leimu and Merilä, 2007; Gordo, 2007) and duration of the migration season has increased (Lehikoinen *et al.*, 2019). The influence of changing climatic conditions on food resources are predicted to influence distances of migration; longer distances to find suitable resources (Doswald *et al.*, 2009; Butchart *et al.*, 2018) and shorter distances as winters become warmer (Visser *et al.*, 2009; Pulido and Berthold, 2010; Teitelbaum *et al.*, 2016). Mechanisms driving changes in migratory behaviour could be individual behavioural flexibility or generational change, with changes in the frequency of individuals undertaking different migratory routes, distances and timings as juveniles respond to different natal or environmental conditions compared to their predecessors and alter the species' migration phenology (Gill, Alves and Gunnarsson, 2019).

Anthropogenic activities also directly drive changes to resources. Humans provide predictable and concentrated food resources, PAFS or predictable anthropogenic food subsidies (Oro *et al.*, 2013), for example rubbish dumps, fishery discards or supplementary food for garden birds. These resources can influence movement and migratory behaviour. They have been shown to result in decreased home range sizes (Plaza and Lambertucci, 2017) as well as the expansion of non-breeding ranges (Furness *et al.*, 2006; Greig, Wood and Bonter, 2017). Changes in frequency of residents and migrants have been shown to be influenced by food availability from anthropogenic sources, for example fewer harvested crops resulted in more migratory blue tits (*Parus caeruleus*, Nilsson *et al.*, 2006). Generalist bird species with a range of migratory distances shown in a breeding population rely on anthropogenic food resources at the wintering grounds closer to the breeding grounds (Shamoun-Baranes *et al*., 2017). PAFS have also influenced changes in migratory route and wintering locations, blackcaps (*Sylvia atricapilla*) have increasingly migrated from central Europe to the UK for the non-breeding period instead of the Mediterranean to feed at garden bird feeders (Plummer *et al*., 2015).

The consumption of organic waste at landfill sites is thought to have facilitated partially migratory behaviour in European white storks (*Ciconia ciconia*) populations (Catry *et al*., 2017; Gilbert *et al.*, 2016). Traditionally the birds migrate to sub-Saharan Africa every year, however over recent decades higher numbers of storks have remained in Iberia for the non-breeding period (Shephard *et al*., 2015; Flack *et al*., 2016; Catry *et al*., 2017). The possible mechanisms leading to this change could be: individuals becoming resident and no longer migrating, increasing proportion of residents joining the population (generational change; Gill, Alves and Gunnarsson, 2019) or increasing numbers of individuals from northern Europe wintering in Iberia (Rotics *et al*., 2017; Cheng *et al*., 2019).

I aim to understand if the use of landfill sites influences the migratory behaviour of juvenile white storks in a partially migratory population where a large proportion of adults are resident (Catry *et al*., 2017). I investigated the influence of juvenile use of landfill sites at the breeding area and along the migration route on migratory behaviour as well as the natal conditions that might influence the extent of landfill use by individuals on migration. Juvenile white storks are known to use social cues from adults for the direction and end point of their first migration (Chernetsov, Berthold and Querner, 2004). I predict that the more juveniles use landfill sites in Iberia, where thousands of white storks remain during the non-breeding season (Arizaga *et al*., 2017; Catry *et al*., 2017), the more likely that they will delay onset of migration due to the lack of social cues for migration. In addition, exploring factors that are associated with use of landfill sites on migration will highlight whether juvenile birds use of landfill sites is related to body size or food that they are fed in the nest. Migratory birds have high levels of site fidelity to wintering areas (Chambon *et al*., 2019) so identifying migratory strategy and wintering area of first year birds can be crucial to understanding factors that influence migration parameters and timings.

I tracked juvenile white storks, with GPS loggers, to investigate the extent to which landfill site use influences (1) start date, (2) duration, (3) flight speed, (4) route efficiency and (5) likelihood of completion of migration. I studied the parameters of migration (2 - 5) for different legs of migration, defined by overcoming three large geographic barriers. Landfill site use prior to migration, during each leg of migration and across the whole of migration were examined as predictors that may influence parameters of migration. I studied an index of body size, proximity of natal nest to landfill sites and date of starting migration as predictors of landfill use during the whole migration.

3.2.2 Methods

3.2.2.1 Data collection

I tracked 99 juvenile white storks from a partially migratory population in Southern Portugal between 2016 and 2018 (Table 5) using GPS/GSM transmitters (Flyway 50 by Movetech Telemetry ©, British Trust for Ornithology, Norwich, UK). The juveniles were from nests located at varying distances from landfill sites (1.6 – 67.6 km, Figure 19). Transmitters were deployed as backpacks with a Teflon harness, sewn together with cotton thread as a weak link (Gilbert *et al*., 2016), one week before fledging (approximately 55-60 days old). Weight, wing and tarsus measurements were taken and the standardised residuals from a model describing the linear relationship between weight (g) and tarsus length (mm) were used (from all white storks juveniles, n = 129, tracked in this population from 2013 to 2018, appendix 3.1) as a body size index. In 2016 and 2017 transmitters recorded locations every 20 minutes from 5 am to 9 pm GMT, with one night position at 1am GMT, and in 2018 locations were recorded every 10 minutes (5 am – 9 pm GMT). Location data from 2018 birds were resampled at 20 minute rate, in order that metrics created from the GPS data were comparable for all juveniles.

Table 5. Summary of tracked individuals across the years of the study (2013 - 2018), the number used in the analysis of predictors of migration characteristics and the number of tracked days per deployment year (days tracked as of 10/04/2019).

Year	Number of tracked juveniles	Mean number of days tracked per bird (range)*
2016	40	216 (14 - 834)
2017	30	143 (4 - 461)
2018	29	101 (4 - 307)

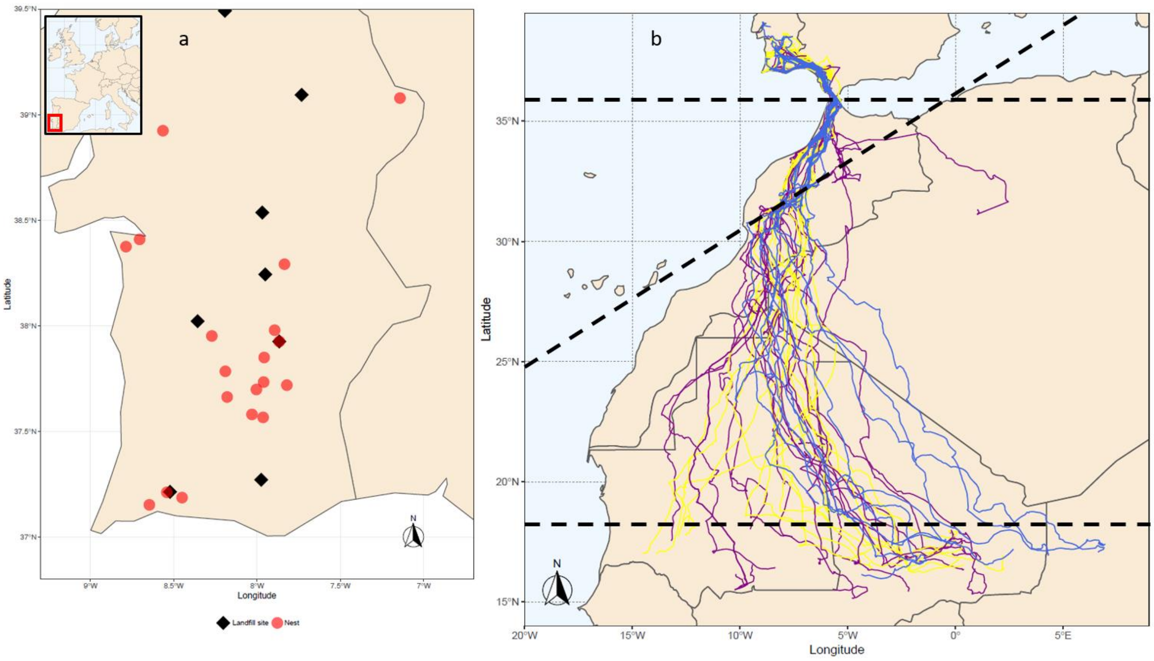

Figure 19. (a) Map of southern Portugal showing colony locations of tracked birds (red circles) and all landfill sites in Portugal (black diamonds). (b) Tracks of first year storks that completed their first migration (yellow = 2016 (n = 13), pink = 2017 (n = 17) and blue = 2018 (n = 9)). Dashed lines show the approximate locations of the three geographical barriers along this migratory flyway: 1. Strait of Gibraltar (36° S); 2. Atlas Mountains (y = 0.5817921x + 36.1213); 3. End of Sahara Desert (18.4° S).

3.2.2.2 Phenology of migration

Key dates of juvenile movements were calculated from GPS data from fledging to the end of their first southward migration (Table 6). Two consecutive locations from the nest were used to calculate fledging date to reduce the chance of picking a position resulting from a GPS error. The start of migration was defined as the date of leaving the colony area and will be used as such for the rest of this chapter. A threshold of 15 km was used because while the tracked juveniles from this study roost at the nest at night the mean maximum distance travelled from the nest per day was 14.7 km. Date of arrival in the Sahel was defined as the end of migration.

Table 6. Definitions of calculating key dates of migration for juvenile white storks.

Key date	Definition
Fledging date	First date a juvenile had two consecutive fixes > 50 m away from the nest.
Date of leaving colony	First date when the juvenile roosts (spends the night) over 15 km from their nest site and does not roost within 15 km of the nest again.
Date of arrival in Sahel	Date of crossing latitude 18.4°N
Date of crossing Strait of Gibraltar	Date of crossing latitude 36°N
Date of crossing Atlas	Day of crossing the line given by: $y = 0.5817921x + 36.1213$

I split the movements of juveniles into pre-migration movements and migration. Pre-migration encompassed the period between fledging and the date of leaving the colony area. Migration was split into three legs defined by crossing geographical barriers along migration (Table 6, Figure 19b). Leg 1 of migration was the period from leaving the colony area to crossing the Strait of Gibraltar, leg 2 of migration was from the Strait of Gibraltar until the crossing of the Atlas Mountains and leg 3 of migration included the crossing of the Saharan desert and finished on arrival in the Sahel region. Duration of each period and whole migration was the number of days from start date to end date of the period.

3.2.2.3 Migration Parameters

For the whole migration and each separate legs of migration I determined the route efficiency (straightness of route taken) and mean maximum flight speed (km/hr) per day. The straightness index (Benhamou, 2004) was calculated as a route efficiency metric and it is the straight-line distance for start point to end point divided by distance moved between flight locations (fixes with speed > 5km/hr) for the same period. As all birds migrate across the Strait of Gibraltar to Africa, rather than crossing the Atlantic Ocean, the straightness index for the whole migration was the straight-line distance between the first location at the date of leaving the colony to Strait of Gibraltar (-5.65 E, 36.0 N) combined with straight-line distance from Strait of Gibraltar to last location on date of arriving in the Sahel, divided by the total distance moved between each flight fixes for the whole migration. Mean maximum flight speed (km/hr day-1) was calculated from the maximum recorded speed for flight fixes (> 5km/hr) per day, divided by the number of days. Completion of each period was achieved (1 or not completed = 0) when individuals survived to start the following period, and was calculated for whole migration and each leg of migration.

3.2.2.4 Landfill site use before and during migration

I quantified the reliance on landfill resources to understand the influence of predictable food sources on migratory behaviour. Landfill site use was determined from the GPS positions given by the tracking devices. It was calculated as the proportion of locations obtained during the day (all fixes between 30 minutes before sunrise and 30 minutes after sunset), excluding flight fixes (speed > 5 km/hr), within a 1000 m radius of the centre of the landfill sites. I calculated the proportion of locations on landfill sites for all individuals in the pre-migration period, three legs of migration and migration as a whole. The locations of all landfill sites in Iberia are known, including those not used by white storks in this study. Landfill sites in Africa were located from looking at ground fixes (speed < 5 km/hr) from tracked white storks in this study and using sentinel satellite imagery from the last 14 months (Sentinel-2, 10m multispectral images, cloud free images, updated 19 December 2018). The imagery was used on ArcGIS© Online (esri, 2018) due to the large area being investigated. If any locations were uncertain due to poor image quality (cloud cover) the location was viewed on recent Google Earth© images (2019) to confirm whether it was a landfill site or not. Landfill sites were differentiated from bare patches of ground, possible unregulated rubbish tips or small quarries by the presence of the water reservoirs which are crucial parts of the waste management process (appendix 3.2). Two landfill sites were visited to ground truth my methods. Sixteen landfill sites were found in North Africa (appendix 3.3 and 3.4).

3.2.2.5 Predictors of landfill site use

I used three variables for natal conditions to understand potential influences on landfill site use on migration: body size index, distance between nest and nearest landfill site, calculated as the distance from nest coordinates to the centre of closest landfill site which provides a proxy for parental use of landfill sites (Gilbert *et al*., 2016), and date of leaving colony.

3.2.2.6 Statistical analysis

Mixed models were used to test the influence of landfill site use on migration parameters (Table 7). The migration parameters investigated are likelihood of completion, duration, route efficiency and mean maximum flight speed. These were investigated separately for the whole migration and the three migration legs. In addition, the influence of pre-migration landfill site use on the date of leaving the colony (start date of migration) was investigated. A further mixed model was used to understand the influence of natal conditions, distance from nest to nearest landfill site, body size index and date of leaving colony on the landfill site use across the whole migration. Mixed models were carried out using R with RStudio (version 3.5.0). All mixed models controlled for year of transmitter deployment (2016, 2017 and 2018).

Table 7. Outline of mixed models undertaken to investigate influences of migration parameters and landfill use on migration. Highlighting response variable, fixed and random effects and the type of statistical model used.

Response variable		Fixed Effect	Random effect	Type of model
	Date of leaving colony	Landfill site use (prior to migration)	Year (2016, 2017 and 2018)	LMM
Whole migration	Date of leaving colony	Landfill site use (whole migration)		LMM
	Completion			GLMM (binomial)
	Duration			GLMM (negative binomial)
	Efficiency			LMM (logit transformed data)
	Flight speed			LMM
	Landfill site use (whole migration)	Distance from nest to landfill site Relative body size Date of leaving colony		GLMM (binomial)
Leg1	Completion	Landfill site use (leg 1)		GLMM (binomial)
	Duration			GLMM (negative binomial)
	Efficiency			LMM (logit transformed data)
	Flight speed			LMM
Leg2	Completion	Landfill site use (leg 2)		GLMM (binomial)
	Duration			GLMM (negative binomial)
	Efficiency			LMM (logit transformed data)
	Flight speed			LMM
Leg3	Completion	Landfill site use (leg 3)		GLMM (binomial)
	Duration			GLMM (negative binomial)
	Efficiency			LMM (logit transformed data)
	Flight speed			LMM

To determine the influence of landfill site use on the likelihood of completion of migration a GLMM with binomial error family was used. For the models investigating whether duration of the periods was influenced by landfill site use a negative binomial GLMM was used (due to over dispersion of the data); date of leaving colony (julian date), route efficiency (transformed with logit function) and mean maximum flight speed during migration were investigated using LMM. For all models (Table 7), stepwise deletions were made (using AIC value) and the best model had the lowest AIC value and the least number of parameters. If multiple models were within Δ2 AIC, the simplest model, with the least number of parameters or the null model, was taken as the most parsimonious. Predicted values from the most parsimonious model were calculated to create graphs showing the strength of the influence of the significant individual characteristics on the migration characteristics. In addition, the marginal and conditional R square values were calculated to understand the full variation explained by the models.

3.2.3 Results

All juveniles crossed the Strait of Gibraltar (65/99) or died/their transmitter stopped before crossing (34/99, appendix 3.5). Forty-nine juveniles survived to start their non-breeding season in Africa, 45 completed migration and arrived in the Sahel with a mean maximum migration distance of 2495 km (SE = 18.2); while four birds spent their non-breeding period in Morocco (2016/17), their mean maximum migration distance was 758 km (SE = 67.7). These four birds were removed from analysis of parameters of the whole migration, leg2 and leg 3 of migration.

3.2.3.1 Migration phenology and duration

The mean date of leaving the colony area, and starting migration, was 28 July (SE = 1.8, appendix 3.6 and 3.7). The mean date of crossing the Strait of Gibraltar was 14 August (SE = 2); all crossed the Strait of Gibraltar before 10th September each year and the mean date of crossing the Atlas Mountains was 23 August (SE = 2.2). The mean date of arrival in the Sahel, and end of migration, was 4 September (SE = 2.4). The mean duration of whole migration, from leaving the colony area to arriving in the Sahel, was 38 days (SE = 3;

appendix 3.6), with the mean duration of leg 1 = 17 days (SE = 2), leg2 = 7 (SE = 1.3) and leg 3 = 12 (SE = 0.3).

3.2.3.2 Influence of landfill use on migratory behaviour

Landfill use while on migration influenced the duration, mean maximum speed per day and date of leaving colony, but did not affect route efficiency or likelihood of completion of migration (Table 8). Juveniles that used landfill sites more during their whole migration had longer migrations, from leaving the colony to entering the Sahel region, spent more days on migration and travelled at slower speeds (Table 8, Figure 20). Juveniles with fewer fixes on landfill sites during the pre-migration period, left their colonies at an earlier date in the season (Figure 20).

Splitting migration into three legs revealed where the predictor variables are most important for the parameters of migration. The maximum speed in leg 1 and leg 2 and route efficiency in leg 3 varied with use of landfill sites during those periods (Table 9; Figure 21). Birds with a greater proportion of fixes on landfill sites in leg 1 and in leg 2 had slower maximum speeds during the two periods and those with a greater proportion of fixes on landfill sites in leg 3 had a straighter route across the Sahara.

Table 8. Output of most parsimonious models investigating how date of leaving the colony area and parameters of migration (duration, completion and route efficiency) varied with landfill site use prior to and on migration, respectively, and the influence of natal conditions (body size index and date of leaving colony) on use of landfill sites across the whole migration. Year was included in all models as a random effect. Bold p values denote a significant influence of the predictors on the migration parameter, significance was defined as $p < 0.05$.

Period	Migration parameter	Model type	Predictors in final model	Estimate	Standard Error	Test statistic	P value	Random effect (variance and standard error)	R^2		N
									Marginal	Conditional	
Whole migration	Date of leaving colony (Julian Day)	LMM	Landfill use	104.21	9.94	10.49	**< 0.001**	7.23 (2.69)	0.57	0.60	79
	Completion	-	-	-	-	-	-	-	-	-	-
	Duration (days)	Negative binomial GLMM	Landfill use	1.22	0.35	3.46	**0.0005**	<0.001 (<0.001)	0.26	0.26	39
	Route efficiency (straightness index)	-	-	-	-	-	-	-	-	-	-
	Mean max. speed	LMM	Landfill use	-12.50	4.34	-2.88	**0.007**	3.27 (1.81)	0.17	0.26	39
	Landfill use	Binomial GLMM	Date of leaving colony Body size indices	-0.01 0.53	0.002 0.035	-6.56 15.67	**< 0.001** **< 0.001**	0.82 (0.91)	0.04	0.23	39

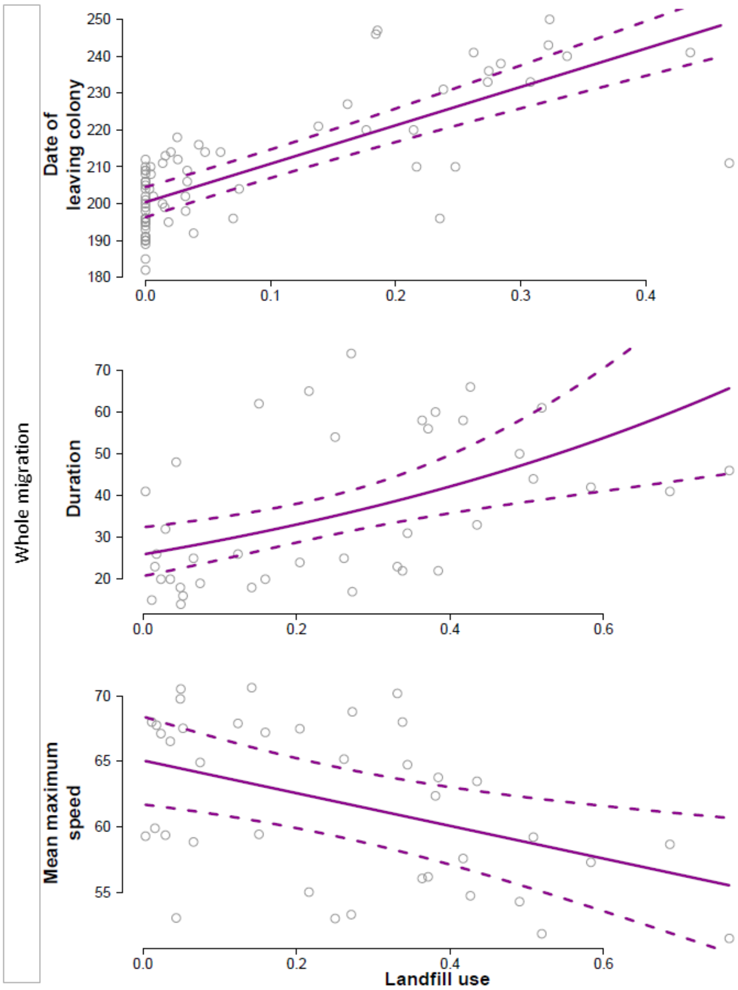

Figure 20. Significant relationships from mixed models showing the association between landfill use on migration and timing, duration and flight speed (Table 8). Figure notation: Date of leaving colony = date of starting migration (Julian days), Landfill use = proportion of fixes on landfill sites across of whole migration, Mean maximum speed = mean maximum flight speed per day across the whole migration, Duration = number of days from date of leaving colony to arriving in Sahel.

Table 9. Parameters of migration split into three periods based on topographical barriers on migration. Output of most parsimonious models investigating how movement parameters of for each leg of migration (duration, completion, route efficiency and speed) varied with use of landfill sites in each leg. Year was included in all models as a random effect. Bold p values denote a significant influence of the predictors on the migration parameter, significance was defined as $p < 0.05$.

Period	Migration parameter	Model type	Predictor in final model	Estimate	Standard Error	Test statistic	P value	Random effect (variance and standard error)	R² Marginal	R² Conditional	N
Leg 1 (Leaving colony to Strait of Gibraltar)	Completion	-	-	-	-	-	-	-	-	-	-
	Duration (days)	-	-	-	-	-	-	-	-	-	-
	Route efficiency (straightness index)	-	-	-	-	-	-	-	-	-	-
	Mean max. speed	LMM	Landfill use	-8.49	4.14	-2.05	**0.04**	< 0.001 (< 0.001)	0.06	0.06	64
Leg 2 (Strait of Gibraltar to Atlas Mountains)	Completion	Binomial GLMM	Landfill use	16.19	14.83	1.09	0.27	< 0.001 (< 0.001)	0.86	0.86	55
	Duration (days)	-	-	-	-	-	-	-	-	-	-
	Route efficiency (straightness index)	-	-	-	-	-	-	-	-	-	-
	Mean max. speed	LMM	Landfill use	-12.39	2.10	-22.43	**0.02**	< 0.001 (< 0.001)	0.11	0.11	48
Leg 3 (Atlas Mountains to Sahel)	Completion	-	-	-	-	-	-	-	-	-	-
	Duration (days)	-	-	-	-	-	-	-	-	-	-
	Route efficiency (straightness index)	LMM	Landfill use	9.01	2.63	3.43	**0.002**	< 0.001 (< 0.001)	0.24	0.24	39
	Mean max. speed	LMM	Landfill use	-37.66	22.77	-1.65	0.11	< 0.001 (< 0.001)	0.07	0.07	39

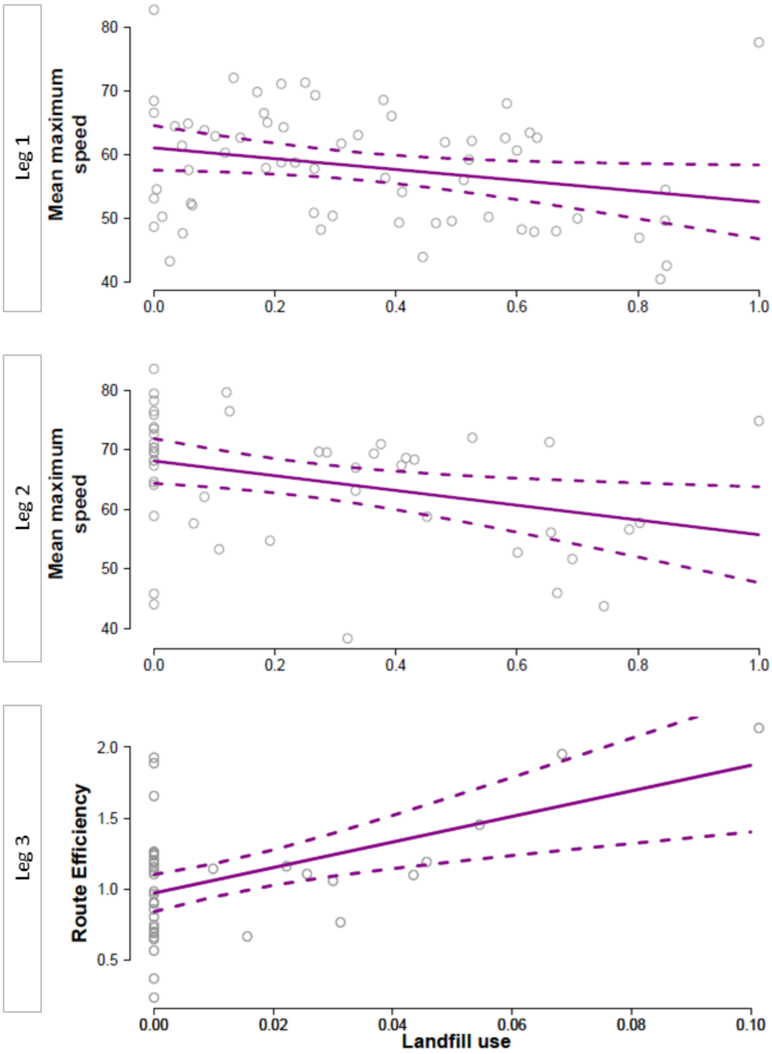

Figure 21. Significant effects of fixed effects on the parameters of each leg of migration (split by topographical barriers on migration) from mixed models (Table 9). Figure notation: Leg 1 = from leaving the colony to crossing the Strait of Gibraltar, leg 2 = from crossing the Strait of Gibraltar to crossing the Atlas Mountains, leg 3 = from crossing the Atlas Mountains to entering the Sahel, Landfill use = proportion of fixes on landfill sites during each period.

3.2.3.3 Predictors of landfill site use while on migration

Landfill site use while on migration was significantly influenced by date of leaving the colony and the body size indices (Table 8, Figure 22). Individuals that departed later from the natal colony used landfill sites less than individuals that left earlier in the season. In addition, birds with larger body size indices used landfill sites more on migration than juveniles with smaller body size indices.

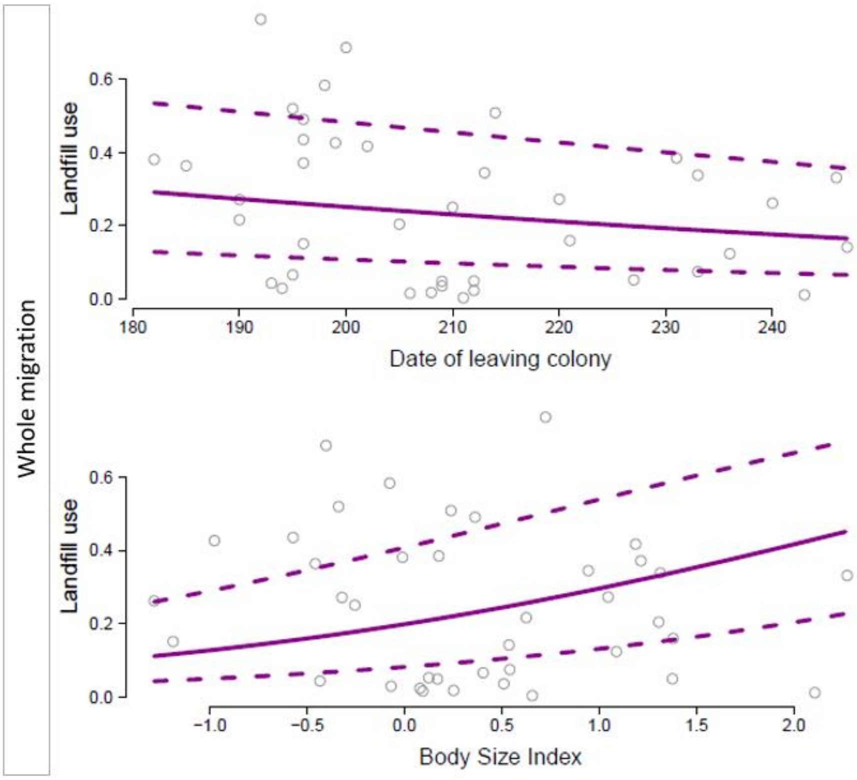

Figure 22. Significant relationships between landfill use across the whole migration and natal conditions: body size indices and date of leaving the colony. Figure notation: Date of leaving colony = date of starting migration (Julian days), Landfill use = proportion of fixes on landfill sites across of whole migration.

3.2.4 Discussion

Greater pre-migration use of landfill sites resulted in delaying the date of leaving the colony area; juvenile white storks that used landfill sites 20% more between fledging and leaving the colony left the colony area 10 days later (here the start date of migration). Greater use of landfill sites on migration resulted in longer migrations and travelling at slower speeds from colony to the Sahel region; the storks that used landfill sites 20% more on migration spent an extra 6 days on migration and had a lower mean maximum speed by 2 km/hr. Landfill site use did not influence the likelihood of individuals surviving to complete migration. This study suggests that once started, the likelihood of completing migration is probably more influenced by stochastic events, such as anthropogenic structures (Martín *et al*., 2018; Nichols *et al*., 2018), poor weather conditions (Vansteelant *et al*., 2015) and poor social cues (Berdahl *et al*., 2018; Nevitt, 2018) than use of landfill sites.

In addition I showed that landfill site use on migration is influenced by date of leaving the colony and body size index but was not associated with distance between nests and nearest landfill sites. The effect size was rather small with juveniles that left the colony area 10 days later using landfill sites 2% on migration and juveniles with 20% greater body size indices using landfill sites 7% more. The results indicate that landfill site use on migration is not influenced by exposure to landfill site food at the nest, by parents, or by proximity of nest to landfill sites. These results combined with other results suggest that birds that start of migration later, use landfill sites more prior to migration, and are more likely to have quicker migrations.

The study of landfill site use by wildlife is particularly relevant at present because waste management is changing in Europe, EU legislation requires member states to reduce the quantity of material deposited at open landfill sites and organic waste to be recycled at the source instead of at landfill sites (EU Directives 1999/31/EC and 2018/851). These changes will influence the wildlife populations that rely on them, as landfill sites can positively impact upon demographic parameters (Gordon *et al*., 2016; Plaza and Lambertucci, 2017). The positive impacts of landfill site use on breeding success and survival has been seen in this study population of white storks (Gilbert *et al*., 2016). My results suggest that, with the removal of resources at landfill sites, I could hypothesis changes in phenology of migration, start dates and duration of migrations; these could be advanced and shortened respectively but mortality on migration is unlikely to increase.

This is the first study to look at landfill site use across the whole of migration for any Afro-Palearctic migratory species. Juvenile white storks use landfill sites in Iberia and North Africa. In this study use of landfill sites in North Africa, leg 2 of migration, was similar in frequency to use of landfill sites in Iberia, leg 1 of migration (mean of 27% and 35% respectively, appendix 3.6). The small amount of landfill site use in leg 3 of migration, crossing the Sahara Desert, is due to the few landfill sites on the south of the Atlas Mountains. High use of landfill sites in North Africa, with no known changes to waste management there, indicates that anthropogenic waste will still be available to migrating white storks. Therefore duration of migration may be maintained by prolonging migration at landfill sites in Africa to fuel up to cross the Sahara Desert. Use of anthropogenic waste resources in North Africa is probably underestimated in this study as only managed landfill sites are included in the analysis. Unregulated rubbish tips are more variable in time and space and were more difficult to determine from satellite images (appendix 3.2). In addition, quality of organic waste at landfill sites in Morocco compared to Iberia is unknown; the differences in the economies and stability of the countries concerned suggest that landfill sites in Morocco are likely to have less organic waste and be of poorer quality compared to landfill sites in Iberia. White storks might be attracted to landfill sites in Africa due to cues not relating to the quality of the food available. One last point, landfill site locations in North Africa used by this study were determined by stationary fixes of these study individuals, therefore I would recommend other researchers to undertake similar investigations with their own study species; other species may use different routes across North Africa and access other landfill sites.

This sample of juveniles from a partially migratory white stork population is interesting because all juveniles were migratory in their first year. Juvenile white storks follow adult birds on migration (Chernetsov, Berthold and Querner, 2004; Berdahl *et al*., 2018) and although a large proportion of adults are resident (Catry *et al*., 2017) all surviving juveniles followed migratory individuals to Africa indicating a probable innate programme for migration (Chernetsov, Berthold and Querner, 2004). My results indicate that greater use of landfill sites delays the start date of migration for first year juveniles. This suggests that they are to some extent responding to social cues from resident adults or to the high abundance of food availability. Then juveniles are either ignoring cues for residency at landfill sites at a later date and start migration or they are outcompeted for the resources at landfill sites by the adults and start migration. However it seems unlikely that Portuguese juvenile storks are outcompeted as juveniles from other Western Europe populations (France and Germany) overwinter in Iberia and use resources at landfill sites (Shephard *et al*., 2015; Rotics *et al*., 2017; Cheng *et al*., 2019).

Despite a potential innate drive to migrate, juveniles migrate with the flexibility to shorten their migratory distance, and four individuals (8%) spent the non-breeding season in Morocco instead of sub-Saharan Africa. It is likely that the flexibility of migratory strategy for white storks, the switch from migratory to resident, is linked with age and the benefits of maintaining territories for adults (Gilbert *et al*., 2016; McCrary *et al*., 2019) made possible by the presence of year-round food resources at landfill sites. Therefore the changes in migratory behaviour in this population may not be down to generational shift in responses to environmental cues (Gill, Alves and Gunnarsson, 2019) but instead be individual plasticity in migratory strategy. In addition, it could be hypothesised that after landfill closures and removal of organic waste in European resident white storks will travel to landfill sites in Morocco but not return to full migratory behaviour and wintering in sub-Saharan Africa.

To conclude I studied the influence of landfill sites on the migratory behaviour of juvenile white storks to understand the benefit of a year-round food resource on juveniles of a traditionally migratory species. I found that greater use of landfill site pre-migration resulted in delaying the start of migration. Greater use of landfill sites on migration increased the time it took to reach sub-Saharan Africa and slower speeds in flight. I found limited flexibility of migratory strategy for juveniles suggesting that cues from resident adults at landfill sites were ignored in favour of cues from migratory individuals. Future changes to organic waste disposal will remove this food resource which is unlikely to greatly impact the success of the migratory juveniles but could influence migration phenology.

Section 2: Parameters of first northward migration are not influenced by use of anthropogenic food subsidies.

3.3.1 Introduction

The first northward migration for juveniles, in their first year of life, between non-breeding and breeding areas is different to their first southward migration as they are no longer completely naïve individuals (Newton, 2008). If individuals are migrating to their natal area to breed their migration is constrained to be able to return to suitable breeding areas with sufficient time to find a mate and breed successfully. Here, I have studied the first northward migration of juvenile white storks; these birds do not breed in their second year so their northward migration is not constrained in timing. However, they may still use social cues from conspecifics or changes in resources in the non-breeding area to facilitate timing of this migration. Use of landfill sites in North Africa may effect duration of northward migration as it did for the southward migration.

I aim to: (1) describe the northward migration of first year juvenile white storks, (2) compare migration parameters between southward and northward migrations, (3) compare characteristics of non-breeding period and start date of migration for individuals that did and did not complete northward migration and (4) understand whether characteristics of non-breeding period, start date of migration or landfill use on migration influences the migration parameters (duration, route efficiency or maximum flight speed) of northward migration.

3.3.2 Methods

3.3.2.1 Phenology of northward migration

Start date of northward migration is defined as the date of crossing northward at 18.4° latitude. This will be termed date of leaving the Sahel region for the rest of this chapter. This date was chosen because white storks are itinerant in their non-breeding areas often displacing large distances throughout the non-breeding season; picking one area that is the 'nonbreeding area' is difficult. The end of northward migration is also difficult to define as these juveniles are not heading back to Europe to breed and they move around constantly after crossing the Sahara desert; I considered crossing northward over the Strait of Gibraltar (36° latitude) as the end of northward migration. I also determined the date of crossing the Atlas Mountains, the day of crossing the line given by: $y = 0.5817921x + 36.1213$. Duration of the whole northward migration and the two legs of migration, leg 1 (from leaving Sahel to crossing the Atlas Mountains) and leg 2 (from crossing the Atlas Mountains to the Strait of Gibraltar), was determined as the number of days from start to end dates.

3.3.2.2 Parameters of northward migration

The parameters determined for northward migration are: route efficiency and mean maximum speed per day. The methods for these two metrics are included in Section 1 of this chapter. The completion of northward migration and the two legs of migration was whether the bird was known to cross the Atlas Mountains and Strait of Gibraltar.

3.3.2.3 Influence of landfill site use on migratory behaviour

To understand the influence of landfill site resources on parameters of northward migration, a metric for landfill site use was determined. Landfill site use was calculated as the proportion of locations obtained during the day, excluding flight fixes, within a 1000 m radius of the centre of the landfill sites. I calculated the proportion of fixes on landfill sites for the whole of northward migration and the two legs of the migration.

3.3.2.4 Parameters of non-breeding period

Two parameters of the non-breeding period, duration and mean daily displacement per day, were calculated in order to understand the influence of these on the northward migration. Duration of the non-breeding period was the number of days between date of entering Sahel on southward migration and leaving on northward migration. Mean daily displacement per day was the mean distance (km) moved between the last fix for each consecutive day.

3.3.2.5 Comparing southward and northward migration parameters

Due to limited sample size of birds on northward migration, univariate statistics (paired t test and paired Wilcoxon signed rank tests) were used to compare the duration, speed and route efficiency between southward and northward migration. The metrics of the whole of both migrations will be compared, as well as comparing the corresponding legs of northward and southward migration.

3.3.2.6 Predicting influences of first northward migration parameters

Correlations between variables were investigated and variables with correlations greater than 0.70 (Pearson's rank coefficient) were considered highly correlated. Completion of northward migration was considered with t-test and Wilcoxon signed rank tests due to small sample sizes. The non-breeding parameters between individulas that did and did not complete northward migration were compared. Linear models were used to determine the influence of landfill site use and parameters of the northward migration on parameters of northward migration. Small sample sizes do not allow for mixed models controlling for year, and only one variable was considered in each model. Duration of northward migration was analysed with a generalised linear model (Poisson family). Route efficiency was logit-transformed and analysed with a linear model. Start date, landfill site use, duration of non-breeding period and daily displacement in non-breeding period were included as fixed effects in separate models. The models were compared to null models and the most parsimonious model had the lowest AIC. If the model and null model were within 2AIC then the null model was the best model. Psuedo-RSquared was calculated for generalised linear models as variance explained/total variance. This analysis was only undertaken for the whole migration due to the small sample size. All statistical analysis was undertaken with R version 3.5.0 in RStudio 1.1.383.

3.3.3 Results

3.3.3.1 Comparison of migration parameters between southward and northward migration

Only ten individuals that were tracked for their northward migration had data for their full southward migration (due to loss of data in the Sahara). Northward migration was longer, had slower mean maximum speeds and more efficient routes than southward migration (Table 10). When looking at the corresponding legs of northward and southward migrations, crossing across the Sahara and crossing North Africa was slower on the northward migration compared to southward migration (Table 11), taking more days and slower flight speeds. Route across North Africa was straighter in the southward migration than the northward migration (Table 11).

Table 10. Comparison of northward and southward migration parameters (welch two-sample t tests and Wilcoxon signed rank tests), including the mean (standard deviation) of the parameters (duration, mean maximum speed and route efficiency). P values were considered significant if < 0.05 and indicated in bold.

Migration parameters	Southward migration (n = 10)	Northward migration (n = 10)	Comparison (test statistic, p value)
Duration (days)	36 (22)	82 (37)	V = 3, **p = 0.01**
Mean maximum speed	62 (7)	37 (3)	V = 55, **p = 0.002**
Route efficiency	0.66 (0.07)	0.73 (0.1)	T9 = -2.76, **p = 0.02**

Table 11. Comparison of parameters between the corresponding legs of northward and southward migration (welch two-sample t tests and Wilcoxon signed rank tests), including the mean (standard deviation) of the parameters (duration, mean maximum speed and route efficiency). Legs of migration covering the crossing of the Sahara desert from Atlas Mountains to Sahel, and crossing of North Africa, from Strait of Gibraltar to Atlas Mountains.

Migration parameters	Crossing Sahara desert			Crossing North Africa		
	Leg 3 Southward migration (n = 16)	Leg 1 Northward migration (n = 16)	Comparison (test statistic, p value)	Leg 2 Southward migration (n = 12)	Leg 2 Northward migration (n = 12)	Comparison (test statistic, p value)
Duration (days)	12 (2)	41 (36)	V = 104.5, **p = 0.01**	7 (10)	46 (24)	V = 66, **p = 0.004**
Mean maximum speed	70 (6)	39 (6)	V = 0, **p < 0.0001**	66 (7)	37 (3)	V = 0, **p = 0.0005**
Route efficiency	0.73 (0.08)	0.79 (0.1)	T_{15} = -1.67, p = 0.1	0.78 (0.1)	0.60 (0.2)	T_{11}=-3.27, **p = 0.007**

3.3.3.2 Likelihood of completing migration influenced by non-breeding period, migration parameters or individual characteristics

Twenty-one individuals started their northward migration and 12 completed the full migration to Iberia (Table 12, Figure 23). Another two storks migrated successfully to Iberia but data was lost due to a back-log of transmissions while they crossed the Sahara and so a full track was not available. Two individuals did not return to Iberia and remained in Morocco after all other tracked individuals had crossed the Strait of Gibraltar (Figure 23c). One did not make it across the Atlas Mountains and four individuals did not make it to Iberia.

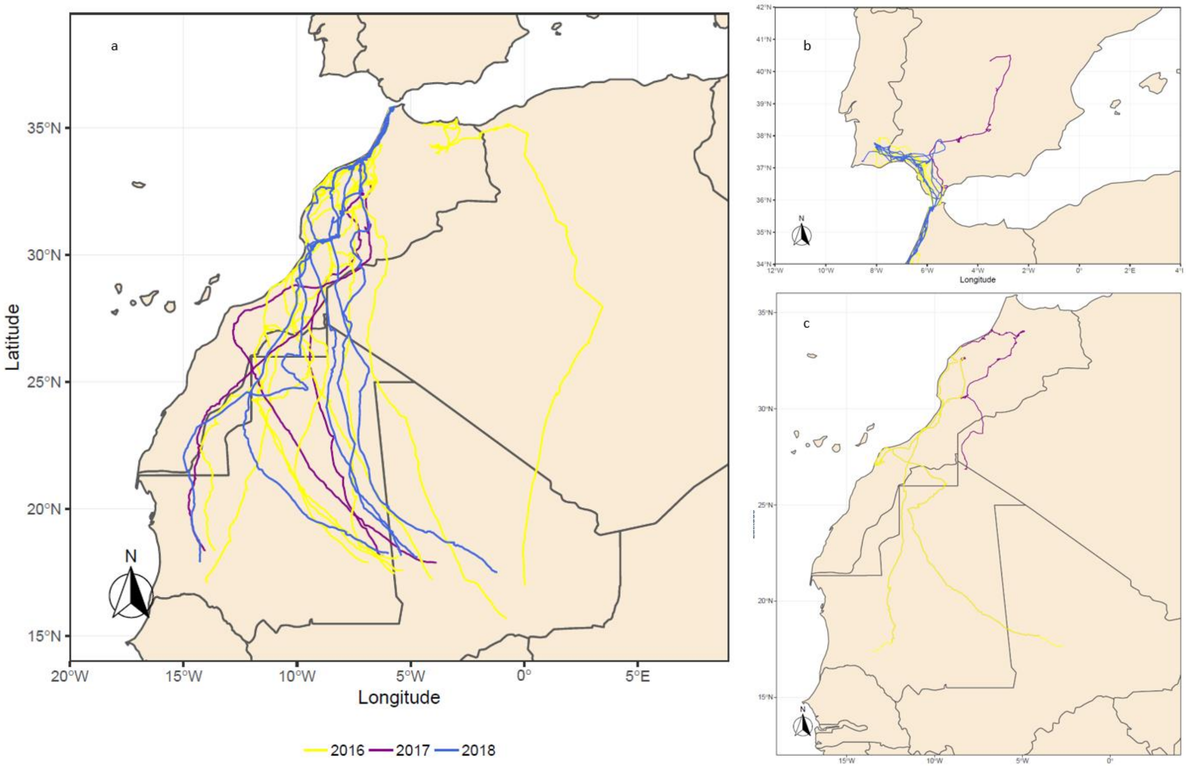

Figure 23. Tracks of juvenile white storks on northward migration. Year of deployment denoted by colour. (a) Tracks from leaving the Sahel to crossing the Strait of Gibraltar or end of transmission (2016 = 11, 2017 = 3, 2018 = 5). (b) Tracks for one month after crossing Strait of Gibraltar (2016 = 6, 2017 = 1, 2018 = 5). (c) Tracks of two birds (from 2016) that did not return to Iberia after northward migration (yellow = track from leaving the Sahel to 1st May 2017 (last date of birds crossing to Iberia), purple = 1st May to end of transmission), showing one bird starting second southward migration from Morocco.

Table 12. Summary of migration phenology and movement parameters including landfill site use on northward migration. Mean and standard deviation are shown and split by year of logger deployment. *only 1 bird had a known date of crossing Strait of Gibraltar. Completion of whole migration and leg 2 of migration was calculated as whether individuals successfully finished migration. The number that completed migration and leg 2 for 2016 and 2017 are not the sample sizes used in the calculation of the summaries of the parameters, 2016 = 6 and 2017 = 1. Two individuals (from 2016) finished their migration in Morocco (stayed past 1-May, last date of crossing Strait of Gibraltar) and two individuals (1 each from 2016 and 2017) did make it to Iberia but part of the journey from Morocco to Iberia was lost due to back log of data being transmitted from over the Sahara (no GSM coverage).

Characteristics		2016	2017	2018
Date of leaving Sahel		01-Jan (46)	31-Jan (25)	18-Jan (44)
Date of crossing Atlas Mountains		19-Feb (56)	22-Feb (10)	18-Feb (59)
Date of crossing Strait of Gibraltar		09-Apr (20)	04-Apr *	13-Apr (9)
Duration	Whole migration	97 (49)	98 *	84 (38)
	Leg 1	49 (47)	26 (29)	31 (26)
	Leg 2	56 (34)	39 *	53 (50)
Landfill site use	Whole migration	0.10 (0.12)	0.53 *	0.18 (0.12)
	Leg 1	0.05 (0.16)	0.17 (0.30)	0.0009 (0.002)
	Leg 2	0.14 (0.12)	0.55 *	0.29 (0.18)
Route efficiency	Whole migration	0.71 (0.10)	0.59 *	0.78 (0.07)
	Leg 1	0.75 (0.15)	0.80 (0.16)	0.85 (0.08)
	Leg 2	0.57 (0.09)	0.64 *	0.70 (0.10)
Mean Maximum speed	Whole migration	35 (3)	38 *	39 (1)
	Leg 1	39 (8)	43 (3)	40 (3)
	Leg 2	34 (2)	37 *	39 (2)
Number completed	Whole migration	9	2	5
	Leg 1	12	3	5
	Leg 2	9	2	5

Individuals that completed northward migration had shorter daily distances (km day-1) in the non-breeding period than individuals that did not survive to finish migration (n = 16 and 5 respectively; mean (SD): 62 km (10) and 75 km (5) respectively; t_{15}= 3.93, p = 0.001). There was no difference in start date of northward migration between individuals that did and did not complete northward migration (W = 43.5, p = 0.80). Duration of stay in the winter period are highly correlated with start date of northward migration, those that spend longer in the Sahel leave later than those that spend a short time in the Sahel (Pearson's product-moment correlation = 0.93, t_{10} = 8.12, p < 0.0001). Further analysis with multivariate statistics therefore only included start date of migration and not duration of non-breeding period.

3.3.3.3 Influence of start date, movements in non-breeding area and use of landfill sites on migration parameters

Individuals that left the Sahel later in the season spent less time in crossing Africa and reaching Iberia (estimate = -0.01, SE = 0.001, z = -12.96, p < 0.0001; pseudo-RSquared = 0.85; Figure 24). Route efficiency and maximum speed for the northward migration were not influenced by start date of northward migration. Duration of northward migration, route efficiency and mean maximum speed are not influenced by distance moved per day in the non-breeding period or use of landfill sites on the migration.

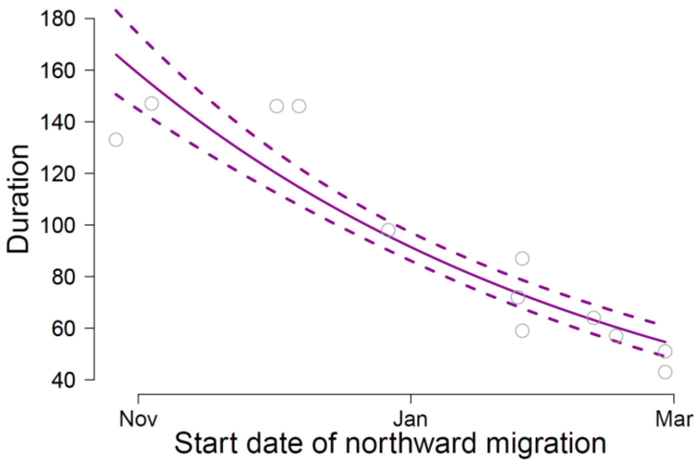

Figure 24. Duration of northward migration is influenced by start date of northward migration. Individuals with an earlier start date have longer migrations to Iberia. Dashed lines show the 95% confidence intervals around the predicted values from the model.

3.3.4 Discussion

Northward migration took longer than southward migration for the individuals that were tracked on their migration. This is the first study to describe and investigate influencing factors of migration parameters for the first northward migration of juvenile white storks. Duration of northward migration was negatively influenced by date of leaving the Sahel. Date of leaving the Sahel was extremely variable, from November to March. Those that started earlier in the season had longer migrations to Iberia. This may have resulted from poor foraging conditions in the Sahel encouraging birds to migrate across the Sahara and continue fuelling in Morocco before heading to Iberia.

The large variability in timing for leaving the Sahel region suggests that the migratory behaviour is flexible; if there are timing constraints for the northward migration to reach breeding areas at a particular time it is more visible in the date of crossing the Strait of Gibraltar which is not as variable for these individuals. However, these individuals were not constrained by breeding as their dates of arriving in Iberia would have been too late to find a nest, mate and breed successfully. Dates of leaving the Sahel region and crossing the Atlas Mountains were much more varied than the corresponding dates on the southward migration (Table 12 and appendix 3.6) in turn suggesting that southward migration is constrained by some variables, such as favourable weather conditions, resource availability or social cues from experienced migrants.

My results show that northward migration was slower, taking more days and using slower speeds than the southward migration, whether across the whole of the migrations or split between the two corresponding legs of both migrations. The route efficiency for the legs of migration covering the crossing of the Sahara desert were similar. However, the routes were less efficient crossing North Africa, north of the Atlas Mountains, in the northward migration, compared to the same area on the southward migration. This suggests that North Africa is an important stop over for birds on their northward migration, and could be considered as another non-breeding area, especially for birds that left the Sahel as early as November.

Mortality was assumed for the birds that stopped transmitting on the northward migration, however as it was almost a year since deployment of the loggers the weak link could have broken on the harness of the logger, or the transmitter may have failed. Those that completed northward migration had shorter daily distances in the non-breeding period. This could have been because the birds that completed their northward migration had been in non-breeding areas with better food resources. In addition, poor weather conditions on their return journey can influence mortality on migration (Lok, Overdijk and Piersma, 2015).

Unlike the southward migration, landfill site use on northward migration was low (Table 12) and did not influence time spent on migration, route efficiency or mean maximum speeds suggesting other foraging areas were used more than landfill sites. The conditions at the other foraging areas and weather conditions had more of an impact on the parameters on northward migration than landfill sites.

In addition, as northward migration did not include movements and landfill sites in Europe, I cannot hypothesise how the change in EU regulations around organic waste management will impact the northward migration. However, two individuals did not return to Iberia at the end of their first northward migration and, as landfill sites in North Africa will not be affected by a change of regulations, storks may choose to spend longer in North Africa. There are breeding populations in North Africa (Djerdali *et al*., 2016; Birdlife International, 2019) and maybe these populations will expand if storks find better resources in North Africa than Southern Europe.

Chapter 4

Quantifying the extent and importance of post-fledging family associations in white storks (*Ciconia ciconia*).

Photo of a family of white storks, adult and juveniles, in Odiáxere, Portugal. The juveniles have been ringed and have tracking devices deployed on them. Photo taken by K Rogerson

4. 1 Abstract

Extended family associations in social species can result in offspring learning movement strategies and foraging behaviour from parents. In colonial species, fledgling birds follow cues from older individuals but the extent of the influence of family associations on the development of foraging and movement strategies is not currently known. Family associations can influence the uptake of novel behaviours if the changes in behaviour are socially transmitted from closely related individuals. I examined the contribution of family associations in the uptake of new movement and foraging behaviours, in a population of white storks in Portugal. Over the last three decades white storks have transitioned from being fully migratory to partially migratory (where some individuals are resident and others are migratory) and started using food subsidies on landfill sites. Using GPS/GSM devices, I tracked the movement behaviour of 23 parent-offspring, 24 sibling and 30 sibling-random juvenile pairs. Family pairs did not differ from random bird associations indicating weak links and learning opportunities between individuals from the same family. Only 16% of offspring visited a landfill site for the first time with their tagged parent and siblings did not visit landfill sites simultaneously. During the study all surviving juveniles migrated to Africa whereas 77% of parents were resident, offspring of migratory parents migrated independently of family members suggesting migratory strategy is not learnt from parents. Durations of parent-offspring associations were shorter if offspring fledged later in the breeding season and duration of sibling associations were shorter if nests were far from landfill sites. This study highlights that a gregarious migratory bird, the white stork, exhibits no specific associations between family members, neither for migration nor post-fledging foraging. The social components of migratory strategy and foraging behaviours are learnt from other non-related individuals, the cues determining which individuals are followed are not yet known.

4.2 Introduction

Family associations are observed in a variety of social species, some live in highly social cooperative groups (Arnold and Owens, 1998) while others are social only at certain times of year (Danchin and Wagner, 1997). Some migratory avian species, such as species within the Anatidae and Gruidae families, form close family units with associations starting at fledging and being maintained throughout migration to non-breeding locations and some associations last until the return to breeding areas (Lazarus and Inglis, 1978; Alonso, Bautista and Alonso, 2004). Other migratory avian species are gregarious during migration, forming flocks with conspecifics. Gregarious behaviour during migration increases the likelihood of finding favourable weather conditions (Loon, Bouten and Davis, 2011), being recruited to large flocks and finding stopover sites and wintering destinations (Helm, Piersma and van der Jeugd, 2006). Gregarious behaviour and family associations facilitate social interactions and social learning, which is important to reduce predation risk and uncertainties during migration (Nemeth and Moore, 2014).

In avian species, close associations between parents and offspring during the post-fledging period are beneficial if increased investment in offspring increases the offspring fitness and survival while offsetting any fitness costs suffered by the parents (Covas, Griesser and Sheffield, 2007). The benefits of extended parental care for the post-fledging period and beyond has been shown to offer protection from predators (Earnst and Bart, 1991), provide access to better resources (Earnst and Bart, 1991), increase offspring food intake (Black and Owen, 1989) and increase offspring survival (Gruebler and Naef-Baenzer, 2010; Weegman *et al*., 2016). However, there are costs for the adults such as reduced availability or poor-quality foraging resources (Black and Owen, 1989; Inger *et al*., 2010; Nolet, Gyimesi and Lith, 2014).

The benefits and costs that constrain parent-offspring associations do not influence the associations between siblings. Studies examining interactions between siblings in other taxa suggest dispersal distances of siblings may be enhanced to promote outbreeding, for example flying squirrel (*Pteromys volans*) siblings settle far from each other and in random directions from the natal nest (Selonen and Hanski, 2010). However, great tit (*Parsus* *major*) siblings associated more than expected by chance (Grabowska-Zhang *et al*., 2016) and for cooperative avian species siblings disperse together and become breeding helpers for their siblings (Sharp *et al*., 2008), these individuals can improve their fitness with potential kin-related benefits. In addition to these benefits, sibling associations may be valuable when increased group size is advantageous (i.e. anti-predation behaviour, access to resources leading to increased fitness; Weegman *et al*., 2016), although this would be the same as associating with nearby juvenile conspecifics. Direct benefits and costs of sibling associations for migratory avian species have not been investigated.

Species or populations with novel migratory or foraging behaviours are known to spread the behaviours genetically (Pulido and Berthold, 2010) or through social learning (Aplin, Sheldon and Morand-Ferron, 2013). There are no previous studies of family associations to explore the possible transmission of preferences for foraging sites or migratory strategies between family members. Advanced tracking technology has allowed us to remotely follow pairs of storks and undertake in depth investigation into their movements, migratory behaviour and family associations. I tracked adult and fledgling white storks (*Ciconia ciconia*) in a population that has recently become partially migratory (with resident and migratory birds breeding in the same colonies), a large proportion of individuals are remaining in Europe instead of undertaking the traditional migration to sub-Saharan Africa (Catry *et al*., 2017). This change in migratory behaviour started in the 1980s (Tortosa, Caballero and Reyes-Lopez, 2002; Catry *et al*., 2017) and has been associated with the use of landfill sites as foraging areas (Gilbert *et al*., 2016). It is likely that the shift in migratory behaviour was facilitated by social learning of migratory behaviour although this has not been thoroughly investigated. Post-fledging white storks (from here on termed juveniles) are known to follow adults on their first migration (Chernetsov, Berthold and Querner, 2004) but it is unknown when the social behaviour is learned, and from whom in the wild. Juveniles are known to winter in Europe on landfill sites (n = 6/54, Rotics *et al*., 2016; 6% of wintering population, Archaux, Henry and Balanca, 2008, n = 142/169, Cheng *et al*., 2019) but large numbers of juveniles are not attracted to stay at these new wintering sites.

I tracked parent-offspring and sibling pairs to understand if family members associate during the post-fledging period. I also created sibling-random juvenile pairs to see if associations with family members are different in extent to associations with random individuals from the same colony. The objectives of this study were to (1) quantify the time juveniles spend with their parents and could possibly learn from their foraging behaviour and migratory strategy, (2) quantify and compare the time sibling and sibling-random pairs spend together to understand the importance of family associations, (3) determine if variation in extent of family associations is influenced by spatial or temporal variables, such as fledging date, body size and proximity to landfill sites, (4) examine whether a juvenile's first use of landfill sites take places with a parent or with siblings, and whether sibling pairs differ from sibling-random juvenile pairs in their use of landfill sites together, (5) compare timing of migration between family pairs and sibling-random pairs and (6) determine if the extent of association with parents or siblings benefits the survival of juveniles up to the start of migration.

4.3 Methods

4.3.1 Data collection

GPS/GSM transmitters (Flyway 50 by Movetech Telemetry ©, British Trust for Ornithology, UK) were deployed on 61 juveniles and 12 adult white storks from 2016 to 2018. Transmitters were deployed as a backpack with a Teflon harness, sewn together with cotton thread as a weak link to prevent lifelong deployment (Gilbert *et al*., 2016). Juveniles were deployed with tracking devices one week before fledging (approximately 55-60 days old) and placed back in the nest immediately after deployment. Adults were caught at landfill sites with leg lassos and a remotely activated clap trap (Gilbert *et al.,* 2016), and at the nest using a remotely activated clap trap. At transmitter deployment, morphometric measurements were taken for each individual, weight, wing and tarsus measurements. Forty-eight juveniles formed 24 sibling pairs and 21 juveniles formed parent-offspring pairs with 12 adults. In 2016 and 2017 transmitters recorded locations every 20 minutes from 5 am to 9 pm GMT with one night fix at 1 am GMT and in 2018 locations were recorded every 10 minutes (5 am – 9pm GMT). Location data from the 2018 birds were resampled at the 20 minute rate to give comparable data.

Random juveniles from the same colonies as the sibling individuals were selected to create sibling-random juveniles pairs. In this study juveniles from the same nest are termed siblings and juveniles from different nests within the same colony are termed random and assumed to be unrelated. However, a recent study shows that 10.5% and 18% of nests in German and Spanish populations contain half siblings (Turjeman *et al.*, 2016); this is likely to be similar in Portugal and some siblings from the same nest may be half-siblings. Sibling pairs had a mean difference of four days in fledging dates (range 0 - 17); I chose random juveniles with fledging dates +/- four days of the sibling juvenile. Thirty sibling-random juvenile pairs were created.

4.3.2 Definition of extent of association

The extent of pair associations was calculated using GPS fixes (0600 – 1900 GMT, every 20 minutes). Fixes +/- 20 mins of each other were matched between individuals and fixes were categorised as in association if the individuals were <= 500 m apart. Flocks of foraging and flying white storks span up to 500 m. Two metrics of extent of association were calculated: the length and strength of association. The length of association is the number of days when a given pair had fixes in association. For parent-offspring pairs this was from the fledging date to last day with fixes within 500 m. For juvenile pairs, from the latest fledging date of the pair to the last day with fixes within 500 m. The association period included days with no fixes in association. The strength of associations was the proportion of fixes in association (< 500 m apart) per day and was determined for each pair using the total number of fixes obtained during the period of association. This calculation occurred after the removal of fixes < 25 m from the nest, to include only foraging locations or flying in flocks.

4.3.3 Migration strategies and phenology

Juveniles and adults were defined as migratory or resident. Migratory individuals crossed the Strait of Gibraltar to Africa and resident individuals remained in Iberia for the non-breeding period. The survival to migration was calculated as whether juveniles were successful at crossing the Strait of Gibraltar (0/1). Timing of movements were: fledging date, the first date an individual had two consecutive fixes 50 m away from the nest and date of crossing Strait of Gibraltar, the day an individual crossed latitude 36° South.

4.3.4 Influence of body size on associations and survival

The standardised residuals from a linear model describing the relationship between weight (g) and tarsus length (mm) for 129 juveniles tracked since 2013 was used to create a body size index (appendix 4.1). I investigated whether the body size indices of individual birds was associated with variation in extent of association and survival.

4.3.5 Timing and frequency of landfill site use

Use of landfill sites during associations was determined by the location of fixes within 1000 m of the centre coordinates of landfill sites in Iberia (Gilbert *et al*., 2016), this captures use of landfill sites and resting in a neighbouring location waiting for the rubbish and organic waste to arrive. Average proportion of fixes (with flight fixes, > 1.38 m/s, removed) on landfill sites per day were calculated for all individuals that used landfill sites during their associations with other individuals. The date of first use of landfill sites for all juveniles was the day of the first fix at a landfill site. Distance between nest and closest landfill site could influence landfill site use, so I calculated the straight-line distance from nest to centre coordinates of the closest landfill sites (km). Nests within 15 km from a landfill site are termed close to landfill sites, based on adult use of landfill sites and regular foraging trips to landfill sites (Gilbert *et al*., 2016), and nests over 15 km from a landfill site are termed far from landfill sites.

4.3.6 Statistical Analysis

To understand if family pairs and pairs of random individuals are similar, the length and strength of association for parent-offspring and sibling pairs and sibling and sibling-random juvenile pairs were compared with t-tests. Log- or square root-transformations were used to normalise the data.

I investigated whether the family associations were influenced by temporal and spatial variables. The length and strength of association could be influenced by distance between nest and landfill site, juvenile fledging date or juvenile pre-fledging body size. Length of association was investigated with linear mixed models. Due to small sample sizes (23 parent-offspring and 24 sibling pairs) variables' influence on length of association were investigated in three separate models. Therefore significance was defined as $p < 0.0125$ (Bonferroni correction). Year (2016, 2017 and 2018) was included as a random effect, to control for differences in sample sizes and environmental conditions in each year. The strength of association per day was investigated using a binomial generalised linear mixed model, variables were removed if there was collinearity, day since fledging was included as a fixed effect, with pair ID and year as random effects. In addition, for the models investigating extent of sibling associations, the mean fledging date and body size indices of each pair were fixed effects. The influence of the length of family associations on survival to start migration (binary outcome) were examined with binomial GLMMs. Models were compared with AIC and the most parsimonious model, with the lowest AIC, was chosen. If two or more models were within Δ2 AIC the model with the fewest parameters was selected.

Behaviour metrics were compared within parent-offspring pairs and between sibling and sibling-random juvenile pairs. Timing and frequency of landfill site use as well as timing of migration were compared. Parent and offspring metrics were compared with univariate tests depending on the normality of the data. The differences in behaviours between individuals in sibling pairs were compared to the differences between individuals in sibling-random juvenile pairs. All statistical analysis was undertaken in R 3.5.0 and RStudio.

4.4 Results

4.4.1 Comparison of extent of associations between pair types

The length of associations of parent-offspring and siblings pairs were not significantly different from each other and neither were the length of associations of sibling and sibling-random juvenile pairs, with mean lengths of 24 and 22 days respectively (Table 13, appendix 4.2). Sibling and sibling-random juvenile pairs do not differ in the strength of their associations with a mean of 59% fixes in association per day (Table 13). The parent-offspring pairs are significantly different from sibling pairs in strength of association, sibling pairs have higher mean association fixes than parent-offspring pairs (Table 13, appendix 4.2).

Table 13. Length (days) and strength (percent of fixes in association per day) of associations were examined for parent-offspring, sibling and sibling-random pairs of white storks (mean and lower-upper 95% confidence intervals). Parent-offspring and sibling pairs, sibling and sibling-random juvenile pairs were compared with Welch Two Sample t-test (t statistics, df and p value). Length of association was square-root transformed to normalise the data for t-tests. P values were considered significant if < 0.05 and indicated in bold.

	Length of association (mean days, 95% CI)	Comparisons in length	Strength of association (mean % day^{-1}, 95% CI)	Comparisons in strength	N
Parent-offspring	28.17 (19.76 - 36.58)	$T_{38.87}$ = -1.51, p = 0.14	24.67 (18.94 – 30.39)	$T_{41.57}$ = 7.64, p **< 0.0001**	23
Siblings	19.75 (15.05 – 24.45)		60.58 (52.71 – 68.45)		24
Sibling-random juvenile	23.87 (19.57 – 28.16)	$T_{45.91}$ = -1.48, p = 0.15	57.49 (50.18 – 64.79)	$T_{50.38}$= 0.59, p = 0.56	30

4.4.2 Drivers of family associations

Parent-offspring associations were influenced by temporal variables. Length of association for parent-offspring pairs was influenced by fledging date (Table 14, Figure 25); offspring with earlier fledging dates had longer associations with their parents. The strength of parent-offspring associations were negatively influenced by day since fledging, with greater time since fledging strength of association reduced (Table 14, Figure 25). Strength of association was not influenced by pre-fledging juvenile body size indices or fledging date.

Sibling associations were influenced by temporal and spatial variables. Length of association between sibling pairs was negatively influenced by distance between nest and closest landfill site (Table 14, Figure 25). Siblings from nests closer to landfill sites had longer associations. The strength of associations were negatively influenced by day since fledging (Table 14, Figure 25) and were not influenced by distance between nest and closest landfill site.

Table 14. Output of most parsimonious models investigating how length and strength of associations for family pairs were influenced by temporal and spatial variables. Variables were considered to have a significant influence on the extent of association if p values were < 0.025 (Bonferroni correction) and are indicated in bold.

Extent of association	Pair type	Variable	Estimate (SE)	df	Test statistic	P value	Random effects (variance, SD)	R squared		n
								Marginal	Conditional	
Length of association	Parent-offspring	Body size index	1.45 (3.29)	18.57	T = 0.44	0.66	Year = 216.5, 14.71	0.32	0.71	23
		Fledging date	-1.27 (0.32)	17.67	T = -3.99	**< 0.0001**				
	Sibling	Distance from nest to landfill site (km)	-0.69 (0.17)	22	T = -4.11	**0.0005**	Year = 73.28, 8.56	0.42	0.42	24
Proportion of fixes in association (per day)	Parent-offspring	Day since fledging	-0.019 (0.001)		Z = -13.61	**< 0.0001**	ID = 0.44, 0.66 Year = 0.08, 0.28	0.03	0.16	620
	Sibling	Day since fledging	-0.07 (0.003)		Z = -25.97	**< 0.0001**	ID = 0.74, 0.86 Year = <0.0001, <0.0001	0.09	0.26	473

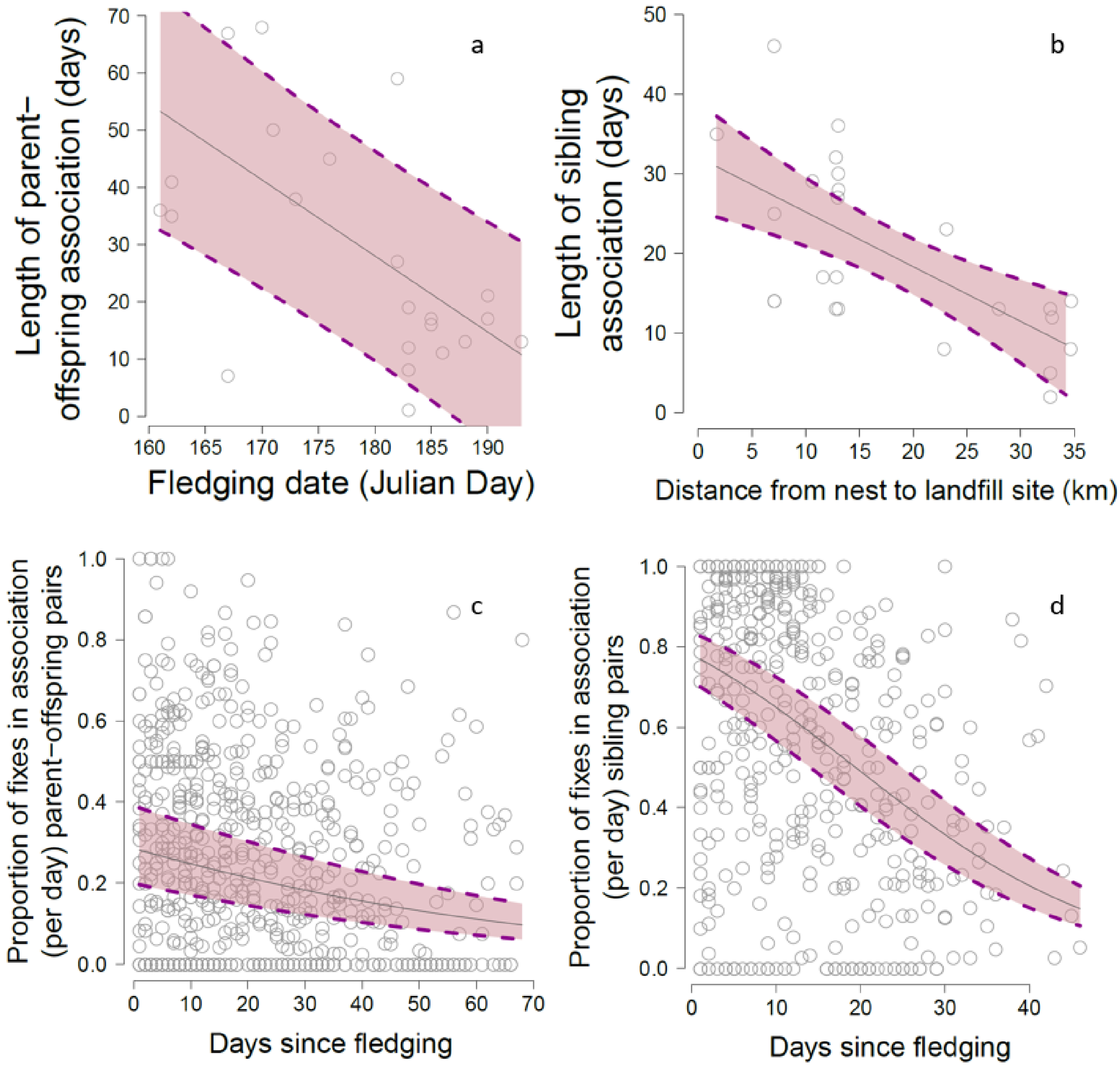

Figure 25. The significant influence of temporal and spatial variables on the extent of the association between family pairs, parent-offspring and sibling pairs. Length of association (a) was influenced by fledging date for parent-offspring pairs and distance from nest to landfill site (b) for sibling pairs. The proportion of fixes in association per day, (c) and (d), for family pairs was influenced by days since fledging.

4.4.3 Landfill site use during associations

Parent-offspring pairs were split between nests close to (n = 10) and far from landfill sites (n = 13; Table 1, appendix 4.3 and 4.4). Three offspring did not use landfill sites: two did not survive > 7 days after fledging from nests > 15 km from a landfill site and their parents did not use landfill sites during their association. The third juvenile survived 41 days after fledging, was from a nest < 15 km from a landfill site and its tagged parent used landfill sites during their association. Thirteen offspring used landfill sites during the association with their parents and four were in association with their tagged parent on their first visit. Adults used landfill sites on average +/- 18 hours from their offspring's first use of landfill sites (Table 15). Parents and offspring did not differ in their use of landfill sites (Table 15). For offspring, a high proportion of their use of landfill sites was in association with parents, whereas for parents the time at landfill sites with offspring was a small amount of their total use of landfill sites (Table 15).

Differences between siblings in timing and frequency of landfill site use were not significantly different from the differences between sibling and a random juveniles (Table 16). One sibling pair (1/12) used landfill sites for the first time within two hours of each other and one sibling-random juvenile pair (1/23) used landfill sites for the first time within an hour of each other. Individuals of five sibling pairs and eleven sibling-random juvenile pairs both used landfill sites during the association.

Table 15. Variation in behaviour metrics of offspring and parents and differences between individuals. The mean and upper and lower 95% confidence intervals are shown. Comparisons between parents and offspring using paired univariate tests, test statistics and p-value are shown. P values were considered significant if < 0.01 (bonferroni correction) and are indicated in bold.

	Offspring mean (95% CI)	Parent mean (95% CI)	Comparison between offspring and parents	Difference between parent and offspring Mean (95% CI)	N (Pairs)
Hours between offspring use and adult use (on day of offspring first use of landfill sites)	-	-	-	18.19 (1.11 – 35.27)	12
Proportion of landfill site use during association	0.41 (0.23 – 0.59)	0.23 (0.16 – 0.29)	W = 61, p = 0.077	0.29 (0.12 – 0.45)	12
Proportion of landfill site use together	0.36 (0.26 – 0.45)	0.07 (0.04 – 0.1)	W = 44, p = **0.008**	0.29 (0.20 – 0.38)	9
Days between fledging and first landfill site use	18.56 (12.08 – 25.05)	3.36 (-1.48 – 8.21)	W = 75, p = **0.0024**	16.13 (9.12 – 23.14)	12
Distance moved (km day-1)	10.20 (7.24 – 13.17)	23.11 (19.14 – 27.08)	T_{22} = -5.05, p **< 0.0001**	12.93 (7.63 – 18.23)	23
Proportion of flight fixes (day-1)	0.06 (0.04 – 0.07)	0.08 (0.07 – 0.10)	T_{22} = -2.42, p = 0.024	0.03 (0.004 - 0.5)	23
Date of migration (Julian date, crossing strait of Gibraltar)	10-Aug (02-Aug – 19-Aug)	04-Aug (19-Jul – 20-Aug)	-	14.80 (2.25 – 27.35)	5

Table 16. Variation in behaviour metrics within sibling and sibling-random juvenile pairs with mean and upper and lower 95% confidence intervals shown. The comparison of the differences between sibling pairs and sibling-random juveniles, undertaken with t-tests and Wilcoxon signed rank tests (test statistic and p-value shown). Time between fledging and first landfill site use in association was square-root transformed to make the data normally distributed. P values were considered significant if < 0.05.

	Sibling Pairs Mean (lower and upper 95% CI)	N (pairs)	Sibling-random juvenile pairs Mean (lower and upper 95% CI)	N (pairs)	Comparison between pair types (test statistic and P-value)
First use of landfill sites (days)	2.83 (2.99 – 8.83)	16	6.96 (4.47 – 9.43)	23	$T_{35.56} = 0.82$, p = 0.42
Proportion of landfill site use during association (day^{-1})	0.17 (-0.04 – 0.39)	5	0.15 (0.09 – 0.21)	11	$T_{4.9}=0.26$, p = 0.81
Proportion of landfill site use together during association	0.07 (-0.03 – 0.18)	4	0.24 (0.04 – 0.44)	10	W = 15, p = 0.54
Time between fledging and first landfill site use during association (days)	4.76 (-2.31 – 11.83)	5	7.98 (2.87 – 13.09)	11	$T_{10.20}=-0.76$, p = 0.46
Distance moved (km day-1)	5.10 (2.69 – 7.50)	24	3.73 (2.33 – 5.13)	30	W = 399, p = 0.50
Proportion of flight fixes (day-1)	0.03 (0.02 – 0.04)	24	0.02 (0.01 – 0.03)	30	$T_{47.64}=0.99$, p = 0.33
Difference in date of migration (Julian date, crossing strait of Gibraltar)	20.78 (8.01 – 33.54)	9	17.5 (13.14 – 21.86)	10	$T_{9.93}=0.55$, p = 0.59

4.4.4 Migratory behaviour and survival to migration

All juveniles that survived to their first non-breeding period (European winter) migrated to Africa. Seven juveniles (30%) from parent-offspring pairs died and one juvenile's tag stopped transmitting before crossing the Strait of Gibraltar. Of the remaining 13 offspring, five had a migratory parent (three adults) and eight had a resident parent (six adults). No parent and offspring migrated on the same day, migration dates between parents and offspring were on average 15 days apart (Table 15).

Out of the 48 juveniles in the sibling pairs, 18 (38%) did not survive to migrate to Africa while the remaining juveniles crossed the Strait of Gibraltar, five individuals had known logger failure and 13 died in Iberia. For the pairs where both individuals migrated, the differences in date of migration between siblings and between sibling and random juveniles were not significantly different (Table 16).

The likelihood of juveniles surviving to cross the Strait of Gibraltar was not influenced by the length of associations with parents or siblings. Length of association did not remain in the most parsimonious model which was the null model for both pair types.

4.5 Discussion

This study highlights that white storks are gregarious and have regular associations with individuals from their colony, however they do not have specific, long standing associations with family members like other gregarious migratory species. The white stork family associations did not surpass 70 days, whereas tight family associations seen in some geese species are seen throughout the juvenile's first migration and non-breeding period, well over 200 days (Gupte *et al*., 2019). Family associations between white storks did not differ in length to associations between two randomly chosen juveniles from the same colony. Many species of social birds learn from conspecifics that are not related to them (Fritz and Kotrschal, 1999; Boogert *et al*., 2014). Interestingly, the proportion of fixes that individuals spent together were significantly greater for juvenile pairs than parent-offspring pairs, suggesting first-year juveniles stay together in post-fledging/pre-migration flocks for foraging and flying, regardless of relatedness.

Fledging date and proximity of nests to landfill sites influenced the length of the family associations I studied. These temporal and spatial variables indicate that the length of association is due to the amount of time juveniles spend around the nest/colony area. Juveniles are more likely to stay close to landfill sites after fledging, before moving on and migrating. In addition, juveniles that fledged earlier in the season stay in the nest/colony area longer before migration further increasing the likelihood of spending time together.

The proportion of fixes in association within family pairs was influenced by time since the start of association. The proportion of fixes in association per day decreases with time since fledging as juveniles become more independent and move greater distances, eventually moving away from the nest/colony area and migrating to Africa. The results indicate that juveniles gradually stop associating with members of their own colony, presumably following cues for other flocks and the environment as they prepare to migrate.

All the juveniles in this study were migratory while 77% of all parents were resident, suggesting small influence between migratory behaviour of parents and offspring. Any potential genetic component for migratory strategy, migratory vs resident behaviour, that could be inherited from a parent needs to be further investigated but this study shows that juvenile migratory behaviour is not socially transmitted from a parent. Additionally, if migratory behaviour is socially transmitted by learning from other conspecifics I would have expected some juveniles to be resident due to the large numbers of storks remaining in Iberia for the non-breeding period (Catry *et al*., 2017; Cheng *et al*., 2019). However there were none observed in this study suggesting that juveniles could have an innate desire to migrate and follow adults that migrate to Africa. Despite social information being available, colonial and gregarious species do not always use it, for example gulls do not use social information from conspecifics to find foraging locations (Racine *et al*., 2012). If migratory strategy was purely socially transmitted in white storks, migration behaviour could be lost if the number of migratory adults becomes too small (Foss-Grant, Bewick and Fagan, 2018).

The use of landfill sites, a novel foraging area, was studied to understand if juveniles follow adults to the best foraging locations. The juveniles in this study did not follow tagged parents to landfill sites, only 16% visited landfill sites for the first time with their parent. However, only one parent of each offspring was tracked and it cannot ruled out that the juvenile followed the other parent. I show that juveniles are gregarious and follow conspecifics to reach landfill sites but they do not specifically follow their parents or siblings.

Survival to migration was not influenced by extent of the associations, or the temporal and spatial variables that correlated with length of association, fledging date and proximity of nest to landfill sites. The cause of mortality for juveniles during the post-fledging period is extremely stochastic, caused by electricity pylons (Garrido and Fernandez-Cruz, 2003) or other anthropogenic or natural causes (Tobolka, 2014). I showed there were no potential benefits of social interactions with a particular individual for survival.

This study shows that siblings, juveniles from the same nest, are independent of each other. This could impact on future studies providing greater sample sizes and increased statistical power if siblings can be treated independently of each other. Potential future studies investigating family members in white storks would benefit from understanding the kin recognition in this species (Nakagawa and Waas, 2004).

Chapter 5

General Conclusions

The end of a good day. Photo taken by K Rogerson.

5.1 Key findings from this study

Juvenile white storks from southern Portugal forage at landfill sites during the post-fledging weeks and, prior to starting migration, the extent to which they use landfill sites varies between individuals (use before migration varied from 0 – 64% of fixes on landfill sites; Chapter 2). Mortality rates of first-year juveniles varied with use of landfill sites before migration, with lower mortality for juveniles that used more landfill sites (Chapter 2). The period with highest juvenile mortality was between fledging and the start of migration, suggesting that the period when juveniles learn how to find resources, fly effectively and avoid predators is critical for their survival. The proximity of nests to landfill sites and pre-fledging body size were not related to juvenile mortality, suggesting that parental use of landfill sites and natal conditions were not associated with mortality.

White storks forage on landfill sites across North Africa, Morocco and Algeria, and the use of landfill sites in Africa has been quantified here for the first time for migratory juvenile white storks (Chapter 3). The phenology of the southward migration during the first year of life varied with use of landfill sites (Chapter 3). Individuals that use landfill sites during the post-fledging period started migration later, and those that used landfill sites more during migration had slower migrations, taking more days and having slower flight speeds, than those that used landfill sites less.

Tracking the migration routes of juvenile white storks from Portugal to Africa showed that 8% stayed in Morocco for their non-breeding season. This shows that North Africa is used during the non-breeding period and should be indicated as such on distribution graphs for the species (Figure 26). The remainder migrated to sub-Saharan Africa (Chapter 4). Migration took an average of 38 days, with a mean start date of 28 July for leaving the colony area and mean end date of 4 September for arriving in the Sahel region. The mean maximum flight speed per day on migration was 41 km/hour. In comparison the northward migration from Sahel to Iberia, was longer and slower, being 82 days on average with a mean maximum flight speed per day of 31 km/hour. In addition, there was huge variation in start date of northward migration with some returning across the Sahara Desert in November while others waited until March to cross the Sahara. This huge variability indicates diversity in migratory strategy for juveniles, either following cues from the local environment, for example resource levels and weather conditions, or following other white storks.

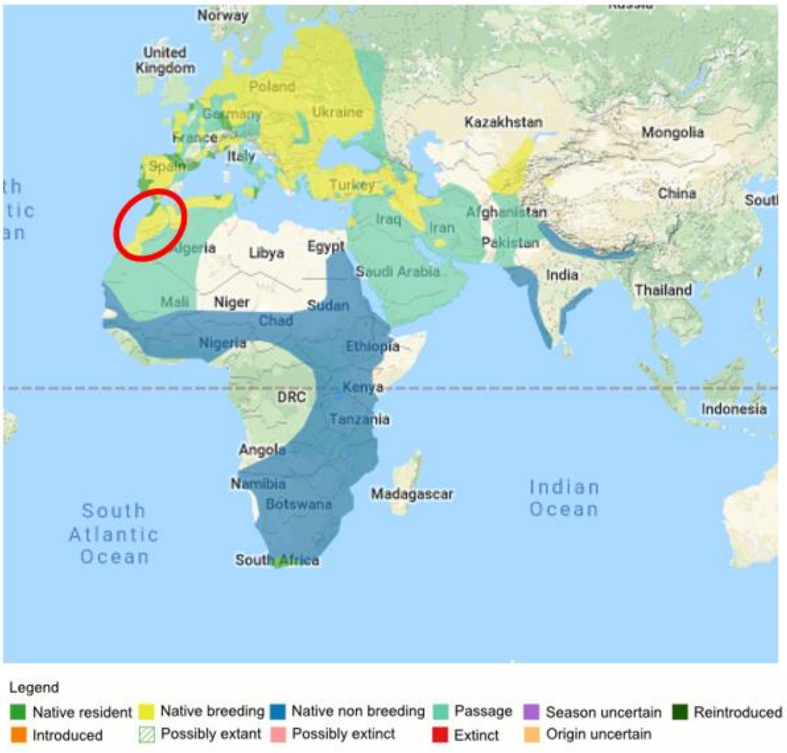

Figure 26. Map of white stork geographic distribution adapted from online map by Birdlife International (2019). The red circle indicates the area where four tracked juveniles stayed during the non-breeding period.

A surprising result from tracking juveniles from this white stork population of southern Portugal, for which a large proportion of adults are resident in Europe (Catry *et al.*, 2017), was that all surviving tracked juveniles (2016 - 2018) migrated to Africa in their first year. Two juveniles from this population tracked in 2013 and 2014, out of 14 with known migratory decisions, were residents and remained in Iberia during their first non-breeding season. Studies from other populations in central Europe indicate that juveniles often stay in Iberia for the non-breeding season (Flack *et al.*, 2016; Arizaga *et al.*, 2017; Cheng *et al.*, 2019). Therefore the expectation was that some tracked juveniles from 2016 to 2018 (n = 107) would be resident and that my research might disentangle differences between resident and migratory juveniles. My results suggest that, for the juveniles tracked since

2016, the use of landfill sites does not influence migratory strategy. In addition, parental migration strategy is unlikely to influence juveniles' migratory behaviour as family members do not associate with each other during the post-fledging period any more than unrelated birds (Chapter 4). All tracked juveniles were migratory, while 62% of juveniles with known strategy and a tracked parent, had a resident parent (Chapter 4). Additionally, juveniles did not appear to learn locations of landfill sites and their use of foraging locations from their parents (Chapter 4). Juveniles are known to follow conspecifics on migration (Chernetsov, Berthold and Querner, 2004; Flack *et al.*, 2018) and are also likely to learn the locations of landfill sites from conspecifics.

My study contributes to the understanding of the drivers behind migratory behaviour of white storks. I have shown that juveniles do not learn from family members in establishing migratory strategies but also are unlikely to respond to potential cues to remain in Iberia from conspecifics and resource availability at landfill sites. This is indicated by such a high proportion of adults remaining in Iberia whilst all Portuguese juveniles in this study were migratory.

5.2 Further points

5.2.1 What is migration?

During this research, questions have arisen around how to define migration. The theoretical definition of migration, as defined by Winger *et al.* (2019), is: *"a regular, seasonal round-trip movement between a region where young are reared … and a non-breeding region or regions*" (Winger *et al.*, 2019). However, practically defining migration is difficult when data is available from tracking devices. White storks have a variety of migratory strategies and stopover durations making the identification of start and end of migration challenging.

Several definitions of when migration starts and ends have been used and proposed in the current literature. Some of the definitions for start and end dates of migration using movement data include: (1) a *distance-moved cut-off*, either relating to daily displacements

(Vansteelant *et al.*, 2015; Vidal-Mateo *et al.*, 2016) or changes in latitude (Flack *et al.*, 2016; Rotics *et al.*, 2016; Cheng *et al.*, 2019). (2) A *speed cut-off* can be used to define the first migratory day at a breeding/non-breeding area (Burnside, Collar and Dolman, 2017), although this method requires a known definition of breeding/non-breeding area. (3) *Direction of movement* can use unidirectional movements of birds on migration to indicate migration compared to local movements of birds within a breeding or non-breeding site (Shamoun-Baranes *et al.*, 2003). However, this requires the breeding and non-breeding site to be known and multiple non-breeding areas used by one individual would make this definition difficult to use for some species. (4) A *geographical cut-off* can be used such as a certain latitude or defining area around the breeding/nonbreeding areas to be able to define start or end dates of migration (Meyburg *et al.*, 2017; Baert *et al.*, 2018).

These practical definitions of migration phenology show the variation in ways that movement data can be used to define the same theoretical behaviour. They highlight how different species, and populations within species, at different geographical locations may require different definitions for the researcher to gain meaningful start and end dates.

There has been a move to quantify migration movements objectively using the Net Squared displacement (NSD) method (Bunnefeld *et al.*, 2011). The NSD method uses nonlinear models to distinguish migratory movements from other types of movements such as nomadic and dispersal ones and calculate start and end dates for these movements. However researchers must carefully consider the start locations, frequency of data sampling and the full extent of movement when they use this technique (Singh, Allen and Ericsson, 2016).

From discussions with colleagues and visual inspection of the location data it seemed a *direction of movement* definition would be a preferable method to define the start of migration for Portuguese birds. However, due to the location of nests across Portugal, juveniles start migration by moving south or east and some even move north first before moving south and east. So, one direction of movement would not fit all juveniles (Figure 27b).

During my research, as my knowledge of migration and movement of white storks developed, and depending on the objectives for the metrics of migration, I used five different methods to define migration phenology. Firstly, I used the NSD method to define start and end dates of migration. However, on visually inspecting dates on maps of migratory movements it seemed that for some individuals movements within the non-breeding areas were being defined as migratory movements (Chapter 2). Secondly, for the birds with NSD dates that didn't match their movements, I used a *distance-moved cut-off* of 70 km daily displacement coupled with allowing 13 days for of < 70 km displacement (mean length of stopovers; Chapter 2). This two-step approach felt unsatisfactory for all birds because I was defining migration differently based on individual movement behaviour rather than using the same rule for all. Thirdly, in Chapter 3, I defined the colony area for each juvenile as 15 km around their nest (based on the mean foraging distance of juveniles while they roost at the nest), and first date of leaving the colony area and not returning to it was used as a proxy for starting migration. This definition meant that movement within Iberia was captured within the migration period for each bird, as fuelling and stop overs are all part of migration behaviour (Alerstam and Bäckman, 2018). Fourthly, to define the end of migration for Chapter 3 I used a *geographical cut-off*, I used the latitude of 18.4°N to define arrival at the non-breeding region, the Sahel. This cut-off was chosen as white stork juveniles' use multiple areas in the Sahel and it would be difficult to distinguish between stop overs and non-breeding areas. Therefore, choosing one non-breeding area or a change in daily displacements did not make sense given the itinerant behaviour they exhibit (Figure 27b). Finally, in Chapter 4 I used a *geographical cut-off* of crossing the barrier of the Strait of Gibraltar (latitude 36°N) to define birds that were migratory, although the analysis in Chapter 4 did not require an exact date of starting migration.

A manuscript is in preparation, written by a colleague, which examines four methods of defining migration phenology. The methods (geographical cut-off, distance-moved, NSD and distance-moved with a temporal restriction) were used on data from eight migratory white storks from our tracked birds of the Portuguese population. The variation in dates of southward migrations was small (with the mean median difference in duration of migration between methods being 3, SE = 0.5), while variation for dates of the northward migrations was larger (mean median difference in duration of migration between methods being 15, SE = 5). Of these four methods explored, the results suggest the method with a distance-moved cut-off coupled with a temporal restriction was best for these individuals as it was less varied across the individuals. Expert knowledge of the study species is needed to be able to calculate spatial and temporal thresholds and reduce arbitrariness of the restrictions. In addition, the practical definition used for migration depends on the biological question being asked for the population, species or migratory behaviour. When comparing migration phenology for species across studies and papers it is crucial to understand the different methods that have been used and could result in different parameters.

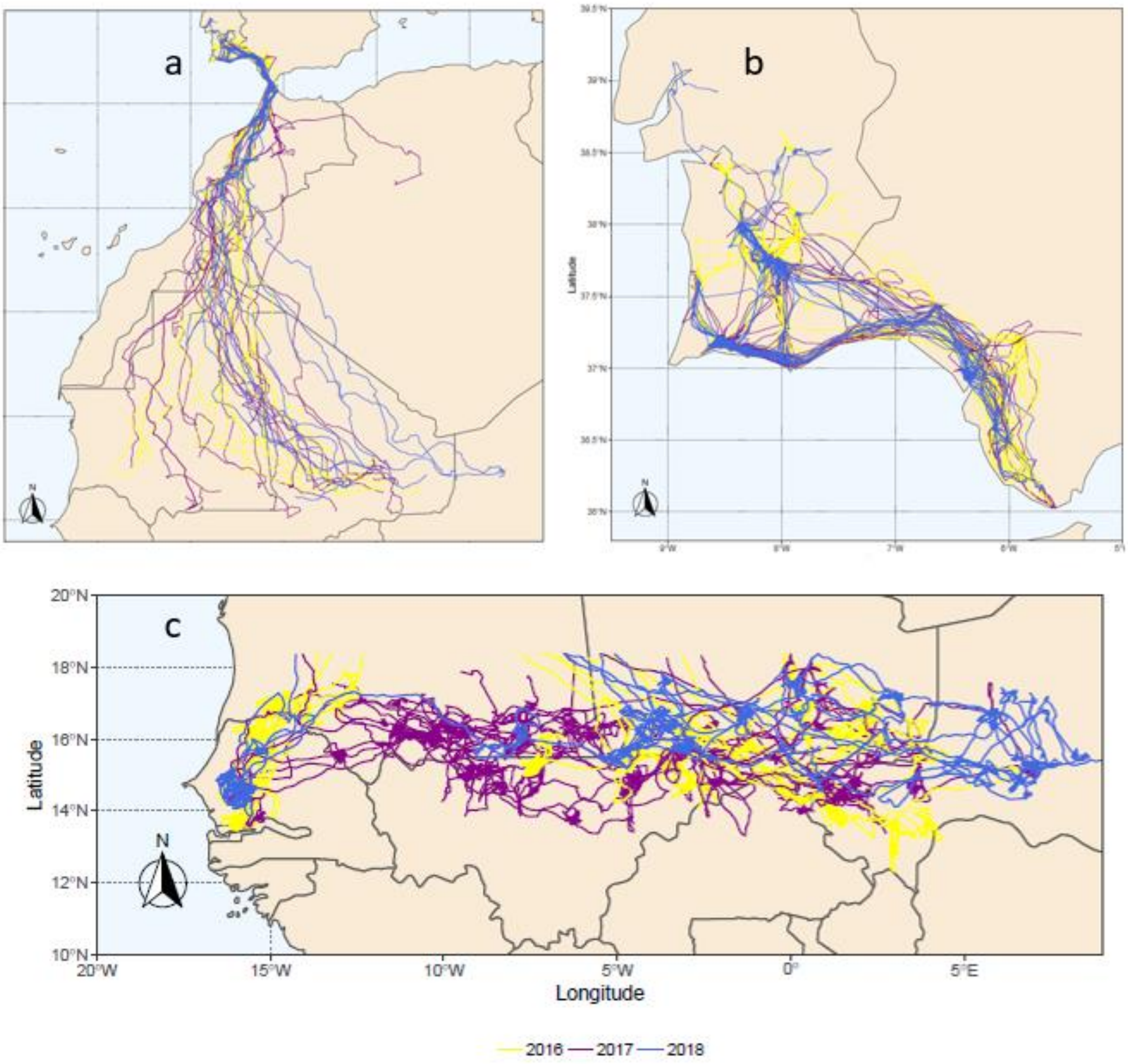

Figure 27. Map of juvenile movements (a) whole southward migration for first year juveniles, from leaving the colony in Portugal to entering the Sahel region, (b) in Europe from fledging to crossing the strait of Gibraltar in Spain and (c) in sub-Saharan Africa, the Sahel (latitude < 18.4°), during their first non-breeding period. Tracks are coloured by year of fledging.

5.2.2 Potential responses of removing anthropogenic food subsidies

Anthropogenic food subsidies are used as a conservation management tool for declining or re-introduced wildlife populations (Ewen *et al.*, 2015). They can benefit such populations, positively influencing survival rates and improving breeding success (Schabo *et al.*, 2017). In addition, subsidies from anthropogenic waste also positively influence wildlife populations across the world (Plaza and Lambertucci, 2017).

It could be considered that these anthropogenic waste subsidies are artificially inflating wildlife populations beyond the limits that would be set by natural resources (from discussions at conferences). This argument might suggest that the removal of the waste subsidies, due to changes in waste policies and regulations, would be a benefit to the wildlife and the local environment. However, these food waste subsidies have influenced ecosystems for decades and removal might detrimentally impact wildlife numbers and influence the wider community.

In addition, the argument that the populations are “artificially inflated” suffers when the term “artificial” is considered. For some it will describe a man-made situation while others will think of it as a situation different from the norm. Ecosystems and communities have been influenced by anthropogenic activities for millennia. Birds associated with farms have been particularly influenced. House sparrows (*Passer domesticus*) and common starlings (*Sturnis vulgaris*) used to have large populations during the early 20th century when they fed off grain in the fields, stores and livestock feed. However agricultural practices changed in the second half of the 20th century (for example intensification with rearing livestock indoors, increased use of pesticides removing invertebrate prey and secure post-harvesting storage of grain) and their populations declined rapidly (Robinson, Siriwardena and Crick, 2005a, 2005b). Farmland bird populations are still in decline (Donald, Green and Heath, 2001). In addition, urban house sparrows were detrimentally affected in the 1920s when reduction of horse-drawn vehicles lead to declines in dung and grain in urban areas (Robinson, Siriwardena and Crick, 2005a). These previous large bird populations from anthropogenic subsidies at farms and in urban areas could be considered artificially high.

Current waste subsidies at landfill sites and fisheries are just following the trend of other anthropogenic subsidies in the past.

An issue with the species that use our waste resources, especially in urban areas, is that they may start to be considered a nuisance or a "pest". In the UK, garden birds that are fed by humans with feeders and bird tables are viewed positively and considered worthy of food provisions (Cox and Gaston, 2018). In addition endangered birds, such as the red kite, are fed in gardens (Orros and Fellowes, 2015b). However, scavenger species in the UK, like herring gulls (*Larus argentatus*), are considered a nuisance and local councils have banned people from feeding them in popular seaside towns (for example East Devon - https://www.independent.co.uk/news/uk/home-news/feeding-seagulls-fined-east-devon-district-council-public-space-protection-order-a7711991.html and West Dorset - https://news.dorsetforyou.gov.uk/2018/04/20/ban-on-feeding-gulls/). This is due to the human-gull conflicts owing to their food scavenging behaviour (Goumas *et al.*, 2019) and is despite the fact that herring gulls have a declining population in the UK (Eaton *et al.*, 2015). White storks, with their increasing population in Portugal (Catry *et al.*, 2017), are beginning to be seen as a pest in the agricultural landscape. During my fieldwork, farmers and landowners talked about their dislike of storks, for example trampling plants in rice fields as they forage on crayfish, and the nuisance of having large nests on their buildings. This is despite the fact that white storks feed on agricultural pests, such as grasshoppers, and can provide a service for farmers.

I do not argue here that reducing food waste should be condoned, reduction will increase food security that is a benefit for our growing human population in the rapidly changing environment (Gordon *et al.*, 2016). However, we could consider giving access to the food that we do waste as a subsidy to wildlife populations. Over the past century, the large proportions of wildlife across taxa and across the world have been negatively influenced by anthropogenic activities, from deforestation to urbanisation and pollution. When our activities, or the side effect of our activities, such as our waste, provide a benefit to wildlife, should we not consider that an advantage?

Additionally, human behaviour could be changed to improve the potential human-wildlife conflicts arising from providing subsidies to wildlife, even those considered as pests (Baruch-Mordo *et al.*, 2009). We consider that some scavengers are performing an ecosystem service by recycling our organic waste (Sekercioglu, 2006); for example vultures that eat the carcasses of livestock or wild animals are removing the carcasses from the landscape, limiting the spread of diseases and maintaining energy flows throughout the food webs (Sekercioglu, 2006; Dupont *et al.*, 2012). Scavengers consuming our organic waste at other locations are providing a similar service. In addition, other cultures interact with wildlife and provide subsidies for their benefit in spite of increasing human-wildlife conflicts, for example Muslims provide meat for black kites in Delhi despite attacks on humans (Kumar *et al.*, 2019). Our attitude to waste and the species that feed on it could be changed, to instead think of the benefits our waste can potentially provide to wildlife.

5.3 Future research

Continued tracking of adults and juvenile white storks in the Portuguese population will improve understanding of the drivers of variation in migratory behaviour. Long term tracking will provide further understanding of the flexibility of migratory behaviour in the population, distinguishing between individual variability of migration behaviour between years, and whether individuals are consistent and the change in frequency of migrants and residents is due to juvenile birds, i.e. generational change (Gill, Alves and Gunnarsson, 2019). It will be crucial to use and develop tracking devices with longer life spans; ©Movetech Telemetry devices used since 2016 have lasted a maximum of 3 years. Tracking of adults and juveniles would be needed, and it would be beneficial to increase the region where birds were tracked from to include northern Portugal, as well as collaborating with researchers in Spain to understand variation in migratory strategies across the Iberian Peninsula and the environmental conditions that are associated with differences in migratory behaviour. Improving the ringing effort of white storks in Portugal and the re-sighting effort across their annual geographic range and throughout the year could have cheaper upfront costs but would require longer time spans to collect sufficient data to investigate variation in migratory strategy.

Further to this study, 11 juveniles that were tracked in 2016 and 2017 were tracked for a second year and four were resident in Iberia for their second non-breeding season while the rest made a second migration to Africa (Figure 28). Increasing the sample size of tracked second year juveniles will enable us to understand the possible factors behind their decision to switch from being a migrant to resident. It could be predicted that use of landfill sites and social cues from resident adults will encourage second year birds to become resident but it could also be attributed to conditions in the region they used for their non-breeding period in their first year or on their first migration.

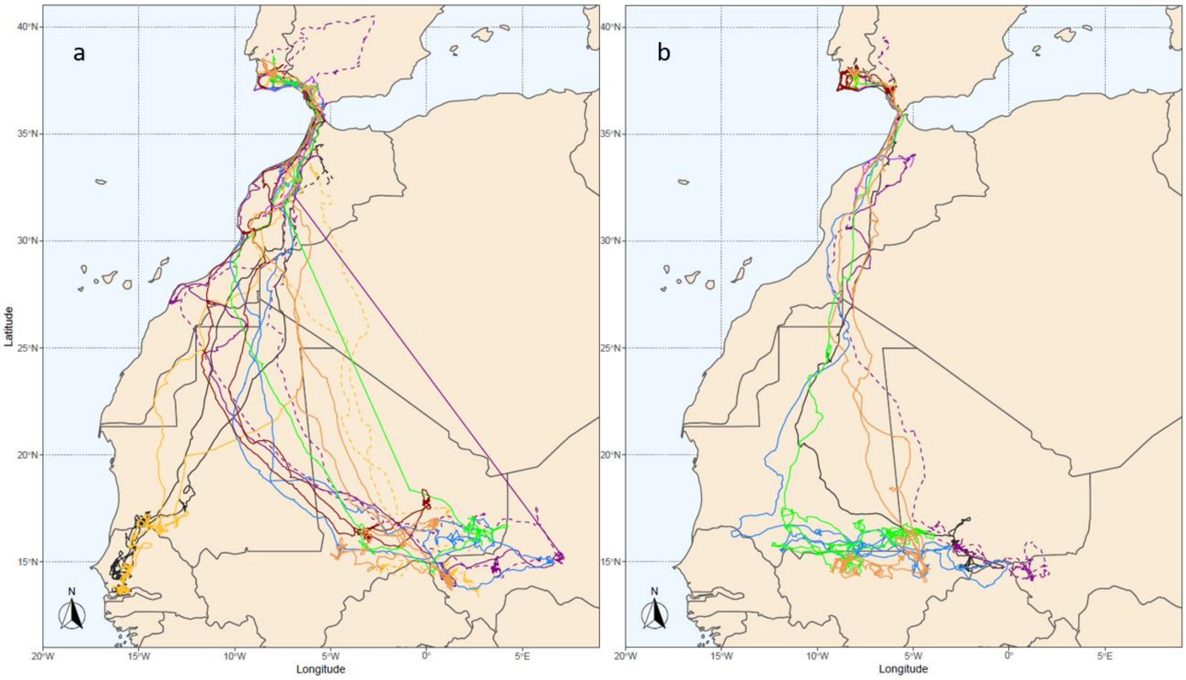

Figure 28. Maps of tracks for juveniles (n = 11) that were tracked for more than 1 year: (a) tracks of the first year, all migrated and (b) tracks of second year, four remained in Iberia. Colours are the same for individuals across maps, birds tracked in 2016 and 2017 have solid lines, while birds tracked in 2017 and 2018 have dashed lines.

In addition, it is important to maintain the tracking and study of white storks migratory behaviour while the amount of organic waste at landfill sites is being reduced, as per EU regulations (*EU Directive 2018/851*, 2018). This would enable us to understand the influence of landfill sites in maintaining the high resident population. This further study would benefit from obtaining information from companies managing landfill sites, to quantify exact levels and the reduction of organic waste at the landfill sites, which has so far been impossible. The information from monitoring migratory and foraging behaviour from GPS devices, as well as continuing observations of numbers in non-breeding populations and breeding success, would provide a full picture on the changes that are occurring in the white stork population with the removal of an important food resource.

As the organic waste at landfill sites in Portugal is reduced, it is important to understand if the resident population will be maintained in Iberia in the non-breeding period (Figure 29). To fully understand the impact of landfill sites as a food resource, and the impacts of the removal of the resource, further research is needed to identify the amounts of natural food available for white storks in the summer and winter, and using this to make predictions of the number of white storks the natural resources can support. This includes gaining a better understanding of the reliance of white storks on invasive crayfish in rice fields and waterways (Tablado *et al.*, 2010; Sanz-Aguilar *et al.*, 2015; Gilbert, 2016).

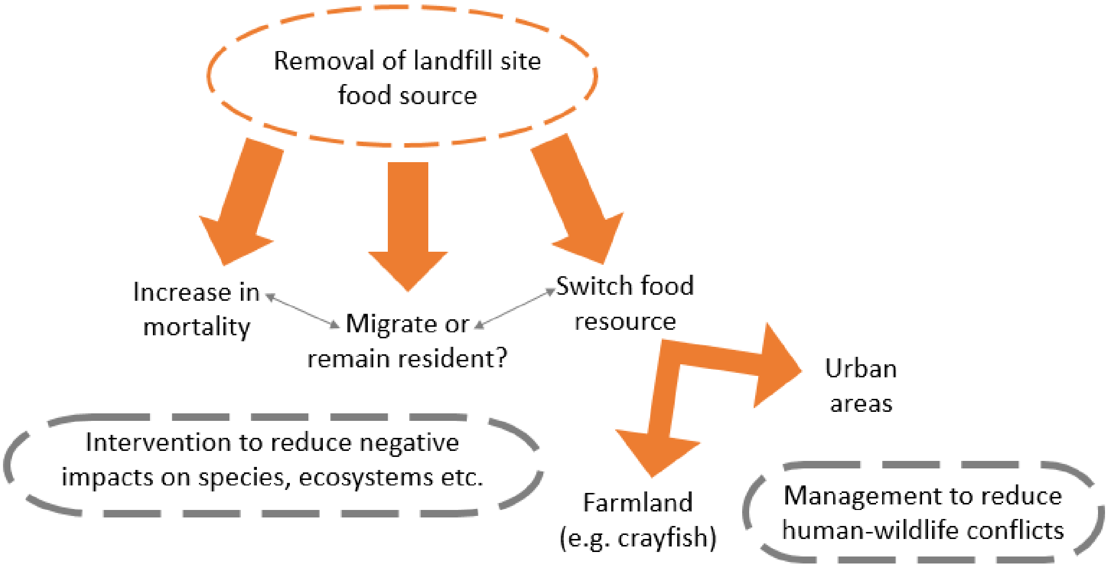

Figure 29. Conceptual diagram of how the removal of the food at landfill sites may impact on white storks and the local ecosystem. Adapted from Figure 3 by Newsome and Eeden (2017), as seen as Figure 1 in Chapter 1.

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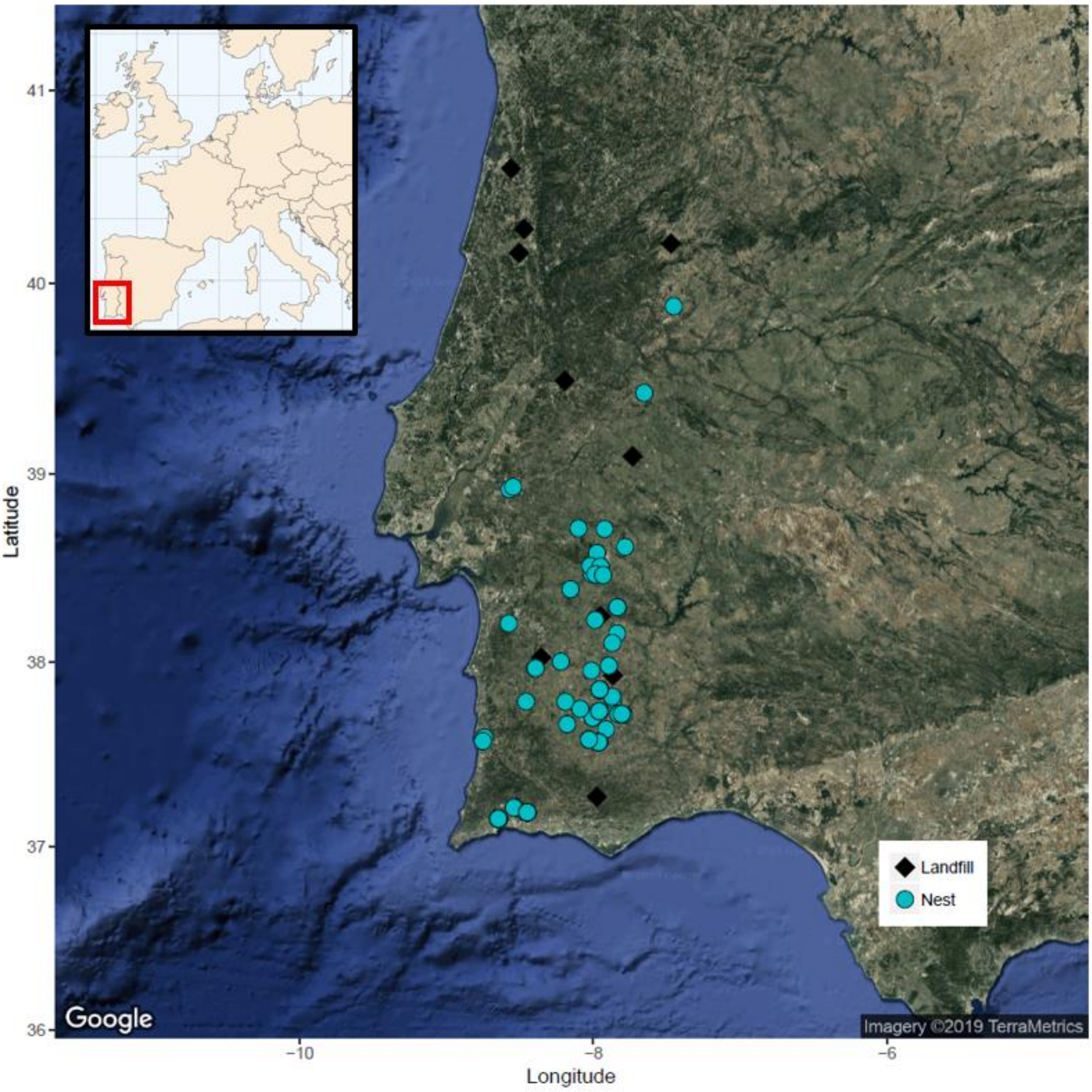
Appendices

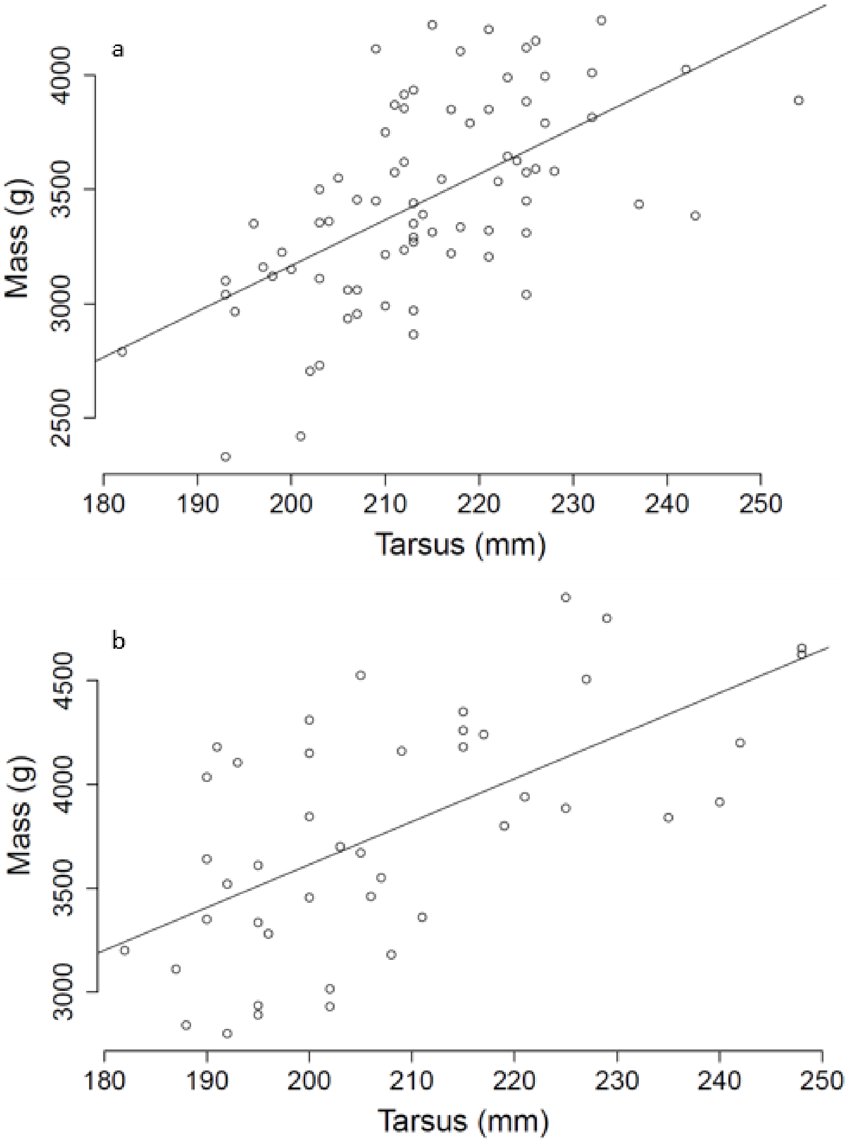
Appendix 2

2.1 Location of nests of tracked birds and landfill sites across Portugal



Nest locations of tracked adult and juveniles white storks (2013 - 2017) and open landfill sites in Portugal.

2.2 Relationship between mass and tarsus length for adult and juveniles



Relationship between mass (g) and tarsus length (mm) for (a) juvenile and (b) adult white storks deployed with GPS transmitters (2013 - 2017). The residuals of the linear models (bold line) are used for a body size index.

2.3 Summary of covariates included in survival analysis for adults and juveniles.

Summary of covariates included in the models to predict survival probabilities for adults (n = 34) and juveniles (n = 69): mean, range and SE of body size index and proportion of fixes on landfill sites.

Covariates	Age	Mean	Range	SE
Body size index (weight ~ tarsus length standardised residuals)	A	-0.001	-1.63 – 1.82	0.15
	J	-0.014	-2.23 – 2.23	0.12
Proportion of fixes on landfill sites	A	0.14	0 – 0.64	0.02
	J	0.15	0 – 0.48	0.02
Distance between nests and landfill sites (km)	A	19.4	3.87 – 48.2	1.79
	J	18.8	1.70 – 75.7	1.54

2.4 Consistency of use of landfill sites for juveniles and adults

Consistency of landfill site use (mean and SD) by adults for breeding periods in Iberia including distance from nest to nearest landfill sites (km).

Logger number	Number of breeding seasons tracked	Mean use of landfill sites in breeding season (SD)	Distance from nest to nearest landfill sites (km)
436	2	0.24 (0.09)	6.60
310	2	0.21 (0.11)	7.08
392	3	0.21 (0.11)	23.75
428	2	0.21 (0.05)	16.48
331	2	0.18 (0.13)	11.61
378	3	0.15 (0.08)	7.07
485	2	0.15 (0.05)	6.35
322	2	0.14 (0.04)	23.12
705	2	0.13 (0.03)	34.67
395	3	0.12 (0.06)	13.02
438	2	0.12 (0.17)	23.11
401	2	0.11 (0.02)	27.97
01	3	0.11 (0.03)	11.61
396	2	0.07 (0.04)	7.77
537	2	0.06 (0.06)	16.22
434	2	0.04 (0.00)	31.60
15	2	0.03 (0.05)	24.28
383	2	0.02 (0.01)	18.07
398	2	0.02 (0.02)	8.97

2.5 Descriptions of status available for each individual in each period included in survival analysis

Description how status for each bird in each period of the survival analysis was assigned.

Outcome	Instances when outcome is assigned
Alive	Individuals alive and transmitting for entire time period.
Dead	Mortality confirmed by visits to last location of transmitter.
	If transmitter was at same location for > three days and transmitter deployed < 12 months before end of transmission.
Unknown	Individual does not have transmitter deployed.
	Individual has died, unknown outcomes assigned for all periods after the period when death occurred.
	Transmitter stopped working due to battery failure (battery over charging or not re charging).
	Transmitter stopped working at approximate end of transmitter life (2 years).
	Transmitter stopped transmitting in North Africa or Sahel, birds assumed to have entered Sahara Desert or other areas with no GSM coverage.

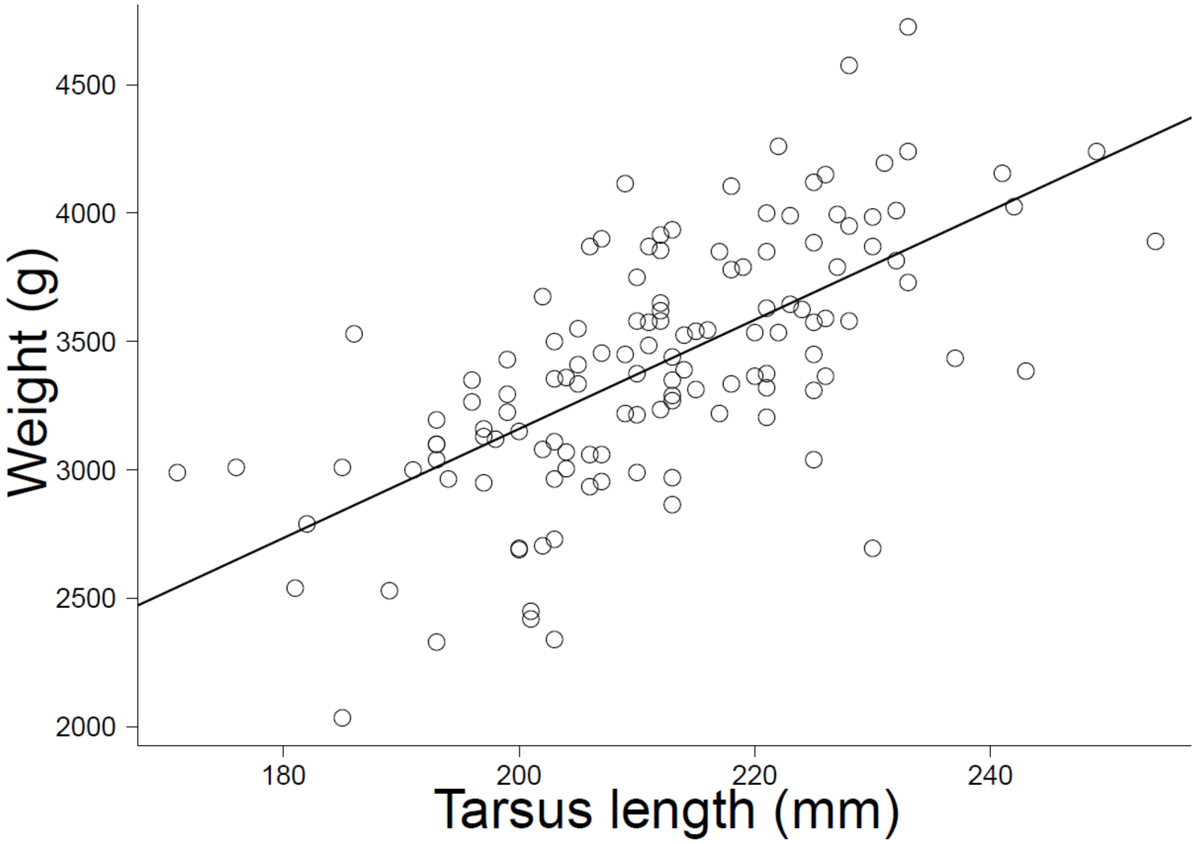
2.6 Transmitter failure rates

Failure of transmitters in the six months following deployment. Here I show the number of transmitters that worked for more than six months, those that stopped transmitting in Africa (unknown if transmitter failure or bird death) and those when the bird was known to die or transmitter failure was recorded. Percentages of transmitters that stopped in first six months, stopped on migration in Africa in first six months and survived first six months in bold. All transmitters deployed in these years are included here, including those that did not have enough data to be included in the survival analysis.

Year	Total transmitters deployed (n = 157)	No. working in 6 months	No. birds died in 6 months	No. stopped in 6 months	No. stopped transmitting in Africa	**Stopped in 6 months (%)**	**Stopped on migration (%)**	**Survived 6 months (%)**
2012	15	11	1	3	0	**20**	**0**	**73**
2013	39	10	1	21	7	**54**	**18**	**26**
2014	10	1	3	3	3	**30**	**30**	**10**
2016	44	17	15	4	8	**9**	**18**	**39**
2017	45	24	7	1	13	**2**	**29**	**53**

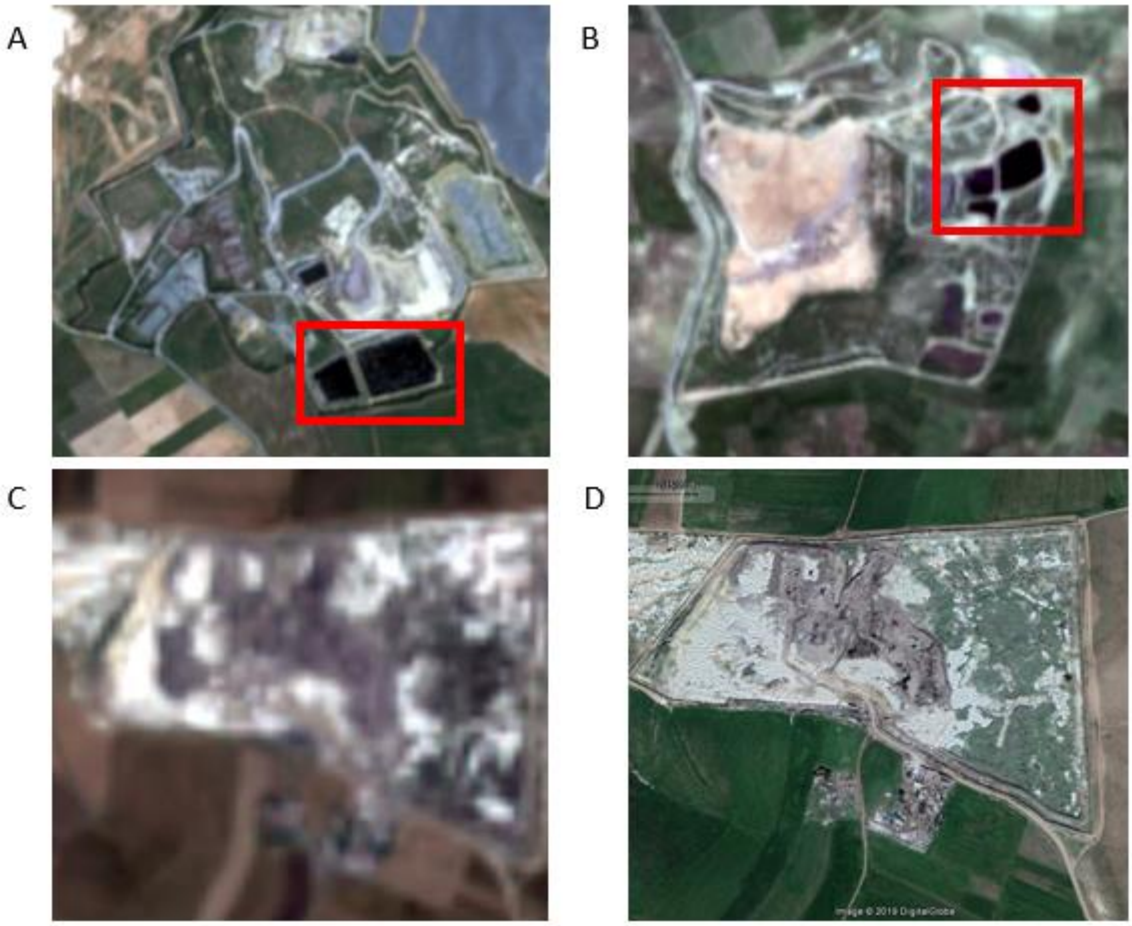
Appendix 3

3.1 Body size index metric for tracked juveniles.



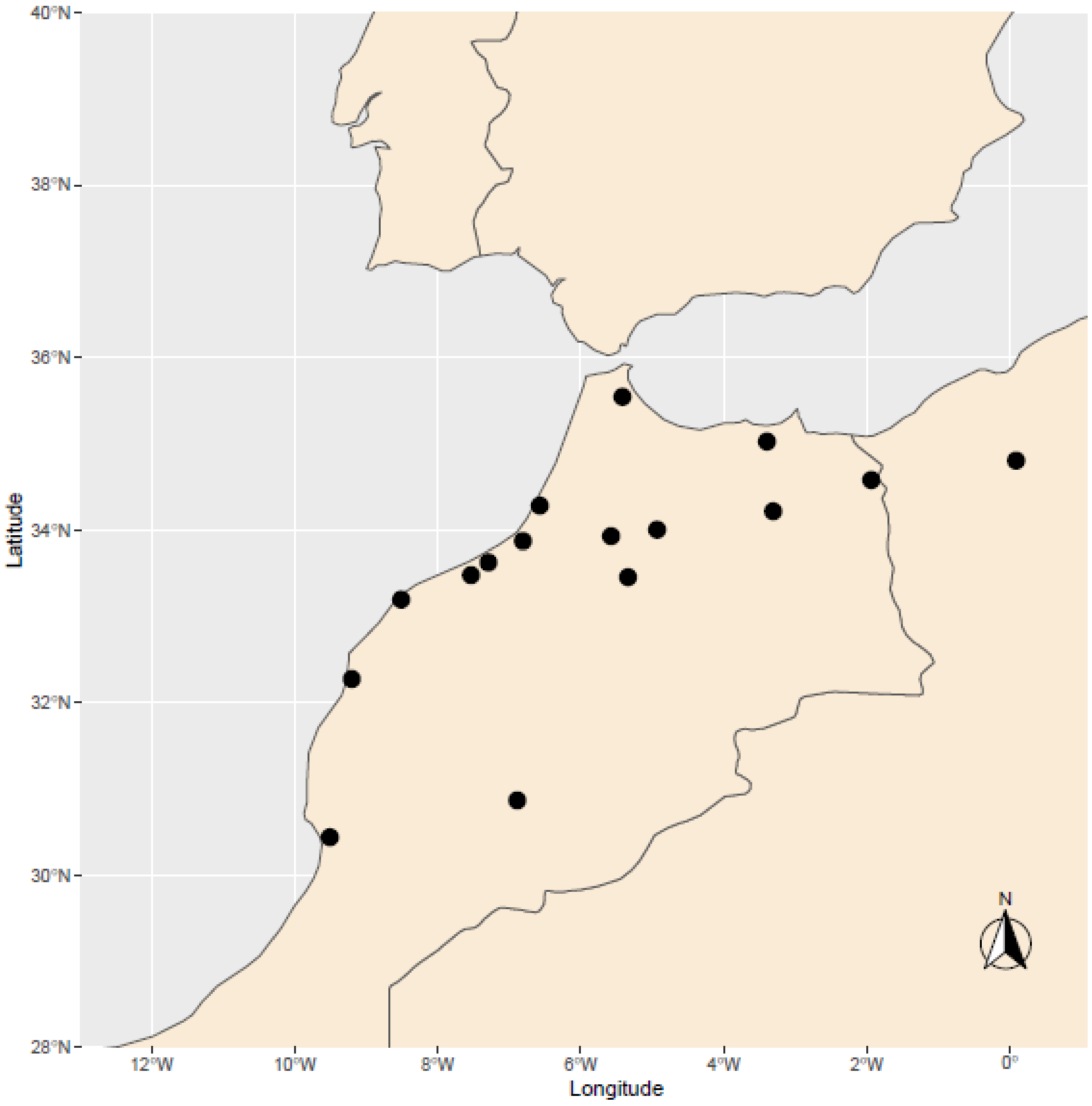
Relationship between weight (g) and tarsus length (mm) for juveniles tracked since 2013 from the Portuguese white stork population. The residuals of this relationship are used as a body size index.

3.2 Landfill sites in North Africa



Images of landfill sites. A) Landfill site in Iberia (Sentinel-2 satellite imagery), red square around water reservoirs; B) Landfill site in North Africa (Sentinel-2 satellite imagery), red square around water reservoirs; C) Possible landfill site, unregulated rubbish tips or bare ground (Sentinel-2 satellite imagery) in Morocco (-7.68633, 32.99827) and D) Same location as C) with Google Earth imagery confirming an unregulated rubbish tip or bare ground.

3.2 Map of landfill sites in North Africa



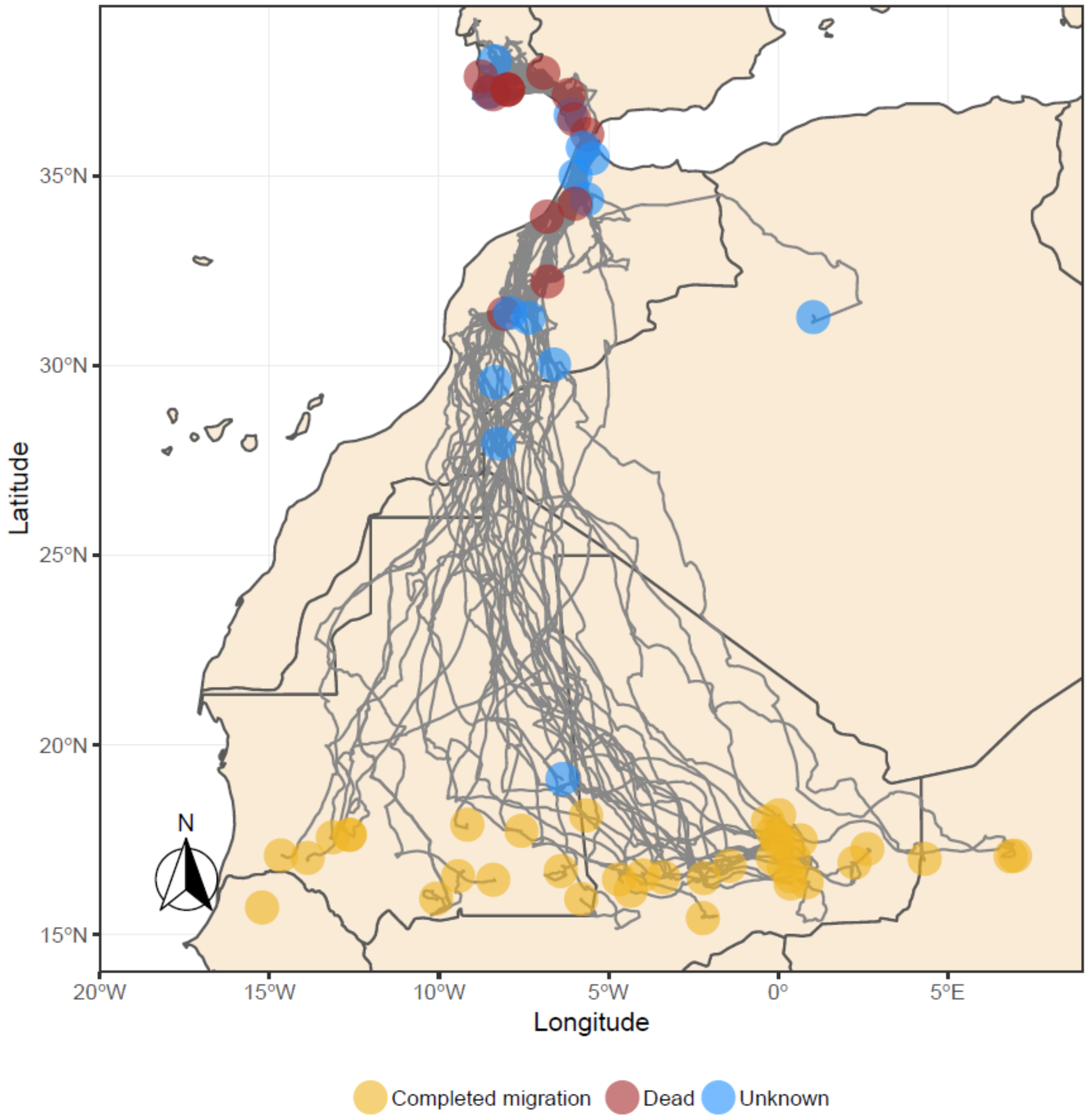
Map of 16 landfill sites in North Africa, coordinates in appendix 3.4.

3.4 Coordinates of landfill sites in North Africa

Degree coordinates, longitude and latitude, of 16 landfill sites located in North Africa from stationary fixes of juvenile white storks.

	longitude	Latitude
1	-6.5741	34.2835
2	-5.577	33.92974
3	-7.29407	33.62936
4	-4.93234	34.00381
5	-3.39486	35.02699
6	-8.51454	33.19885
7	-9.20633	32.27753
8	-6.89012	30.86891
9	-6.81038	33.87302
10	-9.51249	30.44054
11	-5.33956	33.45827
12	-7.53758	33.48255
13	-3.30799	34.21788
14	-5.41828	35.54568
15	-1.94239	34.58048
16	0.086227	34.80621

3.5 Locations of end of transmitters or arrival in the Sahel.



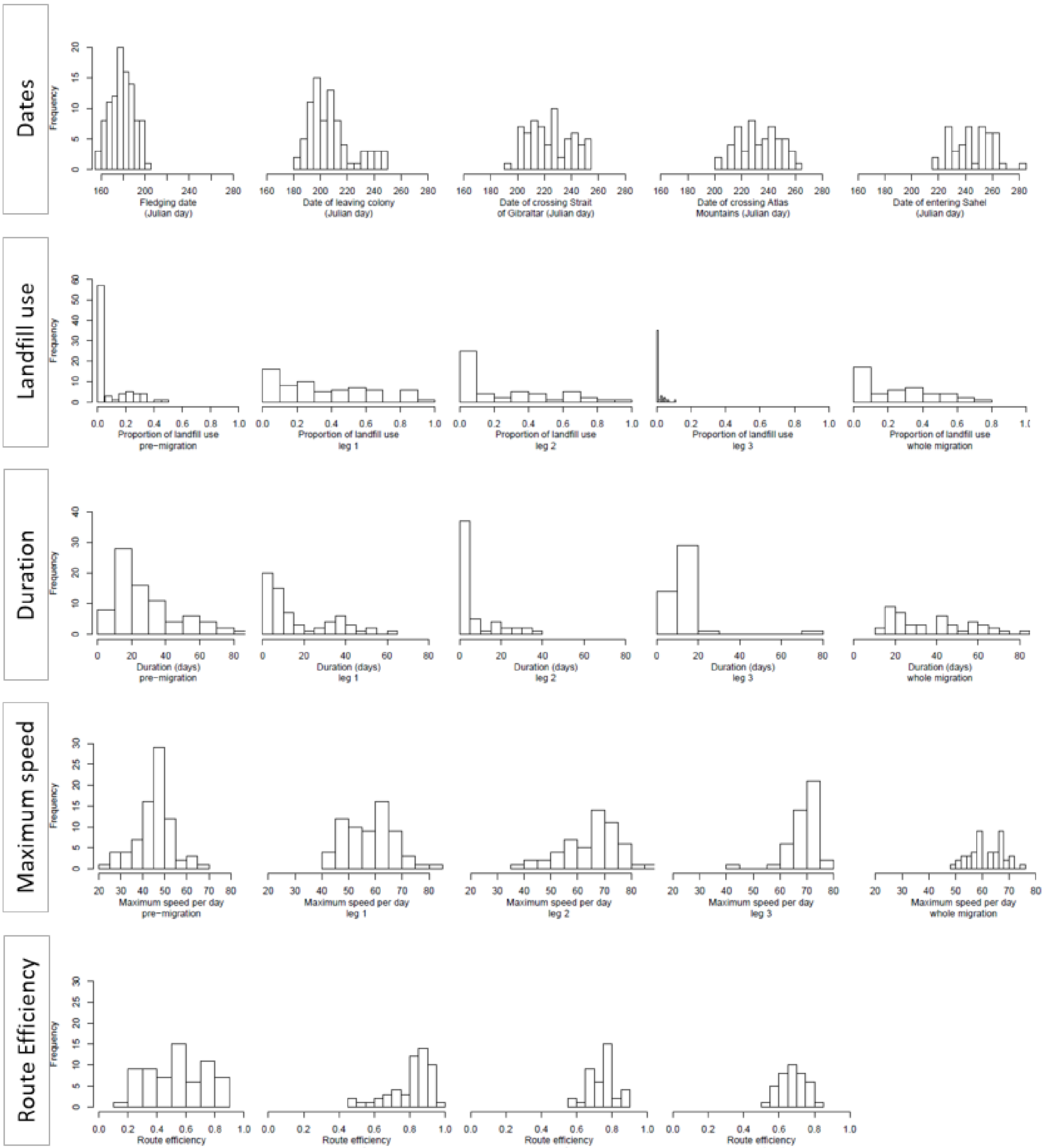
Locations of deaths, logger failure/loss of GSM signal (unknown) and last locations on day of arriving in the Sahel for all juveniles tracked (2016 - 2018). Grey lines show migration routes.

3.6 Summary of migration characteristics

Summary of characteristics of first year migration movements (mean and SD) split by year of transmitter deployment.

Characteristics		2016	2017	2018
Body size index		-0.38 (0.74)	0.01 (1.11)	0.45 (1.02)
Fledging date		26-Jun (11)	26-Jun (10)	03-Jul (11)
Date of leaving colony		24-Jul (17)	24-Jul (18)	31-Jul (12)
Date of crossing Strait of Gibraltar		15-Aug (18)	13-Aug (17)	09-Aug (12)
Date of crossing Atlas Mountains		22-Aug (17)	25-Aug (12)	17-Aug (16)
Date of entering Sahel		03-Sep (17)	05-Sep (14)	28-Aug (14)
Duration	Pre-migration	27 (19)	29 (20)	31 (19)
	Whole migration	43 (19)	38 (18)	24 (7)
	Leg 1	22 (19)	19 (16)	8 (8)
	Leg 2	7 (10)	9 (10)	4 (5)
	Leg 3	11 (2)	12 (2)	13 (1)
Landfill site use	Pre-migration	0.08 (0.14)	0.06 (0.11)	0.08 (0.10)
	Whole migration	0.32 (0.26)	0.28 (0.16)	0.11 (0.12)
	Leg 1	0.35 (0.28)	0.38 (0.26)	0.31 (0.29)
	Leg 2	0.19 (0.29)	0.30 (0.27)	0.25 (0.32)
	Leg 3	0.01 (0.03)	0.01 (0.02)	0.01 (0.02)
Route efficiency	Whole migration	0.67 (0.08)	0.67 (0.07)	0.70 (0.06)
	Leg 1	0.48 (0.23)	0.52 (0.18)	0.65 (0.14)
	Leg 2	0.84 (0.10)	0.77 (0.16)	0.82 (0.07)
	Leg 3	0.75 (0.09)	0.74 (0.07)	0.72 (0.06)
Mean Maximum speed	Pre-migration	33 (5.4)	37 (5.1)	40 (4.6)
	Whole migration	39 (2.9)	42 (2.4)	43 (2.6)
	Leg 1	37 (3.3)	40 (4.0)	40 (3.7)
	Leg 2	41 (5.7)	41 (5.2)	43 (3.5)
	Leg 3	44 (2.6)	45 (2.0)	44 (2.0)
Number completed	Pre-migration	31	25	23
	Whole migration	13	17	9
	Leg 1	23	22	19
	Leg 2	17	18	13
	Leg 3	13	17	9

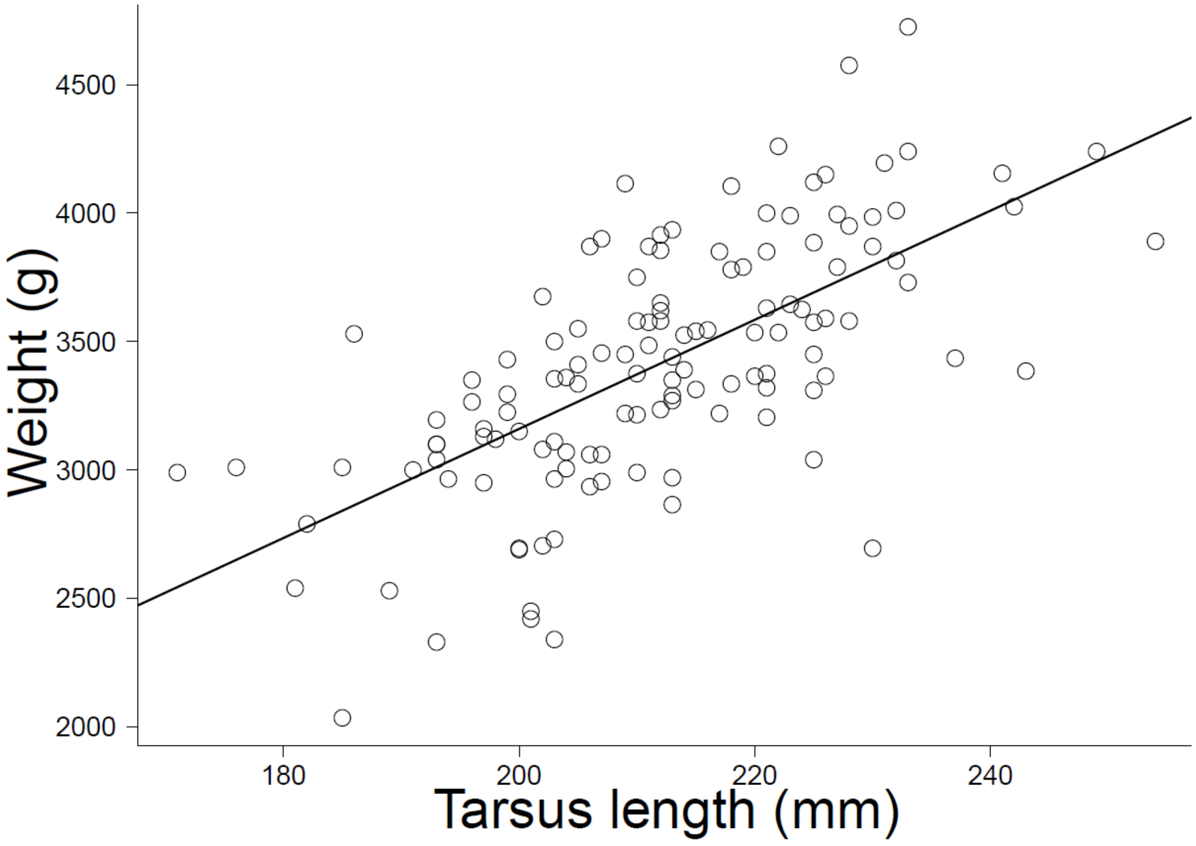
3.7 Frequency distributions of migration parameters



Frequency distributions of individual characteristics and migration parameters, including dates of starting migration and crossing geographical barriers, landfill use, duration, mean maximum speeds and route efficiency across the different migration periods.

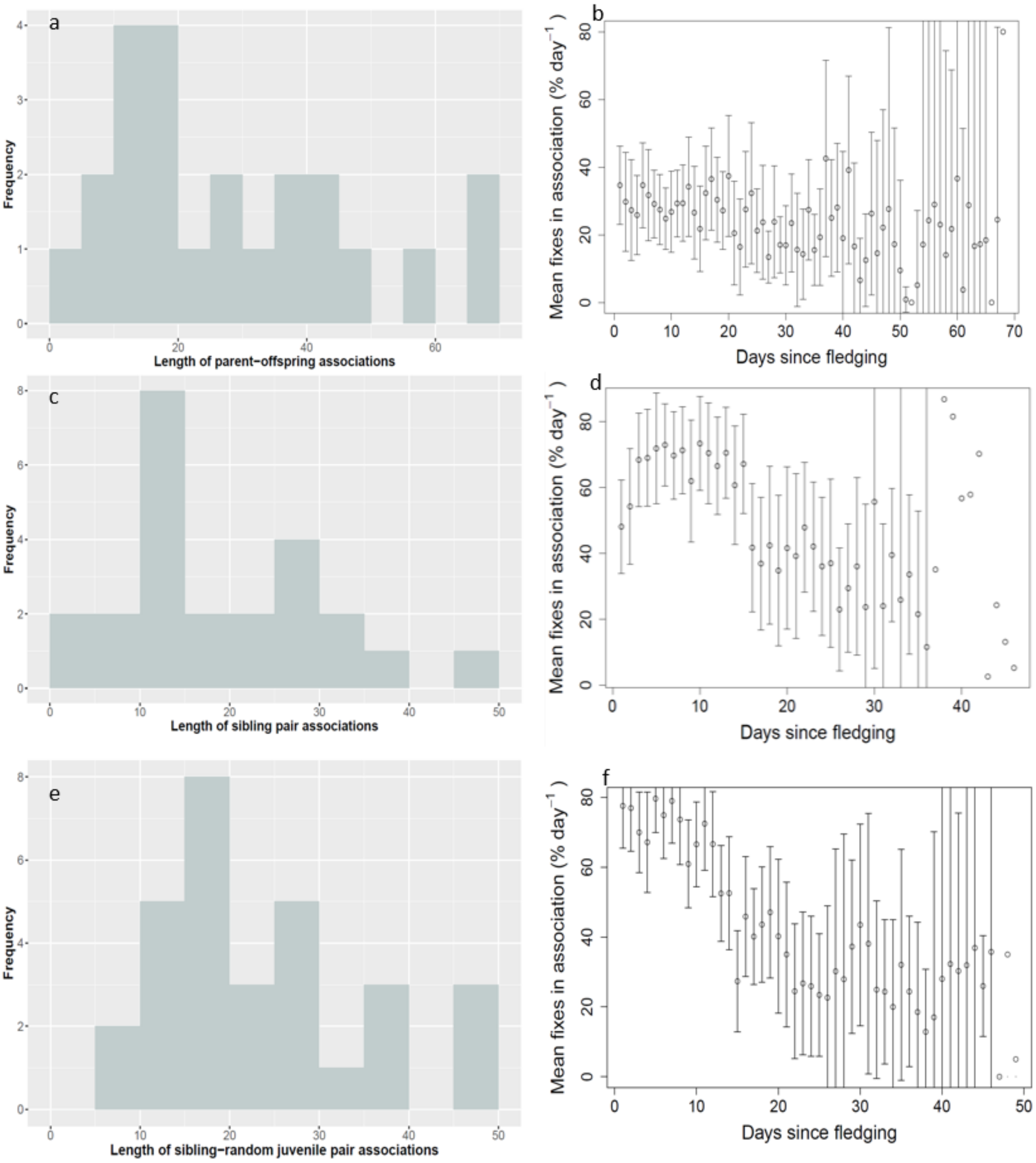
Appendix 4

4.1 Body size index metric for tracked juveniles.



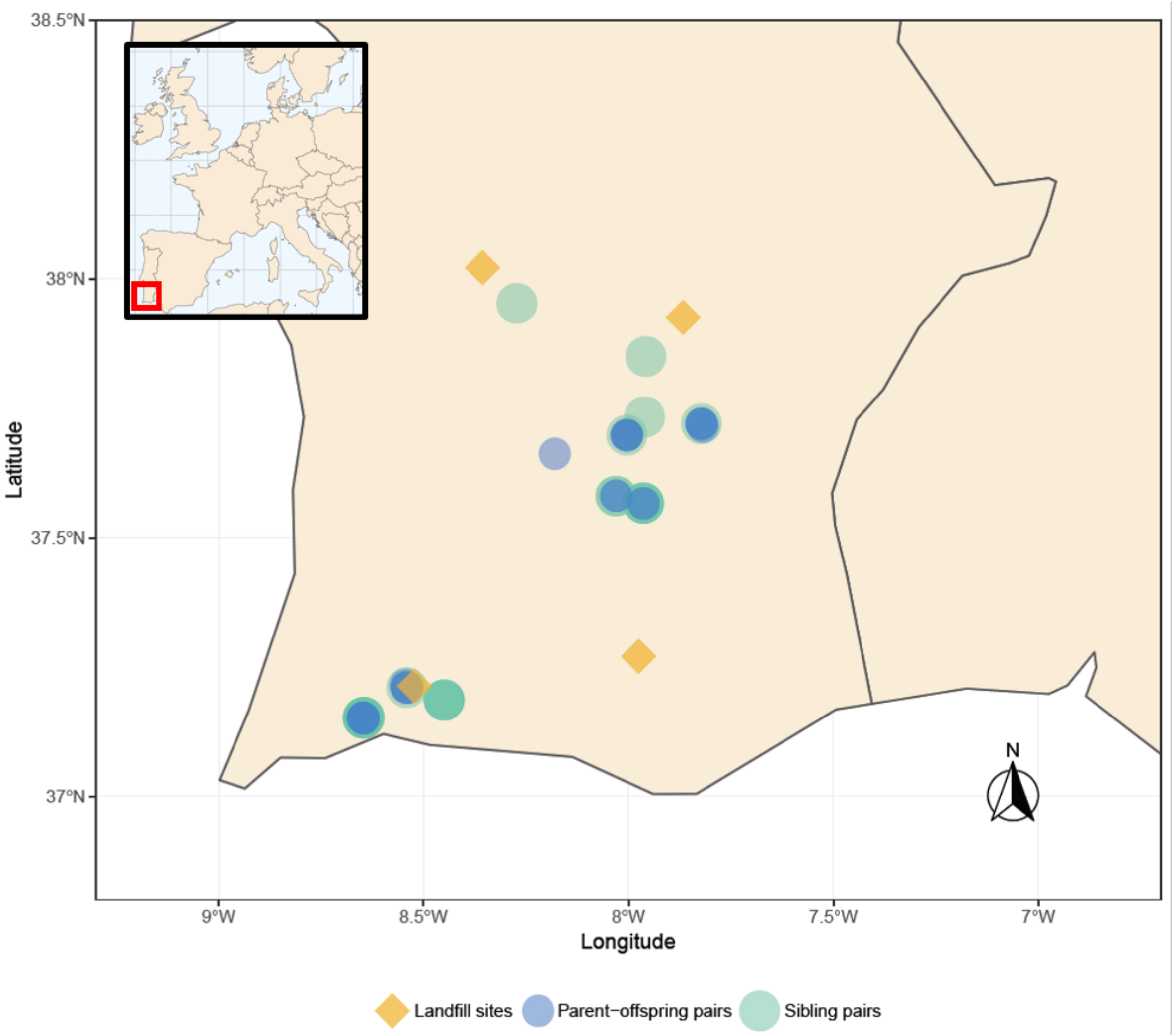
Relationship between weight (g) and tarsus length (mm) for juveniles tracked since 2013 from the Portuguese white stork population. The residuals of this relationship are used as a body size index.

4.2 Extent of associations between family and sibling-random juveniles pairs



Extent of association for parent-offspring (a, b), sibling (c, d) and sibling-random juvenile (e, f) pairs. (a), (c) and (e) show the variation in length of associations. (b), (d) and (e) show the mean percentage of fixes in association per day since the start of association. The error bars show 95% confidence intervals and no error bars indicate days with no fixes in association or only one pair had associations on that day.

4.3 Locations of nests and landfill sites



Nest locations for parent-offspring and sibling pairs and closest landfill sites in southern Portugal.

4.4 Numbers of pair types close to and far from landfill sites

Sibling and sibling-random juvenile pairs were split between nests close to (< 15 km) and far from (> 15 km) landfill sites.

	Number of pairs close to landfill sites	Number of pairs far from landfill sites
Parent-offspring	10	13
Sibling pairs	15	9
Sibling-random juvenile pairs	25	5