

**MIGRATORY BEHAVIOUR AND ECOLOGY OF A TRANS-SAHARAN
MIGRANT RAPTOR, THE OSPREY *PANDION HALIAETUS***

Thesis submitted for the degree of
Doctor of Philosophy
at the University of Leicester

by

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Dept. Neuroscience, Psychology and Behaviour

2017

Migratory behaviour and ecology of a trans-Saharan migrant raptor, the osprey *Pandion haliaetus*

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Abstract

The seasonal migration of birds is one of the great phenomena of the natural world and satellite tracking provides a valuable means to analyse the behavioural and environmental factors that influence it. In this study satellite telemetry was used to track ospreys *Pandion haliaetus* during migration between the United Kingdom and West Africa.

Autumn migrations were faster than those in spring, with more favourable meteorological conditions resulting in ospreys requiring fewer travelling days to reach their destination. They also incorporated time-minimisation techniques during southward journeys, indicating that selection-pressure influences migration speed in autumn as well as during spring migrations. The reclamation of winter territories is likely the key behavioural driver during autumn, particularly as later-departing individuals migrated faster.

High resolution GSM-GPS transmitters provided new insights into the ability of ospreys to adapt flight method to environmental conditions, with tagged individuals exploiting thermal updrafts when available, but swapping to energy-demanding flapping flight when necessary. Very long ocean crossings, particularly across the Bay of Biscay, were regularly undertaken in autumn, when tailwinds aided progress. These flights were predominantly undertaken by flapping, but ospreys sometimes exploited weak thermals and elements of the wind to achieve soaring-gliding flight over the sea, the first time such behaviour has been documented. Individuals also regulated both flapping and gliding airspeed in response to changing wind conditions.

Juvenile ospreys showed clear individual variation in the timing and speed of migration. Migration routes during the first migration were profoundly influenced by weather conditions, with wind drift resulting in very long flights across the ocean. It was also notable that ospreys with the longest post-fledging phase migrated fastest. Juveniles generally exhibited energy-minimisation techniques during migration, indicating that they were less time-constrained than adults. This may be particularly important given that individuals are likely to gain fitness advantages by arriving at the wintering grounds in good condition.

Acknowledgements

I have always been fascinated by bird migration and so this PhD has provided a wonderful opportunity to develop this interest into an academic study. It has been especially rewarding to follow ospreys on migration, given that I have been actively involved in their conservation for the past nineteen years.

I am particularly indebted to Roy Dennis. Roy has been a great mentor to me over the years, and has been at the forefront of satellite tracking research in the UK for the past two decades. Many of the ospreys in this study are from nests that have been monitored by Roy for more than fifty years in Scotland and I am extremely privileged to have been able to include them. Roy also helped to catch and tag ospreys at Rutland Water and provided a constant source of advice and knowledge.

Undertaking a PhD while working at Rutland Water Nature Reserve was a demanding challenge and I am very grateful to Professor David Harper for supporting me through the initial phases. David encouraged and supported me greatly, and crucially, helped me to develop an academic focus. The same is true of Professor Lex Comber whose passion, enthusiasm and knowledge of GIS knows no bounds. We had some very enjoyable discussions and I learnt a great deal. I was sorry to see both David and Lex leave the university during the course of my PhD.

Losing my two supervisors was a blow, but I was extremely fortunate that Dr Will Norton took over from David as my main supervisor. Although avian migration is not Will's subject area he quickly became a constant source of encouragement and advice, particularly while I was writing-up. I thank him sincerely for his enthusiasm and support. I am also very grateful to Dr Kirsten Barrett who, like Will, provided valuable advice during my final year, and to Dr Swidi Ott for his assistance with statistical analyses. Sincere thanks also to Dr Iain Barber and Dr Aldina Franco from the University of East Anglia for a stimulating and thought-provoking viva. I am also grateful to Professor Thomas Alertsam and Dr Ugo Mellone for helpful comments on an earlier version of chapter 3.

This PhD would not have been possible without the support of Leicestershire and Rutland Wildlife Trust. I am grateful to Simon Bentley and Tim Appleton for allowing me to work part-time while writing up this thesis. I am also indebted to my friends and colleagues at Rutland Water, Becky Corby, Lloyd Park, John Wright, Kayleigh Brookes, Paul Stammers, Ken Davies and Jackie and Pete Murray who worked extremely hard in my absence and kept various projects running very smoothly. I also thank John and Lloyd for their company and patience while trying to catch ospreys to satellite-tag at Rutland Water.

I am extremely grateful to Anglian Water for funding my PhD fees. Anglian Water has worked in partnership with LRWT at Rutland Water for the past forty years and achieved some wonderful conservation successes, with the Rutland Osprey Project foremost among them. I particularly thank Andy Brown, Chris Gerrard and Mike Drew for their support.

Finally, special thanks to my wife Louise and also to my parents, Bob and Bev Mackrill, for their constant support and encouragement.

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List of Abbreviations

AIC	Akaike information criterion
ANOVA	Analysis of variance
bl.height	Boundary layer height
BMR	Basal metabolic rate
CA	California, United States of America
Corp	Corporation
circ	Circling
df	Degrees of freedom
D_{ind}	Induced drag
D_{par}	Parasitic drag
D_{pro}	Profile drag
dist	Distance
ECMWF	European Center for Medium-Range Weather Forecasts
et al	And others
F	F statistic
flap.tf	Flapping time fraction
frac	Fraction
g	Acceleration due to gravity
g	Gram
GIS	Geographic information system
GLMM	Generalized linear mixed models
GMT	Greenwich Mean Time
GPS	Global positioning system
GSM	Global System for Mobile Communication
h.wind	Headwind
HD	High resolution data

ID	Identification
Inc	Incorporation (business)
IQR	Inter-quartile range
kg	Kilogram
km	Kilometre
LMM	Linear mixed-effect model
LR	Likelihood ratio statistic
LSD	Least significant difference
m	Body mass
m	Metre
$m\ s^{-1}$	Metres per second
mB	Millibar
MD	Maryland, United States of America
min	Minute
mins	Minutes
N	Number
NOAA	National Oceanic and Atmospheric Administration
ns	Natural cubic spline
NY	New York state, United States of America
ODBA	Overall dynamic body acceleration
P	Power
p	P value
PTT	Platform transmitter terminal
Q-Q	Quantile-quantile
R^2	R squared
s	Second
SD	Standard deviation
Sig	Significance

spp	Species (plural)
Std	Standard
T	Thrust
UK	United Kingdom
USA	United States of America
u-wind	Component of horizontal wind towards east
V	Velocity
V_{bg}	Best glide speed
V_{it}	Inter-thermal gliding speed
V_{max}	Maximum cross-country speed
V_{min}	Minimum (stalling speed) in gliding flight
V_{mp}	Minimum power speed in flapping flight
V_{mr}	Maximum range speed in flapping flight
V_{ms}	Speed of minimum sink in gliding flight
V_{opt}	Optimal inter-thermal glide speed
v-wind	Component of horizontal wind towards north
V_{xc}	Cross-country speed
V_z	Vertical speed component

1. Introduction

The seasonal migration of birds is one of the great phenomena of the natural world. Each year almost 20 % of the world's nearly 10,000 bird species are compelled to make seasonal movements in order to take advantage of changing food availability, reduce competition and avoid predation (Alerstam 1990, Somerville et al. 2015). The selective advantages of these migratory movements are offset by costs associated with such travel (Newton 2008). Many migratory birds undertake remarkable feats of endurance and cross inhospitable environments such as deserts (Strandberg et al. 2010) and oceans (Gill et al. 2008) in order to reach favourable breeding or wintering habitats.

In the past one hundred years the knowledge and understanding of avian migration has increased dramatically as new methods of study have arisen (Alerstam and Hedenström 1998). At the simplest level the introduction of optics – binoculars and high-powered telescopes – enabled greatly-enhanced field study of migratory species. However it was the instigation of ringing that began to reveal the magnitude of bird migration. For instance, the first recovery of a British-ringed barn swallow *Hirundo rustica* from South Africa provoked widespread astonishment (Witherby 1912). Since then technological advancements have enabled the use of specific equipment, most notably radar (e.g. Bruderer and Boldt 1991) and satellite telemetry (e.g. Tomkiewicz et al. 2010) to further our understanding to unprecedented levels (López López 2016).

1.1. Why migrate?

The driving force behind bird migration is the earth's changing seasons. These seasonal changes exert push and pull factors on migrant species that have evolved to take advantage of predictable changes in environmental conditions around the globe (Flegg 2004). Changes in day length, rainfall and temperature control the length of the vegetation period – the time when plants can exploit solar energy in order to germinate and grow – the most extreme examples of which are tundra and dry savannah (Alerstam 1990). The annual movement of migrant species tends to occur in regions where this change shows most seasonal variation. As a result very few migrant species occur in the rainforest areas in South America, Africa and Southeast Asia

where the hot, humid climate allows growth throughout the year, whereas in Scandinavia, where the vegetation period is limited to between 130 and 240 days depending on latitude, the majority of bird species are migratory (Alerstam 1990). That is not to say that migration is an exclusively north-south phenomenon. Owing to warmth from the sea in winter, the 0° isotherm runs almost directly north to south through Europe – from western-most Norway across the south-west Baltic Sea and south to Switzerland and south-east France. As a result many species that breed in Scandinavia and northern Russia migrate west, rather than south in autumn (Alerstam 1990). The choice of wintering location of migrant species can be surprising too. For instance many northern migrants choose to winter during the dry season in the savannah regions south of the Sahara. Despite the heat and drought, species such as warblers, flycatchers, shrikes and wheatears are able to find sufficient food (Alerstam 1990).

The highest migratory bird diversity is found in the Northern Hemisphere where migration dynamics are dominated by intra-continental (rather than inter-continental) movements (Somerville et al. 2013). In an extensive analysis of the global distribution of migratory bird species, Somerville et al. (2013) demonstrated that the proportion of migratory species increases with latitude as documented in earlier studies (Newton and Dale 1996a, Newton and Dale 1996b) but that there is asymmetry in the magnitude of this effect between the Northern and Southern Hemisphere. The local percentage of migratory species reaches a maximum of 60% in the Southern Hemisphere whereas in the Northern Hemisphere the percentages are often considerably higher, with migratory species constituting the majority of the local avifauna at high latitudes. Somerville et al. (2013) hypothesise that this may be due to the fact that climate seasonality is more extreme in the Northern than Southern Hemisphere making it more challenging for species to remain all year round. Other hypotheses relate to the more extensive continental land mass and greater long-term climatic variability of the Northern Hemisphere (Somerville et al. 2013).

Somerville et al. (2015) presented evidence supporting the hypothesis that seasonality is a key driver of the number of breeding migrants in local avian assemblages, with incoming migrants befitting from the surplus of energy and

resources available in areas of high seasonality (Dalby et al. 2014). In contrast, they found evidence that the diversity of non-breeding migrants is driven by a combination of the quality of wintering sites and their location in relation to the breeding grounds. The costs of migration thus play a key role in determining the distance birds are willing to travel between their breeding and wintering grounds (Wikelski et al. 2003, Newton 2008). Somerville et al. (2015) conclude, therefore, that migratory species are predominantly influenced by resource availability (and its relationship with seasonality) during the breeding season but that selection of wintering grounds is a trade-off between local suitability and accessibility to the breeding grounds.

1.2. Conservation of migratory species

As Gilroy et al. (2016) point-out migrants are subjected to 'multiple jeopardy' owing to their reliance on different sites across the annual cycle. Recent research indicates that long-distance migrants of both passerine (Sanderson et al. 2006, Ockendon et al. 2012) and non-passerine species (Oppel et al. 2015) may be more prone to population declines than species that migrate shorter distances. In addition Gilroy et al. 2016 found that species with larger winter ranges relative to breeding range were less likely to be declining than those with more restricted non-breeding ranges. An understanding of migration routes and timing, stop-over sites and wintering locations is thus essential to understanding the natural (Newton 2008) and anthropogenic threats (Brochet et al. 2015, Johnston et al. 2012) posed to migrant species and to guide appropriate conservation action (Wilcove and Wikelski 2008). This is particularly relevant in the face of global environmental change resulting from factors such as climate change and habitat loss, both of which have been shown to result in declines in migratory species in recent years (Both et al. 2006, Møller et al. 2008, Flousek et al. 2015, Piersma et al. 2016).

1.3. Navigation

Perhaps the most intriguing question relating to avian migration is how do migrant birds find their way, particularly first-year birds with no previous experience? Research has shown that juveniles are unable to correct for displacement from their intended

direction during their first autumn migration, suggesting that true navigation - where birds use geographical landmarks or other sensory cues to guide them - is only possible among birds with experience of previous migratory journeys (Guildford et al. 2011). Instead it is thought that many first-year birds rely on an inherited programme of direction and distance often referred to as vector summation, in order to reach their wintering site (Mourtsen 2003). Under this technique, first outlined by Rabøl (1978) and further explained by Alerstam (2000) migration consists of a series of flight steps (vectors), where the orientation between each flight step varies according to a circular probability distribution around the primary (mean) direction. Any subsequent variations in orientation between different flight steps may be caused by limitations in the precision of the birds' navigational abilities and external variables such as wind drift. This supports the 'clock-and-compass concept' (Gwinner 1996) whereby migration of juveniles is controlled by an endogenous temporal/directional programme without any elements of compensation for geographical displacement or goal area navigation (Rabøl 1978).

The location of the sun, stars and the Earth's magnetic field are thought to be important navigational aids for migrant birds but empirical evidence is relatively limited (Åkesson and Henderström 2007, Guildford et al. 2011). Experience of the rotation centre of stars combined with the Earth's geomagnetic field is believed to be crucial in the successful migration of passerines that often fly at night (Weindler et al. 1996), while olfaction (Gagliardo et al. 2009, Pollonara et al. 2015) and land topography (Alerstam 1990, Pollonara et al. 2015) have also been shown to be used as navigational aids by some species. Guildford et al. (2011) suggest that sensory control of navigation may vary according to stage of the migratory journey and the level of previous migratory experience.

1.4. Flight mechanics during migration

In order to understand the adaptive evolution of migration it is first necessary to consider flight mechanics, a subject addressed by Pennycuik (1969) and studied in detail thereafter (e.g. Alerstam 2000, Pennycuik 2008). Birds mainly migrate by two contrasting methods: soaring-gliding, where external energy provides the power to

overcome drag, and flapping flight, in which wing strokes provide the necessary lift and thrust (Alerstam and Henderström 1998). As explained by Alerstam (2000) the power required for flight in both flapping and gliding flight is related to speed according to:

$$P = (D_{ind} + D_{par} + D_{pro}) V$$

where D_{ind} is induced drag, D_{par} parasitic drag, D_{pro} profile drag and V is flight velocity. In this case induced drag is caused by the generation of lift, whereas parasitic and profile drag are the result of pressure and friction acting on the bird's body and wings. In gliding flight power relates to the rate of loss of potential energy ($P = mgV_z$, where m is body mass, g is acceleration due to gravity and V_z the vertical speed component) whereas in flapping flight power is produced by the flight muscles which generate wing beats ($P = T V$, where T is thrust and V is flight velocity). When power is plotted against speed it produces a U-shaped power curve (Figure 1.1.). This is because D_{ind} becomes reduced with increasing flight speed, whereas D_{par} and D_{pro} both increase (Alerstam 2000).

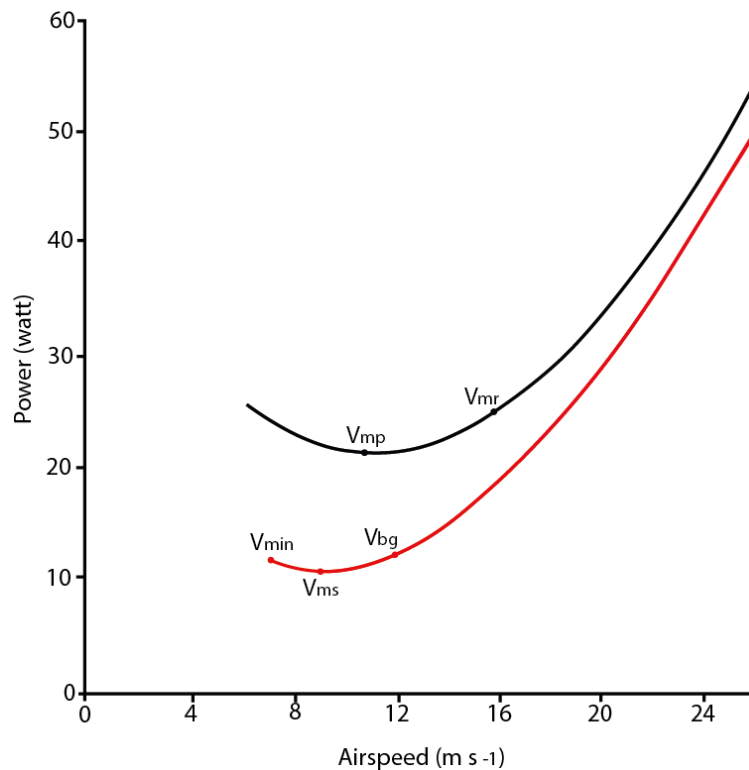


Figure 1.1. Power in relation to speed for flapping (black line) and gliding (red line) flight as exemplified for the osprey *Pandion haliaetus*, according to the theory of flight mechanics (Alerstam 2000). V_{mp} = minimum power speed in flapping flight, V_{mr} = maximum range speed in flapping flight, V_{min} = minimum (stalling speed) in gliding flight, V_{ms} = speed of minimum sink in gliding flight, V_{bg} = speed of best glide in gliding flight. In flapping flight power is generated by wing beats, whereas in gliding flight birds exploit external sources of energy (e.g. thermal updrafts) and power thus relates to the loss of potential energy.

The most common means by which migrating birds attain the power required to sustain soaring-gliding flight is by exploiting thermal updrafts - created by differential heating of the earth's surface - in order to gain altitude (Pennycuick 1998). The strength, spacing and vertical extent of thermals varies in different areas and on different days (Pennycuick 1998) but as long as air mass speed within a thermal exceeds an individual's sinking speed, a bird will gain altitude with minimal energy expenditure (Kerlinger 1989, Pennycuick 1998). It will then glide onwards, gradually losing altitude until it reaches another updraft (Leshem and YomTov 1996, Pennycuick

1998). Under such a scenario, the resulting cross-country speed is determined by climbing speed within thermals and the inter-thermal gliding speed.

The glide polar is a theoretical method to calculate the cross-country speed of a bird in thermal flight (Pennycuick 1998). The key element of this is a performance curve that shows the bird's sinking speed, relative to the air, versus forward speed (Figure 1.2). The cross-country speed (V_{xc}) can be determined by drawing a straight-line from the relevant vertical climbing speed (V_c) to the inter-thermal gliding speed (V_{it}). The point at which this line intersects the x axis is V_{xc} . Two points on the glide polar represent alternative behavioural strategies (Horvitz et al. 2014). The first, the best glide speed (V_{bg}), is independent of V_c because it represents the highest ratio of V_{it} to inter-thermal sinking speed (V_s), thereby maximising gliding distance. The second, defined as the optimum inter-thermal speed (V_{opt}), occurs when the bird adjusts its gliding airspeed to the rate of ascent in the preceding soaring phase (Horvitz et al. 2014), thereby making a tangent to the glide polar (Pennycuick 1998). As a result V_{opt} increases with increasing V_c (Pennycuick 1998) and a bird aiming to maximise its cross-country speed should glide at V_{opt} (MacCready 1958). However flying at V_{opt} entails a greater risk of forced landing or switching to flapping flight due to the variable nature of thermals in time and space (Pennycuick 1998). Thus a risk-averse bird is expected to glide at V_{bg} at the cost of slower onward progress compared to a risk-prone bird aiming to maximise cross-country distance (Horvitz et al. 2014). For most birds the glide polar is such that time spent gliding between thermals is close to 50% in typical thermal soaring flight (Alerstam 2000).

The power required for soaring-gliding flight can also be attained through slope soaring, whereby birds exploit orographic updrafts created when horizontal winds are deflected upwards by ridges and hills (Kerlinger 1989, Shepard et al. 2013). Under constant wind conditions orographic lift has the potential to provide a continuous source of lift along specific terrain features. As a result onward progress may be less staggered during slope soaring than in thermal flight (Kerlinger 1989, Pennycuick 1998). However, slope soaring birds may be forced to deviate from the most direct migratory course in order to follow the terrain feature that is generating lift (Dueer et al. 2012). The only occasions when birds in thermal flight do not need to interrupt

onward progress in the manner of slope soaring are rare occasions when thermals become aligned in 'thermal streets'. Under such circumstances it is possible for birds to either maintain or gain altitude while gliding (Pennycuick 1998).

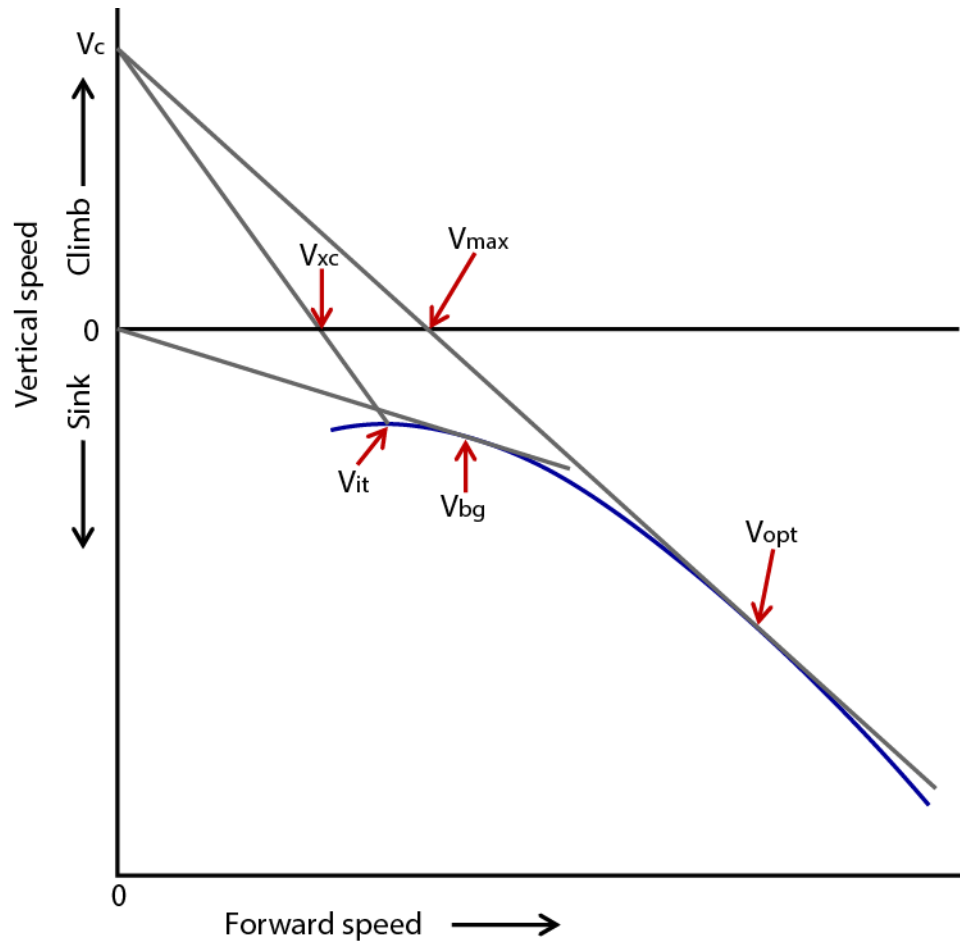


Figure 1.2. Glide polar for a given bird, showing its sinking speed relative to the air, versus forward speed. This is the classic theory for finding the cross-country speed attained by a bird climbing in discrete thermals, and flying through stationary air between thermals (Pennycuick 1998). V_{xc} = cross-country speed, V_{max} = maximum cross-country speed, V_{it} = inter-thermal gliding speed, V_{bg} = best glide speed, V_{opt} = optimal inter-thermal glide speed. See text for full explanation. V_{xc} can be determined by drawing a straight-line from the relevant V_c to V_{it} . The point at which this line intersects the x axis is V_{xc} . Two points on the glide polar (blue curve) represent alternative behavioural strategies. The first V_{bg} is independent of V_c because it represents the highest ratio of V_{it} to V_s , thereby maximising gliding distance. The second V_{opt} occurs

when the bird adjusts its gliding airspeed to the rate of ascent in the preceding soaring phase thereby making a tangent to the glide polar (Pennycuick 1998).

Alerstam (2000) argued that the mechanical power required for flapping flight is always higher than the corresponding curve for gliding flight. As a result, the ability of a given species to utilise these contrasting flight modes during migration is determined by its size, morphology and ability to adjust its wings and tail at different speeds (Alerstam 2000, Thomas 1996, Tucker 1987, 1998).

1.5. Flight method during migration

The power curve provides compelling evidence to explain the evolution of flight behaviour and range during bird migration. Flapping flight is highly metabolically costly because the power used for forward propulsion is produced by the bird's own flight muscles, rather than an external energy source. As a result the power requirements for flapping flight increase with body mass (Pennycuick 1989). Using calculations based on the power curve, Alerstam (2000) demonstrated that given a basal metabolic rate (BMR) of 1.5, an osprey *Pandion haliaetus* is expected to fly at 17 m s^{-1} to maximise migration speed, whereas the optimum flight speed of the Arctic tern *Sterna paradisaea* at the same BMR is slower (11 m s^{-1}). However, because the tern is considerably smaller and lighter it can fly at this optimum speed for 13 % longer, meaning that it could theoretically travel 187 km day^{-1} by flapping compared to just 97 km day^{-1} for the osprey. This adaptive ability of the Arctic tern to migrate efficiently by flapping flight enables it to undertake the longest recorded bird migrations, with some individuals from Iceland and Greenland migrating in excess of 60,000 km annually between their breeding grounds and wintering sites in the Antarctic Sea (Egevang et al. 2010). The osprey also undertakes long migrations between Europe and Africa (e.g. Hake et al. 2001) and North America and South America (e.g. Martell et al. 2001) but it travels predominantly by soaring-gliding flight as opposed to flapping, thereby enabling it to cover greater daily distances (Mellone et al. 2012). The differences in migratory range are even more pronounced when very large species are considered. Alerstam (2000) calculated that based on the same criteria as the Arctic tern and osprey, whooper swans *Cygnus cygnus* would require almost 400 days to complete a

migration similar to those undertaken by Arctic terns because of the very high energetic costs of flapping flight in such a large species. Instead they migrate shorter distances, such as between Iceland and the United Kingdom (Pennycuick et al. 1999) and Russia and Japan (Shimada et al. 2014).

Soaring-gliding flight is far less metabolically costly than flapping because the majority of energy required to power flight is extracted from thermal updrafts (Alerstam 2000). As a result more than 300 larger species of various taxonomic groups migrate long distances by this method (Del Hoyo et al. 1992). Wing loading, calculated by dividing body mass by wing surface area, is of particular importance in determining the ability of birds to migrate by soaring-gliding flight, because it influences their ability to exploit lift. Species with a lower wing loading are able to exploit weaker lift because they have a lower sinking speed (Pennycuick 2008). Conversely, species with higher wing loading can glide faster between thermals (Kerlinger 1989). As a result species with very large wing loadings such as black stork *Ciconia nigra*, white stork *Ciconia ciconia* and steppe eagle *Aquila nipalensis* are particularly dependent on favourable thermal conditions to aid migration, meaning that daily travel time is restricted to periods when thermals are available (Chevallier et al. 2010, Shamoun-Baranes 2003, Spaar and Bruderer 1996). In contrast, species with a lower wing loading such as marsh harrier *Circus aeruginosus* and Montagu's harrier *Circus pygargus* are less restricted by thermal availability, even though they migrate by soaring-gliding where possible (Liminana et al. 2013, Mellone et al. 2012). It is notable however that even these latter 'facultative soaring' migrants (Vansteelant et al. 2015) rarely undertake nocturnal migration; generally only doing so when migrating over unfavourable habitats or when migration is time-limited (Alerstam 2006). This contrasts markedly with species that migrate solely by flapping flight. Many passerine species, for example, migrate almost exclusively at night (Gwinner 1996, Alerstam et al. 2011)

The majority of birds that migrate by soaring-gliding flight are restricted to flight over land where the strongest thermal conditions prevail (Shepard et al. 2013). However some seabirds are specifically adapted to soaring-gliding flight over the ocean. The best example relates to frigatebirds which have extremely low wing loadings (Weimerskirch et al. 2003). These species are specially adapted to exploit narrow or

weak thermals and stay airborne for very long periods over the ocean (Pennycuik 1983, Brewer and Hertel 2007) to such an extent that they can roost on the wing (Weimerskirch et al. 2003). This is especially important given their inability to land on the water (Weimerskirch et al. 2003). Albatrosses, meanwhile, are able to fly very long distances over the ocean without flapping their wings through a combination of dynamic soaring and wave slope soaring (Richardson 2011). In each case birds exploit the interaction between wind and ocean waves by characteristic zigzag flight close to the ocean surface. In dynamic soaring albatrosses swoop across an area of wind shear just above the ocean surface to increase their airspeed (Sachs 2005). This is then converted to potential energy through a gain in height, similar to the motion of a pendulum, and may account for 80–90% of the total energy required for sustained soaring (Richardson 2011). On other occasions albatrosses are able to sustain soaring-gliding flight through wave slope soaring, whereby they exploit updrafts caused by wind interacting with waves to gain altitude and thus potential energy (Richardson 2011). These techniques enable albatrosses to cover vast distances across the ocean, including complete round-the-world journeys which can involve birds flying 950 km per day (Croxall et al. 2005).

1.6. Migration strategy

In addition to its impact on flight performance, flight method often constrains the routes that migratory land birds are able to use. The fact that species that migrate by soaring-gliding are usually confined to flight over land results in large concentrations of migratory soaring birds in spring and autumn at well-known geographical bottlenecks, such as the Bosphorus (Porter and Willis 1968, Fülöp et al. 2014), the Strait of Gibraltar (Evans and Lathbury 1973, Martín et al. 2016), Eilat in Israel (Christenson et al. 1981, Lott 2002) and South-west Georgia (Verhelst et al. 2011) in order to avoid long energy-demanding flights over the sea. Many soaring-gliding species make long detours during migration to pass through these locations. For instance Italian short-toed eagles *Circaetus gallicus* follow a lengthy overland route in order to cross the Strait of Gibraltar rather than make a more direct, but much longer, ocean flight across the Mediterranean from Italy (Panuccio et al. 2012). Some land bird

species, however, are adapted to very long continuous flights across water. The most extreme examples are wader species that make remarkable non-stop flights across oceans by flapping flight. Far eastern curlews *Numenius madagascariensis* have been shown to fly non-stop for 3 – 5 days across the Pacific Ocean between Australia and China, a distance of approximately 6500 km (Driscoll and Ueta 2002) while some bar-tailed godwits *Limosa lapponica* fly non-stop for 9 days across the Pacific Ocean from Alaska to New Zealand a distance of over 10,000 km (Gill et al. 2009). The latter flight involves the godwits maintaining an estimated metabolic rate of 8-10 times BMR that far exceeds any other documented sustained energy budget (Hammond and Diamond 1997). Such extreme flights require birds to deposit sufficient fuel to power the complete migratory flight prior to departure. It is essential therefore that they originate from sites where food resources are plentiful and can be acquired without other appreciable costs, most notably predation-risk (Houston 1998). In the case of the godwits, the intertidal infauna of the central and southern Yukon-Kuskokwim, the principal staging autumn staging site, provide extremely rich foraging, with few avian predators (Gill et al. 2009).

Most migratory species deposit fuel prior to departure, but few are able to complete migrations in a single continuous flight in the manner of bar-tailed godwits (Alerstam 1990). Soaring-gliding migrants are usually constrained by thermal conditions (Mellone et al. 2012, Shepard et al. 2013), while flapping migrants are directly influenced by fuel load. As fuel reserves increase so does the potential flight range, but this does not increase linearly with added fuel mass (Alerstam and Lindström 1990). Instead the basis for theoretical predictions of fuel deposition rates is based on the range curve; the decelerating function of flight range in relation to fuel load where the marginal rate of range increase will become reduced with successively heavier fuel burdens (Alerstam and Lindström 1990). As a result most species that migrate by flapping flight interrupt their migration with re-fuelling stops, often referred to as stop-overs.

1.7. Stop-overs

The duration and frequency of stop-overs has been the subject of numerous theoretical and empirical studies and provides valuable information on the trade-offs

involved in avian migration. A key driver in determining stop-over behaviour is the extent to which migration is time or energy selected. In time-selected migration birds are under selection pressure to complete the migration as quickly as possible, thereby assuming quick accumulation of large fat reserves at stop-over sites and considerable distances travelled on each flight leg (Alerstam and Lindström 1990). In energy-selected migration the need to conserve energy is the key driver and, as such, energy-selected migrants tend to fly short distances with low fat loads which are slowly restored at frequent stop-over sites (Alerstam and Lindström 1990). Of the various theoretical rules proposed to explain stop-over behaviour of birds that migrate by flapping flight, Alerstam (2011) suggested that time-minimisation combined with the 'global update rule' proposed by Houston (1998) provided the best fit in a majority of stop-over studies of passerine species. Under this scenario migrating birds use the fuel deposition rate experienced at each new stop-over site to determine stop-over strategy for the remainder of the journey.

Seasonal differences in stop-over duration provide further evidence of the selection pressures acting on migrating birds. In a thorough review of migration studies Nilsson et al. (2013) found that stop-over duration was generally shorter in spring than autumn, and proposed four possible explanations (1) degree of pre-migratory fuelling, (2) feeding conditions, (3) feeding intensity and behaviour, or (4) that stop-overs are not used for fuel deposition. Of these factors, changes in foraging behaviour may be particularly indicative of time-selection since total migration time is almost directly proportional to fuel deposition rate (Houston 1998). Adopting a more risk-prone strategy while foraging for instance may lead to more intensive fuel deposition and thus shorter stop-over duration in spring (Alerstam and Lindström 1990).

Soaring-gliding migrants are less constrained by fuel load than species that migrate by flapping flight because the bulk of power for migration is extracted from thermal updrafts. In fact high fuel loads have the potential to increase inter-thermal gliding speed Pennycuik (1975). As a result cross-country speed will increase with increasing mass under strong thermals, but be reduced under weak lift conditions (Pennycuik 1975). This key difference between soaring-gliding and flapping species means that large fuel loads that last for all or a significant proportion of the migration should be

more common among the former (Alertsam and Henderström 1998, Alerstam 2000). This has been borne out by recent satellite tracking studies which indicate that soaring-gliding species such as booted eagles *Aquila pennata* do not appear to forage on migration (Mellone et al. 2015). Nevertheless many soaring species do incorporate stop-overs into their migratory flights (e.g. Chevallier 2013, Kanai 2002).

In fly-and-forage migration birds combine foraging with covering migration distance (Strandberg and Alerstam 2007). As such it can provide a time-saving alternative to stop-overs among species that fly extensively during foraging. This is exemplified by the common swift *Apus apus* which employs a mixed fly-and-forage technique while migrating (Akesson et al. 2012). This, facilitated by its aerodynamic morphology, allows common swifts to reach average migration speeds well above 300 km per day in spring, which is higher than similar sized passerines (Akesson et al. 2012). Hobbies *Falco subbuteo* are able to extend their daily flight distances by using the fly-and-forage strategy (Strandberg et al. 2009) and it is also a technique regularly incorporated into migratory flights by ospreys (Strandberg and Alerstam 2007).

1.8. The triangle of velocities

As explained by Alerstam (2000) wind is an omnipresent and extremely powerful factor in bird migration. The track vector of a flying bird (direction and speed relative to the ground) is the sum of the wind vector and the bird's heading vector (flight direction and speed relative to the air) in relation to different wind conditions. Under the rules of optimum bird migration (Alerstam and Lindström 1990) birds migrating by flapping flight are expected to adjust both their heading and airspeed (flight speed relative to the air) in relation to different wind conditions. The extent to which birds concede to wind drift or compensate for it depends on different migratory conditions, as reviewed by Alerstam (2000):

- i) If wind is expected to vary considerably between different flight steps and the bird is many flight steps from its next goal, it will gain time and energy by allowing itself to be drifted by the wind (Alerstam 1979). Furthermore, it should adjust its airspeed according to wind conditions, increasing airspeed

when flying into a headwind, and reducing it with tailwind support (Alerstam and Henderström 1998).

- ii) Complete compensation is the optimal solution if wind remains constant or similar throughout the journey to the next goal (Alerstam 1979). Under this scenario the airspeed is expected to be reduced when it exceeds the corresponding groundspeed, and increased when it is slower (Liechti 1995). When migrating in strong crosswinds a bird is also expected to increase its airspeed and adjust its heading in order to fully compensate for wind drift (Alerstam 2000).
- iii) When wind varies independently between flight steps a strategy of adapted drift is optimal. In this case the bird should submit to wind drift away from the goal in the initial flight steps, and then compensate to a higher and higher degree when approaching the goal (Alerstam 1979). As such the rules for adjustment of airspeed are intermediate between the two former cases (Alerstam 2000).
- iv) If winds vary more predictably between departure site and the next goal according to some regular pattern, the 'minimal time path' will provide the best solution (Alerstam 2000). This involves varying degrees of partial drift and compensation depending on expected winds at different stages in the journey (Alerstam 2000).

There is an increasing body of empirical evidence to support these theoretical predictions. For instance Karlsson et al. (2010) demonstrated that common swifts increase their airspeed in response to strengthening crosswinds. Similarly Sapir et al. (2014) found that European bee-eaters *Merops apiaster*, a species that migrates by both flapping and soaring-gliding flight, fully-compensate for the effect of crosswinds, and that this response was not dependent on bird flight mode. In nocturnal passerine migration full or partial wind drift in response to crosswinds is frequently recorded (e.g. Cochran and Kjos 1985, Liechti 2006, Zehnder et al. 2001) but Backman and Alerstam (2003) showed that wind drift is more pronounced in autumn when there is a greater degree of naïve individuals migrating for the first time. This suggests that

experience plays a key role in the extent to which migrating birds are able to compensate for the effects of wind.

Seasonal differences in wind can also play a key role in influencing migratory flights. Liechti and Bruderer (1995) found that ground speeds of species using flapping flight during migration over Israel were faster in autumn when they were supported by tailwinds. Mean airspeed, however, was slightly higher in spring than in autumn, indicating a tendency to compensate for opposing winds. Kemp et al. (2010) demonstrated a similar effect of wind on species that migrate by flapping flight, recording a 16.9% increase in migration speed through the Netherlands in spring compared to autumn due to the positive effect of tailwinds on ground speeds.

Although the rules of optimal adjustment relate to species that migrate by flapping flight only, soaring-gliding species are expected to respond to wind drift by adjusting their heading (Alerstam and Henderström 1998). Klaassen et al. (2011) found that marsh harriers and ospreys respond to crosswinds according to local conditions; drifting when favourable and compensating or overcompensating when approaching a goal or facing the risk of being blown into hazardous habitats. Klaassen et al. (2011) go on to suggest that this flexibility in response indicates that migrating raptors have excellent navigational skills and are able to estimate drift while aloft. Some studies have also demonstrated that gliding speed is regulated according to wind conditions, with gliding airspeed increased in response to headwinds and reduced with tailwind support (Spaar 1997). However, the majority of published work demonstrates the clear advantages of migrating with tailwinds. Vansteelant et al. (2015) showed that weather accounted for 30–40% of variability in daily distance and daily mean speed achieved by honey-buzzards *Pernis apivorus* and Montagu's harriers, with tailwinds having the most significant impact. Similarly, tailwinds have been shown to have a significant impact on daily distances flown by booted eagles (Mellone et al. 2015), white storks (Shamoun-Baranes et al. 2003) and by four species of raptor while migrating across the Sahara (Mellone et al. 2012).

1.9. Hazards of migration

The selective advantages of migration are off-set by an increased risk of mortality during the journey (Klaassen et al. 2014). Migratory flights are associated with enhanced risk of predation, diseases, exhaustion, food shortage and mass mortality associated with weather and wind conditions which may have short-term effects on population sizes (Newton 2008). It may also expose migrating birds to increased risk of mortality due to anthropogenic factors, such as hunting (Brochet et al. 2015) and collisions with wind turbines (Johnston et al. 2012). Sillett and Holmes (2002) found that 85% of Black-throated Blue Warbler *Setophaga caerulescens* mortality occurred during migration and Klaassen et al. (2014) showed that mortality rate among three raptor species was six times higher during migration periods than on the breeding or wintering grounds. Furthermore there was a tendency for a higher mortality rate during spring migration, when mortality was most likely to occur in the Sahara desert (Klaassen et al. (2014). This corresponds with the findings of Lok et al. (2015) who found that Eurasian spoonbill *Platalea leucorodia* mortality was highest during spring, and specifically among populations crossing the Sahara.

1.10. Juvenile migration

Juvenile birds have inferior navigational abilities (Guildford et al. 2011, Mueller et al. 2013), expend more energy when flying (Rotics et al. 2016), are more susceptible to adverse weather (Thorup et al. 2003) and are less efficient foragers than adults (Skorka and Wojcik 2008). As such the first migration presents a highly demanding challenge (Alerstam 1990, Newton 2010, Rotics et al. 2016) and juveniles often exhibit considerably lower annual survival compared to adults as a result (Strandberg et al. 2010, Sergio et al. 2011, Guillemain et al. 2013).

In many species social learning is key to the survival chances of young birds with juveniles following experienced conspecifics on migration. For instance some shorebird species such as dunlin *Calidris alpina* migrate in mixed-age flocks (Henningsson and Karlsson 2009), while juvenile geese, cranes and swans migrate with their parents (Newton 2008). Soaring-gliding species tend to be social migrants

because such behaviour facilitates the location of thermal updrafts and learning of optimum routes by inexperienced individuals (Kerlinger 1989, Newton 2008). Avoiding long water crossings - where thermals updrafts are completely absent or very weak - is particularly important for soaring species because of the high metabolic costs of swapping to energy-demanding flapping flight. This is particularly the case for juvenile birds whose inferior flight skills make the switch to flapping flight even more costly than for adult birds (Rotics et al. 2016). The hazards of long sea crossings for soaring species is exemplified by the high degree of mortality among juvenile Egyptian vultures *Neophron percnopterus* which attempt long crossings of the Mediterranean between the Balkan peninsular and North Africa. Oppel et al. (2015) found that all except one of the birds that attempted the crossing died, whereas all juveniles that used an alternative route through Turkey and the Middle East survived.

The migratory periods of adults and juvenile raptors do not always overlap despite the clear advantages to juvenile birds of following experienced conspecifics on migration. Adult honey buzzards usually leave before juveniles (Agostini and Logozzo 1995) which may lead to juveniles attempting long sea crossings if they do not encounter later-departing adult birds en route (Agostini 2004). The migration routes used by juvenile short-toed eagles is also strongly dependent on social learning, with juveniles only incorporating detours to avoid long sea crossings if they encounter experienced adult birds during migration (Agostini et al. 2016, Mellone et al. 2016). Like honey buzzards, adult short-toed eagles depart earlier than juveniles, meaning that earlier departing juveniles are more likely to encounter adults and thus incorporate detours into their migration than those that depart later (Agostini et al. 2016, Mellone et al. 2016).

When migrating alone juvenile raptors rely entirely on an inherited programme of direction and distance, often referred to as vector summation in order to reach a suitable wintering site (Mourtsen 2003). Perhaps the best example of this strategy is that of ospreys which always migrate singly despite readily incorporating soaring-gliding flight into migration (Mellone et al. 2012, Agostini et al. 2015). The morphology of ospreys means that they are better-adapted to long sea crossings than most other migrant raptors (Agostini et al. 2015), but adult birds tend to be more selective in their water-crossing tendencies than juveniles (Horton et al. 2014) and are

able to compensate for crosswinds when necessary to avoid being blown into hazardous habitats (Klaassen et al. 2011). Like most first year birds juvenile ospreys are more susceptible to wind drift (Thorup et al. 2003) and this has implications for migration routes, and ultimately, their final wintering destination (Hakke et al. 2001, Martell et al. 2001).

Recent studies have demonstrated that juvenile birds expend more energy on migration than adults (Duerr et al. 2015, Rotics et al. 2016). Rotics et al. (2016) estimated that juvenile white storks used 14% more energy on migration as a result of an increased use of flapping flight compared to adults, even though they migrated with experienced conspecifics. These increased energetic costs coupled with vector-based orientation (compared to goal-based navigation by adults where there may be fitness benefits associated with an early arrival on the wintering grounds) mean that juvenile migration is more likely to be influenced by energetic constraints than time (Miller et al. 2016). This explains why juveniles of some species have been shown to migrate slower than adults (Mellone et al. 2013, Miller et al. 2016) and spend more time on stop-overs during migration (Hake et al. 2003, Mellone et al. 2013). In this case stop-overs provide a valuable opportunity for juveniles to replenish fuel reserves (Yosef et al. 2006) and, potentially, an additional chance to improve foraging skills (Mellone et al. 2013). The risks of juvenile birds attempting to migrate too quickly was exemplified by Rotics et al. (2016) who found that juvenile white storks that died during or just after migration exhibited higher levels of flight energy expenditure compared to surviving juveniles. They hypothesised that in the case of species that migrate with experienced conspecifics there is a trade-off between attempting to keep pace with experienced adult birds (who migrate faster and more efficiently) and saving energy but, in doing so losing contact with flocks and increasing the risk of being left behind.

1.11. Seasonal differences in migration

The empirical evidence that mortality is often higher during spring migration is indicative the birds may be under selective pressure to complete spring migration faster than autumn because of the advantages of returning earlier (Kokko 1999). As

Nilsson et al. (2013) point out, birds that arrive at breeding sites early can initiate breeding earlier (Moore et al. 2005) and in doing so potentially increase reproductive performance (van Noordwijk et al. 1995). However these benefits are off-set by the dangers associated with a faster migration, as demonstrated by increased mortality in the Sahara in spring that may be associated with a riskier migration strategy (Klaassen et al. 2014, Lok et al. 2015). In time-selected migration, migration speed may be characterised by a distinct shift from a maximum sustained speed to a final sprint regardless of the associated costs of doing so (Alerstam 2006). This may involve extending daily flight times (Alerstam 2006), changing from soaring flight to energy-demanding flapping flight (Mellone et al. 2012), and migrating in unfavourable meteorological conditions such as in strong headwinds, thereby extending airspeeds beyond those that are optimal in flapping flight (Alerstam and Henderström 1998).

In a thorough comparison of published studies comparing seasonal variation in migration, Nilsson et al. (2013) found that journeys in spring were usually faster for all migration variables analysed. Nevertheless seasonal differences were considerably smaller in magnitude for flight speed variables (airspeed, groundspeed and daily travel speed) than for variables affected by foraging behaviour (stop-over duration, total migration speed, and total duration of migratory journey).

Of the various flight speed variables assessed by Nilsson et al. (2013), airspeed (a bird's flight speed relative to the surrounding air) is the best means of determining the urgency of migration because it is independent of external variables - most notably wind - that may artificially increase ground speed (Alerstam 2000). However in flapping flight the increased flight costs of a faster airspeed will limit the distance a migrating bird is able to fly as already discussed (Alerstam 2000, Alerstam and Lindström 1990). Nilsson et al. 2013 found that airspeeds were generally faster in spring, but that the most convincing examples of time-selected migration were common swifts (Henningsson et al. 2009) and nocturnal long-distance passerine migrants tracked by radar in Scandinavia (Karlsson et al. 2012).

Of the variables affected by foraging behaviour, the tendency for birds to make fewer and shorter stop-overs during spring migration has already been discussed. This

corroborates with the fact that in the majority of cases birds also showed a faster migration speed and shorter duration of migration in spring (Nilsson et al. 2013). The one notable exception was soaring-gliding species, for which there was no seasonal difference in duration of migration and only a weak trend for faster spring migration speed (Nilsson et al. 2013). This suggests that these species are constrained by their reliance on thermal conditions, even if there is increased urgency in spring.

1.12. Methods of study

Recent years have seen significant technological advances that have greatly aided the study of avian migration (López-López 2016). Of particular note was the development of the first satellite transmitters in the 1980s (Fuller et al. 1984). This allowed birds to be tracked during complete migratory journeys for the first time, thereby providing valuable new information on route, speed and duration of migration (Börger 2016). The incorporation of Global Positioning System (GPS) receivers, data transmission through the Argos system (a global satellite-based location and data collection system dedicated to studying animal movement) and the increase of data storage and battery capacity (most recently through incorporation of solar power) has provided steadily improving data ever since (López-López 2016). The most recent Platform Transmitter Terminals (PTTs) provide highly accurate three-dimensional detail with altitude, speed and orientation logged at the same time intervals as location. Another exciting recent development is the deployment of Global System for Mobile Communication (GSM)/GPS transmitters. These transmitters which send data through the mobile phone network are capable of transmitting more data than an Argos/GPS PTT and, ultimately, are more cost effective per unit of data transmitted. The high temporal resolution data collected by GSM/GPS transmitters make it possible to undertake in-depth analysis of flight behaviour across complete migrations for the first time (López-López 2016).

As López-López (2016) pointed out, studies using individual-based tracking systems are based on the underlying principle that bird behaviour is not affected by carrying the transmitter. Some studies have identified negative impacts, specifically relating to rates of mortality and breeding success (Constantini and Møller 2013), but others have

found no such trends (Igual et al. 2005) and argue that the sample size of studies reporting negative effects are too low to make such inferences (Sergio et al. 2015). All researchers agree, however, that the correct choice of transmitter and method of attachment is key (Blackburn et al. 2016). Most studies adhere to the recommendation that the weight of transmitters should not exceed 3-5% of the bird's body mass (Kenward 2001). Nevertheless López-López (2016) suggests that further research is needed to assess the most appropriate tracking methods, both from the perspective of transmitter weight, and also how it affects aerodynamics in flight (Penycuik et al. 2012). In the UK the use of satellite transmitters is strictly licenced by the British Trust for Ornithology.

1.13. The osprey

The osprey is a medium-sized raptor with a cosmopolitan distribution. It is one of only six land bird species that occurs on every continent except Antarctica (Monti et al. 2015). The most widely accepted taxonomic arrangement recognises four sub-species of Osprey: *P. h. haliaetus* (Linnaeus, 1758) which breeds in the Palearctic including Europe, north-west Africa, and Asia north of the Himalayas, *P. h. carolinensis* (Gmelin, 1788) in North America, *P. h. ridgwayi* (Maynard, 1887) in Caribbean Islands, and *P. h. cristatus* (Vieillot, 1816) in the Indo-Pacific and Oceania. Christidis and Boles (2008) split *Pandion haliaetus* and *Pandion cristatus* into separate species but this has been controversial and not widely accepted (Birdlife International 2016).

As a specialist piscivore that hunts by plunge diving and then catching prey in specially-adapted talons, ospreys can forage in both freshwater and marine environments (Poole 1989). Northern populations are generally migratory with European and Asian ospreys wintering in sub-Saharan Africa (Dennis 2002, Alerstam et al. 2006), the Indian sub-continent and South-east Asia respectively (Poole 1989), and North American birds wintering in South America (Martell et al. 2014). In contrast, individuals from lower latitudes (e.g. Caribbean, Atlantic islands and Mediterranean basin) are mostly sedentary, or make limited post-breeding movements (Poole 1989, Thibault et al. 1996). Ospreys show strong natal philopatry, with males in particular usually returning to the area from which they fledged in order to breed (Poole 1989). Nests usually

consist of large stick-built structures situated on a prominent tree or artificial structure, such as electricity pylons (Schmidt-Rothmund et al. 2014), although ospreys may nest on cliffs or on the ground in some localities (Poole 1989). Once established, nests are often used for many years by successive generations of ospreys (Dennis 2008, Poole 1989).

1.14. Osprey migration

Osprey migration has been studied using a combination of ringing (Strandberg et al. 2009), radar (Meyer 2000, Kjellen et al. 2001) and, most recently, satellite tracking. The earliest satellite tracking studies (Kjellen et al. 1997, Martell et al. 2001) generally verified migration routes and overwintering regions first indicated by ringing recoveries, but added considerable detail in terms of speed, duration and timing of migration (Stranberg et al. 2009). Of particular note among these early studies were long ocean crossings undertaken by North American ospreys migrating between the Dominican Republic and Venezuela (Martell et al. 2001), and the first documentation of flights across the Sahara which took up to ten days to complete (Kjellen et al. 1997). It was also notable that two females from the same region of Sweden used contrasting migration routes to the Ivory Coast and Mozambique respectively (Kjellen et al. 1997).

In subsequent years further satellite tracking studies have significantly increased knowledge of osprey migration. Studies where individual ospreys have been followed for successive migrations using solar-powered PTTs (Figure 1.3) have been particularly revealing, demonstrating that adult birds show a high degree of repeatability in routes (Vardanis et al. 2016), thereby indicating the existence of up to three intermediary goal areas along the route of individual birds (Alerstam et al. 2006). Adult birds are also faithful to the same wintering site each year and are largely sedentary after arriving in autumn (Washburn et al. 2014). This contrasts with the behaviour of juvenile birds, which wander widely on the wintering grounds upon arrival (Hake et al. 2001).

In addition to differences in behaviour following arrival at the wintering grounds, juvenile ospreys show a larger variability in orientation during autumn migration than

adults (Hake et al. 2001). In North America this results in some juvenile birds making very long non-stop flights (mean 52 hours, 2162 km) across the western Atlantic Ocean direct from New England to the Caribbean, a flight not undertaken by adult birds that choose to migrate along the eastern seaboard instead (Horton et al. 2014). Unexpectedly, juvenile ospreys maintain a remarkably direct route during these flights, fully compensating for wind drift despite an absence of visual clues. Furthermore they regulate airspeed according to the rules of optimum bird migration theory (Alerstam and Lindström 1990), increasing airspeed in headwinds and reducing them with tailwind support (Horton et al. 2014). Horton et al. (2014.) suggest that none of the existing theoretical frameworks of animal navigation are capable of explaining such advanced navigational abilities of juvenile ospreys and instead proposed a 'chord and clock' system of navigation. Under this system they suggest that the migrating individual is able to use external information (e.g. magnetic field and celestial cues) to determine the scalar distance between two locations (chord) and gauge the passage of time calibrated against exogenous time dependent cues (clock). This contrasts with the conclusions of Thorup et al. (2003) who suggested that the migration patterns of juvenile ospreys could be explained by extended vector summation, whereby the vector summation model (Rabøl 1978) described earlier also includes an initial phase of less concentrated orientation.

The results of satellite tracking studies have verified the suggestion that ospreys migrate by a combination of soaring-gliding flight and flapping flight (Alerstam 2000) given that they do not limit flight to land in the manner of true soaring migrants, and also incorporate nocturnal flight into migration (Alerstam 2006, Horton et al 2014). Agostini et al. (2015) suggest that the osprey's ability to undertake long sea crossings may be due to morphological adaptations; specifically its long, relatively narrow wings that reduce drag. The osprey's ability to supplement soaring-gliding flight with flapping was also referenced by Mellone et al. (2012) who suggest that on occasions ospreys may employ the technique of powered glides where birds flap sporadically during inter-thermal gliding. This has the effect of increasing flight speed and, when coupled with the ability for longer flight times each day, may explain why ospreys often achieve

greater daily distances on migration than true soaring migrants (Hake et al. 2001, Mellone et al. 2012).



Figure 1.3. Osprey with solar-powered GPS Platform Transmitter Terminal (PTT) at Rutland Water. *This type of PTT weighs 35 g and is attached to the bird using a Teflon harness secured with cotton. Transmitters log location, altitude, speed and orientation at pre-determined time intervals. All of the ospreys in this study were tagged under licence from the British Trust for Ornithology.*

Satellite tracking has also demonstrated the hazards that ospreys face on migration. Klaassen et al. (2014) showed that the rate of mortality was six times higher during migration than breeding and wintering periods among ospreys, marsh harriers and Montagu's harriers. It is particularly notable that a significant proportion of migration occurred in the Sahara during spring. This corresponds with previous research which demonstrated that the Sahara is a clear hazard to migrating ospreys and other species tracked by satellite telemetry (Strandberg et al. 2010). Sea crossings have also been shown to result in mortality among ospreys, particularly juveniles during their first autumn migration (Dennis 2002, Horton et al. 2014, Klaassen et al. 2014).

Previous studies of osprey migration have shown that spring flights are faster than autumn (Alerstam et al. 2006, Martell et al. 2014). Alerstam et al. (2006) found that this was due to the fact that Swedish ospreys incorporated fewer stop-over days in spring. North American birds also spent fewer days on stop-overs during spring migration, but in addition they travelled by more direct routes and also flew further per day compared to autumn (Martell et al. 2014). In addition Alerstam (2006) suggests that on occasions some ospreys display the attributes of sprinting migrants by incorporating nocturnal flight into the latter stages of migration. This enables them to return to the breeding site faster and thereby demonstrates the benefits of a flexible flight method.

1.15. Ospreys in the UK

In the United Kingdom the osprey was formerly widespread with breeding pairs distributed throughout England, Scotland and Wales (Dennis 2008). However, intense persecution, most notably during the Victorian era, resulted in a drastic decline and by the 1920s they had almost been completely exterminated as a breeding species (Dennis 2008). It was not until 1954 that breeding was documented again when a pair reared two chicks at Loch Garten in northern Scotland (Brown and Waterston 1962). Since then the population in Scotland has increased to more than 230 pairs, thanks to a dedicated conservation effort in the form of protection of established nests and erection of artificial new ones (Schmidt-Rothmund et al. 2014). Ospreys returned to England in 2001 as a result of natural expansion into Cumbria and a re-introduction project based at Rutland Water in the East Midlands (Mackrill 2013). Breeding was subsequently confirmed in Wales for the first time in 2004 (Evans 2014). The population in England and Wales constitutes at least 25 breeding pairs in 2016 (Dennis 2016 *pers. comm.*).

1.16. Aims of thesis

Ringling and previous satellite tracking studies have shown that ospreys from the UK usually migrate to West Africa, with the majority of birds wintering on the coast between Mauritania and Ivory Coast (Dennis 2002). These early satellite tracking

studies were carried out using transmitters with relatively low temporal resolution (Dennis 2002), but GPS PTTs and GPS/GSM PTTs now have the potential to provide much more extensive datasets. The key aims of this thesis are to use these advances in satellite tracking to further our understanding of osprey migration from the UK and to put it in the wider context of avian migration by addressing three key research questions:

1.16.1. To what extent does osprey migration vary by season and how is it influenced by environmental and behavioural factors?

Seasonal differences in osprey migration speed have been reported from Europe (Alerstam et al. 2006) and also North America (Martell et al. 2014), with spring flights faster. However, it has been difficult to determine the relative influence of selection pressure (time and energy) on the faster spring flights because previous studies have not incorporated environmental data. It is widely accepted that, like many species, ospreys gain a selective advantage through an early arrival at their breeding grounds in the spring, but recent evidence suggests that several species of migratory raptors are also under time-pressure in autumn, with reclamation of winter territories important to individual fitness. A key aim of this thesis, therefore, is to attempt to determine the relative influence of time and energy minimisation on migration during autumn and spring and to determine how this affects migration speed and routes, when environmental variables are controlled for.

1.16.2. How does flight method vary according to region and associated environmental conditions, and what is the subsequent effect on migratory performance?

The osprey's ability to migrate long distances by flapping flight means that it is less-reliant on thermal updrafts than most other medium-large raptors and, as such, can make very long ocean crossings. The same adaptability in flight mode also enables it to undertake nocturnal flight when necessary. Until recently, however, it was not possible to determine the extent to which ospreys adapt their flight method during complete migratory journeys and across geographical barriers such as oceans. Instead studies were confined to single sites using visual observations or radar. The advent of high-definition GSM tracking technology now permits such research for the first time.

The second key aim of this thesis is to devise a simple method to categorise flight method from high-resolution GSM data and to determine how ospreys adapt their flight mode according to changing environmental conditions, particularly during flights over land and sea.

1.16.3. To what extent do juvenile ospreys show individual variation in migratory behaviour, performance and routes?

During their first migration juvenile ospreys migrate singly, and as such rely on an endogenous programme of direction and distance, known as vector summation in order to migrate to distant wintering grounds. The lack of previous migratory experience and absence of social learning during migration has the potential to result in highly individual flights, particularly as first year birds are unlikely to be capable of correcting for displacement. The final key aim of this thesis, therefore, is to understand the driving forces behind any such individual variation in juvenile osprey migration, and to determine how this affects routes, timing and, ultimately, destination of migration.

1.17. Ethics statement

All of the ospreys in this study were satellite-tagged by Roy Dennis, with assistance from Tim Mackrill and others, under licence issued by the British Trust for Ornithology. All transmitters were of a size and weight in accordance with the recommendations of Kenward (2001). Birds were trapped according to licence criteria using either an eagle owl decoy and Dho-Gaza net or a simple noose placed on the nest or nearby perch. None of the birds sustained injuries during the trapping process and all were handled for the minimum period of time possible. All birds were monitored closely after release, and no adverse effects caused by the deployment of the transmitters were observed.

2. The role of weather and time-minimisation in determining seasonal variation in osprey migration.

2.1. Abstract

The use of time-minimisation strategies during avian migration has profound effects on migration speed. There is a growing body of evidence that in addition to spring migration, selection pressure acts as a key driver in shaping migratory journeys in autumn. In this study we compared the autumn and spring migration of ospreys migrating between the UK and West Africa at three temporal scales (hourly, daily and journey) using satellite telemetry. Contrary to expectations ospreys required fewer days to complete autumn migration because they flew greater distances on travelling days and used more direct routes, with no seasonal difference in the number of stop-over days. Meteorological factors were the key driver in shaping differences in daily and hourly speeds, with birds travelling faster when supported by tailwinds and in favourable thermal conditions. However, ospreys also incorporated time-minimisation strategies during autumn migration, most notably a greater propensity for nocturnal flight. This was frequently recorded during crossings of the Bay of Biscay, which were usually only undertaken in autumn when supported by tailwinds. In some cases Bay of Biscay crossings constituted sections of very long non-stop flights from the UK with a maximum distance of 1365 km. We argue that the time-minimisation strategies used by ospreys during autumn support a growing body of evidence that selection pressure to reclaim winter territories is an important factor in determining migratory behaviour of trans-Saharan raptors even if, as in this case, meteorological variables are the primary factor in determining migration speed.

Keywords: Raptor, GPS telemetry, migration, Bay of Biscay, Sahara, time-minimisation.

2.2. Introduction

In recent years our knowledge of bird migration has been enhanced by advances in satellite tracking technology. These data have generally shown that birds migrate faster in spring than autumn (Nilsson et al. 2013) because of the selective advantages of returning to the breeding site earlier (Kokko 1999, Newton 2008). However, there is a trade-off between fast spring flights and risk-taking on migration. Mortality rate can be up to six times higher during migration than in stationary periods and there is a tendency for higher mortality during migration in spring than autumn (Lok et al. 2013; Klaassen et al. 2014).

Seasonal differences in migration speed differ in magnitude according to which factors are tested, with flight speed varying less than factors such as stopover duration and total duration of migration (Nilsson et al. 2013). Some species may be further constrained by their flight method (Alerstam 2000). For instance daily flight times of soaring migrants such as raptors and storks are limited to periods when thermal updrafts are available (Melone et al. 2012) and cross-country speed is constrained by climbing speed within thermals and inter-thermal gliding speed (Spaar and Bruderer 1996, Pennycuik 1998, Horvitz et al. 2014). As a result soaring-gliding migrants show less seasonal variation in total duration of migration than passerines which migrate by flapping flight (Nilsson et al. 2013).

Wind also has a profound effect on soaring migrants (Alerstam 2000) with migration speed enhanced by tailwinds (Vansteelant et al. 2015) but decreased by crosswinds (Kerlinger 1989). Several studies have shown that tailwinds have the most significant impact on daily distances of migrant raptors by increasing hourly speeds. Vansteelant et al. (2015) found that weather accounted for between 40 % and 50 % of variability in hourly speeds achieved by honey-buzzards *Pernis apivorus* and Montagu's harriers *Circus pygargus*, with tailwinds having the most significant impact. Similarly, Mellone et al. (2012) showed that tailwind strength was the most important factor in determining the daily distance flown by ospreys *Pandion haliaetus* and three other species of raptors across the Sahara. Crosswinds, like tailwinds, are also likely to influence daily distance, in this case through their influence on straightness and the extent to which a

migrating bird either submits to, or compensates for, wind drift (Liechti 1995, Alerstam 2000). Klaassen et al. (2011) found that marsh harriers *Circus aeruginosus* and ospreys respond to crosswinds according to local conditions; drifting when favourable and compensating or overcompensating when approaching a goal or facing the risk of being blown into hazardous habitats. Klaassen et al. (2011) go on to suggest that this flexibility in response indicates that migrating raptors have excellent navigational skills and are able to estimate drift while aloft.

The influence of weather is exemplified by the fact that some migratory raptors and storks have unexpectedly been shown to migrate faster in autumn than spring as a result of more favourable meteorological conditions (Shamoun-Baranes et al. 2003, López López et al. 2014). Weather may also influence the migration route used, which has been shown to vary according to season in some species. Such loop migrations reflect predictable seasonal differences in environmental conditions, particularly in relation to crossing ecological barriers (Newton 2008, Alerstam 2011).

The profound influence of weather makes extricating the relative importance of behavioural drivers in determining bird migration speed difficult. As such airspeed, a measure of a bird's speed relative to the air rather than the ground, is a useful attribute because it is determined solely by the bird's flight behaviour rather than meteorological conditions (Nilsson et al. 2013). Flight theory suggests that optimal airspeed will be faster during time-selected migration (where a bird is expected to minimise overall duration of migration) compared to energy selected migration (when minimising energetic costs is the key driver) (Alerstam and Lindström 1990). This has been borne out by radar tracking studies of common swifts *Apus apus* (Henningsson et al. 2009) and nocturnal passerine migrants (Karlsson et al. 2012) with faster airspeeds recorded in spring according to the time-minimisation hypothesis. There is also some limited evidence that species that migrate by soaring-gliding fly at faster airspeeds in spring (Spaar et al. 1998). These species can achieve faster airspeeds by increasing the angle of descent during glides between thermals (Horvitz et al. 2014). However this increases the risk of grounding, or swapping to energy-demanding flapping flight which is particularly costly for larger species (Horvitz et al. 2014).

In the past time- and energy-selected migrations have been presented as being independent of one another (Henderstöm 1993) but in recent years it has been suggested that birds use components of both strategies (Alerstam 2011). For instance Miller et al (2016) found that spring migration of golden eagles *Aquila chrysaetos* is predominantly time-limited, but that individuals that migrate the furthest also incorporate energy-saving strategies. In contrast autumn migration is predominantly energy-selected but with some elements of time-minimisation, particularly among later departing birds.

In time-selected migration, speed may be characterised by a distinct shift from a maximum sustained speed to a final sprint regardless of the associated costs (Alerstam 2006). This may involve extending daily flight times, sometimes to include nocturnal flight (Alerstam 2006), changing from soaring flight to energy-demanding flapping flight (Mellone et al. 2012), and migrating in unfavourable meteorological conditions such as in strong headwinds and thereby extending airspeeds beyond those that are optimal in flapping flight (Alerstam and Henderström 1998). There is growing evidence that in addition to the well-documented spring migrations, autumn migration in some species may also be time-selected due to competition for resources on the wintering grounds (Panuccio et al. 2014, Mellone et al. 2015).

The osprey *Pandion haliaetus* is a long distance migratory raptor that breeds in much of northern Europe and winters in sub-Saharan Africa, with a smaller number of individuals spending the winter in Iberia (Dennis 2002, Alerstam et al. 2006). Other migratory populations of the species also breed in North America (Martel et al. 2014). The United Kingdom supports almost 300 pairs of breeding ospreys, the majority of which occur in Scotland (Dennis 2008). Other smaller populations also occur in England and Wales (Mackrill 2013). Ospreys use the fly-and-forage strategy during migration, whereby birds pause to feed before, during or after a day's flight (Strandberg and Alerstam 2007, Klassen et al. 2008), as well as incorporating stop-overs into their journeys (Kjellén et al. 2001).

Seasonal differences in osprey migration speed have been reported from Europe (Alerstam et al. 2006) and also North America (Martell et al. 2014) but there has been

some debate as to the influence of selection pressure in determining this variation. Alerstam et al. (2006) found that ospreys incorporated fewer stop-over days in spring, but suggest that this is not necessarily indicative of time-minimisation because other factors such as pre-migratory fuelling and stop-over site quality may be important. Furthermore there was minimal seasonal variation in flight performance or timings on travelling days. Martell et al. (2014) meanwhile suggest that shorter routes used by ospreys that breed on the East Coast of North America in spring may be indicative of a time-minimisation strategy. However, like Alerstam et al. (2006), meteorological conditions were not controlled for. For ospreys returning to breeding sites in Europe weather conditions encountered during spring migration are likely to be less favourable than autumn, particularly as they approach the breeding grounds (Shamoun-Baranes et al. 2003, Mellone et al 2012). Although ospreys migrate predominantly by soaring-gliding flight, their morphology – specifically long narrow wings that reduce drag - enables them to switch to flapping flight in adverse weather conditions (Kerlinger 1989, Agostini 2015). As a result they are better adapted to a final sprint than pure soaring migrants. Alerstam (2006) suggests that some ospreys migrating to nests in Sweden exhibit such behaviour.

The UK's position in Western Europe makes the analysis of flights to and from this region particularly interesting because of the close proximity to the Bay of Biscay. The osprey's ability to utilise flapping flight enables it to make long sea crossings during migration (Meyer et al. 2000, Dennis 2002, Martel et al. 2014, Horton et al. 2015) with hourly speeds exceeding those over land (Klaassen et al. 2008). Migrant ospreys have been recorded flying across the Bay of Biscay from the UK to northern Spain (Dennis 2002) but such flights can involve considerable risk, and have been shown to result in mortality, particularly among juvenile birds (Dennis 2008). Time-selection theory suggests that flights across the Bay of Biscay are more likely to be undertaken in spring, but the climate of Europe may prohibit such flights even by birds behaving in the manner of sprinting migrants. Furthermore migrant ospreys may be more inclined to make long crossings of the Bay of Biscay in autumn when they have had the opportunity to deposit fuel on the breeding grounds (Alerstam 2000) or at stop-over sites.

The Sahara presents another ecological barrier to ospreys migrating between Northern Europe and West Africa and it has been shown to increase mortality among migrant raptors, particularly in spring (Klaassen et al. 2014). Furthermore, difficulties encountered when crossing the Sahara – often relating to adverse weather – can result in migratory species arriving late at the breeding grounds, thus leading to a reduction in breeding success (Strandberg et al. 2010). Nonetheless the migration speed of ospreys across the Sahara has been shown to be faster in spring than autumn (Mellone et al. 2012).

2.2.1. Aims

In this study the repeated journeys of adult ospreys satellite-tagged in the UK were analysed in order to determine:

- i. The extent to which migration routes and speed vary seasonally, and specifically to test the hypothesis that selection pressure to incorporate time-minimisation strategies is greater in spring, resulting in faster migrations. Conditions for thermal soaring-gliding are likely to be more favourable in Africa than Europe (Chevallier et al. 2010) but this is off-set by the fact that fewer foraging sites are available in Africa - particularly while crossing the Sahara - which has implications for fly-and-forage migrants such as ospreys (Strandberg and Alerstam 2006). Furthermore, in time-selected spring migration ospreys should migrate faster and for longer through Europe as they approach their breeding site, even if environmental conditions are unfavourable (Alerstam 2006). Including region, departure date, and key meteorological factors as explanatory variables enables potential confounding factors to be disentangled in order to identify the key behavioural and environmental drivers determining migration speed and routes.
- ii. Whether strategies used by ospreys to cross two key ecological barriers – the Bay of Biscay and Sahara - differ between spring and autumn. The UK's close proximity to the Bay of Biscay means that ospreys migrating to and from the Iberian peninsula are more likely to attempt ocean crossings than

ospreys from populations further east in Europe. Previous research has demonstrated that ospreys are able to make such crossings, but that these flights involve increased risk compared to flight over land. The Sahara is another key ecological barrier to ospreys migrating to sub-Saharan African, as demonstrated by increased mortality of migratory birds during flights across it, particularly in spring. The analysis of flights across these two ecological barriers and how they vary between seasons, thus has the potential to add to our understanding of the trade-offs involved in avian migration.

2.3. Methodology

A total of 14 adult ospreys from Highland and Moray in Northern Scotland and Rutland and Leicestershire in Central England were trapped under licence and fitted with Platform Transmitter Terminals (PTTs) manufactured by Microwave Telemetry Inc., Columbia, MD 21045, United States. Of these birds, nine were males and five were females. Three of the birds (two males and one female) were from a population centred on Rutland Water in central England that was established by a reintroduction project in the late 1990s. The individuals translocated as part of this project were taken from the same population in Northern Scotland that the remainder of the satellite-tagged birds in this study originate from. Of the English birds, one (bird 1) was translocated from Northern Scotland and released at Rutland Water as a juvenile and the two others (bird 2 and bird 3) are wild-fledged offspring of translocated birds. The transmitters were fitted using a Teflon harness and weighed 35g: equivalent to less than 3% of an Osprey's body weight as recommended by Kenward (2001). The transmitters, with an in-built Global Positioning System (GPS) logged the bird's location (± 18 m), altitude (± 22 m), speed (km) and orientation (degrees) once every hour. Three of the birds were fitted with Global System for Mobile Communication (GSM)/Global Positioning System (GPS) satellite transmitters that have the same degree of accuracy, but log data as regularly as once per minute during the middle part of the day (when battery voltage is highest) and less frequently (0.5 - 4 hours) at night. For consistency, and for comparison with the standard transmitters, only one

data point per hour from the GSM transmitters was used in the flight analysis. In each case the data point closest in time to the start of the hour was used. Satellite data were accessed through the Argos system based in France.

2.3.1. Timescale

Migration patterns were analysed at three scales: hourly, daily and journey (Mellone et al. 2015). Flight data were first analysed to determine start time and end time of each day's flight. If the exact start time was not logged by the transmitter, it was estimated to the nearest 15 minutes by calculating the time required to fly to the location of the first GPS observation after the bird had begun its daily flight, based upon the bird's average speed during the morning. Time of arrival at the evening roost site was estimated by calculating the time required to fly from the last flying GPS observation (i.e. speed > 0 km) to the first stationary GPS observation based on the bird's average speed during the afternoon. Daily distance was then determined by calculating the great circle distance between the departure location and evening roost site. Days where an individual flew > 25 km in the intended direction of migration were classed as travelling days, while days where the bird remained in the same area and flew less than 25 km were classed as stop-over days. If a bird continued to fly for more than one day the flight was deemed to be a single sector and analysed in the same way as a single day. Migration distance was calculated as the sum of all daily/sector distances flown on travelling days. Journey straightness was calculated as the ratio between migration distance and the total great circle distance between the start point and end point of the migration. Actual flying time was calculated for days with hourly GPS observations, using start time and end time and discounting any periods where the bird remained stationary during the day. Daily straightness was also calculated for days with hourly GPS observations as the ratio between actual distance travelled (sum of hourly distances flown) and daily distance (great circle distance between start location and roosting site as described in Mellone et al. (2015). The final day of migration was discounted from this analysis to account for the fact that birds may not have needed to maximise daily distance on this day. On the hourly scale, migration speed on travelling days was determined by calculating distance flown during one hour segments where travelling speed recorded by the transmitter was > 0 km at the

beginning and end of each hour and where the bird flew > 5km during the 1 hour period (as per Strandberg et. al 2009, Mellone et al. (2012) and Mellone et. al 2015).

Adult Ospreys are sedentary in winter (Hake et al. 2001, Dennis 2008, Washburn et al. 2014), so a bird was considered to have completed its autumn migration if it remained in the same area for four consecutive weeks. Data for any days where the bird was at its wintering site were subsequently discarded from the analysis. Spring was deemed to have been completed once the bird returned to its breeding nest or summering location since all the birds were of known origin.

2.3.2. Environmental variables

To determine the impact of meteorological conditions on migration speed, wind data and boundary layer height (m) were downloaded from the European Center for Medium-Range Weather Forecasts (ECMWF) Global Reanalysis Project at a resolution of 0.25° and 3 h. Wind strength and direction may vary with altitude (Stull 1988) and so u- and v-wind components (i.e. latitudinal and longitudinal wind velocities, m s^{-1}) were downloaded for the barometric pressure level (950 mB, equating to an altitude of 540 m) closest to the median altitude flying altitude of the ospreys in this study (585 m). Wind data were linearly interpolated for hourly locations when the bird was travelling (i.e. excluding all resting hours) using ArcMap 10.3.1. Head/tailwind and absolute crosswind components were then calculated for each hourly location based on the bird's hourly flight heading (Vansteelant et al. 2015). In this case headwinds were expressed as positive values, and tailwinds as negative. According to the triangle of velocities described by Alerstam (2000) a bird's groundspeed and track direction is the sum of the bird's flight vector (heading direction and airspeed) and the wind vector (wind direction and speed). Therefore we calculated hourly airspeeds by summing hourly groundspeed with head/tailwind component based on the bird's hourly heading. Based on this calculation a flapping groundspeed of 10 m s^{-1} with a headwind component of 3 m s^{-1} would give an airspeed of 13 m s^{-1} . Boundary layer is a proxy for the strength and spacing of thermals, with a higher boundary layer indicative of stronger and more densely spaced thermals (Stull 1988). Boundary layer was thus linearly interpolated for hourly locations in the same way as wind data

(Vansteelant et al. 2015). In order to determine the impact of weather variables on a daily scale, head/tailwind and crosswind components were calculated for each hourly location relative to the bird's daily heading and then averaged across the day. Hourly boundary layer data were averaged in the same way. Day length was expressed as minutes between sunrise and sunset as experienced by each individual during each daily flight (i.e. minutes between sunrise at the departure site and sunset at the roosting site). Sunrise and sunset were calculated for the relevant locations using a formula provided by National Oceanic and Atmospheric Administration (NOAA) <http://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html>.

All environmental variables were sub-divided into categories according to the criteria required for use of the LMM procedure in IBM SPSS Statistics 22. This categorisation also enabled direct comparisons to be made with previous research on osprey migration which used the same methodology (Mellone et al. 2012). Headwinds exceeding 2.5 ms^{-1} classified as 'opposing winds', head/tailwind between 2.5 ms^{-1} and -2.5 ms^{-1} as 'weak winds' and tailwinds exceeding -2.5 ms^{-1} as 'following winds'.. Absolute crosswinds were classified as either 'weak' ($0 \text{ ms}^{-1} - 2.5 \text{ ms}^{-1}$), 'moderate' ($2.5 \text{ ms}^{-1} - 7.5 \text{ ms}^{-1}$) or 'strong' ($> 7.5 \text{ ms}^{-1}$). Boundary layer was classified as 'low' ($< 1500 \text{ m}$), 'medium' ($1500\text{m} - 3000\text{m}$) or 'high' ($> 3000\text{m} +$). Finally day length was classified as 'short' ($< 700 \text{ mins}$), 'medium' ($700 \text{ mins} - 750 \text{ mins}$) or 'long' ($> 750 \text{ mins}$).

2.3.3. Regions

Since environmental conditions and flight behaviour are likely to vary both regionally and seasonally (Alerstam 2006) data were sub-divided into four separate categories for the analysis of daily speeds: 'Europe in autumn', 'Africa in autumn', 'Europe in spring', and 'Africa in spring'. For the purposes of this analysis GPS observations north of 36°N were categorised as 'Europe' and south of 35.9°N were categorised as 'Africa'. Where a bird crossed between regions the relevant data were excluded from the analysis.

The analysis of hourly speeds enabled ocean crossings to be included as separate variables in order to check for differing flight strategies between land and sea. In this

case ‘ocean in autumn’ and ‘ocean in spring’ were included along with ‘Europe in autumn’, ‘Africa in autumn’, ‘Europe in spring’, and ‘Africa in spring’. The latitudinal and longitudinal constraints outlined above were used for the land regions, with all ocean flights incorporated together.

2.3.4. Departure date

In order to determine the effect of departure date on migration speed, the start date of autumn and spring migrations were categorised as early, medium or late. This categorisation is shown in Table 2.1 and was based on the frequency distributions of departure dates in each season.

Table 2.1. Departure date categorisation. *Birds were classified as early, medium or late departing in the LMMs according to the dates that they set-off on migration.*

Season	Early	Medium	Late
Autumn	2 – 22 August	23 August – 6 September	7 September – 26 September
Spring	26 February – 15 March	16 March – 31 st March	1 st April – 12 April

2.3.5. Flight across ecological barriers

Flights across the Bay of Biscay and Sahara were included in the main analysis, but were also investigated separately to check for seasonal differences in relation to the crossing of these ecological barriers. The median altitude of ospreys flying over the Bay of Biscay was lower (267 m) than the corresponding figure for complete migrations and so u- and v-wind components for a pressure level of 975 mB (323 m) were used in this analysis. If the exact start time of the flight over the sea was not logged by the transmitter, it was estimated using mean flight speed during the sea crossing. The same method was used to determine the finish time if necessary. For the purposes of this analysis, the Bay of Biscay relates to any sea crossings made by Ospreys over the Atlantic Ocean between the UK and northern Spain (55° N and 43° N). As such, parts of the Irish Sea and Celtic Sea were also included. Flights between latitudes of 30° and 16° N were included in the analysis of migration across the Sahara and any flights that exceeded these geographic parameters were excluded from the analysis.

2.3.6. Statistical Analysis

At the journey scale, Generalized Linear Mixed Models (GLMM) with Poisson error distribution and log-link function were used to test for the effect of season on total duration of migration, number of travelling days and number of stop-over days. In each case bird ID was included as a random factor to account for the fact that birds were migrating between start and end points unique to them. A Linear Mixed-effect Model (LMM) was used to determine whether logit-transformed (Warton and Hui 2011) journey straightness varied between seasons. Bird ID was again incorporated into this model as a random factor.

Further LMMs were used to determine the impact of season and other explanatory variables on log-transformed daily distance, daily straightness and daily flying time with bird ID included as a random factor (with repeated measures for years) on each occasion. If appropriate, non-significant explanatory variables were removed through a process of step-wise model selection in order to identify the most parsimonious models. The same LMM process was also applied to hourly data in order to determine the effect of explanatory variables on hourly groundspeeds. Model-fit was assessed in all cases by examining the distribution of model residuals (Appendix 1). Estimated marginal means were calculated for each category of all explanatory variables included in final LMMs. This technique provides a valuable method by which to assess the effect of each variable whilst controlling for the effects of other significant factors.

In addition Mann-Whitney U tests were used to check for seasonal difference in meteorological variables. All means are displayed with standard deviations throughout the paper. All statistical analyses were undertaken using IBM SPSS Statistics 22.

2.4. Results

The GPS transmitters logged 21106 observations during 63 migrations (35 in autumn, 28 in spring) undertaken by 14 ospreys (Figure 2.1 and Figure 2.2). Twelve of the birds wintered in West Africa and two in Spain (Table 2.2). Where birds were tracked for more than one migration season, they always returned to the same wintering site in successive years. In addition to the complete migrations summarised in Table 2.1, data

from one incomplete autumn migration (Bird 1) and one incomplete spring migration (Bird 7) were analysed where appropriate. Evidence suggests that Bird 1 was predated by a desert eagle owl *Bubo ascalaphus* while roosting in mountains in the northern Sahara. Bird 7's transmitter failed while it was migrating north through Spain. Summaries of all of the migrations are shown in Table 2.3. This table also includes each bird's age at the start of each migration and the outcome of any breeding attempts prior to autumn flights.

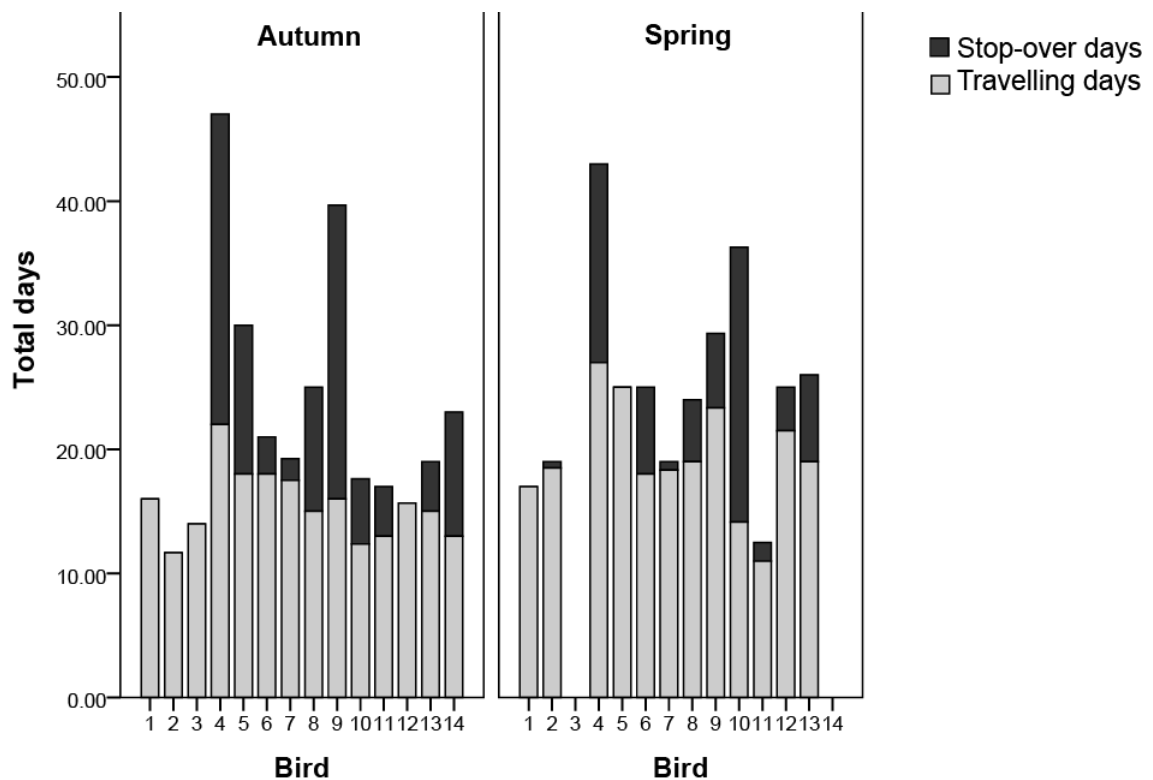


Figure 2.1. Number of travelling days and stop-over days during completed migrations. Mean values shown where appropriate. There was no seasonal difference in stop-over duration (GLMM, $F = 2.031$, $p = 0.160$) but ospreys required fewer travelling days to complete autumn migrations (GLMM, $F = 12.168$, $p < 0.001$).

Table 2.2. Summary of complete migratory flights undertaken by ospreys. *Means and standard deviations shown where appropriate. Straightness is ratio between total distance flown on travelling days and direct distance between summer and winter site.*

Bird	Sex	Summer	Winter	Autumn			Spring		
				N	Total days	Straightness	N	Total days	Straightness
1	M	England	Senegal	1	16	0.94	1	17	0.95
2	F	England	Senegal	3	12	0.98	2	19	0.89
					(SD = 1)	(SD = 0.01)		(SD = 7)	(SD = 0.05)
3	M	England	Guinea	1	14	0.96			
4	F	Scotland	Guinea-Bissau	1	47	0.97	1	43	0.93
5	M	Scotland	Senegal	3	30	0.94	3	25	0.93
					(SD = 9)	(SD = 0.02)		(SD = 4)	(SD = 0.02)
6	F	Scotland	Mauritania	1	21	0.89	1	25	0.94
7	M	Scotland	Senegal	4	20	0.94	3	19	0.94
					(SD = 5)	(SD = 0.02)		(SD = 5)	(SD = 0.02)
8	M	Scotland	Guinea-Bissau	2	25	0.95	1	24	0.94
					(SD = 0)	(SD = 0.02)			
9	M	Scotland	Senegal	3	40	0.91	3	29	0.87
					(SD = 9)	(SD = 0.01)		(SD = 6)	(SD = 0.04)
10	F	Scotland	Spain	8	18	0.95	7	36	0.95
					(SD = 5)	(SD = 0.01)		(SD = 4)	(SD = 0.01)
11	F	Scotland	Spain	2	17	0.90	2	13	0.89
					(SD = 7)	(SD = 0.01)		(SD = 4)	(SD = 0.04)
12	M	Scotland	Senegal	3	16	0.97	2	25	0.90
					(SD = 2)	(SD = 0.02)		(SD = 3)	(SD = 0.05)
13	M	Scotland	Senegal	1	19	0.95	1	26	0.94
14	M	Scotland	Senegal	1	23	0.92			

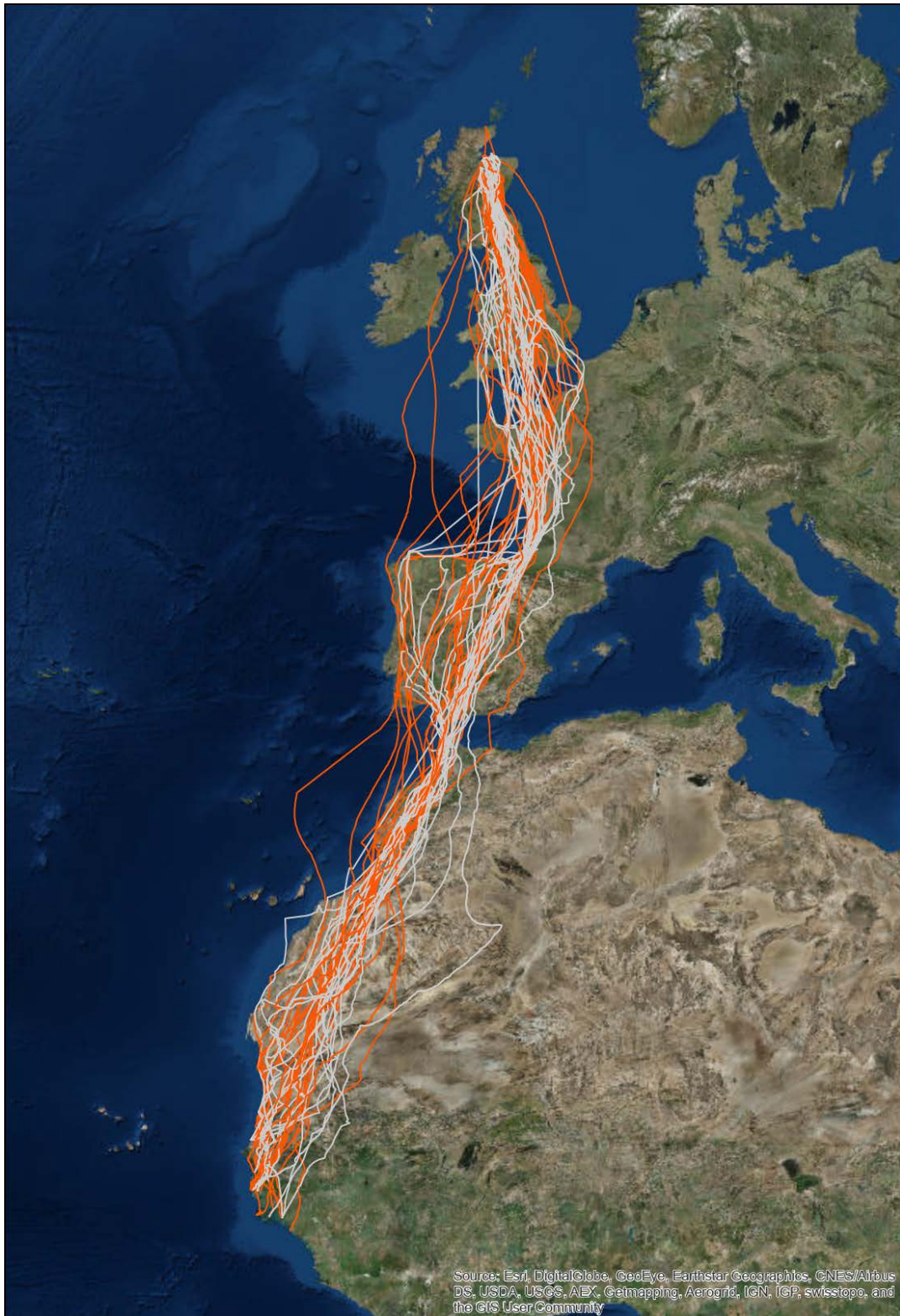


Figure 2.2. Map showing all migrations completed by satellite-tagged ospreys. Orange lines indicate autumn migration and white lines show spring migrations.

Table 2.3. Summary of all autumn migrations and breeding success prior to departure. *Travel fraction is the fraction of travelling days compared to total days of migration, i.e. a travelling fraction of 1.00 means that the bird did not incorporate any stop-over days into its migration.*

Bird	Sex	Year	Age	Bred?	No of off- spring	Dep. date	Total days	Travel frac.	Night flights	Non- stop night flights	Night frac.
1	M	2011	13	N		2/9	16	1.00			0
2	F	2013	8	N		29/8	12	1.00	1		0.08
2	F	2014	9	N		31/8	12	1.00			0
2	F	2015	10	Y	2	31/8	11	1.00	1		0.09
3	M	2011	5	Y	3	27/8	14	1.00	1		0.07
4	F	2007	5 +	Y	2	4/8	47	0.47			0
5	M	2008	7	Y	3	22/9	22	0.82	1	1	0.06
5	M	2009	8	Y	1	16/9	28	0.68	3	2	0.18
5	M	2010	9	Y	1	12/9	40	0.53	3		0.14
6	F	2008	5	N		23/8	21	0.86			0
7	M	2009	8	Y	2	7/9	16	1.00	2	1	0.13
7	M	2010	9	Y	2	8/9	18	0.94	1	1	0.06
7	M	2011	10	Y	0	30/8	26	0.81	1		0.05
7	M	2012	11	Y	2	7/9	17	0.94	2		0.13
8	M	2009	10	Y	1	22/9	25	0.56	3	1	0.23
8	M	2010	11	Y	2	23/9	25	0.64	1		0.06
9	M	2011	2	N		7/9	31	0.58	1	1	0.06
9	M	2012	3	N		22/8	48	0.27	3		0.23

9	M	2013	4	N		2/9	40	0.43	4		0.24
10	F	2008	8	Y	2	10/8	22	0.77			0
10	F	2009	9	Y	2	9/8	26	0.54			0
10	F	2010	10	Y	3	10/8	14	0.79			0
10	F	2011	11	Y	2	12/8	19	0.74			0
10	F	2012	12	Y	2	8/8	16	0.69			0
10	F	2013	13	Y	1	9/8	12	0.67			0
10	F	2014	14	Y	3	9/8	15	0.80	1		0.08
10	F	2015	15	Y	2	2/8	17	0.71			0
11	F	2013	22	Y	1	19/8	12	0.75			0
11	F	2014	23	Y	0	7/8	22	0.77			0
12	M	2013	15 +	Y	1	10/9	13	1.00	1	1	0.08
12	M	2014	16	Y	0	6/9	17	1.00	2		0.12
12	M	2015	17	Y	0	1/9	17	1.00	1		0.06
13	M	2013	10	Y	3	26/9	19	0.79	1		0.07
14	M	2015	2	N		3/9	23	0.57	2	2	0.18

2.4.1. Departure date

Ospreys departed on autumn migration over a period of 56 days (2 August – 26 September), with all birds setting-off on days when they were supported by tailwinds. These winds were predominantly from the north-west (mean = 300°, SD = 48.5°, range 279° - 357°) with a mean speed of 10 m s⁻¹ (SD = 1.14 m s⁻¹). The mean duration (643 mins, SD = 477 mins) and distance (392 km, SD = 422 km) of the first day/sector of migration varied widely, but heading was predominantly south-south-east (mean = 166°, SD = 14°) with birds appearing to submit to wind drift. The median autumn departure date according to sex and breeding success is shown in Table 2.4. In this

case males that reared young departed later than those that did not, whereas females that bred successfully departed earlier than those that did not.

Table 2.4. Autumn departure dates according to sex and breeding success.

Breeding success	Male		Female	
	Failed/did not breed	Reared young	Failed/did not breed	Reared young
N	5	14	3	12
Median departure date	2 Sept	9 Sept	29 Aug	9 Aug

There was a trend for some birds to make very long continuous flights on the first day of autumn migration. Nocturnal flight (defined as more than two hours after the sunset time experienced by the bird that day, i.e. according to geographic location) was recorded during the first night of migration on six occasions by five birds, with three individuals flying continuously for more than 24 hours, with a maximum flight of 1924 km.

Ospreys departed over a shorter period of 46 days in spring (26 February – 12 April). The median departure date of males (14 migrations) was 20 March and females (13 migrations) 6 March. However the female date was skewed by the fact that seven of these migrations were undertaken by bird 10 which had the earliest median departure date of all birds (1 March). Like autumn, winds were predominantly from the north-west (mean = 310° , SD = 46.2°) with a mean speed of 6.5 m s^{-1} (SD = 1.54), generating a headwind component. Mean duration (397 mins, SD = 98 mins) and distance (181 km, SD = 55 km) were significantly lower than the first day/sector of autumn migration (Mann-Whitney U tests: duration $p < 0.005$, distance $p = 0.024$) and showed less variation. As in autumn, birds appeared to submit to wind drift during the first day of spring migration with a mean heading of 63° (SD = 102°), albeit with greater variation than autumn. There were no instances of nocturnal flight during the first night of spring migration.

2.4.2. Journey speed

GLMMs with bird ID as a random factor (Table 2.5) showed that ospreys required fewer travelling days to complete migration in autumn (mean = 22 days, SD = 9 days, range 11 – 48 days) than spring (mean = 27 days, SD = 10 days, range 10 – 43 days), but that there was no significant seasonal difference in stop-over duration (autumn mean = 7 days, SD = 8 days, range 0 – 35 days, spring mean = 8 days, SD = 9 days, range 0 – 27 days). As a result autumn migrations (mean = 22 days, SD = 9 days, range 11 – 48 days) were completed in fewer days than spring (mean = 27 days, SD = 10 days, range 10 – 43 days). Autumn migrations (mean = 0.943, SD = 0.026) were straighter than spring (mean = 0.923, SD = 0.035) and a LMM with logit transformed straightness as the dependent variable, bird ID as a random factor and season and bird sex as explanatory variable showed that this seasonal variation was significant ($F = 8.742$, $p = 0.005$). Bird sex had no effect on any of the variables tested.

Table 2.5. GLMMs (with Poisson error distribution and log-link function) showing the effect of season on three variables.

Dependent variable	df	F	Sig.
Total days	1	6.283	0.015
Travelling days	1	12.168	0.001
Stop-over days	1	2.031	0.160

2.4.3. Daily speed

Ospreys flew a mean 308 km (SD = 245.6 km) per day/sector during autumn migration compared to 243 km (SD = 131.6 km) during spring. A LMM with log-transformed daily distance as the dependent variable, bird ID as a random factor (with repeated measures for year), and season and bird sex as explanatory variables demonstrated that this seasonal difference was significant ($F = 12.049$, $p = 0.001$). A second LMM

identified significant region/season effects ($F = 5.599$, $p = 0.001$). Subsequent LSD post-hoc tests of marginal means determined that daily/sector distances achieved in Africa during autumn were greater than elsewhere (all $p < 0.05$), and that daily/sector distances flown in Europe during spring were significantly lower than the two autumn regions (both $p < 0.05$). Daily flight data are summarised in Table 2.6.

Table 2.6 Regional variation in daily migratory flights

Season/Region	N	Day length (hh:mm)		Flying time (mins)		Daily distance (km)		Actual distance flown (km)		Daily straightness	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Autumn Europe	269	13:32	01:05	515	275	263.5	210.9	291.0	265.2	0.941	0.067
Autumn Africa	171	12:11	00:20	577	119	307.0	123.1	317.3	119.0	0.951	0.075
Spring Europe	251	12:53	00:53	454	173	220.7	172.9	229.5	133.6	0.938	0.086
Spring Africa	191	12:12	00:16	525	109	268.1	108.8	277.5	118.1	0.928	0.093

2.4.4. Effect of environmental variables on daily scale

Overall, wind was more favourable during autumn migration (Figure 2.3) ($p < 0.001$) when birds were assisted by light tailwinds in both Europe and Africa. In spring, birds experienced headwinds in both Africa and Europe. Ospreys experienced stronger absolute crosswinds in Europe than Africa in both autumn and spring ($p < 0.05$). There was no seasonal variation in boundary layer but it was higher in Africa than Europe in both autumn and spring (Figure 2.4) ($p < 0.001$).

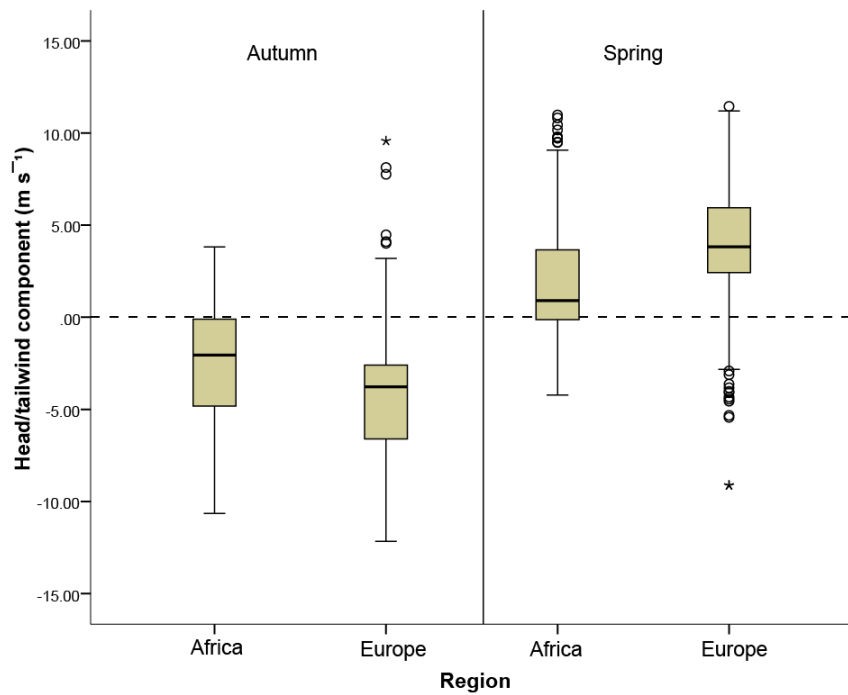


Figure 2.3. Head/tailwind component experienced by ospreys during migration. Positive values indicate headwinds, negative values indicate tailwinds.

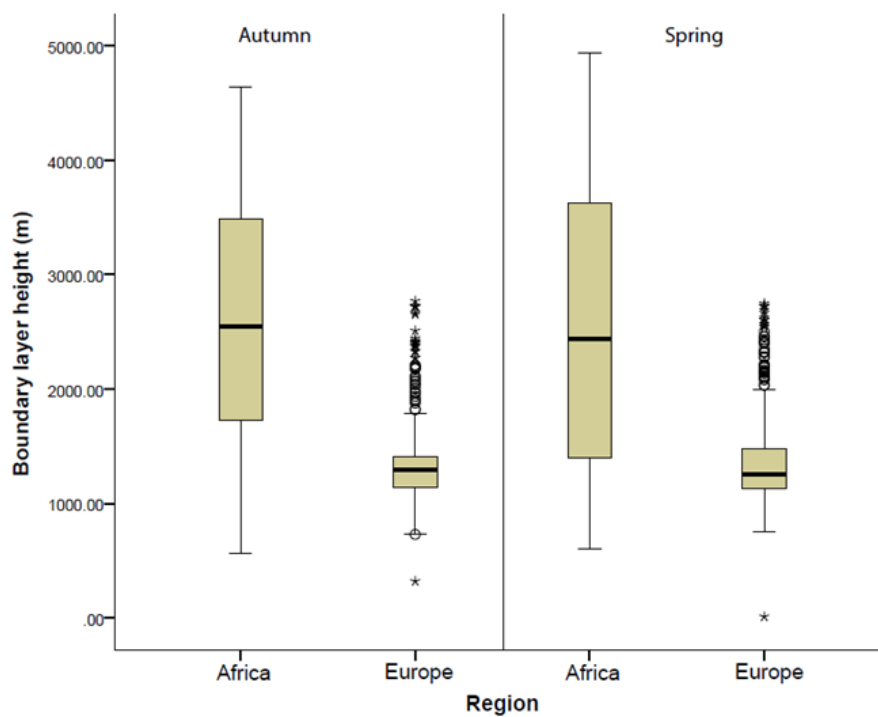


Figure 2.4. Regional and seasonal variation in boundary layer height. A higher boundary layer is indicative of stronger and more densely spaced thermals.

A LMM with log transformed daily/sector distance flown as the dependent variable and bird ID (with repeated measures for years) included as a random factor was used to determine the extent to which the seasonal/regional variation was influenced by environmental factors and timing of migration. The initial LMM included season/region, bird sex, day length, migration departure date (and interaction between season and departure date), crosswind, head/tailwind and boundary layer height as explanatory variables. Non-significant variables ($p > 0.05$) were then removed through a process of stepwise model simplification in order to identify the most parsimonious model. The final model consisted of the three meteorological variables and migration departure date (Table 2.7), indicating that they were the key drivers. LSD post-hoc tests on the marginal means of these variables demonstrated that ospreys migrated further per day/sector with following winds, and under the best thermal conditions. Conversely, strong absolute crosswinds limited progress compared to the two other crosswind categories. Birds that began migrating earlier migrated shorter distances per day/sector in both autumn and spring. These results are summarised graphically in Figure 2.5.

Table 2.7. Final LMM showing the effect of significant explanatory variables on log transformed daily/sector distance.

Explanatory variable	Denominator df	F	Sig.
Intercept	16.186	9621.722	< 0.001
Head/tailwind	857.620	6.635	0.001
Crosswind	854.505	4.111	0.017
Boundary layer	857.554	12.474	< 0.001
Departure date	175.093	7.213	0.001

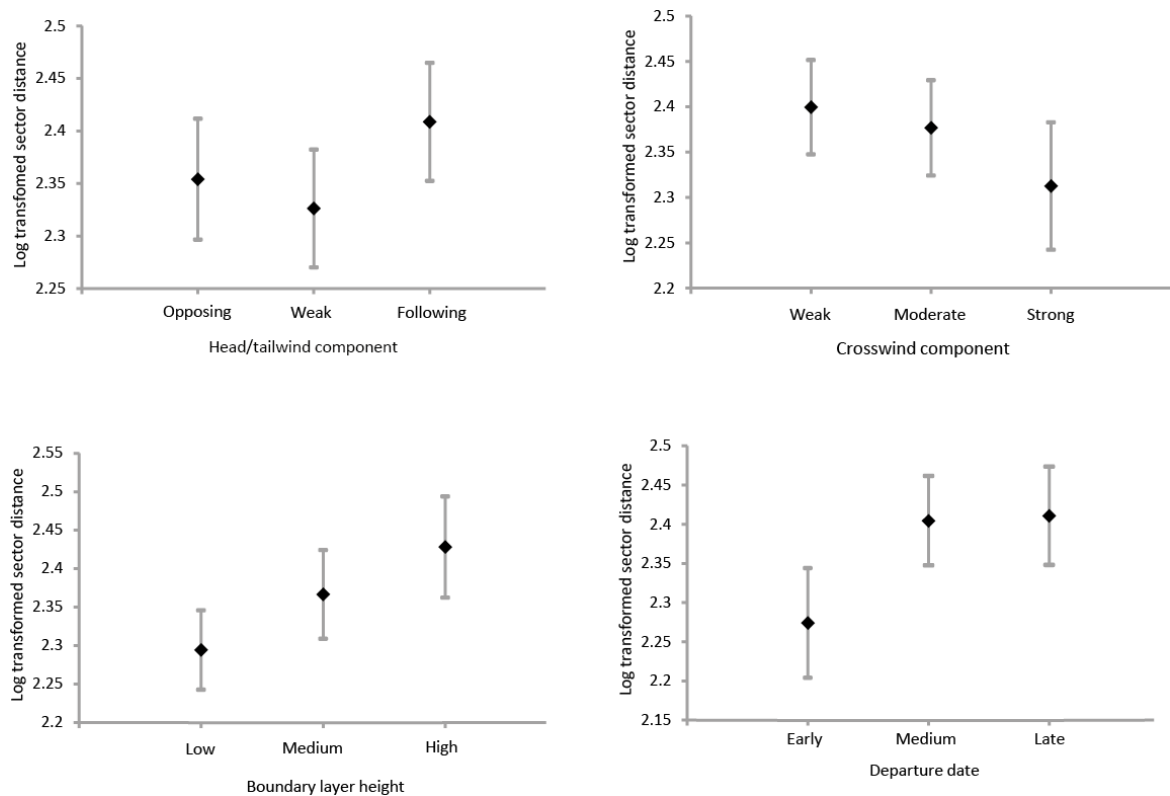


Figure 2.5. Estimated marginal means of significant explanatory variables in the final LMM for daily/sector distance. Grey bars indicate 95 % confidence intervals. Birds migrated further per day/sector with following winds, weak crosswinds and high boundary layer. Birds that departed early in autumn and spring migrated shorter distances per day/sector.

Within the subset of days with hourly GPS observations ($n = 707$ days) there was a tendency for daily/sector flights during autumn (mean straightness = 0.95, $SD = 0.07$) to be more direct than those in spring (mean straightness = 0.93, $SD = 0.09$). However a LMM with logit transformed straightness as the dependent variable, bird ID as a random factor, and season and bird sex as explanatory variables established that this seasonal difference was not significant. Bird sex also had no effect. Analysis of the same subset of data showed that ospreys flew for longer during autumn (mean = 563 minutes, $SD = 256$ minutes) than spring (mean = 498 minutes, $SD = 161$ minutes). A LMM with log transformed daily/sector flying time as the dependent variable verified that this seasonal difference was significant ($F = 7.348$, $p = 0.007$). A second LMM identified significant region/season effects ($F = 7.982$, $p < 0.001$) with ospreys flying for longest per day in Africa during autumn and for the shortest periods in Europe during

spring. Finally region/season, bird sex, day length, headwind, crosswind and boundary layer height were incorporated into a LMM as explanatory variables with bird ID as a random factor in order to determine how these regional differences were influenced by environmental factors. Boundary layer was the only explanatory variable with a significant effect ($F = 4.567$, $p = 0.011$), indicating that it was the key driver, with birds flying for longer when thermal conditions were most favourable (i.e. boundary layer category = high). It should be noted, however, that model fit was poor for each of the daily flying time models (Appendix 2, Figure A2.3.), indicating that these results should be interpreted with caution.

2.4.5. Hourly speed

Analysis of hourly data enabled comparisons to be made between flight speeds over land and ocean as well as between land regions and season. A LMM with log transformed hourly groundspeed as the dependent factor and bird ID as a random factor demonstrated that hourly groundspeeds were faster in autumn ($F = 35.495$, $p < 0.001$), but that there was no sex-based variation. A second LMM was then performed to determine how seasonal affects varied between regions, with a six-level region/season categorical variable included as the explanatory variable. This constituted ocean spring, ocean autumn, Africa spring, Africa autumn, Europe spring and Europe autumn. Bird sex was also included as an explanatory variable and Bird ID as a random factor. This demonstrated clear region/season affects ($F = 99.324$, $p < 0.001$), but no sex-based variation.

2.4.6. Effect of environmental variables on hourly scale

A LMM with log transformed groundspeed as the dependent variable and bird ID (with repeated measures for years) included as a random factor was used to determine the extent to which the season/region variation was influenced by environmental factors and migration departure date. Non-significant variables ($p > 0.05$) were removed by stepwise model simplification and the final model consisted of the three meteorological variables, region/season and migration departure date (Table 2.8). In this case the meteorological variables had similar effects to those observed for daily/sector distance, with birds achieving faster groundspeeds with following winds

and weak crosswinds. Hourly groundspeeds also increased significantly with boundary layer height. Region/season also had a significant effect, indicating that birds adapted their flight behaviour according to regional and season cues. This is best exemplified by the fact that the marginal means of log transformed hourly groundspeeds was faster over the ocean in both spring and autumn than each of the four land categories (all $p < 0.001$). It is also notable that the marginal mean for spring in Europe was significantly higher than the corresponding figures for Africa in autumn and spring ($p < 0.05$), indicating that when other factors were controlled for ospreys migrated faster at the hourly scale in Europe during spring. This contrasts with the observed means (Figure 2.6), thereby demonstrating the constraining impact of the meteorological variables. During autumn birds that departed earlier (in terms of Julian days) flew at slower groundspeeds than later departing individuals, but this trend was not evident during spring.

Table 2.8. Final LMM showing the effect of significant explanatory variables on log transformed hourly groundspeeds.

Explanatory variable	Denominator df	F	Sig.
Intercept	17.993	15252.696	< 0.001
Region/season	5554.650	134.921	< 0.001
Boundary layer	5851.444	62.481	<0.001
Crosswind	5854.961	7.149	0.001
Head/tailwind	5836.920	12.799	<0.001
Departure date	470.035	20.729	<0.001
Departure date*season	938.331	38.548	<0.001

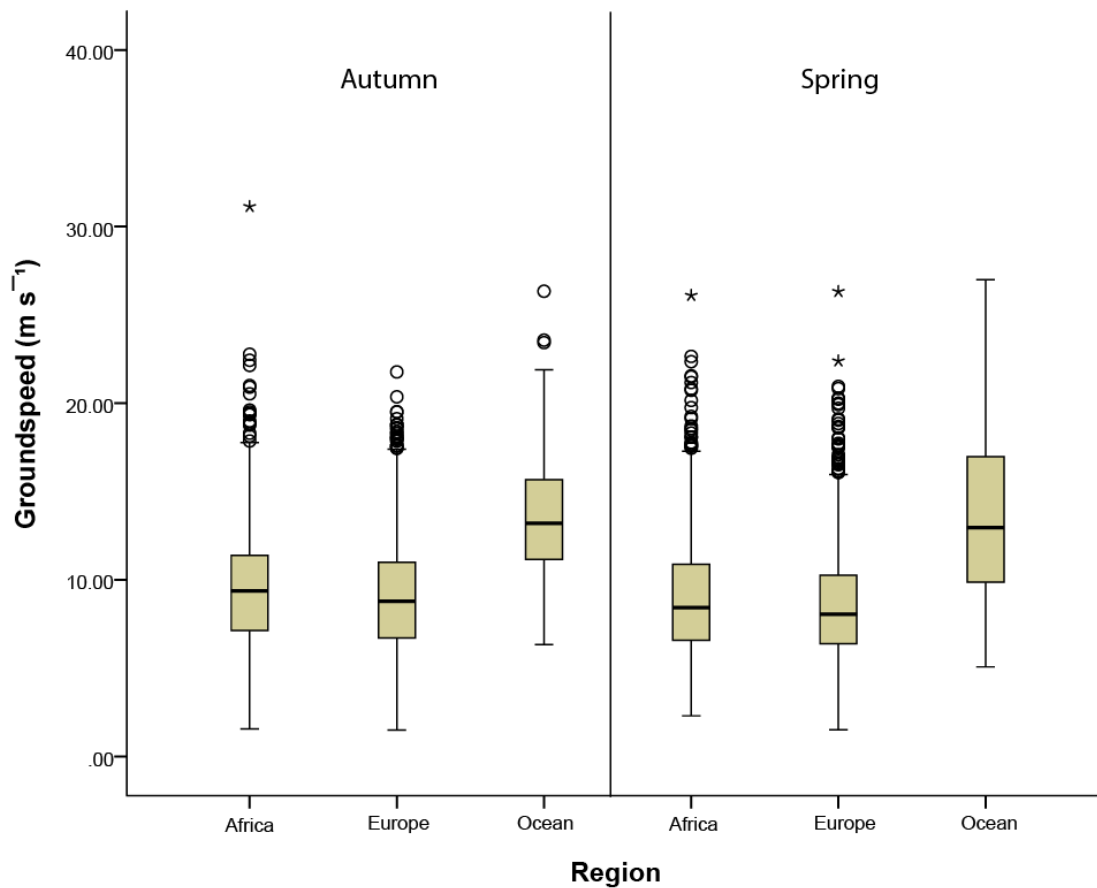


Figure 2.6. Box plot showing regional and seasonal variation in observed hourly groundspeeds achieved by ospreys. *The fastest speeds were achieved over the ocean.*

2.4.7. Nocturnal flights

There were 61 instances of nocturnal flight undertaken by 11 birds (mean duration of nocturnal flight = 319 minutes, SD = 203 minutes). Birds continued flying for two hours or more after sunset on 55 occasions, while the remaining cases involved birds setting-off two or more hours before sunrise. Birds flew continuously through the night on ten occasions, all during autumn: six in Europe and four between Europe and Africa. Nine of these flights involved significant flights across the Bay of Biscay or Atlantic Ocean between Spain and Morocco. Nocturnal flight was most commonly undertaken in Europe during autumn with 21 flight sectors including elements of nocturnal flight, nine of which relate to crossings of the Bay of Biscay. These data are summarised in Figure 2.7 and Table 2.10.

Of the 11 birds that were recorded making nocturnal flights, nine were males (Table 2.9). Furthermore all of the individuals that continued flying continuously through the night on at least one occasion were males. Individual variation in nocturnal flight is shown in Figure 2.8 and Figure 2.9. Later departing birds incorporated more nocturnal flight during autumn than those that set-off earlier (Figure 2.10, $R^2 = 0.304$, $F = 13.952$, $p = 0.01$). There was no such relationship during spring ($R^2 = 0.025$, $F = 0.648$, $p = 0.429$).

Table 2.9. Summary of nocturnal flight per bird and season (A = autumn, S = spring).

Bird	Sex	Number of migrations		Instances of nocturnal flight		Proportion of flight sectors with nocturnal flight per migration		Mean duration of nocturnal flight	
		A	S	A	S	Autumn	Spring	Autumn	Spring
1	M	1	1		5	0	0.29		372 (SD= 267)
3	M	1	0	1		0.07		379	
5	M	3	3	7	5	0.13 (SD = 0.06)	0.07 (SD = 0.03)	460 (SD = 229)	167 (SD = 87)
7	M	4	3	6	5	0.09 (SD = 0.04)	0.07 (SD = 0.12)	391 (SD = 252)	150 (SD = 33)
8	M	2	1	5	1	0.15 (SD = 0.12)	0.05	392 (SD = 220)	203
9	M	3	3	8	3	0.18 (SD = 0.10)	0.05 (SD = 0.06)	352 (SD = 200)	207 (SD = 96)
12	M	3	2	4	1	0.09 (SD = 0.03)	0.03 (SD = 0.04)	350 (SD = 233)	195
13	M	1	1	1		0.07	0	276	
14	M	1	0	2		0.18		614 (SD = 23)	
2	F	3	2	2	3	0.06 (SD = 0.05)	0.09 (SD = 0.07)	182 (SD = 79)	220 (SD = 103)
4	F	1	1	0		0	0		
6	F	1	1	0		0	0		
10	F	8	7	1	0	0.01 (SD = 0.03)	0	161	168
11	F	2	2	0		0	0		

Table 2.10. Summary of nocturnal flight per region and season (A = autumn, S = spring).

Region	Instances of nocturnal flight		Mean duration of nocturnal flight (minutes)	
	Autumn	Spring	Autumn	Spring
Europe	21	8	402 (SD = 211)	153 (SD = 35)
Europe-Africa	11	4	409 (SD = 226)	296 (SD = 250)
Africa	5	12	242 (SD = 127)	241 (SD = 153)

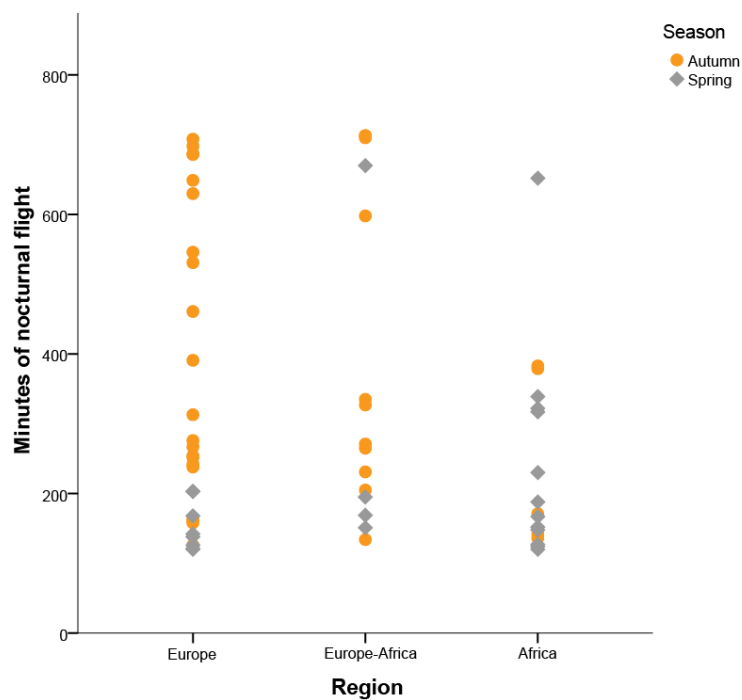


Figure 2.7. Nocturnal flights per region and season. *Each point represents the total duration of nocturnal flight during individual flight sectors.*

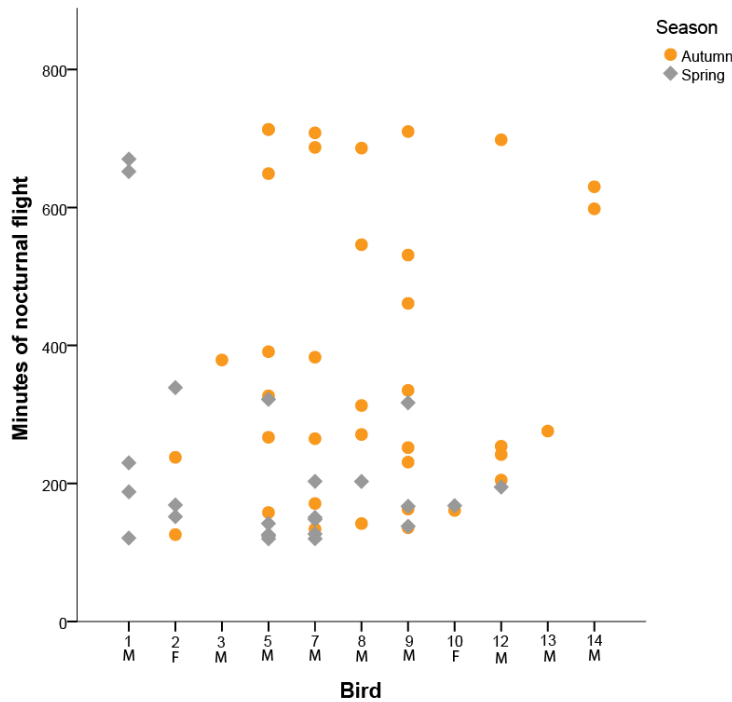


Figure 2.8. Nocturnal flights per bird and season. Each point represents the total duration of nocturnal flight during individual flight sectors. The sex of each bird is indicated on the y axis.

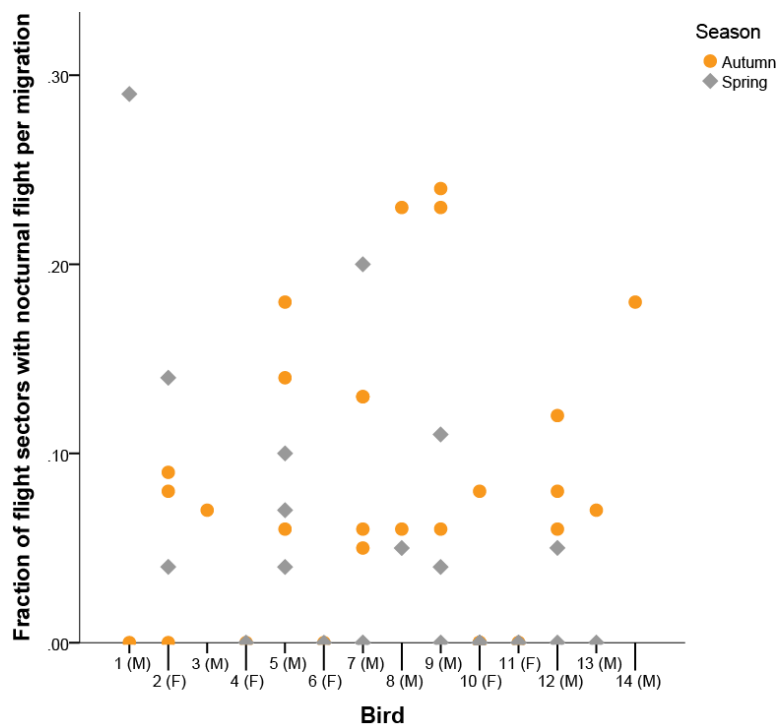


Figure 2.9. Proportion of flight sectors with nocturnal flight per bird and per migration.

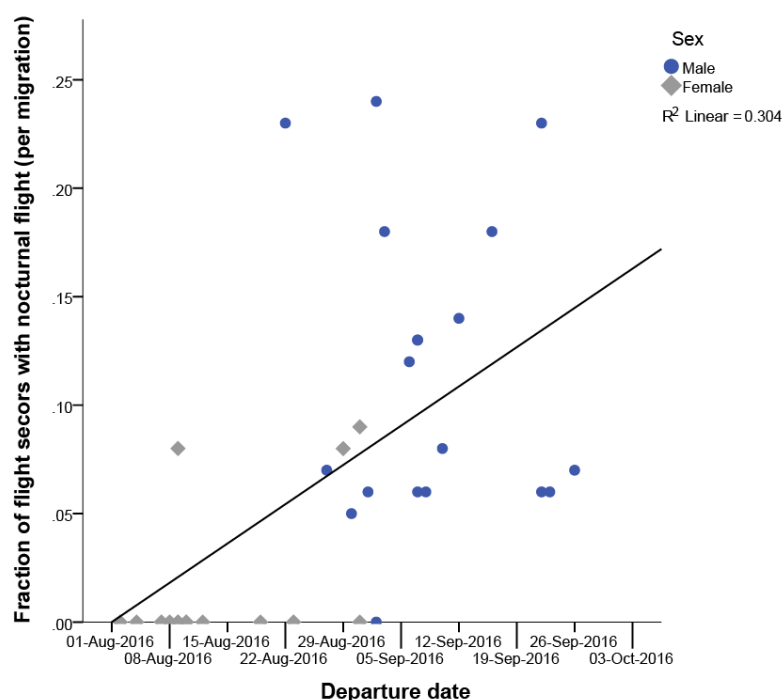


Figure 2.10. Relationship between departure date and proportion of sectors with nocturnal flight during autumn. *Later departing birds tended to incorporate more nocturnal flight.*

2.4.8. Flights across the Bay of Biscay

Eighteen flights in excess of 300 km were made by ten birds across the Bay of Biscay (Figure 2.12). Fourteen were made during autumn (thus 40 % of autumn migrations) and four in spring (14 % of spring migrations) (Table 2.11). All of the autumn flights were undertaken when wind was from the north-east (mean wind direction = 37° , SD = 19, range 5° - 71° ; mean speed = 5.2 m s^{-1} , SD = 2.3), thereby providing a tailwind component (mean = -4.2 m s^{-1} , SD = 1.7 m s^{-1}), with only light crosswinds (mean crosswind component = 2.6 m s^{-1} , SD = 1.8 m s^{-1}). The four spring flights were made into light north-easterly winds (mean wind direction = 21° , SD = 10.0, range 8° - 31° ; mean speed = 4.8 m s^{-1} , SD = 1.3) with a mean headwind component of 4.1 m s^{-1} (SD = 0.6 m s^{-1}) and mean crosswind component of 1.6 m s^{-1} (SD = 0.9 m s^{-1}). As a result the head/tailwind component varied significantly between seasons (Mann-Whitney U test: $p < 0.003$), but differences in crosswind and boundary layer (autumn mean = 767 m, SD = 109 m; spring mean = 793 m, SD = 78 m) were not significant (Mann-Whitney U tests: $p > 0.05$).

Surprisingly given wind conditions, mean hourly groundspeeds were faster during the four spring flights. A LMM with log transformed groundspeed as the dependent variable, bird ID as a random factor and season and bird sex as fixed factors showed that this seasonal difference was significant ($F = 28.865$, $p < 0.001$). In this case ospreys achieved faster groundspeeds in spring by increasing their airspeed in response to the headwind conditions (Figure 2.11). In contrast the favourable wind conditions encountered during autumn enabled them to migrate at a reduced airspeed.

Birds continued flying for two hours or more after sunset on nine occasions (eight autumn, one spring) and three autumn flights involved continuous migration through the night. Nine of the ten longest flights were made during autumn with a maximum of 1365 km from south-west Scotland to northern Spain.

Table 2.11. Flights (> 300 km) made by ospreys across the Bay of Biscay.

Season	N	Distance (km)		Duration (mins)		Groundspeed (m s ⁻¹)		Airspeed (m s ⁻¹)		Altitude (m)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Autumn	14	519	286	650	319	13.8	2.3	9.1	2.8	304	203
Spring	4	403	111	356	129	19.9	3.8	23.7	4.0	683	293

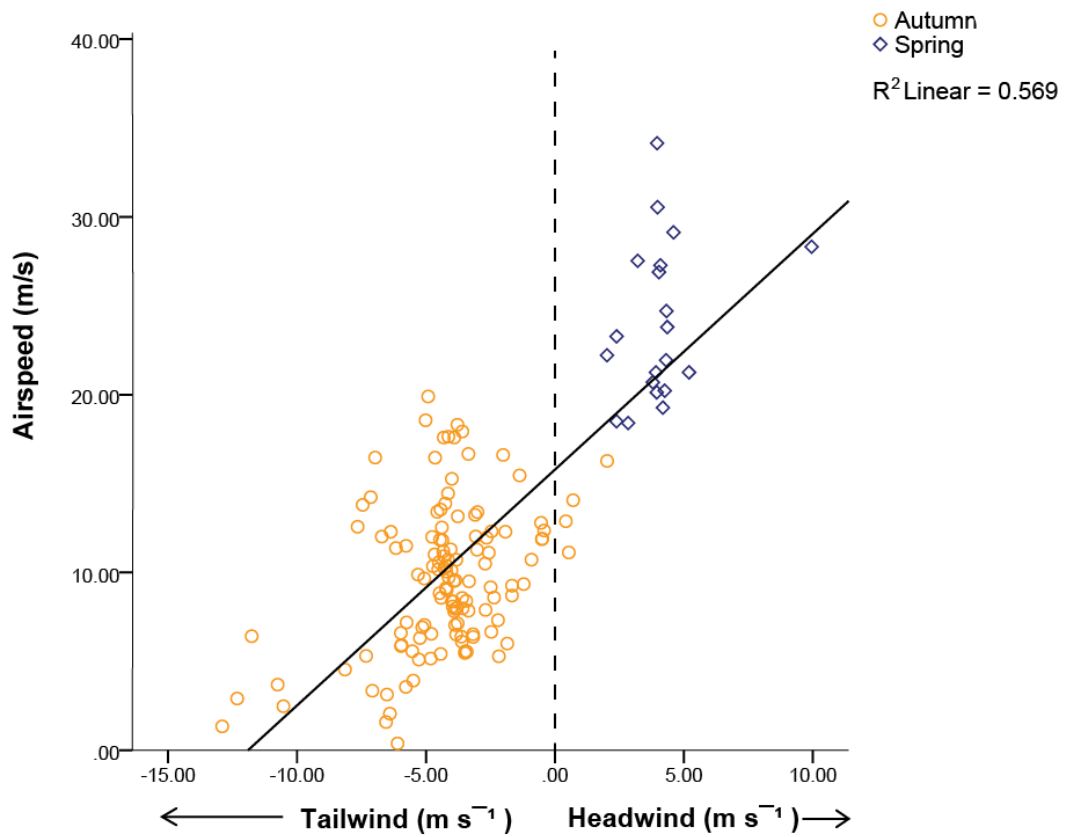


Figure 2.11. Scatter plot showing relationship between hourly airspeed and head/tailwind component during Bay of Biscay crossings. *Ospreys flew at faster airspeeds during spring in response to headwind conditions.*

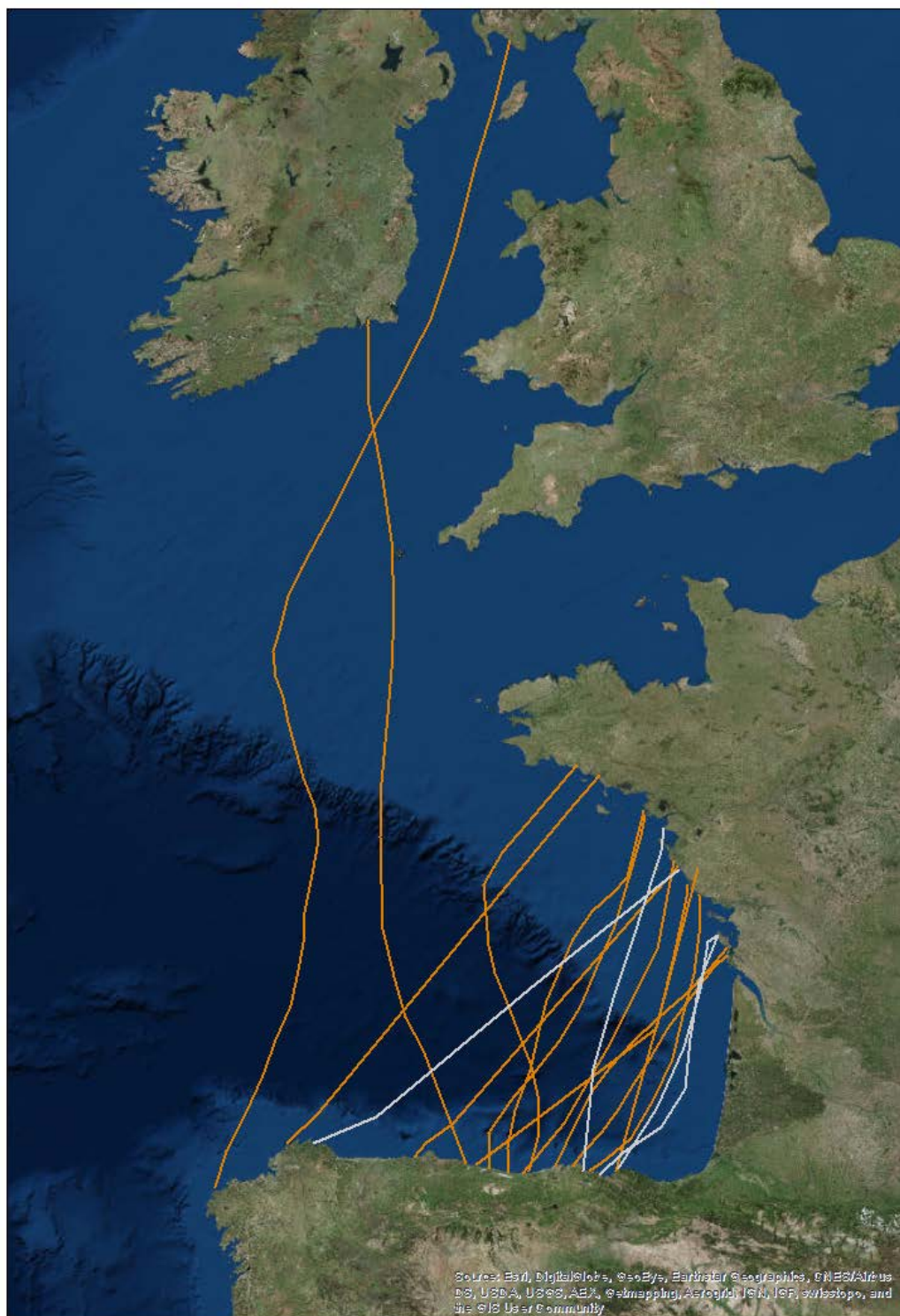


Figure 2.12. Flights in excess of 300 km across the Bay of Biscay.

Orange lines indicate autumn flights, grey lines indicate spring flights.

2.4.9. Flights across the Sahara

Ospreys required a mean 4 days (SD = 1 day) to cross the Sahara during 23 autumn migrations compared to a mean 5 days (SD = 1 day) during 19 spring migrations but a GLMM with bird ID as a random factor indicated that this seasonal difference was not significant ($F = 1.680$, $p = 0.202$). Flights across the desert (Figure 2.13) were more direct in autumn (mean journey straightness = 0.973, SD = 0.033) than spring (mean = 0.917, SD = 0.145). A LMM with logit transformed straightness as the dependent variable and bird ID as a random factor confirmed that season had a significant effect ($F = 9.118$, $p = 0.005$), but that bird sex did not. Day length, head/tailwind, crosswind and boundary layer were then incorporated into a second LMM as additional explanatory variables, but season remained the only significant factor ($F = 5.001$, $p = 0.034$).

There was a tendency for median start time to be earlier in autumn but migration during both seasons was generally confined to daylight hours (Table 2.12). Nocturnal flight was relatively rare with birds flying for more than two hours after sunset twice during autumn and four times in spring. Ospreys flew further per day across the desert in autumn (Table 2.8), and a LMM demonstrated that this seasonal difference was significant ($F = 6.561$, $p = 0.011$). Environmental variables (day length, headwind, crosswind and boundary layer) were then incorporated into a second LMM as additional explanatory variables. This identified boundary layer as the key driver ($F = 4.842$, $p = 0.009$), with ospreys flying furthest when boundary layer was high. None of the other explanatory variables exhibited a significant effect.

Table 2.12. Daily flights across the Sahara.

	Start time (mins after sunrise)		End time (mins before sunset)		Daily Distance (km)	
	Median	IQR	Median	IQR	Mean	SD
Autumn	132	101	14	95	319.2	125.9
Spring	170	39	-1	71	276.7	1104



Figure 2.13. Map showing the migration routes of ospreys across the Sahara. *Daily flights beginning and ending between the red lines were analysed. Orange lines indicate autumn migrations and white lines show spring migrations.*

2.5. Discussion

The selective advantages of returning to the breeding site earlier have been shown to result in faster spring migrations in many migratory species (Nilsson et al 2013). However, the results presented here demonstrate that ospreys migrated faster during autumn at all three temporal scales: hourly, daily and journey. It is also significant that long energy-demanding flights over the Bay of Biscay were frequently undertaken in autumn but rarely in spring. These findings corroborate with a growing body of evidence that autumn migration is faster in some species due to more favourable meteorological conditions (Shaumoun-Barnes et al. 2003, Mellone et al. 2012), and potentially, additional selection pressure (Panuccio et al. 2014, Mellone et al. 2015). Therefore, the key question is to what extent is the seasonal variation in osprey migration speed driven by meteorological conditions and/or selective cues.

2.5.1. Relative influence of meteorological conditions and time-minimisation

A key finding of this study was that autumn migration was shorter in overall duration than spring with ospreys requiring fewer travelling days. It is also notable that there was no seasonal difference in stop-over duration and that autumn routes were more direct than spring. This contrasts with the results of many migration studies, but is not entirely unexpected given that ospreys, like most medium-large raptors, migrate predominantly by soaring-gliding flight (Alerstam 2000) and are thus constrained by thermal conditions, even if there is increased urgency in spring (Nilsson et al. 2013). Nilsson et al. (2013) found that there was no seasonal difference in total duration of migration by thermal soaring migrants, thereby contrasting with a clear trend for shorter spring migrations by songbirds. Meteorological conditions encountered by ospreys in this study were more favourable during autumn and this is likely the key driver in determining the number of travelling days required to complete migration, particularly as meteorological variables were found to be a key driver determining daily distance flown. However, the fact that later departing individuals migrated faster at both hourly and daily scales and that nocturnal flight was more frequently undertaken in autumn, particularly by later departing individuals, supports a growing body of evidence that raptor migration speed is influenced by additional selection pressure

relating to reclamation of wintering sites. Panuccio et al. (2014) and Mellone et al. (2015) suggest that black kite *Milvus migrans* and booted eagle *Aquila pennata* migration may be time-constrained in autumn because of competition for resources in the African wintering grounds. Ospreys have been shown to remain highly faithful to the same wintering site each year (Dennis 2008, Washburn et al. 2014), and all of the birds in this study returned to the same site in successive winters. The reclamation of these winter territories may therefore act as a strong selective cue influencing daily travel routines and time-budgets during autumn migration given the potential fitness benefits of returning to a known site.

2.5.2. Stop-overs

It is notable from a time-minimisation perspective that there was no seasonal difference in stop-over duration. Nilsson et al. (2013) demonstrated that stop-over duration is usually shorter in spring and suggested that such pronounced seasonal variation may be caused by differing levels of pre-migratory fuelling as well as variations in foraging conditions and feeding intensity and behaviour at stop-over sites. Strategies that reduce stop-over duration are important from a time-minimisation perspective and the osprey's use of fly-and-forage migration (Strandberg and Alerstam 2007) may limit the requirement for them. Indeed over a quarter of migrations in this study were completed without stop-overs. Alerstam et al. (2006) found that ospreys returning to nest sites in Sweden incorporated fewer-stop over days into spring migration than autumn but concluded that this was not necessarily indicative of time-minimisation because other factors such as pre-migratory fuelling and stop-over site quality could not be accounted for. North American ospreys also spent fewer days on stop-overs during spring migration (Martell et al. 2014) but like Alerstam et al. (2006) a critical examination of this from a time-minimisation perspective was not possible because other confounding factors were not assessed. The lack of seasonal variation in stop-over duration in this study is interesting and likely indicative of time-minimisation during autumn. However, like Alerstam et al. (2006) and Martell et al. (2014) additional information on levels of pre-migratory fuelling and foraging at stop-over sites is necessary in order to extract the relative influence of each.

2.5.3. Timing of departure in autumn

The propensity for very long continuous flights at the beginning of autumn migration provides strong support for the time-minimisation hypothesis, although meteorological conditions were also a factor. Our results indicate that ospreys increase daily distance at the start of autumn migration by departing when north-westerly winds provide tailwind support. This is exemplified by the fact that nocturnal flight was recorded during the first night of migration on six occasions in autumn, but not in spring when winds were less favourable. This finding corresponds with Maransky et al. (1997) who demonstrated that red-tailed hawks *Buteo jamaicensis* wait for supportive tailwinds before migrating south in autumn. Wind selectivity is indicative of energy-minimisation (Alerstam and Lindström 1990), but extending flight times, particularly into the night when thermals are limited, is a clear example of a time-minimisation technique (Alerstam and Lindström 1990). This is particularly the case given that there was a clear trend during autumn for later departing individuals – usually male birds that reared young - to incorporate more nocturnal flight into their migrations than birds that departed earlier. These results are in agreement with Miller et al. (2016) who found that later departing golden eagles behaved in a more time-limited manner than earlier departing birds, in that case by flying more direct routes. The fact that male ospreys that reared young were the latest to depart is in agreement with previous research which shows that it mainly males who provision young during the post-fledging phase, and generally do not migrate until all of their offspring have departed on migration (Poole 1989).

2.5.4. Bay of Biscay

Many of the very long flights undertaken at the start of autumn migration included crossings of the Bay of Biscay, over half of which involved some degree of nocturnal flight. The morphology of ospreys enables them to undertake long sea crossings, but flights across the Bay of Biscay have been shown to result in mortality among juvenile ospreys in particular (Dennis, 2002; Dennis, 2008; Mackrill 2013). Therefore, previous migratory experience appears important in determining whether flights across the Bay of Biscay are successful, and, crucially, whether they are attempted at all. Our data

indicate that during autumn adult ospreys only cross the Bay of Biscay when supported by tailwinds from the north-east. This is particularly important during nocturnal flight when a lack of visual clues make it more difficult for migrant ospreys to adjust to wind drift (Klassen et al. 2011). Winds along the French continental shelf show considerable variability but north-west winds tend to prevail in late summer (Puillat et al. 2006). Under such circumstances it is beneficial for migrating ospreys to keep to land as they migrate south through France. However, when the wind shifts to the north-east, ospreys appear to concede to wind drift, thereby necessitating flights across the Bay of Biscay. In doing so, they save time according to the triangle of velocities described by Alerstam (2000), by maintaining a south-westerly heading to maximise tailwind assistance. This enables the birds to reduce airspeed (whilst maintaining a fast groundspeed) to a greater extent than if they flew south along the coast, because the latter option would involve some degree of compensation for wind drift through an increase in airspeed (Liechti et al. 1995). Nevertheless the usual energetic savings gained by conceding to wind drift are reduced over the ocean because an absence of thermal updrafts usually necessitates flapping flight (Agostini et al. 2015). However, the results of chapter 3 suggest suggests that in autumn ospreys are sometimes able to exploit weak thermals to aid soaring-gliding flight over the Bay of Biscay which would provide valuable energetic savings in addition to time-minimisation benefits. This is particularly important during the very long non-stop flights undertaken in autumn. The propensity for ospreys to make long crossings of the Bay of Biscay during autumn made a clear contribution to the increased instances of nocturnal flight in Europe during autumn (9 of 21 cases) but given that all of the birds in this study had previous migratory experience it seems likely that the increased instances of flights across the Bay of Biscay in autumn is indicative of a time minimisation strategy, rather than a consequence of wind drift. Klaassen et al. (2011) concluded that adult ospreys respond to crosswinds according to local conditions; drifting when favourable and compensating to avoid being blown into unfavourable habitats. In the majority of cases, therefore, the flights across the Bay of Biscay recorded in this study appear to be conscious decisions by individual birds to save time. North-westerly winds also tend to prevail across the Bay of Biscay in spring (Puillat et al. 2006). This prohibits flights across the ocean on the northward migration

and may explain why ospreys attempted significantly fewer crossings in this season. Our data indicate that ospreys avoid spring crossings by migrating through north western France, but on occasions when they arrive on the north coast of Spain, time pressure forces them to cross the ocean. In such a situation they behave in the manner of 'sprinting migrants' (Alerstam 2006) by increasing airspeeds to those at the upper end of those achievable by ospreys (Alerstam 2000). The favourable meteorological conditions in autumn and increased urgency in spring enabled ospreys to achieve faster groundspeeds over the Bay of Biscay – and during other ocean crossings – than the corresponding figures over land. This corroborates with the findings of Klaassen et al. (2008) who reported the same trend for fast ocean crossings by Swedish ospreys. The data from the Bay of Biscay indicates that during sea crossings ospreys conform to the rules of optimal adjustment of airspeed (Liechti et al. 1994) and it is notable that Horton et al. (2014) described similar airspeed regulation among juvenile ospreys during long flights across the western Atlantic Ocean. In autumn this regulation of airspeed is likely to save valuable energy, thereby permitting the very long sea crossings presented here.

The seasonal variation in Bay of Biscay crossings correspond with other studies of migratory raptors. Yamaguchi et al. (2013) found that Oriental honey-buzzards *Pernis ptilorhynchus* only make a 650 km crossing of the East China Sea in autumn when they were supported by tailwinds. Eleanor's falcons *Falco eleonarae*, meanwhile, undertake shorter sea crossings in autumn when prevailing winds are less favourable (Mellone et al. 2013). Seasonal differences in ocean crossings have also been documented for North American ospreys which make longer crossings of the Caribbean Sea in spring, reducing the overall distance of migration (Martell et al. 2014). The spring crossings are indicative of a time-minimisation strategy, but are less hazardous than autumn, when migration coincides with the hurricane season.

2.5.5. Effect of meteorological conditions on daily distance

Meteorological conditions were a key driver in determining daily distance flown and, as a result, more favourable conditions encountered during autumn enabled ospreys to migrate further per day. This is an agreement with other raptor migration studies

that have demonstrated the positive effects of tailwinds (Mellone et al. 2012, Vansteelant et al. 2015, Mellone et al. 2015) and thermal conditions (Borher et al. 2012, Vansteelant et al. 2015) on hourly speeds and daily distance, as well as the negative effect of strong crosswinds (Vansteelant et al. 2015). This reiterates that a critical examination of migration speeds from a time minimisation perspective is only possible in conjunction with meteorological data. Martell et al. (2014) found that North American ospreys flew further per day in spring. This, combined with more direct routes and fewer stop-over days compared to autumn, meant that spring migration was faster. However, because weather conditions were not accounted for it is not possible to determine the influence of time-selection on this seasonal variation. Alerstam et al. (2006) found that there was minimal season variation in flight behaviour and performance on travelling days of Swedish ospreys but like the American study, weather data was not analysed. As such our study is the first to explicitly evaluate the potential influence of time minimisation on seasonal variation in osprey migration.

2.5.6. Sahara crossings

The greatest variability in flight times occurred in Europe during autumn due to a greater propensity for nocturnal flight, but it is notable that the longest mean flight times occurred during autumn in Africa. Klaassen et al. (2008) identified the same trend among Swedish ospreys, with birds flying for a mean 2.7 hours longer in Africa than Europe. This variation occurred because birds behaved in the manner of fly-and-forage migrants in Europe, regularly interrupting migration to feed. However in Africa, particularly during crossings of the Sahara where foraging opportunities are absent, ospreys behave like 'sprinting migrants', maximising flying times to ensure a rapid crossing of this geographic barrier. Although ospreys are able to migrate long distances by flapping flight it is notable that they behaved in the manner of true soaring migrants during crossings of the Sahara, limiting daily flight times to periods when thermals were available, with boundary layer height the main factor determining daily distance. It is notable, however, that spring flights across the desert were less direct than those in autumn. Given that mean crosswind strength did not vary between seasons this suggests that ospreys compensated for the effects of

crosswinds in autumn, but allowed themselves to be drifted by the wind in spring. This conforms to the theory of 'adapted drift' whereby a bird should submit to wind drift away from the goal in the initial flight steps, and then compensate to an increasing degree when approaching the goal (Alerstam 1979). These findings support the conclusions of Klaassen et al. (2011) who suggested that marsh harriers and ospreys respond to crosswinds according to local conditions; drifting when favourable and compensating or overcompensating when approaching a goal or facing the risk of being blown into hazardous habitats. Previous research has shown that when meteorological variables are controlled for ospreys migrate faster over the Sahara in spring (Mellone et al. 2012) but our analysis failed to detect this seasonal effect.

2.5.7. Conclusion

Given that ospreys are usually faithful to the same nest site and mate each year (Poole 1989) it is generally accepted that they are under selection pressure to migrate quickly in spring (Mellone et al. 2012). This study provides evidence to support this theory, most notably fast speeds during ocean crossings and an increased urgency during migration through Europe in spring. However time-minimisation also appears to play a key role in shaping autumn migration routes and speed. Two studies have demonstrated that spring migration by ospreys is faster than autumn, but neither explicitly tested the influence of meteorological variables on migration speed. As such our results shed new light on the relative importance of meteorological factors and selection pressure in shaping osprey migration speed. Our findings are in agreement with Miller et al. (2016) who suggested that migration usually consists of elements of both energy and time-saving strategies. They also support a growing body of evidence that selection pressure to reclaim winter territories is an important factor in determining the migration speeds of trans-Saharan raptors (Panuccio et al. 2014, Mellone et al. 2015), even if, as in this case, meteorological variables are also a key factor in determining migration speed. Further analysis of the pre-migratory fuelling periods and the foraging behaviour of ospreys during stop-overs would help to shed more light on this interesting element of migration ecology.

3. Why do ospreys *Pandion haliaetus* migrate over ocean and land?

Variation in the flight strategies of a soaring gliding bird.

Timothy R. Mackrill, Swidbert R. Ott, Kirsten Barrett, David M. Harper, William H.J. Norton, and Roy H. Dennis

3.1. Abstract

Data from high resolution Global System for Mobile Communication (GSM) / Global Positioning System (GPS) transmitters tracking ospreys *Pandion haliaetus* migrating between Scotland and West Africa showed that flight method differed between regions and across geographic barriers. A total of 109 days of migration were analysed, 63 during autumn and 46 in spring. Flight method was categorised according to distance, altitude and orientation changes for periods during these days (accounting for 40 % of flight time and 42 % of total migratory distance flown) when high temporal resolution data were available. Ospreys spent 82% of time in soaring-gliding flight, only switching to energy-demanding flapping flight when conditions for thermal migration were poor, most notably during ocean crossings. Ospreys generally travelled slower while migrating over land (mean speed = 10.9 m s^{-1}) than during flights across the ocean (mean speed = 14.7 m s^{-1}).

While migrating over land ospreys travelled faster while gliding, as predicted by flight theory. Ospreys also regulated airspeed in response to wind, increasing both gliding and flapping airspeeds in headwinds and reducing them when flying with tailwind support. This was particularly evident during spring migration when ospreys experienced headwind conditions more often than in autumn.

Unexpectedly, ospreys were able to migrate by soaring-gliding flight during three ocean crossings in autumn. In each case the birds appeared to exploit weak thermals and wind elements to power gliding phases, and were aided by tailwinds. When soaring-gliding flight was not possible, flapping speeds were sometimes considerably higher than over land, indicating that ospreys attempt to cross the sea as quickly as possible, perhaps at the expense of higher metabolic costs. It is notable that the

fastest ocean flapping speeds were recorded in spring, indicating that an urgency to return to breeding sites may have been important, with birds behaving like sprinting migrants.

Keywords: GSM transmitters, raptor migration, ocean crossings, airspeed regulation.

3.2. Introduction

During migration most species use a combination of two flight modes: soaring-gliding, where birds circle in order to gain altitude and then glide forward, and flapping, where birds use flight muscles to maintain altitude and power onward progress. Larger species tend to favour the former method because of the high energy costs of flapping flight, which can be several times their basal metabolic rate (BMR) and significantly greater than soaring-gliding (Spaar 1997, Pennycuick 1998, Alerstam 2000, Duerr et al. 2012).

Two methods are regularly used by migrating birds in order to attain soaring-gliding flight – thermal flight and slope soaring. In thermal flight, birds exploit warm updrafts of air created by differential heating of the earth's surface to gain altitude (Pennycuick 1998). The strength, spacing and vertical extent of thermals varies in different areas and on different days (Pennycuick 1998) but as long as air mass speed within a thermal exceeds an individual's sinking speed, a bird will gain altitude with minimal energy expenditure (Kerlinger 1989, Pennycuick 1989). It will then glide onwards, gradually losing altitude until it reaches another updraft (Leshem and YomTov 1996, Spaar and Bruderer 1996, Pennycuick 1998). During slope soaring birds exploit orographic lift, created when horizontal winds are deflected upwards by ridges and hills (Kerlinger 1989, Shepard et al. 2013). Orographic lift can provide a continuous source of lift along ridges (Kerlinger 1989, Pennycuick 1989), but birds may be forced to deviate from the most direct migratory course in order to follow the terrain feature (Duerr et al. 2012).

Wing loading, calculated by dividing body mass by wing surface area, is specifically related to the ability of birds to exploit lift. Species with a lower wing loading are able to exploit weaker lift because they have a lower sinking speed (Pennycuick 2008).

Conversely, species with higher wing loading can glide faster between thermals (Kerlinger 1989).

The majority of birds that migrate by soaring-gliding flight are restricted to migration over land where the strongest thermal conditions prevail (Shepard et al. 2013). As a result many species of raptor in temperate zones deviate from the most direct migratory route in order to avoid long ocean crossings, where thermal and orographic lift are either limited or absent. In such circumstances the absence of lift means that the only way of maintaining altitude and making onwards progress is by flapping-gliding flight (Kerlinger 1989, Alerstam 2001). Furthermore there are no opportunities to land during ocean crossings if raptors encounter adverse weather conditions during the flight (Zu-Aretz and Leshem 1983). Agostini et al. (2002) and Mellone et al. (2011) showed that short-toed eagles *Circaetus gallicus* extended their migration routes by 500–1700 km in order to cross the Mediterranean at the shortest point, the Strait of Gibraltar. Large concentrations of migratory soaring birds are recorded in spring and autumn at well-known geographical bottlenecks, at well-known geographical bottlenecks, such as the Bosphorus (Fülöp et al. 2014), the Strait of Gibraltar (Martín et al. 2016), Eilat in Israel (Lott 2002) and South-west Georgia (Verhelst et al. 2011) for the same reason. In an extensive analysis of the water crossing tendencies of Afro-Palearctic raptors during migration Agostini et al. (2015) concluded that energy consumption during powered flight was the key factor determining the ability of raptors to make long ocean flights, thereby influencing whether they needed to make detours during migration to avoid long ocean flights (Alerstam 2001).

The osprey *Pandion haliaetus* is a piscivorous raptor that migrates long distances between Northern Europe and sub-Saharan Africa, as well as from North to South America. Its wing loading (4.9 kg m^{-2}) allows it to exploit thermals (Mellone et al. 2012), but it appears to use flapping flight more than other similar-sized migratory raptors such as honey-buzzards *Pernis apivorus* and black kites *Milvus migrans* (Meyer et al. 2000), possibly because its long, relatively narrow wings reduce drag (Kerlinger 1989, Agostini 2015). This enables it to make longer sea crossings (Meyer et al. 2000, Dennis 2002, Martel et al. 2014, Horton et al. 2015) than other similarly-sized raptors (Alerstam 2001, Agostini et al. 2002 and Mellone et al. 2011). Osprey migration has

been extensively studied using satellite telemetry (e.g. Hake et al. 2001, Kjellen et al. 2001, Martell et al. 2001, Alerstam et al. 2006, DeCandido et al. 2006, Dennis 2008, Stout et al. 2009, Bedrosian et al. 2015) but research into flight strategy has been limited to hourly or daily scales (Kjellen et al. 2001, Klaassen et al. 2008, Mellone et al. 2012) or to fixed locations using visual observations or radar (Meyer 2000, Kjellen et al. 2001). Recent advances in technology now make it possible to analyse flight method at a higher temporal resolution using solar powered Global System for Mobile Communication (GSM) / Global Positioning System (GPS) transmitters which log the location, altitude, speed and orientation of migrating birds as frequently as once every 30 – 60 s. Such data have the potential to demonstrate how flight method varies along complete migratory journeys and how this impacts overall migratory performance. The osprey is a particularly interesting species to study in this regard because its flexible approach to migration, through the use of both soaring-gliding and flapping flight, as well as its ability to undertake long sea crossings makes it unusual among migratory raptors. The analysis of high resolution GSM data therefore has the potential to demonstrate how individual ospreys adapt their flight mode according to changing environmental conditions experienced during migration, particularly in relation to ocean crossings which most other migratory raptors avoid.

Alerstam (2000) calculated that given their morphology, the expected migration speed of ospreys should be faster during thermal soaring flight than flapping, even though soaring requires the interruption of forward progress in order to gain altitude. In soaring-gliding flight the fraction of time spent circling in thermals is generally around 50% (Alerstam 2000), but the fast cross-country speeds achieved in glides between thermals compensate for the lost time. As a result ospreys should always favour soaring-gliding flight where conditions permit it. During migration ospreys use the fly-and-forage strategy whereby birds exploit opportunities to feed before, during or after a day's flight (Strandberg and Alerstam 2007, Klaassen et al. 2008). Thus in areas where foraging opportunities are scarce or absent it is particularly important to conserve energy. This is most significant during crossings of the Sahara, known to be a hazard for birds migrating between northern Europe and sub-Saharan Africa (Strandberg et al. 2010, Klaassen et al. 2014).

During the course of migrations between northern Europe and West Africa, ospreys encounter varying environmental conditions that may impact flight method. Thermals are likely to be weaker and more sporadic in Europe than the African land regions (Chevallier et al. 2010), whilst in North Africa variable topography, most notably the Atlas Mountains, provides favourable conditions for the generation of orographic lift (Shepard et al. 2013). Conditions for thermal migration should be excellent in the Sahara and West Africa (Strandberg et al. 2009, Mellone et al. 2012) but the flat terrain in West Africa means that opportunities to exploit orographic lift are likely limited there (Shepard et al. 2013). Thermals develop over the ocean in the trade wind zone, but given that ocean flights undertaken by ospreys migrating from the UK occur to the north of this zone, where thermals are likely to be scarce or completely absent (Kerlinger 1989), ocean crossings are likely to be made by flapping flight. Such variations in environmental conditions are likely to drive differing flight modes by this highly-flexible raptor.

3.2.1. Aims

In this study, we devise and review a simple approach to determine the method of flight using high resolution GSM data from ospreys migrating between the UK and West Africa in order to determine how they adapt flight method according to changing environmental conditions experienced en route. In particular we analyse the extent to which flight strategy varies between land regions and also during flights across the ocean and how this affects overall migratory performance.

In particular, we test the hypotheses:

- (i) that ospreys preferentially migrate by soaring-gliding flight;
- (ii) that they only resort to flapping flight when lift is limited or not available such as during sea crossings or in poor weather;
- (iii) that an increased proportion of soaring-gliding flight leads to a faster migration speed.

This is the first study to use high resolution GSM data to analyse variations in osprey flight method and demonstrates the value of this technique in the study of avian

migration. Such data has the potential to provide new insights into the techniques used by ospreys that enable them to migrate on a much broader front between Europe and Africa than most other migratory raptors.

3.3. Methodology

3.3.1. GSM transmitters

Three adult male ospreys were trapped in northern Scotland under licence (from the British Trust for Ornithology) using a Dho-Gaza net and decoy eagle owl. Solar-powered backpack GPS-GSM transmitters (Microwave Telemetry Inc., Columbia, MD, USA) were fitted to the birds using a Teflon harness. The transmitters logged location (± 18 m), altitude (± 22 m), heading (degrees) and speed (knots) at rates up to once per minute during the middle part of the day (when battery voltage is highest) and less frequently (0.5 - 4 hours) at night, in the absence of sunlight and when birds are less likely to be flying. Two of the birds (bird 1 and bird 2 were tagged in 2013 and bird 3 was tagged in 2015). The transmitters subsequently logged a total of five migratory journeys by bird 1 (three autumn, two spring), two by bird 2 (one autumn, one spring) and one by bird 3 (one autumn).

3.3.2. Flight method classification

Only flight periods with the highest resolution data logged during migration travelling days, henceforth referred to as 'HD sectors' were used to analyse flight method. These were limited to the middle part of the day when battery voltage was highest (thereby permitting collection of high resolution data). In order to be classified as a HD sector a minimum of 45 GPS observations were required per hour (i.e. one GPS observation per 1:20 minutes). The length HD sectors varied between 79 minutes and 565 minutes and were limited to one per day.

The altitude of successive GPS fixes within HD sectors was analysed to determine whether the bird had gained or lost altitude in the intervening period (i.e. since the previous GPS observation). In addition, heading in degrees and great-circle distance (the shortest distance between two points on the surface of a sphere, i.e. the Earth) between successive GPS observations - henceforth referred to as segments - were

calculated. The vertical height accuracy of the GSM transmitters used in this study is ± 22 m (<http://www.microwavetelemetry.com/bird/GSMspecifications.cfm>) and thus only altitude gains in excess of 22 m were considered as an increase in altitude and losses of more than 22 m as a decrease in altitude.

Segments where the bird gained more than 22 m in altitude were classified as circling if distance flown was less than 500 m, or soaring if distance flown exceeded 500 m, thereby allowing inferences to be made about the type of lift exploited by the ospreys. In this classification, circling is likely a proxy for thermal altitude gain since in the time-step of high resolution GPS observations a bird circling in thermals is unlikely to make onward progress of more than 500 m (Pennycuik 1998). Climbing rate (m s^{-1}) was calculated for each daily HD sector by dividing total altitude gain during circling segments by total time spent in circling segments. Soaring, on the other hand, is likely to be more indicative of slope soaring or other forms of linear lift such as thermal streets since, in the time-step being considered, the birds continue to make onward progress while gaining altitude (Pennycuik 1998). In this categorisation, circling and soaring are unrelated to orientation because, during periods of altitude gain, the bird may face any direction.

When gliding or flapping the bird should be orientated in the intended direction of migration (Alerstam 2000). In order to account for this, a third element — based on instantaneous orientation data logged by the transmitters — was incorporated into the classification for these flight methods. In each case the bird was required to have made a minimum onward progress of 250 m — well below the predicted distances achievable by ospreys in flapping or gliding flight — in order to account for the potential impact of headwinds. Ospreys tracked by radar during flapping flight achieved a mean airspeed of 13.3 m s^{-1} (Alerstam et al. 2007) which equates to flying a distance 798 m per minute (the minimum time-step of the high resolution data). However, a migrating osprey is unlikely to maintain such speeds because of the high energetic costs, and speed may be further curtailed by headwinds. In gliding flight the maximal cross-country speed in weak thermals (climb rate 1 m s^{-1}) is 16 m s^{-1} , which equates to 960 metres per minute (Alerstam 2000) but this may also be reduced by headwinds. Gliding is the only flight method where the osprey will lose altitude and

make onward progress, thus a bird was categorised as gliding if it lost more than 22 m in altitude, segment distance exceeded 250 m and orientation change was less than 22.5°. In this case orientation change refers to the difference between transmitter orientation at the start and end of the segment, or the difference between segment heading and transmitter orientation at either the start or end of the segment, whichever is lower. This classification accounts for the fact that gliding may consist of either a single segment or multiple segments and that the bird may have been circling or soaring at either the start or end of it, and therefore orientated in a different direction. Restricting the classification to only instantaneous orientation information logged by the transmitters would otherwise omit some gliding segments. Flapping was classified according to the same orientation and distance criteria, where altitude change was less than 22 m. A sensitivity analysis was carried out to determine the effect of changing the orientation threshold value from 22.5° to a range of other values.

The classification criteria are shown in Table 3.1. Any segments that did not meet these criteria were omitted from the analysis because reliable interpretation of flight method was not possible. These unclassified segments accounted for a mean 6 % (SD = 5 %) of total time.

Once each flight segment had been classified, the total time spent circling, soaring, gliding and flapping were calculated for each daily HD sector and expressed as a fraction of overall time. The great-circle distance between the start and end point of each daily HD sector was calculated and HD sector headway speed was determined by dividing great-circle distance by time. The mean HD sector time was 287 mins which constituted 50 % of daily flying time (mean = 577 mins). Data were validated by cross-referencing where possible with theoretical values calculated by Alerstam (2000) and Pennycuick (2008) and also observed values (Alerstam et al. 2007). Flight for Windows software version 1.24 (C.J. Pennycuick; <http://www.bio.bristol.ac.uk/people/pennycuick.html>) was used to calculate maximum achievable flapping speeds and glide ratios (ratio between horizontal distance gained and altitude change during glides) for ospreys during specific stages of flight.

Table 3.1. Flight method classification. *Flight method was determined through analysis of altitude and orientation changes between successive GPS segments.*

Flight method	Distance flown	Altitude change	Orientation change
Circling	Less than 500 m	Increase in excess of 22 m	
Soaring	500 m or more	Increase in excess of 22 m	
Gliding	250 m or more	Decrease in excess of 22 m	22.5° or less *
Flapping	250 m or more	Increase or decrease by 22 m or less	± 22.5° or less *

**difference between successive transmitter orientations, or difference between segment heading and transmitter orientation at start or end of segment, whichever is lower*

3.3.3. Weather data

To determine the impact of meteorological conditions on flight method, wind data and boundary layer height (m) were downloaded from the European Center for Medium-Range Weather Forecasts (ECMWF) Global Reanalysis Project at a resolution of 0.25° and 3 h. Wind strength and direction may vary with altitude (Stull 1988) and so u- and v-wind components (i.e. latitudinal and longitudinal wind velocities, m s^{-1}) 10 m above sea level and at barometric pressure levels of 925 and 850 mB (equating to altitudes of 762 m, 1457 m) were downloaded. The wind and boundary layer data were then linearly interpolated for hourly locations from each HD sector using ArcMap 10.3.1 (Environmental Systems Research Institute, Redlands, CA). Head/tailwind component (wind speed multiplied by the cosine for the angle between the wind direction and the bird's heading) was calculated for each hourly location based on the bird's heading during the HD sector and the wind speed and direction closest to the bird's median altitude for the same period. Headwinds were expressed as positive values and tailwinds as negative values. Mean daily values were then calculated for headwind component and boundary layer height. A higher boundary layer is associated with

stronger and more densely spaced thermals (Stull 1988, Vansteelant 2015). According to the triangle of velocities described by Alerstam (2000) a bird's groundspeed and track direction is the sum of the bird's flight vector (heading direction and airspeed) and the wind vector (wind direction and speed). Therefore we calculated gliding and flapping airspeeds of individual segments by first calculating the bird's heading. The head/tailwind component was then calculated in relation to this segment heading. The segment groundspeed and head/tailwind component were then summed in order to give the segment airspeed. Based on this calculation a flapping groundspeed of 10 m s^{-1} with a headwind component of 3 m s^{-1} would give an airspeed of 13 m s^{-1} .

3.3.4. Geographic Regions

The migratory flyway was sub-divided into five geographic regions - Europe, North Africa, the Sahara, West Africa and oceans (Figure 3.1). All ocean crossings were classified together irrespective of geographic location. HD sectors were assigned to a specific region; flights where birds crossed regional boundaries were removed from the analysis.

3.3.5. Statistical Analysis

Data were analysed in [R version 3.3.0](#) (R Core Team 2016). Fractions of time spent in each flight mode were calculated for each HD sector by dividing total minutes spent in each flight mode (circling, soaring, gliding, flapping) by the total duration (in minutes) of each HD sector. These time fractions were then logit-transformed for analysis (Warton and Hui 2011). Linear mixed-effects models (fitted in R package '[nlme](#)', version 3.1-128; Pinheiro et al. 2016) were used to determine the effect of region, season (autumn versus spring), wind (headwind component) and boundary layer height on flight method. The effect of boundary layer height was modelled using natural (restricted) cubic splines (R package '[splines](#)'; R Core Team 2016). Bird identity was included as a random factor and logit-transformed flapping time fraction as the response variable. Flapping was chosen as the response variable because under optimum conditions ospreys are expected to migrate by soaring-gliding flight to minimise metabolic costs and maximise the distance flown. Thus we were particularly

interested in understanding under what conditions, and in which regions, ospreys switch to flapping flight.

Model fit was assessed in diagnostic plots (Supplementary material Appendix 2, Figure A2.1, Figure A2.2) including standardised residuals plotted against fitted values and quantile-quantile comparison plots (Q-Q plots) against the standard normal distribution.

The effect of flight method on migratory performance was analysed using Spearman's rank correlation between HD sector headway speed and different potential explanatory variables: flight method time-fractions, headwind, boundary layer height, region and season (function 'spearman2' in package 'Hmisc').

3.4. Results

3.4.1. Flight method

Flight method was determined for HD sectors where ospreys were flying continuously (mean = 287 min, SD = 58 min), collected during a total of 109 days. The number of HD sectors per bird, season and geographic region is shown in Table 3.2 and a comparison of the length of HD sectors between land and ocean is shown in Figure 3.1. The HD sectors consisted of 31246 GPS observations (thus 15623 segments) and constituted 40 % of total flying time during eight migratory flights made by three birds. Five were made by bird 1 (three autumn, two spring), two by bird 2 (one autumn, one spring) and one by bird 3 in autumn (Figure 3.2, Table 3.2.).

All eight of the migratory journeys were completed successfully, with each of the three birds wintering in Senegal. The birds travelled a total of 17907 km during HD sectors (mean distance = 164 km, SD = 60 km), which constituted 42 % of total distance flown during the eight migrations. Mean time fractions for the different flight modes during HD sectors are shown in Table 3.3 along with the mean time spent in each flight mode before swapping to an alternative method of flight (i.e. time spent circling before swapping to gliding etc.). The results of sensitivity analyses into the effect of varying the threshold value of orientation change for flapping and gliding segments from 22.5°

to figures ranging from 10.5° to 32.5° are shown in Figure 3.3 (flapping) and Figure 3.4 (gliding).

Table 3.2. Summary of migrations undertaken by ospreys equipped with GSM transmitters. *Information on breeding attempts prior to autumn migrations is also shown in the table with ‘Yes’ referring to a breeding attempt and the figure in brackets showing the number of young fledged). The number of HD sector is shown per region for Europe (E), North Africa (NA), ocean (O), Sahara (S) and West Africa (WA).*

Bird	Year	Bred	Start date	End date	Total mins	Total dist. flown (km)	No of HD sectors							HD sectors				
							E	N A	O	S	W A	Total mins	Mean mins	Total dist.	Mean dist.	Total GPS obs.	Mean GPS obs.	
Autumn																		
1	2013	Yes (1)	10/9	22/9	8565	5156	3	3	2	3	3	3815	273 (SD = 59)	2255	163 (SD = 61)	3417	244 (SD = 57)	
1	2014	Yes (0)	6/9	21/9	10230	5255	4	3	1	3	2	3996	307 (SD = 26)	2159	166 (SD = 54)	3520	271 (SD = 27)	
1	2015	Yes (0)	2/9	16/9	9705	5349	3	2	0	5	3	3900	300 (SD = 1)	2076	160 (SD = 53)	3570	275 (SD = 16)	
2	2013	Yes (3)	26/9	14/10	8925	5274	5	1	2	3	2	3259	251 (SD = 77)	2063	159 (SD = 64)	2927	225 (SD = 78)	
3	2015	No	6/9	24/9	8205	5188	3	1	2	4	0	3287	329 (SD = 83)	1911	191 (SD = 100)	3003	300 (SD = 64)	
Spring																		
1	2014	N/A	16/3	11/4	10876	5420	4	2	2	4	3	4088	273 (SD = 74)	2223	148 (SD = 49)	3708	247 (SD = 75)	
1	2015	N/A	19/3	8/4	11880	5869	6	2	1	5	3	4952	291 (SD = 35)	2750	162 (SD = 35)	4676	275 (SD = 36)	
2	2014	N/A	16/3	10/4	9750	5337	2	3	2	5	2	3949	282 (SD = 46)	2470	171 (SD = 74)	3711	265 (SD = 47)	

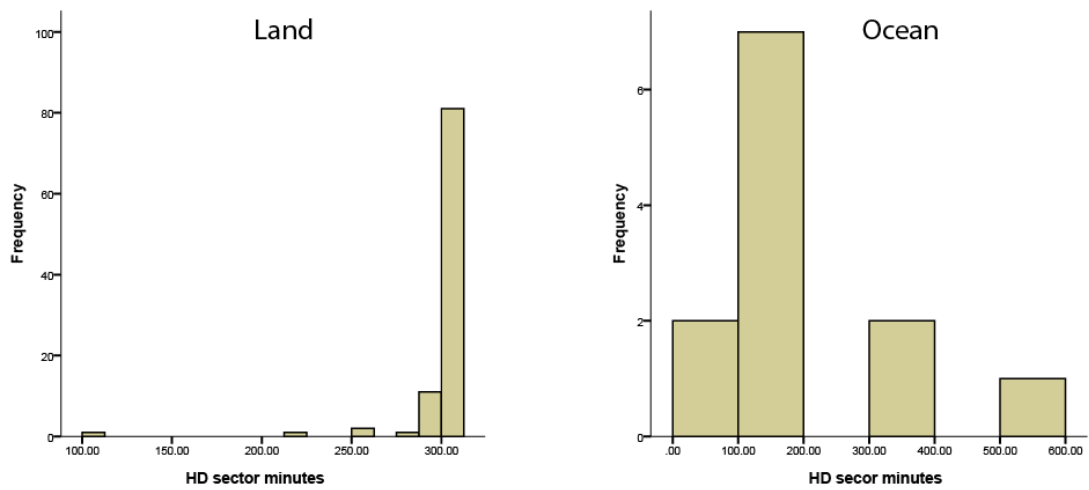


Figure 3.1. Frequency histogram showing the variation in the length (in time) of HD sectors over land and ocean. *HD sectors were daily periods of high-resolution GSM data that enabled flight method to be categorised during that period of time.*

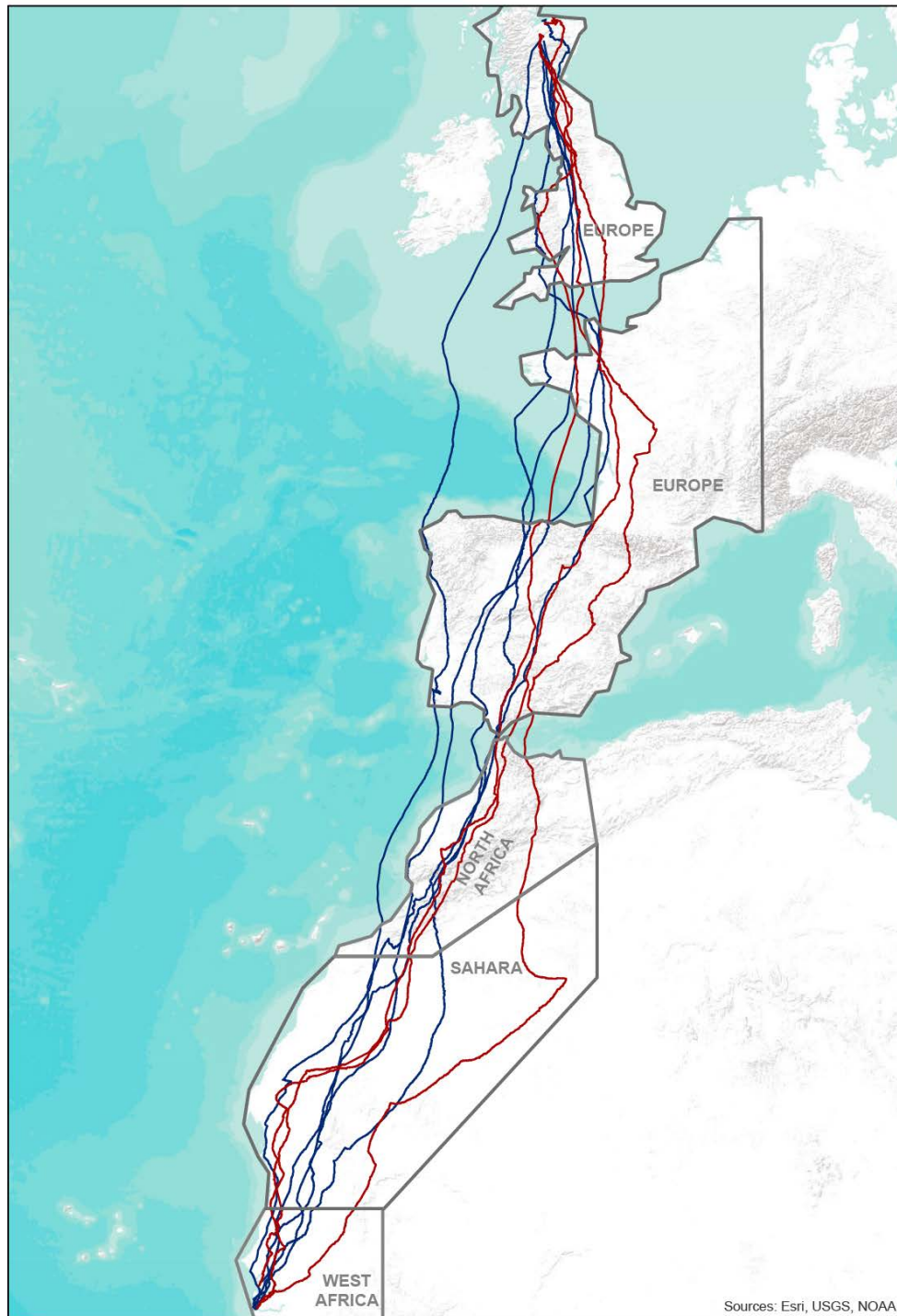


Figure 3.2. Migratory flights of the satellite-tagged ospreys and geographic regions in the study. *Blue lines indicate autumn migration, red lines spring migration. Flights across the ocean were included as a fifth region.*

Table 3.3. Fraction of time spent in different flight methods during HD sectors.

Flight method	Time fraction during HD sectors				Time in flight mode (seconds)	
	mean	SD	median	IQR	mean	SD
Circling	0.25	0.11	0.29	0.12	139	92
Soaring	0.18	0.10	0.17	0.11	104	82
Gliding	0.39	0.11	0.39	0.10	172	130
Flapping	0.18	0.20	0.18	0.08	102	175

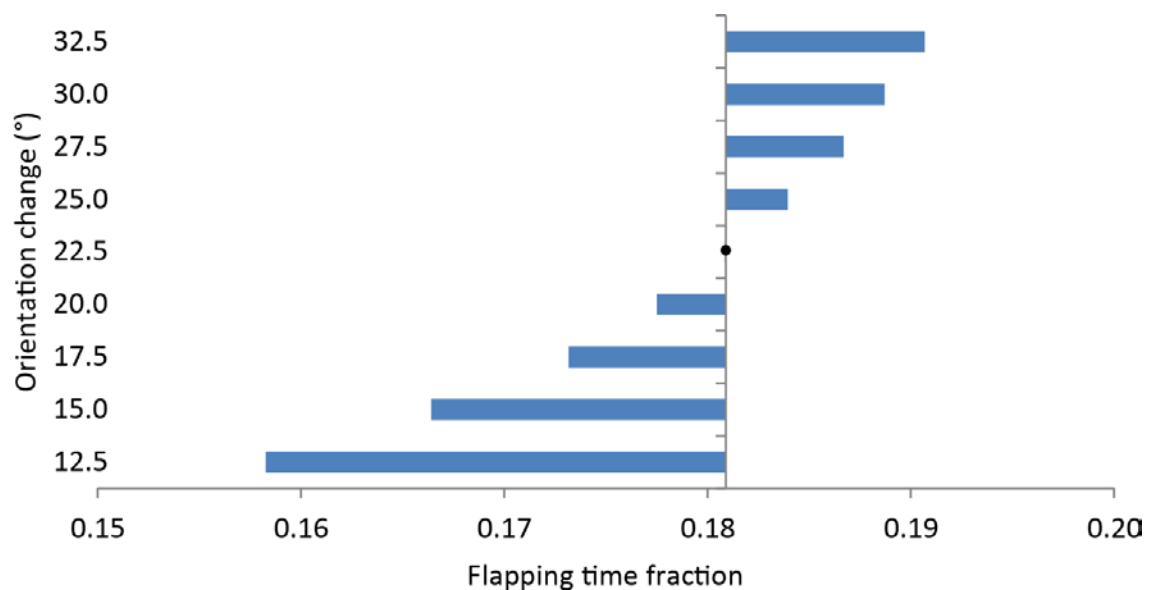


Figure 3.3. Sensitivity analysis showing the effect of varying the threshold level of orientation change for the flapping classification. Bars represent difference in mean flapping time fraction compared to 22.5° (the threshold figure used in the flight method classification) for eight other threshold levels.

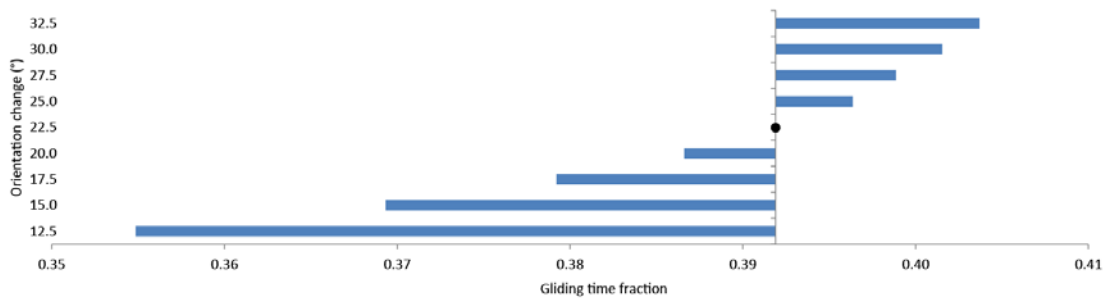


Figure 3.4. Sensitivity analysis showing the effect of varying the threshold level of orientation change for the gliding classification. Bars represent difference in mean flapping time fraction compared to 22.5° (the threshold figure used in the flight method classification) for eight other threshold levels.

3.4.2. Factors determining flight method

Ospreys showed a clear preference for soaring-gliding flight (Table 3.3.), but switched to flapping flight where necessary, particularly during sea crossings (Figure 3.6). The pronounced variation in flight method over land and ocean is summarised in Table 3.4 and Figure 3.5.

Table 3.4. Summary data for flights over land and ocean during HD sectors.

	Mean dist. (km)	Mean speed of flight segm- ents (m s ⁻¹)	Circ. time frac.	Rate of climb (m s ⁻¹)	Soar time frac.	Mean alt. gain	Mean glide frac.	Mean dist. gliding (km)	Mean glide ratio	Mean dist. flapping (km)	Mean flap frac.
Land	161.63(SD = 53.85)	10.9 (SD = 7.9)	0.28 (SD = 0.08)	1.82 (SD = 0.46)	0.12 (SD = 0.08)	11995 (SD = 3914)	0.42 (SD = 0.06)	117.31 (SD = 33.92)	10:1	23.25 (SD = 9.86)	0.12 (SD = 0.06)
Ocean	179.5 (SD = 100.6)	14.7 (SD = 6.5)	0.05 (SD = 0.08)	1.35 (SD = 0.56)	0.11 (SD = 0.08)	1623 (SD = 2919)	0.16 (SD = 0.11)	41.819 (SD = 58.375)	33:1	114.1 (SD = 67.73)	0.67 (SD = 0.26)

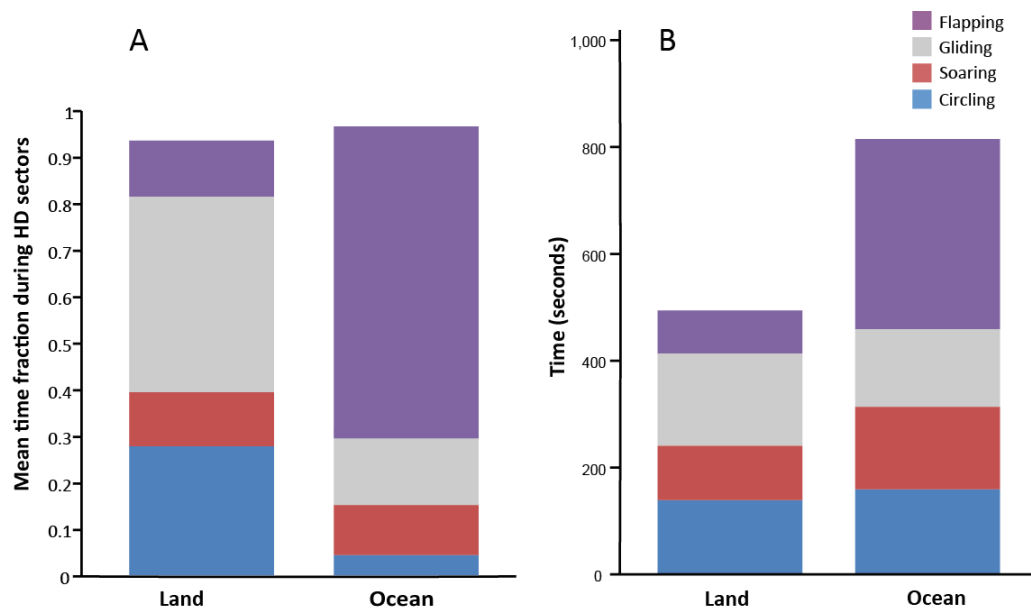


Figure 3.5. Differences in flight method over land and ocean. A) Mean time fractions for circling, soaring, gliding and flapping flight during HD sectors over land and ocean, and B) Mean time spent circling, soaring, gliding and flapping flight over land and ocean before alternating to a different flight mode. *Flight over the ocean generally involved a much greater proportion of flapping flight than over land.*

As expected, ospreys encountered pronounced variation in thermal conditions (Figure 3.7). Boundary layer height was lowest during sea crossings, but also showed marked regional and seasonal differences over land (linear model on log-transformed boundary layer heights over land, $F_{7,87} = 8.887$, $p = 3.24 \times 10^{-8}$; region \times season interaction, $p = 0.00162$). We considered geographic region, season, headwind and boundary layer height as possible explanatory variables for the proportion of time spent in flapping flight. Fitting a mixed-effects model to the over-land data (Table 3.5, Figure 3.8) identified boundary layer height as a key factor (likelihood ratio statistic $LR = 26.74$, $df = 4$, $p = 2.24 \times 10^{-5}$) while region, season and headwind were not significant (all $p > 0.3$), indicating that ospreys exploited land thermals when they were available regardless of region, season and headwind. The regional and seasonal differences in flapping over land (Figure 3.6) were thus largely explained by regional and seasonal variation in thermal conditions (Figure 3.7) rather than by birds selecting differing flight methods depending upon region or season. In general, ospreys experienced the

best thermal conditions in the Sahara and North Africa, resulting in them flapping less than in Europe where thermal conditions were most variable.

The relationship between flapping and boundary layer height over land was non-linear, flattening as boundary layers exceed about 1500 m with birds typically spending about 0.1 of flight time flapping when boundary layer exceeded 2000 m (Figure 3.8). It is also notable that flapping time fraction did not exceed 0.31 while ospreys were migrating over land, indicating that thermals were always strong enough to sustain some degree of thermal flight.

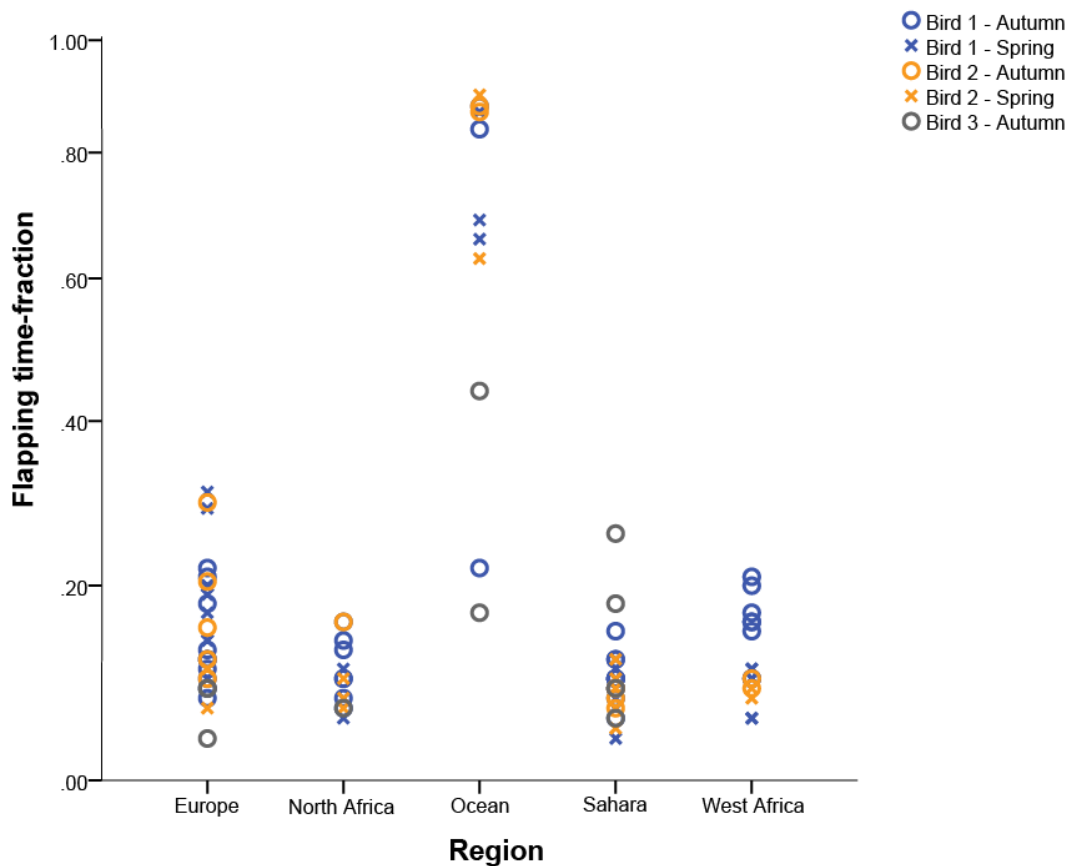


Figure 3.6. Relationship between flapping time-fraction and region.

Untransformed values of flapping time fraction are plotted on a logit-transformed scale. Ospreys generally used a much greater proportion of flapping flight over the ocean, other than during three occasions in autumn.

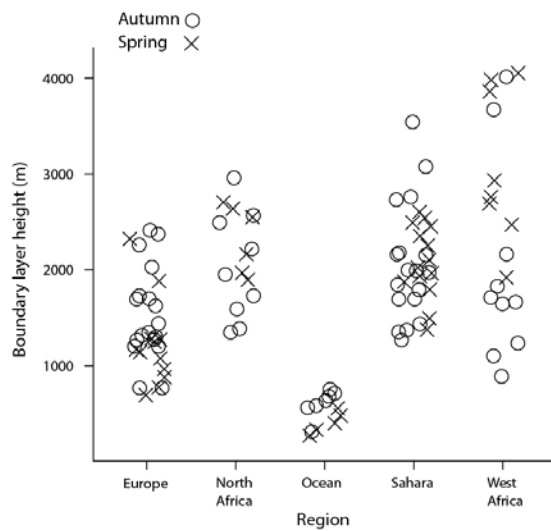


Figure 3.7. Regional and seasonal variation in boundary layer height. *A higher boundary layer is indicative of stronger and more densely spaced thermals.*

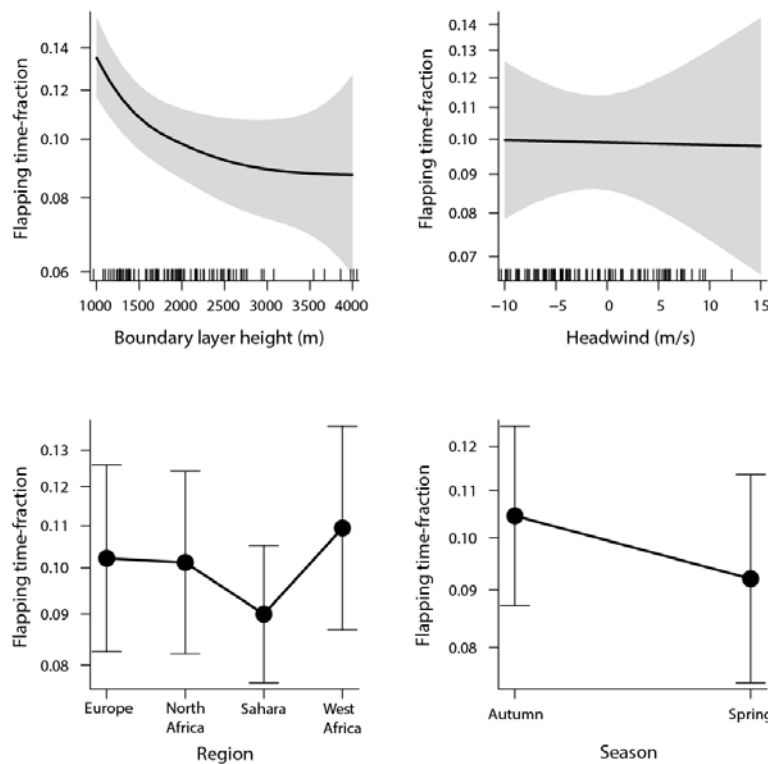


Figure 3.8. Effect estimates from the model for the proportion of time spent in flapping flight over land. *Grey bands and error bars indicate the 95% confidence intervals. Regional differences in the fraction of time spent flapping were driven by changing boundary layer (thermal) conditions, rather than birds altering their flight technique according to region or season.*

Table 3.5. ANOVA-style term deletions for the mixed-effects model of the effects of region, season, headwind (h.wind) and boundary layer height (bl.height) on logit-transformed flapping time fraction (flap.tf) over land, with bird identity as random effect. Boundary-layer height was modelled as a natural cubic spline (ns) with five knots. The model is summarised graphically in figure 4; df, degrees of freedom; AIC, Akaike information criterion; LR, likelihood ratio statistic.

Model: logit(flap.tf) ~ region + season + region + h.wind + ns(bl.height)

	<i>df</i>	<i>AIC</i>	<i>LR</i>	<i>P</i>
full model	12	111.25		
<i>region</i>	3	108.82	3.5645	0.313
<i>season</i>	1	110.19	0.9374	0.333
<i>h.wind</i>	1	109.26	0.0055	0.941
<i>bl.height</i>	4	130.00	26.7430	2.24×10^{-5}
—nonlinear	3	116.11	10.8615	0.0125

Boundary layer height appears to be a less reliable predictor of flight method over the ocean (Fig. 3.9B). The flapping time fraction over the ocean was typically very high (median = 0.765, IQR = [0.5825, 0.8725]), but varied widely between 0.17 and 0.90 despite the fact that boundary layer was always low (mean = 523 m, SD = 164 m) compared to over land (mean 1952 m, SD = 752 m). This variation is only partly explained by the steep rise of the flapping time-fraction as boundary layer height drops below 1000 m. Refitting the model with ocean crossings included (Table 3.6, Figure 3.10) gave a poorer model fit (Supplementary material Appendix 2, Figure A2.2) primarily due to two ocean flights made by bird 1 and bird 3 where the flapping time-fraction was unusually low at ca. 0.2. Boundary layer height was still strongly significant ($LR = 18.74$, $df = 4$, $p = 0.00088$), and the effect of headwind remained non-significant ($LR = 1.54$, $df = 1$, $p = 0.22$) when the sea data were included. However,

birds typically spent more time in flapping flight over the ocean than predicted from the (low) boundary layer (effect for region, $LR = 20.68$, $p = 0.00037$).

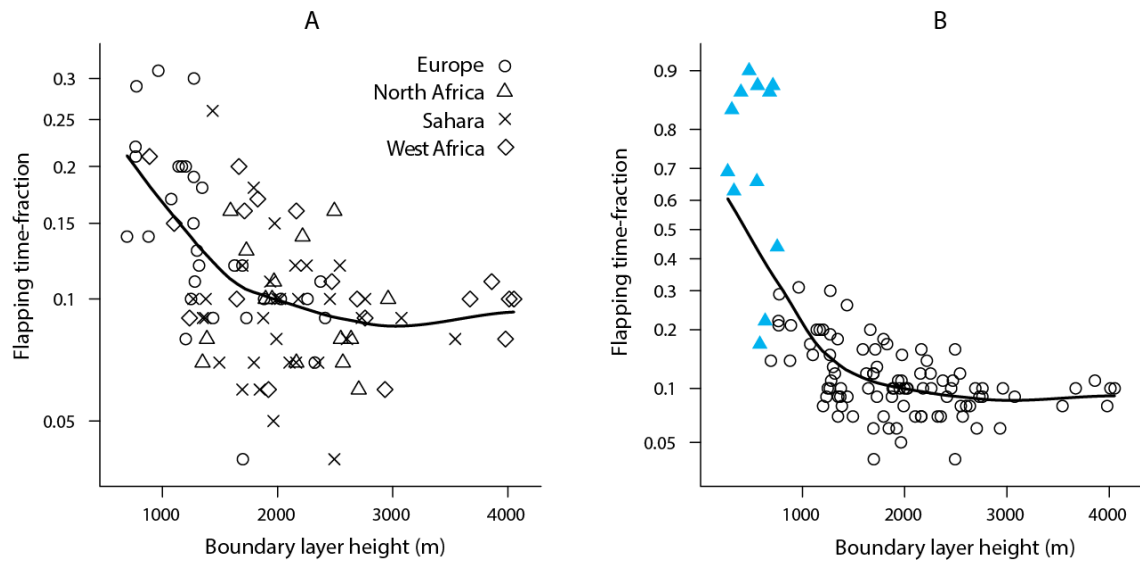


Figure 3.9. Relationship between boundary layer height and time spent in flapping flight. *Flapping time-fraction is shown as untransformed values on a logit-transformed scale. (A) Flights over land only. (B) Ocean flights are shown in blue triangles, land flights as black circles. The lines represent Loess-regressions.*

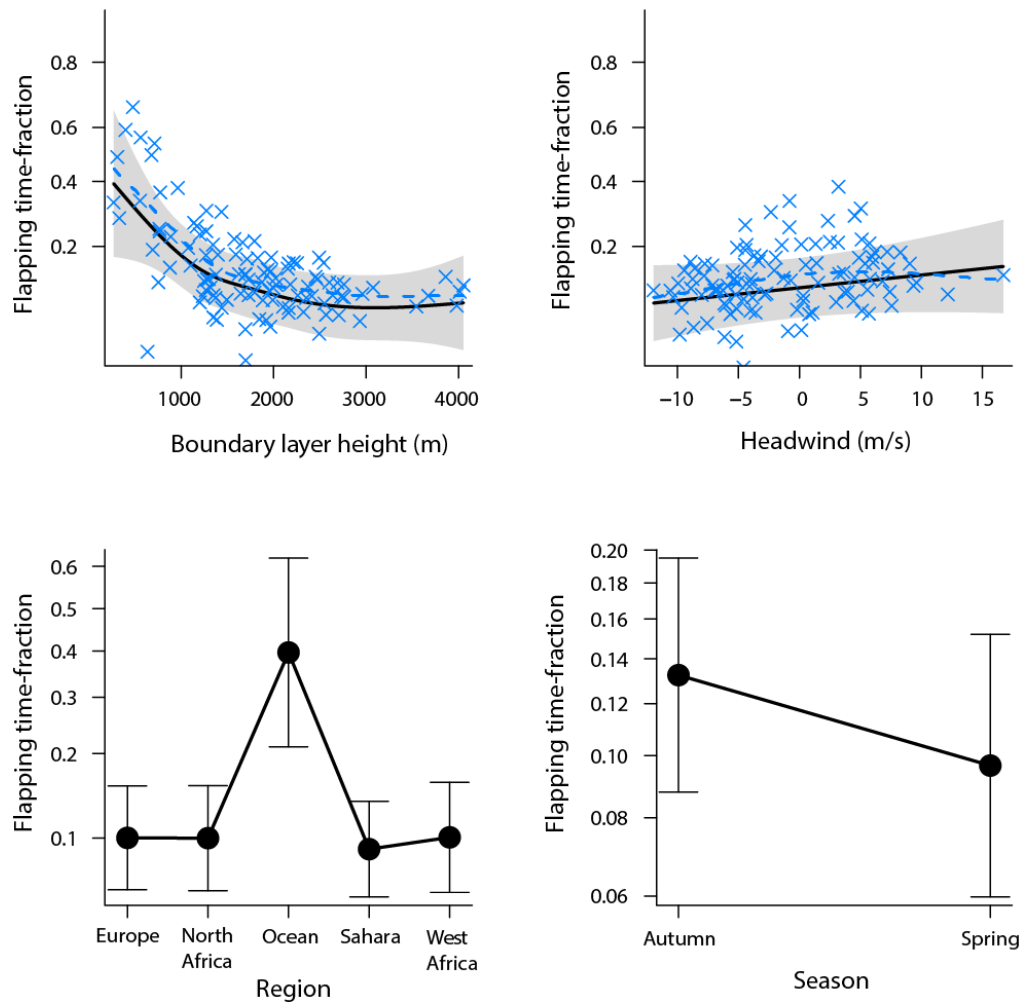


Figure 3.10. Effect estimates from the model for the proportion of time spent in flapping flight over land and sea. Grey bands and error bars indicate the 95% confidence intervals. Boundary layer is a less reliable predictor of flight method over the ocean, than land.

Table 3.6. Mixed-effects model of the effects of region, season, headwind (h.wind) and boundary layer height (bl.height) on logit-transformed flapping time fraction (flap.tf) over land and sea, with bird identity as random effect. Boundary-layer height was modelled as a natural cubic spline (ns) with five knots. The model is summarised graphically in figure S1; df, degrees of freedom; AIC, Akaike information criterion; LR, likelihood ratio.

Model: logit(flap.tf) ~ region + season + region + h.wind + ns(bl.height)

	<i>df</i>	<i>AIC</i>	<i>LR</i>	<i>P</i>
full model	13	199.40		
<i>region</i>	4	212.07	20.6775	0.000367
<i>season</i>	1	200.71	3.3179	0.0685
<i>h.wind</i>	1	198.94	1.5404	0.215
<i>bl.height</i>	4	210.14	18.7415	0.000883
—nonlinear	3	200.67	7.2912	0.0632

3.4.3. Ocean crossings

Ospreys appear to use a different flying mode over the ocean compared to over land. To investigate this in more detail, individual flights made across the sea ($N = 12$) were analysed, focussing in particular on three flights where flapping time fraction was below 0.5, indicating that the birds travelled significant distances by soaring and gliding. In most cases the HD sectors (mean distance 180 km, mean duration 209 mins) did not cover complete sea crossings, instead constituting a mean 59% of total flying time over the sea. Ospreys gained altitude through a combination of circling and soaring during the three flights where flapping time fraction was less than 0.5 and these were the only ocean flights where circling time fraction was greater than 0.02; in

other words, during the other flights almost all climbing was achieved by soaring alone. In our classification circling is likely a proxy for altitude gain on thermals, suggesting that in each case, the ospreys were able to exploit weak thermals over the sea. The climbing rates shown in Table 3.7 give an indication of the likely strength of the thermals encountered by the birds and cross-sections of these flights phases of climb and descent are shown in Figure 3.11. Figure 3.12 provides examples of climbing behaviour of bird 1 (Figure 3.12A) and bird 3 (Figure 3.12B) over the ocean, with flights over Europe (Figure 3.12C) and Sahara (Figure 3.12D) shown for comparison. It is notable that all three flights with significant climbing occurred in autumn and constituted three of the four longest ocean crossings recorded, covering distances (including all data) of 480 km, 1245 km and 1610 km.

The data indicate that these ocean flights did not consist of pure gliding, because the calculated glide ratios exceed the theoretical glide ratios achievable by ospreys at the respective airspeeds (Pennycuick 2008) (Table 3.7). Instead it seems likely that glides between bouts of circling or soaring were interspersed with occasional flapping in order to prolong gliding segments. Each flight was made with tailwind support, which would reduce the amount of flapping required compared to still air conditions.

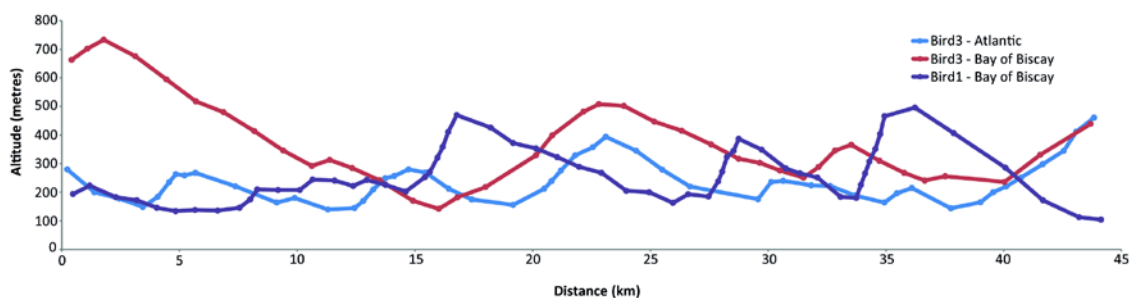


Figure 3.11. Flight profiles of sectors of three flights with significant climbing intervals over the ocean. *These flight profiles indicate that birds were exploiting weak thermals and elements of the wind in order to gain altitude.*

Table 3.7. Circling, soaring and gliding data of three flights across the ocean with significant climbing intervals.

Loc.	Total dist. (km)*	Circ. time- frac.	Rate of climb (m s ⁻¹)	BL height (m)	Soar. time- frac.	Total alt. gain (m)	Dist. gliding (km)	Gliding air- speed (m s ⁻¹)	Glide ratio	Max glide ratio **
Biscay Bird 1	113 (23 %)	0.2	1.01	636	0.18	2657	58.83	14.0	22:1	15:1
Biscay Bird 3	404 (41 %)	0.11	1.39	584	0.26	10523	212.6	15.9	20:1	14:1
Atlantic Bird 3	228 (16 %)	0.2	2.01	754	0.14	1032	81.35	11.1	38:1	15:1

**total distance with high-resolution data; figures in brackets indicate percentage of total distance of the ocean crossing. **Max theoretical glide ratio for given airspeed based on Pennycuick (2008). Glide ratio refers to the ratio between onward distance and altitude loss, i.e. a glide ratio of 15:1 means that for every 15 metres the bird glides forward, it will loses 1 metre in altitude.*

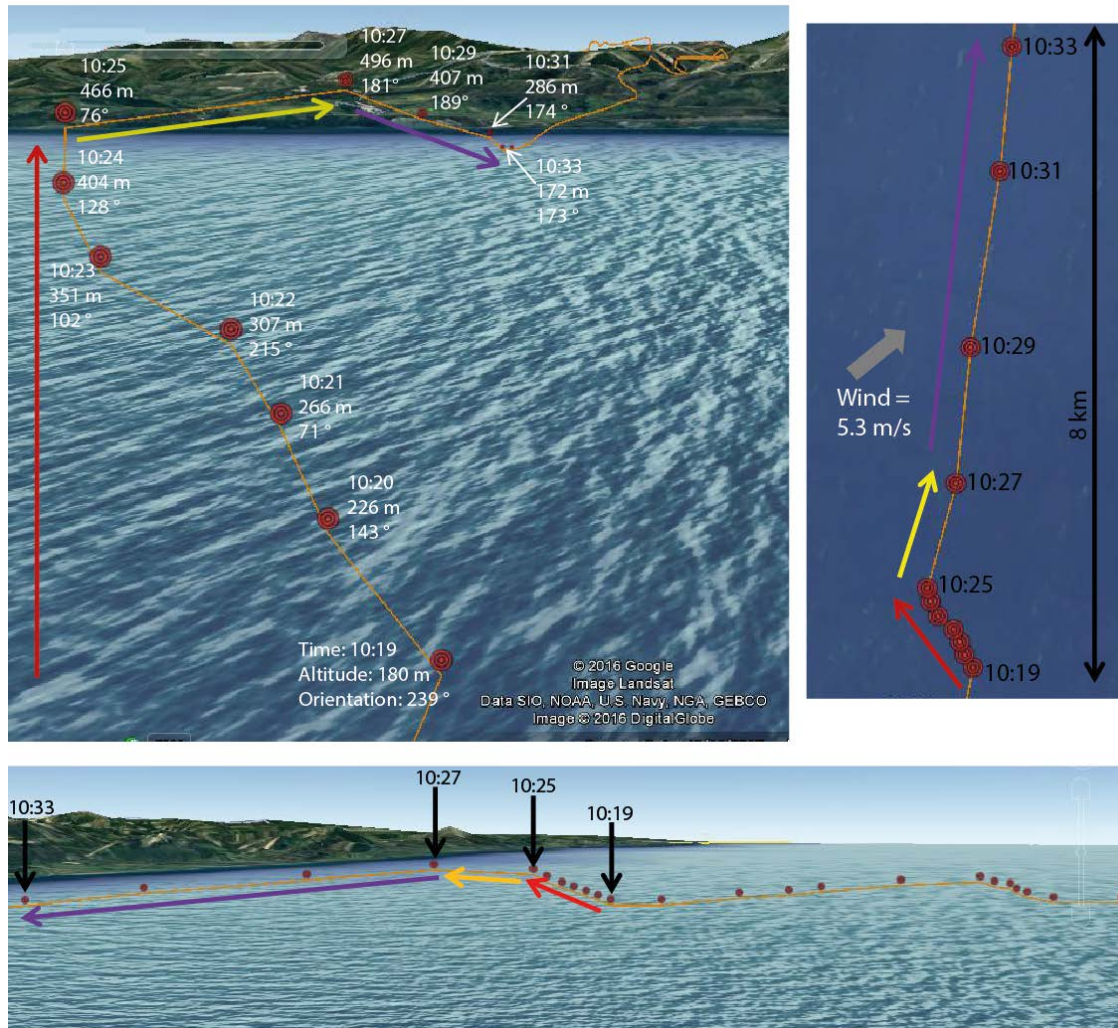


Figure 3.12.A. Climbing and gliding behaviour of bird 1 during a crossing of the Bay of Biscay. Red circles show the location of GPS observations, with accompanying time and instantaneous altitude and orientation data. All times GMT. Wind direction indicated by grey arrow. Circling segments indicated by red arrows, soaring segments by yellow arrows and gliding segments by purple arrows.

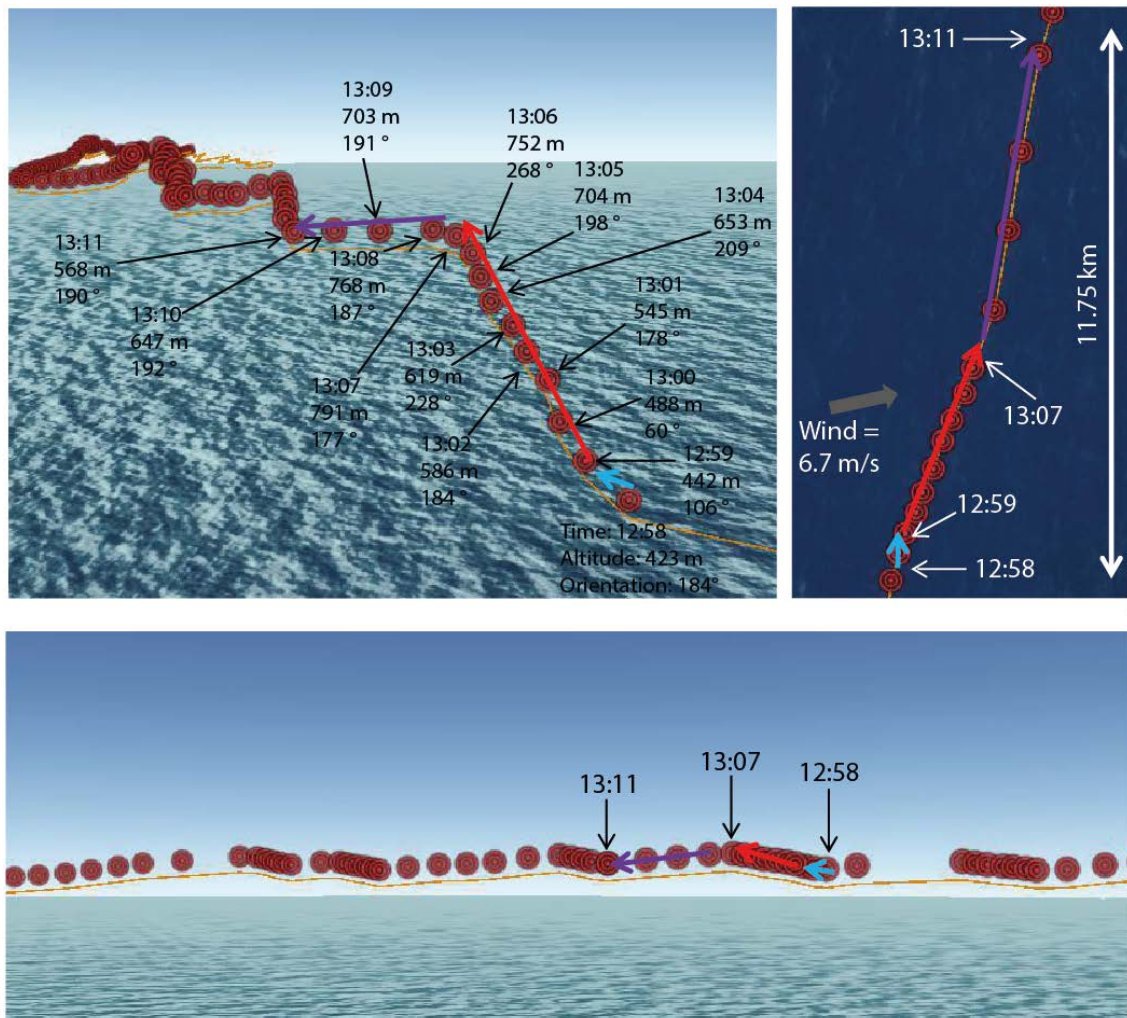


Figure 3.12.B. Climbing and gliding behaviour of bird 3 during crossing of the Bay of Biscay. Red circles show the location of GPS observations, with accompanying time and instantaneous altitude and orientation data. All times GMT. Wind direction indicated by grey arrow. Circling segments indicated by red arrows, soaring segments by yellow arrows, gliding segments by purple arrows and flapping segments by blue arrows.

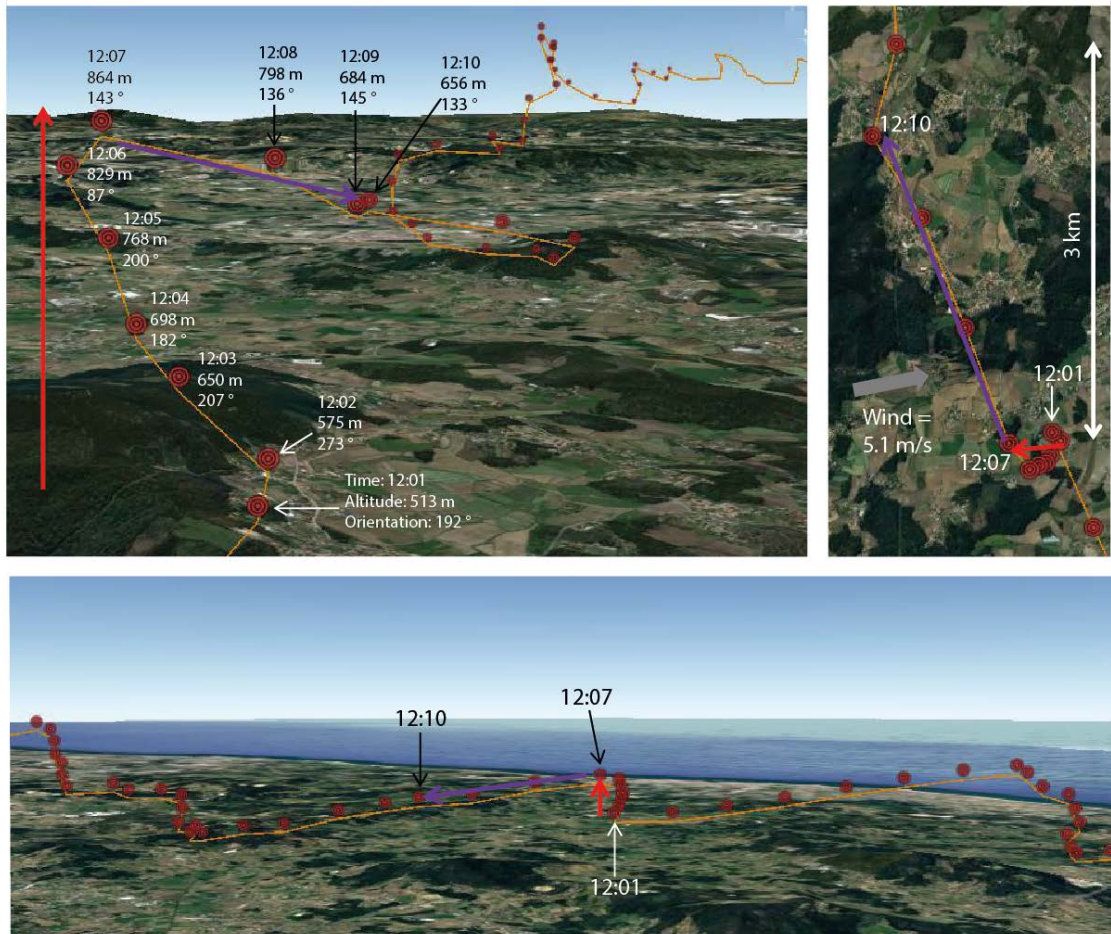


Figure 3.12.C. Climbing and gliding behaviour of bird 3 during flight over Portugal (European region). Red circles show the location of GPS observations, with accompanying time and instantaneous altitude and orientation data. All times GMT. Wind direction indicated by grey arrow. Circling segments indicated by red arrows, soaring segments by yellow arrows and gliding segments by purple arrows.

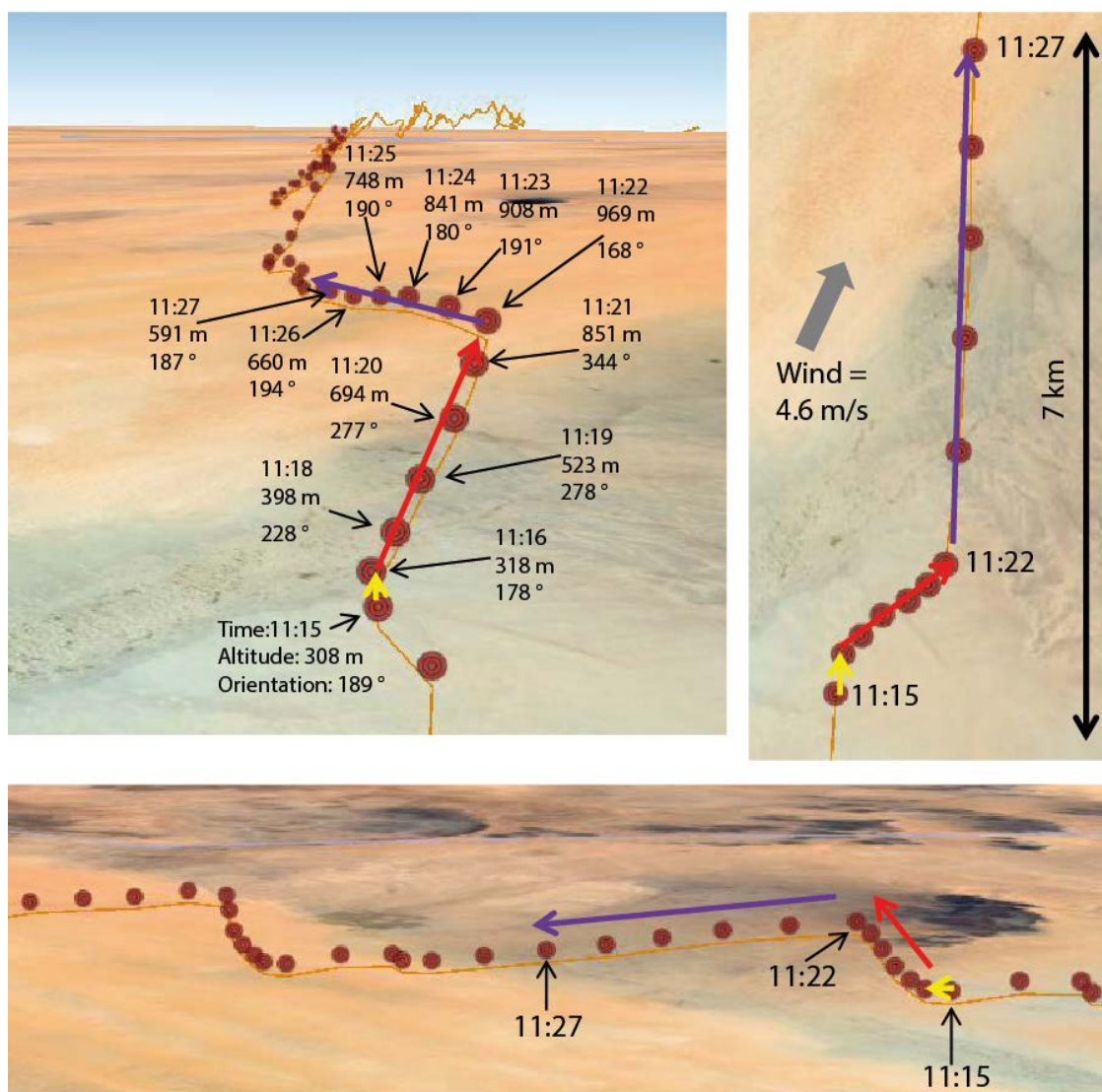


Figure 3.12.D. Climbing and gliding behaviour of bird 1 during flight over Sahara. Red circles show the location of GPS observations, with accompanying time and instantaneous altitude and orientation data. All times GMT. Wind direction indicated by grey arrow. Circling segments indicated by red arrows, soaring segments by yellow arrows and gliding segments by purple arrows.

3.4.4. Flight method and migratory performance

An analysis of univariate associations indicated that HD sector headway speed is associated with different factors over land and sea (Appendix 2, Figure A2.3, Table A2.1 and A2.2). Over land, HD sector headway speed was most strongly associated with gliding flight (adj. $\rho^2 = 0.432$, $F = 72.36$, $df = 95$, $p < 0.0001$) and was essentially uncorrelated with headwind (adj. $\rho^2 = 0.029$, $F = 2.88$, $df = 95$, $p = 0.0928$). Over the ocean, by contrast, HD sector headway speed was most strongly associated with altitude (adj. $\rho^2 = 0.539$, $F = 11.70$, $df = 10$, $p = 0.0065$) — with birds migrating faster at higher altitudes — and not with gliding flight ($\rho^2 = 0.000$, $F = 0.00$, $df = 10$, $p = 0.9656$) or headwind (adj. $\rho^2 = 0.063$, $F = 0.68$, $df = 10$, $p = 0.4299$).

There were significant correlations between the airspeeds of ospreys and wind conditions with birds increasing airspeed when faced with headwind and reducing it with tailwind support. This was true for both flapping ($R^2 = 0.467$, $p < 0.001$, Figure 3.13A) and gliding ($R^2 = 0.510$, $p < 0.001$, Figure 3.13B) airspeeds. The marked seasonal difference in wind conditions encountered by ospreys resulted in a clear trend for faster flapping and gliding airspeeds in spring (Figure 3.13A and 3.13B) when they encountered headwinds more frequently ($p < 0.001$) (Figure 3.14). Ospreys increased both flapping ($R^2 = 0.112$, $p = 0.023$, Figure 3.13E) and gliding ($R^2 = 0.211$, $p = 0.001$, Figure 3.13F) airspeeds in response to headwinds during spring, thereby enabling them to increase groundspeed. They also regulated flapping airspeed during autumn ($R^2 = 0.135$, $p = 0.003$, Figure 3.13C), but there was no significant correlation in gliding airspeeds ($R^2 = 0.045$, $p = 0.094$, Figure 3.13D). It is notable that the fastest airspeeds were recorded over the ocean and in Europe during spring, indicating increased urgency (Figure 3.13E and Figure 3.13F). Mean glide ratios were within the range of gliding performance of ospreys, other than over the ocean as already discussed (Alerstam 2000, Pennycuick 2008).

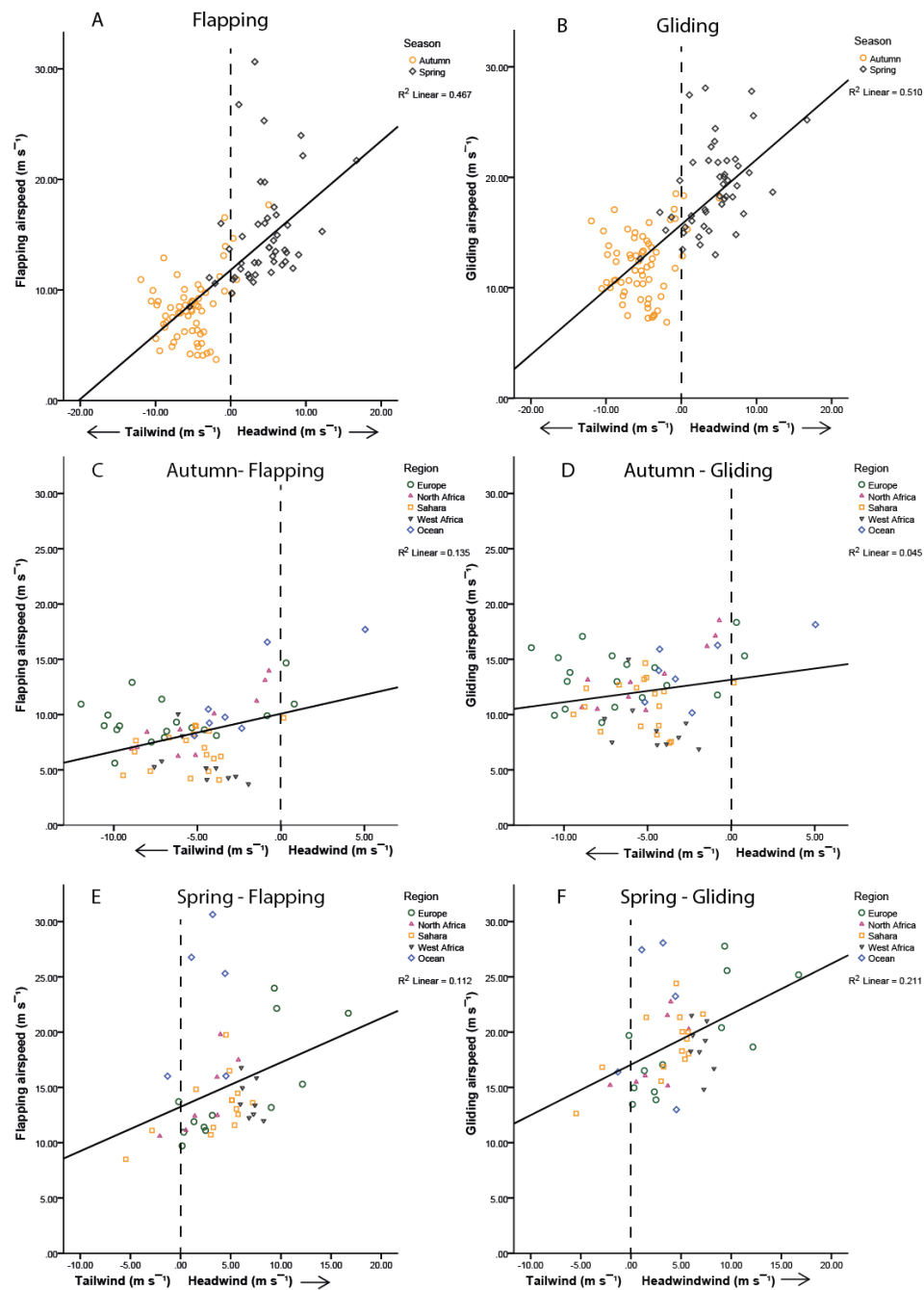


Figure 3.13. Mean flapping and gliding airspeeds achieved by ospreys. Each data point shows mean value for a single HD sector and are colour marked according to individual figure legends. The data show that ospreys regulate both flapping (A) and gliding (B) airspeeds according to wind conditions, increasing airspeeds when flying into a headwind, and reducing them with tailwind support. A marked seasonal difference in wind conditions encountered during migration resulted in ospreys increasing both flapping (E) and gliding (F) airspeeds in spring, but only flapping airspeed in autumn (C) when wind conditions were more favourable.

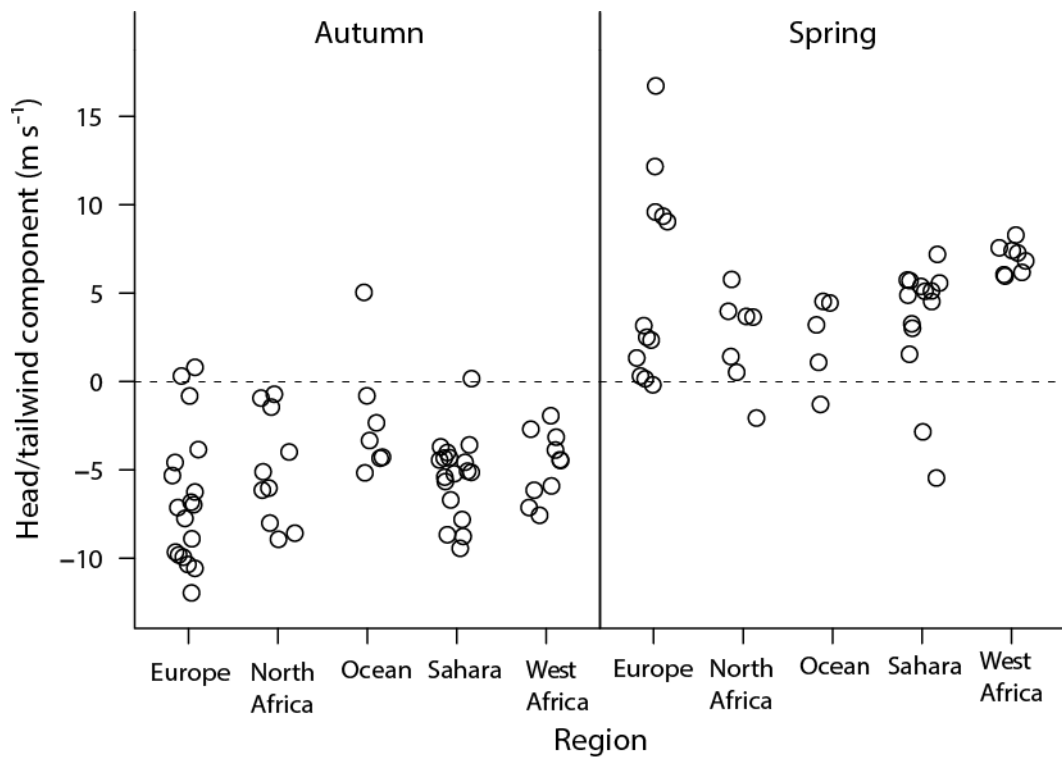


Figure 3.14. Head/tailwind component experienced by ospreys during autumn and spring migrations. *Each data point displays mean value for a single HD sector. Ospreys generally migrated with supportive winds in autumn, but headwinds in spring.*

3.5. Discussion

The high temporal resolution data generated by the GSM transmitters provide unprecedented insights into the flight of migrating birds. Our results demonstrate that ospreys preferentially migrate by soaring-gliding flight, regardless of region or season, and that they migrate faster when doing so. The most notable finding, however, was that ospreys were able to exploit sufficient lift to support soaring-gliding flight during three flights across the ocean; disproving our hypothesis that such flights are undertaken by flapping flight alone.

3.5.1. Flight mode classification

In this study we devised a method that can be applied to high temporal resolution GSM data in order to determine flight mode. The flight categories analysed here represent best estimates of flight method according to altitude and orientation changes. These data were validated as much as possible by cross-referencing specific flight performance data (e.g. glide ratios, flapping and gliding airspeeds) with theoretical values calculated by Alerstam (2000) and Pennycuik (2008). Other studies have recently used accelerometer data to classify flight method (Rotics et al. 2016) using a technique devised by Resheff et al. (2014). However this classification requires that transmitters collect Overall Dynamic Body Acceleration (ODBA) or related metrics (Resheff et al. 2014) which those deployed in this study did not. As such our method provides a means by which to classify flight method when accelerometer data are not available. Nevertheless this novel technique would benefit from further validation, specifically through comparison with classifications based on accelerometer data and by information from visual observations. This latter method would involve classifying periods of flight and then comparing the results with classifications of the same flight period based on visual observations made in the field, as is done with 'ground-truthed' accelerometer data (Rotics et al. 2016). The result presented here should therefore be viewed within this context. Nevertheless comparisons with theoretical predictions and other published studies indicate that the categories provide an accurate representation of osprey flight given these limitations.

3.5.2. Ocean crossings

This study provides the first evidence that ospreys are able to achieve soaring-gliding flight over the sea. Although the osprey's ability to make very ocean crossings is well documented (e.g. Meyer et al. 2000, Dennis 2002, Martel et al. 2014, Horton et al. 2015), we provide a potential new insight into how this uniquely adapted species is able to achieve very long energy-demanding flights over the sea. Soaring-gliding flight was achieved during a quarter of flights across the ocean, with climbing rates during two of these flights within the range reported for migrating ospreys tracked by radar over land in southern Sweden (Kjellén et al. 2001). This indicates that ospreys are able to exploit weak thermals that sometimes develop over the sea under specific environmental conditions. It is notable that the soaring-gliding flights were all made during autumn, when wind was more favourable than in spring. Furthermore, three of the four longest ocean crossings consisted of prolonged periods of soaring-gliding, which would reduce energy expenditure during such flights. During the sections of these flights with high resolution data (i.e. the HD sectors) the individuals concerned covered 52.1%, 52.6% and 35.7% of total distance by gliding respectively. Even if, as seems likely, they incorporated sporadic flapping to prolong gliding phases, this would provide considerable energetic savings given that the bulk of power required for gliding is extracted from external sources (i.e. thermal/orographic lift) whereas in flapping flight the bird produces the necessary lift and thrust using its flight muscles (Alerstam and Henderström 1998). Based on calculations made using Pennycuik (2008) an osprey might be expected to burn approximately 1500 kJ of fuel if it was flapping continuously during the longest HD sector over the ocean (total distance = 404 km) but given that this individual covered 52.6% of total distance flown during the HD sector by gliding, the total fuel burned may have been reduced by as much as half.

The ability of ospreys to achieve soaring-gliding flight over the ocean is highly unusual, particularly given that the flights occurred at relatively northerly latitudes. Frigatebirds *Fregata spp.* have very low wing loadings which enable them to exploit narrow or weak thermals and stay airborne for extremely long periods over the ocean (Pennycuik 1983, Brewer and Hertel 2007). However they are generally confined to the trade-wind zones (Weimerskirch et al. 2003), where soaring conditions are optimal

throughout the year and may even permit soaring by some raptors (Bildstein 2006). Sea thermals are less likely to develop at more northerly latitudes but Yamaguchi et al. (2012) suggested that Oriental honey-buzzards *Pernis ptilorhynchus* may be able to exploit thermals that develop over the East China Sea in autumn. Like the flights documented in our study, this region is situated to the north of the trade wind zone. Bearing this in mind it is notable that the soaring-gliding flights we recorded all occurred in autumn when sea temperatures are warmer than in spring. Under such circumstances Elkins (1995) suggests that weak thermals can develop in this region when cool air flows over the warmer water surface, and our evidence supports this.

It is likely that ospreys can also exploit elements of the wind, such as lee waves and wind shear (which can occur anywhere in the atmosphere) to aid their flight across the ocean. Such waves and vortices are difficult to predict, but can extend as far as 300–400 km downwind of the topographic features generating them, and migrating ospreys may be able to recognise them by the associated Cumulus clouds which form in the rising air (Elkins 1995). In our study this behaviour is most likely to be associated with the soaring classification as per orographic lift over land. It is notable that in the three ocean flights with significant periods of soaring-gliding, altitude gain was achieved through a combination of circling and soaring. In other words, the birds probably exploited both thermals and elements of the wind in order to sustain soaring-gliding flight. On days when thermals and lee waves were limited or not available a greater degree of flapping was necessary. In this case, fast flapping speeds probably reflect the necessity to complete ocean crossings as quickly as possible, with an increased migration speed more important than energy conservation. A similar trend was reported by Vansteelant et al. (2015) who found that honey-buzzards *Pernis apivorus* and Montagu's harriers *Circus pygarrus* travelled faster over the ocean than land. It is notable that the fastest ocean flapping speeds were recorded in spring, indicating that an urgency to return to breeding sites may have been important, with birds behaving like sprinting migrants (Alerstam 2006). These fast flapping flights were made at higher altitudes than other ocean crossings, indicating that birds were able to achieve faster ground speeds by flying higher, perhaps as a result of more favourable wind conditions (Mateos-Rodriguez and Liechti 2012).

Whilst it is possible for ospreys to gain altitude by flapping flight, there would appear to be no biological advantage to doing so during long ocean crossings. Furthermore the climbing behaviour observed during the three ocean crossings with significant circling/soaring segments is very similar to thermal flight over land, even though thermals are weaker, resulting in slower climbs (mean rate of climb over land = 1.82 m s^{-1} , mean rate of climb over ocean = 1.35 m s^{-1} (Table 3.4)). We therefore conclude that the osprey's wing loading enables it to exploit weak ocean thermals that sometime develop in autumn, thereby providing valuable energetic savings during long flights across the sea. Further study using transmitters with in-built accelerometers would help to further verify this finding.

3.5.3. Flight over land

Our data confirm our hypothesis that, over land, ospreys migrate by soaring-gliding flight whenever possible, with flapping flight never constituting more than 30 % of total flying time. The advantages of this are two-fold. First, migrating by soaring-gliding enables them to make valuable metabolic savings, which is particularly important during crossings of the Sahara where excellent thermal conditions usually prevail (Chevallier et al. 2010). This supports previous research which indicated that ospreys delay the start of migration in the desert until thermals develop (Mellone et al. 2012). Second, we found that when migrating over land, ospreys travelled faster when soaring-gliding than flapping. This conforms to the theoretical predictions of Alerstam (2000) who calculated that ospreys should achieve greater cross-country speeds in soaring-gliding flight than when flapping.

The fact that wind did not affect distance flown during HD sectors over land was more surprising. Vansteelant et al. (2015) found that weather accounted for 30–40% of variability in daily distance achieved by honey-buzzards and Montagu's harriers, with tailwinds having the most significant impact. Similarly, Mellone et al. (2012) showed that tailwind strength was the most important factor in determining daily distance flown by ospreys and three other species of raptors across the Sahara. Our results, however, are not directly comparable to these studies because we only analysed HD sectors which represented approximately 40% of total flying time and 42% of total

migratory distance flown. Furthermore to make more accurate inferences about flight performance we only included data where the bird was flying continuously.

The lack of a correlation between HD sector distance and head/tailwind was partly attributable to clear seasonal differences in airspeed. During spring, when winds were generally unfavourable, ospreys increased both gliding and flapping airspeeds. The corresponding increase in groundspeed enable ospreys to cover similar HD sector distances to autumn when winds were generally supportive. These findings conform to the rules of optimal adjustment of airspeed reviewed by Liechti et al. (1994) and further expanded on by Alterstam (2000) that airspeed during flapping flight is expected to be reduced when the resulting groundspeed exceeds the airspeed and to be increased when groundspeed falls short of the airspeed. Horton et al. (2014) described such airspeed regulation by juvenile ospreys during long flights across the western Atlantic Ocean. Although the rules of optimal adjustment of airspeed refer to flapping flight Spaar (1997) reported gliding speed adjustments in relation to head- and tail-winds, with six species of raptor reducing airspeeds with a tailwind component. Horvitz et al. (2014) suggest that soaring-gliding species achieve faster gliding airspeeds by flying closer to optimal glide speed (V_{opt}), which necessitates steeper glides and increased risk of grounding or swapping to flapping flight. Ospreys, however, are well-adapted to flying at V_{opt} because the switch to flapping flight is less energetically costly than for larger species with high wing loadings (Horvitz et al. 2014). Our data appear to agree with these findings given that in spring ospreys increased both flapping and gliding airspeeds in response to headwinds, and also that on occasions they covered significant distances by flapping flight. It is also notable that we recorded some high gliding airspeeds, suggesting that the ospreys may have undertaken sporadic flapping during the gliding phase in order to increase airspeed further when faced with headwinds, particularly during spring when wind was generally unfavourable. This supports the observations that ospreys are not pure soaring migrants, but also flap during descents from thermals (Mellone et al. 2012)..

Author contributions: Satellite transmitters were deployed under licence by RD as part of the Highland Foundation for Wildlife's Osprey Project. Tracking data were collated by RD and TM. TM devised the flight categorisation method with support from WN, collated environmental data and wrote the manuscript. Statistical analysis was undertaken by SO with TM and WN. WN, SO, RD, KB and DH read and commented on the manuscript.

4. Post-fledging and migration of juvenile ospreys *Pandion haliaetus*

4.1. Abstract

Many satellite tracking studies of first-year birds limit their analysis to the migratory flight, thereby discounting the important post-fledging period prior to departure. In this study satellite telemetry was used to determine the extent of individual variability in the post-fledging period and first migration of ten juvenile ospreys from Northern Scotland. Data were collected from fledging until the completion of the birds' first migration to West Africa.

An increase in exploratory flights – both in terms of distance flown and frequency of flights – usually occurred two to three weeks after fledging. In some cases this coincided with departure on migration, but most birds remained in the natal area for longer, making frequent exploratory flights and returning to the nest at regular intervals. In contrast some longer-staying birds remained more sedentary throughout the post-fledging period.

Migration routes were highly variable, with wind playing a key role. Juvenile ospreys were able to compensate for the effect of wind on some occasions, but wind drift resulted in some very long flights over the Atlantic Ocean. This appears to corroborate previous research suggesting that ospreys navigate by vector summation with limited or no compensation for geographical displacement. Juvenile ospreys generally exhibited the traits of energy-minimisers during migration, but it was also notable that birds with the longest post-fledging periods did not interrupt their southward migration with stop-overs, perhaps aided by increased fuel deposition and the development of more efficient flight skills prior to departure.

Keywords: Post-fledging, satellite-tracking, migration, wind drift, osprey

4.2. Introduction

The length of the post-fledging period and timing of subsequent first migration have important implications for survival and natural selection among birds (Newton 1972, Greenwood and Harvey 1982). Juveniles face a high probability of mortality in the first weeks after leaving the nest due to a lack of crucial life skills (Marchetti and Price 1989, Yoda et al. 2004). In migratory species the post-fledging period (from fledging until onset of migration) is of further importance because inexperienced juvenile birds undergo important behavioural (Kitowski 2005) and physiological changes that are essential for migration (Newton 2010), during which juvenile mortality is often very high (Strandberg et al. 2010, Sergio et al. 2014).

Juvenile raptors and owls remain dependent on parental care after fledging and usually stay within the vicinity of the nest for several weeks before dispersing or migrating (Newton 1979). During the post-fledging period they develop the flying and hunting skills necessary for future survival (Bustamante 1993, Bustamante 1994a). Most post-fledging studies have demonstrated a gradual dispersal away from the natal nest over a period of weeks (Delgado et al. 2009, Soutullo et al. 2006, Yamac and Bilgin 2012), although there may be considerable individual variation in dispersal distance (Stupik et al. 2015, Yamac and Bilgin 2012). In a study of burrowing owls *Athene cunicularia* Todd et al. (2007) found that such variation was influenced by habitat: owls that fledged in larger patches of suitable habitat generally moved a greater distance from the nest prior to migration than birds in smaller patches. Conversely Rahman et al. (2014) showed that in juvenile saker falcons *Falco cherrug* post-fledging range size was related to both fledging date and brood size.

In addition to the importance of the post-fledging period from a behavioural and physiological perspective, Brown (1993) proposed that post-fledging exploratory flights may also help determine the choice of future nest sites. This has been difficult to test empirically, but Bai et al. (2009) suggest that recognition of landscape patterns by juvenile ospreys *Pandion haliaetus* may have influenced a gradual shift from forest-dominated landscapes to agricultural-dominated landscapes in a German breeding population.

In many species the duration of the post-fledging period has been shown to be influenced by a reduction in parental investment which prompts juveniles to disperse (Balbontin and Ferrer 2005, Vergara and Fargallo 2008). In others, such as the black kite *Milvus migrans*, there is no such reduction in food provision and the urge to initiate dispersal or migration originates from the juveniles themselves (Bustamante and Hiraldo 1989, Bustamante 1994).

Juvenile birds have inferior navigational abilities (Guildford et al. 2011, Mueller et al. 2013), are more susceptible to adverse weather (Thorup et al. 2003) and are less efficient foragers than adults (Skorka and Wojcik 2008). As a result the first migration presents a highly demanding challenge (Alerstam 1990, Newton 2010, Rotics et al. 2016). Although juveniles of some species follow experienced conspecifics on migration (Rotics et al. 2016), many first-year birds rely on an inherited programme of direction and distance, often referred to as vector summation, in order to reach their wintering site (Mourtsen 2003). As a result Guildford et al. (2011) suggest that true navigation is only possible for birds with experience of previous migratory journeys. This is exemplified by the fact that the migration routes used by adult birds are often either more direct (Hake et al 2001, Sergio et al. 2014) or less hazardous than those used by juveniles (Horton et al. 2014, Oppel et al. 2015). Furthermore, juveniles of some species have been found to migrate at slower speeds (Mellone et al. 2013), migrate less efficiently (Rotics et al. 2016) and spend more time on stop-overs during migration (Hake et al. 2003, Mellone et al. 2013). In this case stop-overs provide a valuable opportunity for juveniles to replenish fuel reserves (Yosef et al. 2006) and, potentially, an additional chance to improve foraging skills (Mellone et al. 2013). Stop-over behaviour is thus diagnostic of the relative importance of energy minimisation during migration (Alerstam and Lindström 1990). For instance Miller et al. (2016) suggest that increased use of stop-overs by golden eagles *Aquila chrysaetos* during autumn migration is indicative of an energy-minimisation strategy, which may be particularly important for inexperienced first-year birds.

In recent decades technological advances have aided the study of avian migration (López-López 2016) and provided new insights into the post-fledging behaviour and migration of juveniles. Of particular note was the development of the first satellite

transmitters in the 1980s (Fuller et al. 1984). This allowed birds to be tracked during complete migratory journeys for the first time, thereby providing valuable new information on route, speed and duration of migration (Börger 2016). However, there are comparatively few studies that combine analyses of both the post-fledging period and first migration, even though they are intrinsically linked.

The osprey is a medium-sized raptor with a cosmopolitan distribution (Monti et al. 2015). It is a specialist piscivore that hunts in both freshwater and marine environments (Poole 1989). Northern populations are generally migratory with European ospreys wintering in sub-Saharan Africa (Dennis 2002, Hake et al. 2001) and North American birds wintering in South America (Martell et al. 2015). Ospreys show strong natal philopatry, with males in particular usually returning to breed in the area where they fledged (Poole 1989).

In the United Kingdom the osprey was formerly widespread with breeding pairs distributed throughout England, Scotland and Wales (Dennis 2008). However, intense persecution, most notably during the Victorian era, resulted in a drastic population decline, and by the 1920s the species had been almost completely exterminated as a breeding species (Dennis 2008). It was not until 1954 that breeding was documented again when two chicks were pair reared at Loch Garten in northern Scotland (Brown and Waterston 1962). Since then the population in Scotland has increased to more than 230 pairs, thanks to a concerted conservation effort in the form of protection of established nests and erection of new artificial ones (Schmidt-Rothmund et al. 2014).

Field observations have shown that juvenile ospreys usually fledge at seven to eight weeks of age and remain dependent on their parents for food until they set-out on migration (Poole 1989). Juveniles fledging from the same nest in northern Scotland over a period of twenty years remained in the natal area for a mean 30 days before migrating, but the length of the post-fledging period was not related to either fledging date or brood size (Bustamante 1995). Monti et al. (2012) found that juvenile ospreys released in central Italy as part of a reintroduction project remained within a 1 km radius of the release site for twenty days, before making longer exploratory flights, with a maximum distance of 14.3 km recorded.

Like many raptors ospreys migrate alone and are thought to follow the rules of vector summation (Alerstam et al. 2006). As a result juvenile ospreys often have a wider orientational scatter on their first migration than adult birds (Hake et al. 2001, Martell et al. 2001) and are more likely to be influenced by wind drift (Thorup et al. 2003). Juvenile ospreys migrating between New England and South America undertake very long energy-demanding flights directly across the western Atlantic, whereas adults migrate south along the eastern seaboard of the United States (Horton et al. 2014). The demanding nature of the first migration means that mortality is usually high among first-year ospreys from migratory populations (Wahl & Barbraud 2014, Eriksson and Wallin 1994).

4.2.1. Aims

In this study we used satellite transmitters to track the post-fledging and migratory movements of ospreys from Scotland in order to test the following hypotheses:

- i) That juvenile ospreys show a predictable pattern of dispersal away from the nest during the post-fledging phase, with birds venturing further from the nest and spending longer periods away prior to departure on migration
- ii) That migration routes and orientation are highly individual and , given that juvenile ospreys are expected to migrate by the laws of vector summation, shaped by the effects of wind in particular, with individuals unable to correct for displacement.
- iii) That ospreys with a longer post-fledging phase, and therefore more opportunity to deposit fuel prior to departure and to refine flying skills, will require fewer stop-over days during migration and, therefore, require less days to complete their migration.

4.3. Methodology

A total of ten juvenile Ospreys from nests in Highland and Moray in Northern Scotland were fitted with Platform Transmitter Terminals (PTTs) (Microwave Telemetry Inc., Columbia, MD, USA) under licence from the British Trust for Ornithology. The transmitters each weighed 35 g: equivalent to less than 3% of an Osprey's body weight

as recommended by Kenward (2001). They were fitted to the juvenile Ospreys using a Teflon harness approximately one week prior to fledging. The transmitters, with an in-built Global Positioning System (GPS) logged the bird's location (± 18 m), altitude (± 22 m), speed (km) and orientation (degrees) once every hour. Satellite data were accessed through the Argos system, based in France.

4.3.1. Post-fledging period

The satellite data were analysed using ArcMap 10.3.1 (Environmental Systems Research Institute, Redlands, CA) in order to determine daily movements of the birds after fledging. Fledging was deemed to have occurred once the satellite data (i.e. an accurate GPS observation) showed that the bird had made at least one flight in excess of 36 metres (twice the location error margin of the satellite transmitters) from the nest and that subsequent data showed a clear pattern of movement away from it.

The distance of each GPS point to the nest was determined in order to analyse how far juvenile ospreys dispersed during the post-fledging period, and how this changed over time. Data from fledging until the onset of migration for each bird were sub-divided into week-long periods in order to make comparisons between individual birds and weeks. Data were further sub-divided according to hourly GPS observations in order to analyse the timing of exploratory flights. These data were then analysed using Kruskal-Wallis tests in IBM SPSS Statistics for Windows 22.0 (IBM Corp., Armonk, NY). The Kernel-Density tool in ArcGIS was used to analyse weeks with more than 20 GPS observations to identify trends in the orientation and location of exploratory flights of the satellite-tagged birds. Key outlying locations were then identified using Google Earth and aerial imagery.

4.3.2. Migration

Ospreys were deemed to have initiated migration when satellite data indicated a clear movement of at least 25 km away from the nest. Migratory flights were then analysed at three temporal scales: hourly, daily and journey (Mellone et al. 2015). Flight data were first analysed to determine the start time and end time of each day's flight. If the exact start time was not logged by the transmitter, it was estimated to the nearest 15

minutes by calculating the time required to fly to the location of the first GPS observation after the bird had begun its daily flight, based on the bird's average speed during the morning. Time of arrival at the evening roost site was estimated by calculating time required to fly from the last flying GPS observation (i.e. speed > 0 km) to the first stationary GPS observation based on the bird's average speed during the afternoon. Daily distance was then determined by calculating the great circle distance between departure location and evening roost site. Days where an individual flew > 25 km in the intended direction of migration were classed as travelling days, while days where the bird remained in the same area and flew less than 25 km were classed as stop-over days. If a bird continued to fly for more than one day, this flight was deemed to be a single sector and analysed in the same way as a single day. Migration distance was calculated as the sum of all sector distances. Journey straightness was calculated as the ratio between migration distance and the great circle distance between the start point and end point of the migration. At the hourly scale, migration speed on travelling days was determined by calculating distance flown during one hour segments where travelling speed recorded by the transmitter was >0 km at the beginning and end of each hour and where the bird flew > 5km during the 1 hour period (Strandberg et al 2009 and Mellone et al. 2015).

Previous research has shown that juvenile ospreys wander widely on the wintering grounds (Hake et al. 2001, Martell et al. 2001), making it problematic to determine when migration has been completed compared to adult birds that are faithful to the same wintering site each year (Alerstam et al. 2006). Taking this into consideration a bird lingering at a site in sub-Saharan Africa was deemed to have completed its migration if it remained there for two or more days. Any subsequent movements were considered to be post-migratory flights.

4.3.3. Environmental data

To determine the impact of meteorological conditions on migration speed, wind data and boundary layer height (m) were downloaded from the European Center for Medium-Range Weather Forecasts (ECMWF) Global Reanalysis Project at a resolution of 0.125° and 3 h. Wind strength and direction may vary with altitude (Stull 1988) and

so u- and v-wind components (i.e. latitudinal and longitudinal wind velocities, m s^{-1}) were downloaded for the barometric pressure level (950 mB, equating to an altitude of 540 m) closest to the median flying altitude of the ospreys in this study (541 m). Wind data were linearly interpolated for hourly locations where the bird was travelling (i.e. excluding all resting hours) using ArcMap 10.3.1. Boundary layer is a proxy for the strength and spacing of thermals, with a higher boundary layer indicative of stronger and more densely spaced thermals (Stull 1988). Boundary layer was thus linearly interpolated for hourly locations in the same way as wind data. In order to determine the impact of weather variables at a daily scale, head/tailwind (wind speed multiplied by the cosine for the angle between the wind direction and the bird's heading) and crosswind (wind speed multiplied by the sine for the angle between the wind direction and the bird's heading) components were calculated for each hourly location relative to the bird's daily heading and then averaged across the day (Vansteelant et al. 2014). Hourly boundary layer data were averaged in the same way. Groundspeed was calculated for hourly segments where travelling speed recorded by the transmitter was > 0 km at the beginning and end of each hour and where the bird flew > 5 km during the 1 hour period (Strandberg et al 2009 and Mellone et al. 2015). The head/tailwind component was first calculated for each hourly location based on the bird's heading during that hour. This figure was added to the hourly groundspeed to give the hourly airspeed (Karlsson et al. 2011). Based on this calculation a groundspeed of 10 ms^{-1} with a headwind component of 3 ms^{-1} would give an airspeed of 13 ms^{-1} , while a groundspeed of 10 m s^{-1} with a tailwind component of -2 ms^{-1} would give an airspeed of 8 ms^{-1} .

In order to determine the impact of crosswinds on migration routes, the sector heading of flights in excess of 100 km made with a mean crosswind component exceeding 2 ms^{-1} (2 on Beaufort scale) was compared to the mean sector heading for all birds (Thorup et al. 2003), which was 190.792° . The mean sector heading was most appropriate for this calculation because ospreys are thought to migrate in an inherited direction by vector summation during their first autumn, and thus the mean sector heading for all birds gives the best estimation of this endogenous direction (Thorup et al. 2003). The crosswind component was calculated according to the mean heading for

all birds, rather than the bird's own sector heading to determine the effect of wind in relation to the intended direction of migration. Flight sectors were classified as wind drift if heading varied by more than 15° with the wind, over-compensation if heading varied by more than 15° against the wind, and compensation if heading varied by less than 15°. A 15° change in heading gives a 65 km shift in perpendicular movement (compared to a flight on the mean heading) at the point of median distance of flight sectors analysed (250.5 km) (cf Klaassen et al. 2011). Absolute deviation from the mean heading (190.792 °) was calculated for each flight sector.

Day length was expressed as minutes between sunrise and sunset as experienced by each individual during each daily flight (i.e. minutes between sunrise at the departure site and sunset at the roosting site). Sunrise and sunset were calculated for the relevant locations using a formula provided by National Oceanic and Atmospheric Administration (NOAA) <http://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html>.

All environmental variables were sub-divided into categories with headwinds exceeding 2.5 ms⁻¹ classified as 'opposing winds', head/tailwind between 2.5 ms⁻¹ and -2.5 ms⁻¹ as 'weak winds' and tailwinds exceeding -2.5 ms⁻¹ as 'following winds' (Mellone et al. 2012). Absolute crosswinds were classified as either 'weak' (0 ms⁻¹ – 2.5 ms⁻¹), 'moderate' (2.5 ms⁻¹ - 7.5 ms⁻¹) or 'strong' (> 7.5 ms⁻¹). Boundary layer was classified as 'low' (< 1250 m), 'medium' (1250 m – 2500 m) or 'high' (> 2500 m +). Finally day length was classified as 'short' (< 700 mins), 'medium' (700 mins – 750 mins) or 'long' (> 750 mins).

4.3.4. Statistical analysis

Migration speeds and distances were compared between birds using one-way ANOVAs followed by Games-Howell post-hoc tests with data log transformed when required. Linear Mixed Models (LMMs) were used to determine the impact of environmental variables on hourly groundspeeds and sector distance. In each case data were log transformed when required and bird ID was included as a random factor to account for variation between individual birds. Model-fit was assessed by examining the distribution of model residuals (Appendix 3). Estimated marginal means were calculated for each significant variable in LMMs. This technique provides a valuable

means method by which to assess the effect of each variable whilst controlling for the effects of other significant factors. LMM were also used to compare the daily/sector distance and journey straightness of juvenile birds to those of the autumn migrations of adult birds described in chapter 2. Finally Generalized Linear Mixed Models (GLMM) with Poisson error distribution and log-link function were used to compare the total duration of migration and as well as number of traveling and stop-over days of the juvenile birds with those of the autumn migrations of adult birds described in chapter 2.

One-way ANOVAs were used to test for differences in log transformed sector deviation (from the mean sector heading) in the crosswinds analysis. All statistics were performed using in IBM SPSS Statistics for Windows 22.0 (IBM Corp., Armonk, NY).

4.4. Results

4.4.1. Post-fledging

The duration of the post-fledging period varied from 18 to 55 days (Table 4.1). The data for all birds consisted of 5041 GPS observations.

Table 4.1. Summary of post-fledging period of ten satellite-tagged juvenile ospreys.

Year tagged	Bird	Sex	Brood size	Date of first flight	Date of migration	Post-fledging period	Number of GPS fixes
2008	10	M	2*	3/8	26/8	23 days	314
2008	9	M	2*	8/8	26/8	18 days	247
2009	6	M	3	17/8	6/9	20 days	284
2010	4	M	2	19/7	12/9	55 days	769
2011	1	M	3	20/7	22/8	32 days	542
2011	2	M	3	14/7	16/8	34 days	455
2012	7	F	2	12/7	25/8	44 days	623
2012	5	F	3**	14/7	30/8	47 days	614
2012	3	F	3**	14/7	8/9	56 days	688
2012	8	M	1	21/7	12/9	53 days	790

Asterisks indicate individuals from the same nest.

Each bird made only short flights to and from the nest during the first week after fledging. All birds began to make longer flights during the second week, but generally remained within 500 metres of the nest with a maximum distance of 931 metres recorded. The earliest departing birds set out on migration during week three, and the remaining birds began to explore more widely. The general trend for a gradual

increase in distance from the nest during the post-fledging period is shown in Figure

4.1. Variation between birds

Overall 93 % of GPS observations were located within 1 km of the nest, but there was considerable variation in exploratory behaviour, exemplified by the fact that mean distance from the nest varied significantly between birds ($p < 0.001$). Bird 8 was logged 1 km or more from the nest on 101 occasions, while bird 4 made the longest exploratory flight of 17.7 km prior to migration. In contrast bird 7 made the shortest flights, with a maximum distance of 659 m despite a relatively long post-fledging period of 44 days (Table 4.2).

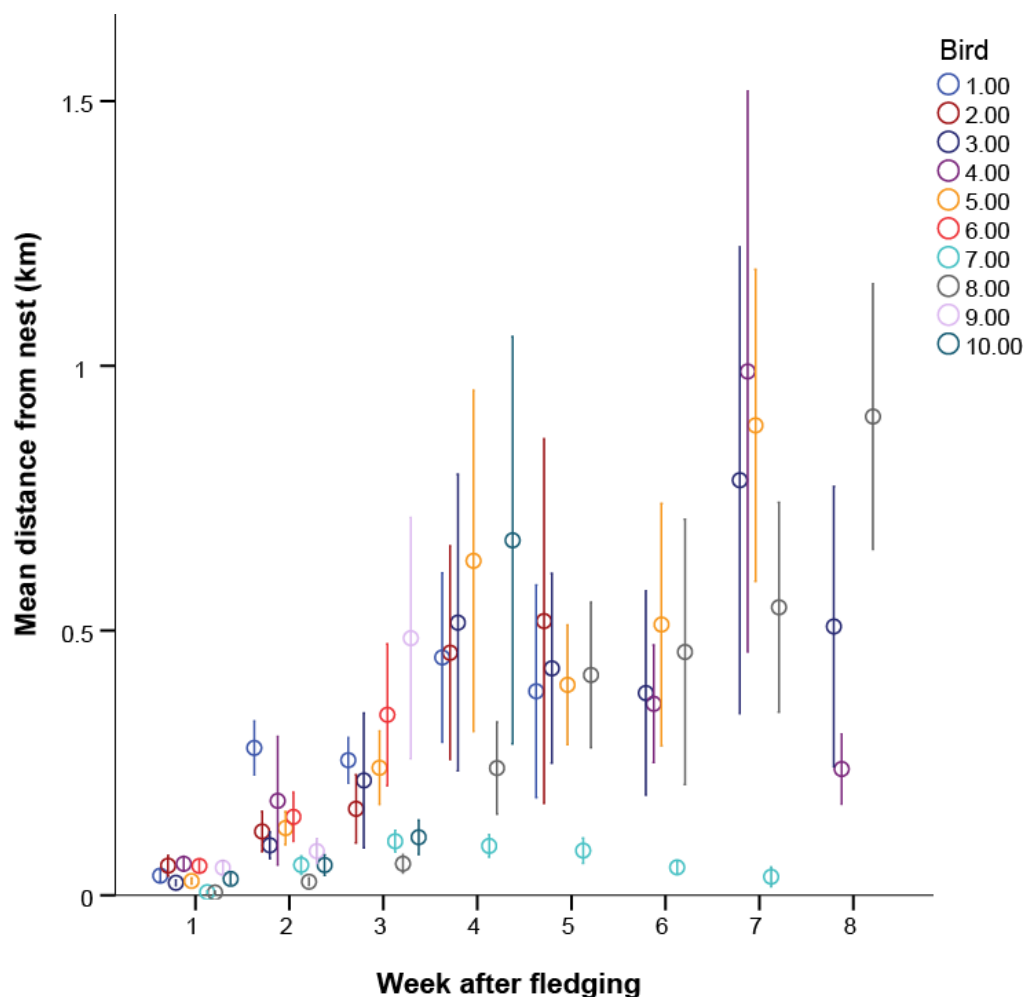


Figure 4.1. Relationship between mean distance from the nest and week after fledging. *There are fewer data points over time as birds departed on migration.*

Table 4.2. Total number of flights in excess of 1 km from the nest made by each of the satellite-tagged birds. A ‘journey’ refers to periods where successive GPS observations were > 1 km from the nest to account for the fact that some birds spent periods of several hours away from the nest.

Bird	Duration of post-fledging period	Number of GPS fixes > 1 km from nest	Total number of ‘journeys’	Maximum distance from nest (km)	Total number of nights roosting > 1 km from the nest
8	53	101	36	9.1	1
4	55	75	32	17.7	0
5	47	61	18	8.6	1
3	56	55	26	13.9	0
2	34	25	15	6.0	0
6	20	9	4	4.3	3
1	40	8	7	7.9	0
9	18	8	4	2.9	1
10	23	7	2	3.6	1
7	44	0	0	0.7	0

4.4.1.1. Kernel density analysis

Kernel density analysis demonstrated that the nest remained the focal point of each bird's activity until migration indicating that juveniles remained dependent on parental food provision until the onset of migration. Kernel density hotspots (indicative of frequently used perching sites) more than 1 km from the nest were first detected one to two weeks prior to migration. These sites were identified as overnight roosts used by five birds immediately prior to migration. Additional hotspots detected for birds 5 and 8 (Figure 4.2) were identified as favoured daytime perching locations. Thus in the two weeks prior to migration these individuals were not exploring further from the nest, but spending longer perched at favoured sites away from it.

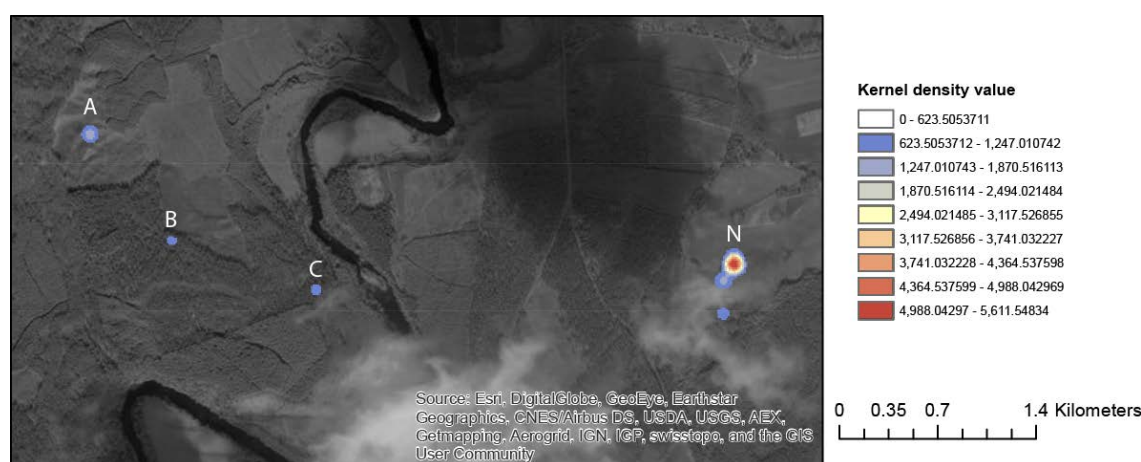


Figure 4.2. Kernel density analysis of GPS observations for bird 8 during week 8 after fledging. The kernel density hotspots show that the nest was the most frequently visited location (N) but that outlying points A, B and C were frequent perching localities. A higher kernel density value (highest = red) indicates a more frequently visited location.

4.4.1.2. Time of day

Kruskall-Wallis tests showed that distance from the nest varied significantly according to time of day among eight individuals (all $p < 0.05$) but that there was no such hourly variation for bird 9 ($p = 0.398$) or bird 10 ($p = 0.704$). There was a general trend for exploratory flights to be undertaken during the middle part of the day (Figure 4.3A and

Figure 4.3B) and this was most evident among the four birds that explored most widely (Figure 4.3C) but less so among the remaining birds (Figure 4.3D).

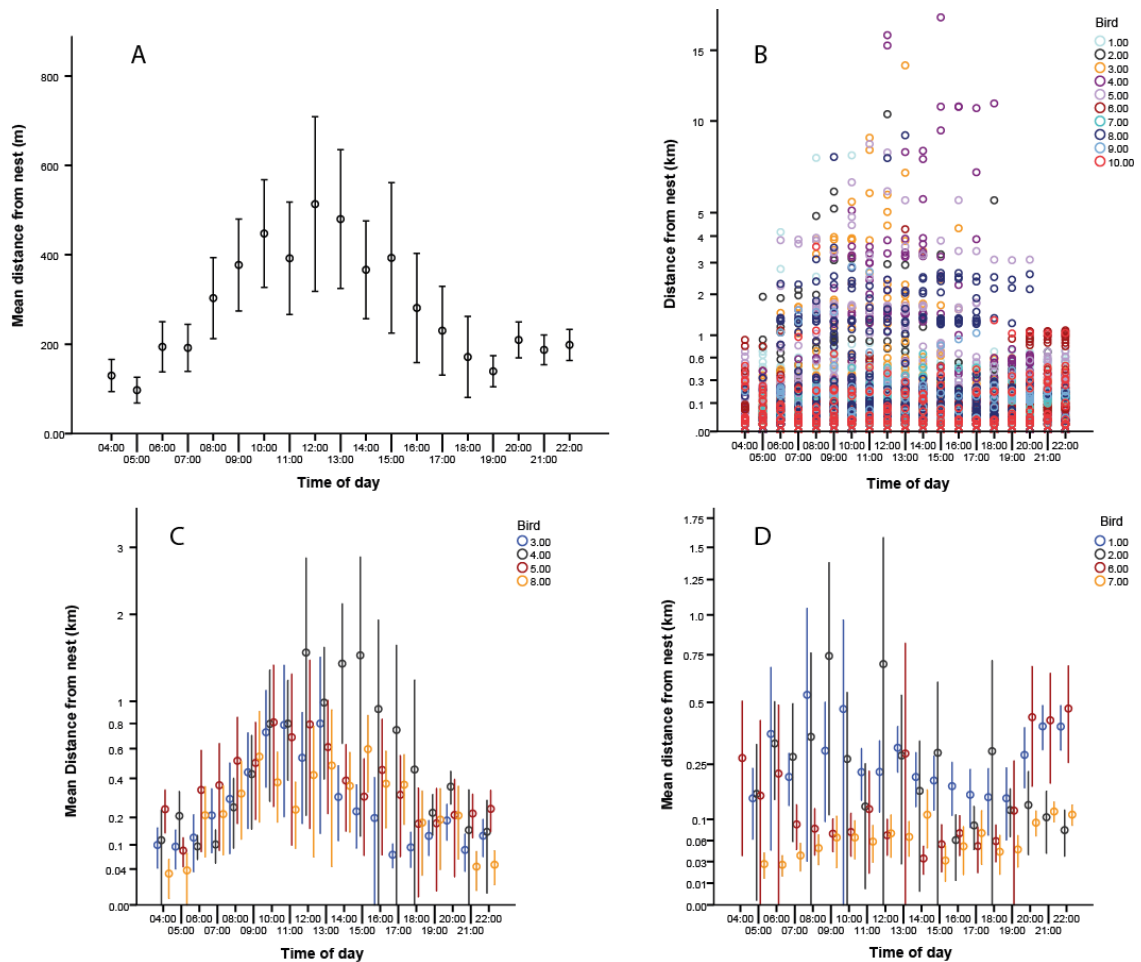


Figure 4.3. Relationship between time of day and distance from the nest. 4.3A shows the mean distance from the nest with 95% confidence intervals for all birds combined and 4.3B a scatter plot of all GPS observations for each bird. 4.3C and 4.3D show the mean distance from nest of birds 1-8 according to the time of day. 4.3C shows the trend for birds that explored most widely (according to mean distance from the nest) and 4.3D shows birds that remained more sedentary. Note the scales for 4.3C and 4.3D are different to account for differing variance of data.

4.4.2. Migration

The juvenile ospreys all set-off on migration between 16th August and 12th September. It is notable that all initiated migration on days when wind was from the west (mean direction = 288°, SD = 9°; mean speed = 10.6 ms⁻¹, SD = 1.2 ms⁻¹). Seven birds made successful migrations to sub-Saharan West Africa. Bird 8 made a very fast migration across the Atlantic Ocean to Cape Verde, after which transmissions ceased. For the purposes of the migration analysis this journey was considered complete because the bird had reached a potential over-wintering location according to the criteria detailed in the methods section prior to the loss of transmissions. Transmissions from bird 9's transmitter stopped while it was migrating south through Ireland and no further data were received. Bird 10 was found dead and extremely underweight in Scotland 12 days after leaving its nest site after a short post-fledging period. The migration routes are shown in Figure 4.4.

4.4.2.1. Overall duration of migration

There was considerable variation in the duration of completed migrations, with flights ranging from eight to 90 days. The migratory flights are summarised in Table 4.3. The fastest journey was made by bird 8 which completed a highly unusual migration to Cape Verde. This flight involved extremely long sea crossings between the UK and Spain, Spain and Canary Islands and the Canary Islands and Cape Verde. Two other individuals – bird 3 and bird 4 - also completed migrations without stop-overs. These three birds were the individuals with the longest post-fledging period but fastest migration (in terms of number of days). The remaining five birds all incorporated stop-overs, resulting in slower migrations. Bird 2 spent the greatest proportion of migration on stop-overs (71 %) and took longer to complete its migration than all other birds as a result.

Journey straightness also varied between individuals, ranging from 0.761 to 0.972. It is notable that the two most direct flights involved long sea crossings. The least direct migration was made by bird 2. This was exacerbated by an apparent false-start to migration that involved the bird flying a loop of Scotland prior to the main migratory movement. This flight was included in the migration analysis because the bird did not

return to its nest site after leaving on 16th August, despite remaining in Scotland for an extended stop-over period of 50 days after this initial movement.

Table 4.3. Summary of migratory flights of all satellite-tagged juvenile ospreys.

Bird	Post-fledging days	Start date	End date	Destination	Distance flown (km)	Journey straight-ness	Travel days	Stop-over days	Total days
1	40	22 Aug	28 Sep	Senegal	5391	0.928	20	17	37
2	34	16 Aug	13 Nov	Mauritania	5672	0.761	26	64	90
3	56	8 Sep	29 Sep	Senegal	5147	0.918	22	0	22
4	55	12 Sep	1 Oct	Mali	5415	0.877	22	0	22
5	47	30 Aug	29 Oct	Senegal	5516	0.919	16	35	51
6	20	7 Sep	28 Oct	Senegal	4791	0.972	13	34	47
7	44	26 Aug	12 Nov	Senegal	5046	0.912	24	55	79
8	53	12 Sep	18 Sep	Cape Verde	5142	0.949	8	0	8
9	18	26 Aug	N/A	Died, Scotland	531		8	0	8
10	23	26 Aug	N/A	Transmitter failure, Ireland	633		10	3	13

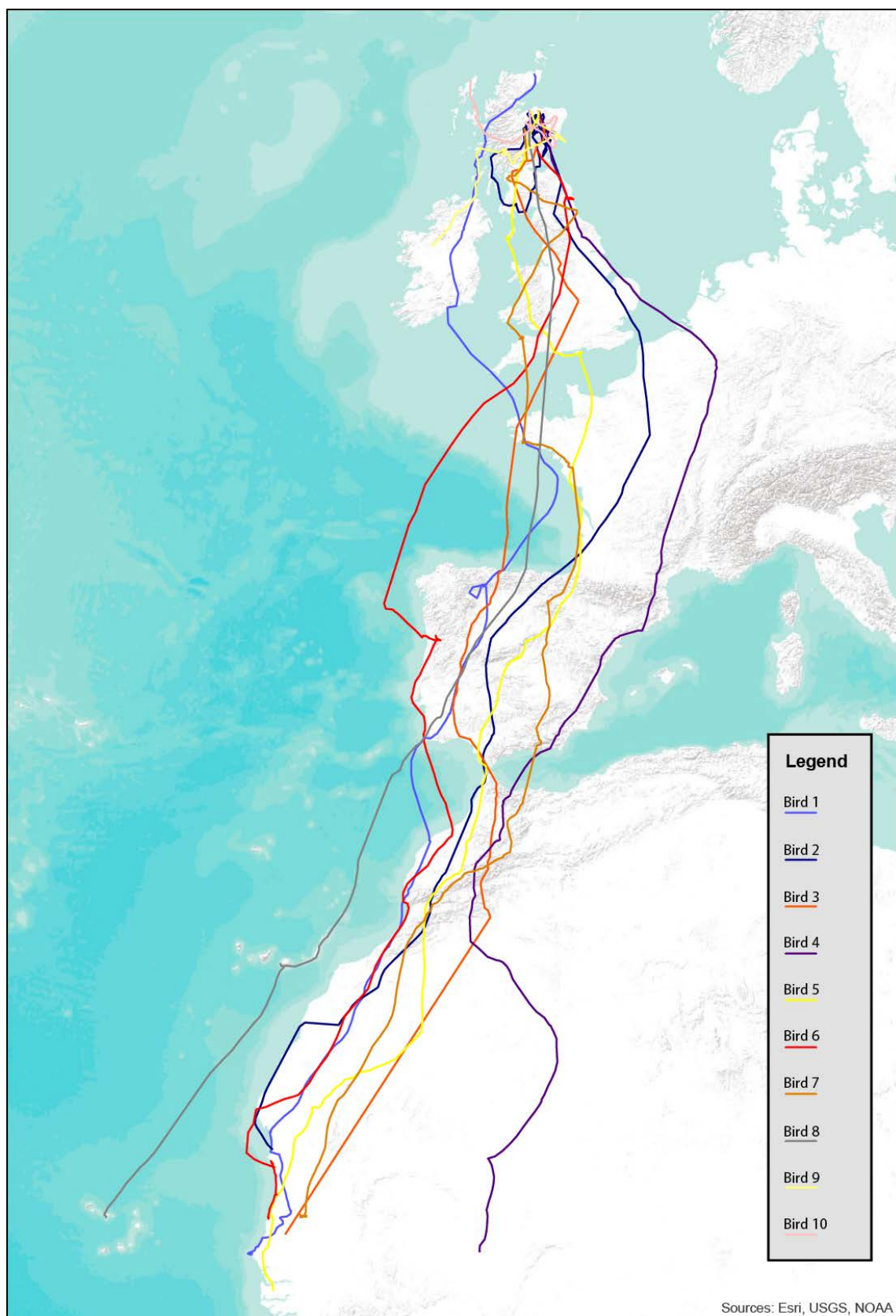


Figure 4.4. Map of all migrations undertaken by juvenile ospreys.

4.4.2.2. Sector distance

Mean daily/sector distance was 290 km (SD = 250 km). Bird 8 flew significantly further per sector than all others, except bird 6 (all $p < 0.05$). There was no other significant variation between individuals (Figure 4.5). Sector distance was strongly correlated with total flying time ($R^2 = 0.835$, $P < 0.001$) (Figure 4.6). Mean flying time was 594 mins (SD = 331 mins) per sector.

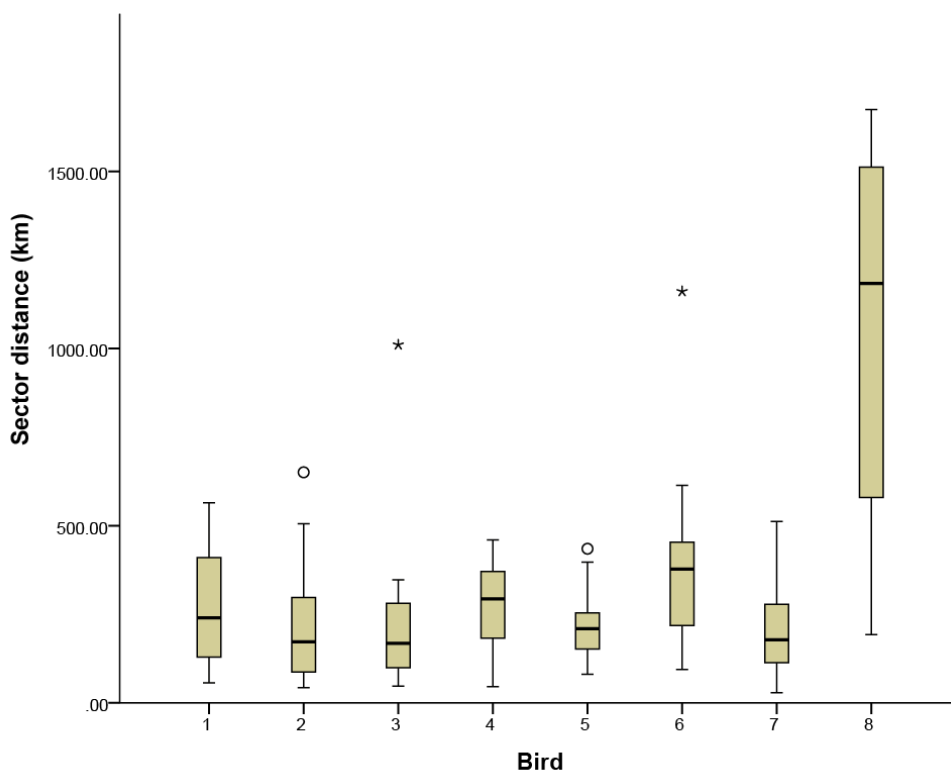


Figure 4.5. Boxplot showing differences between birds in terms of sector distance flown. *Bird 8's very long daily sectors were the result of an unusual migration to Cape Verde that necessitated long ocean crossings.*

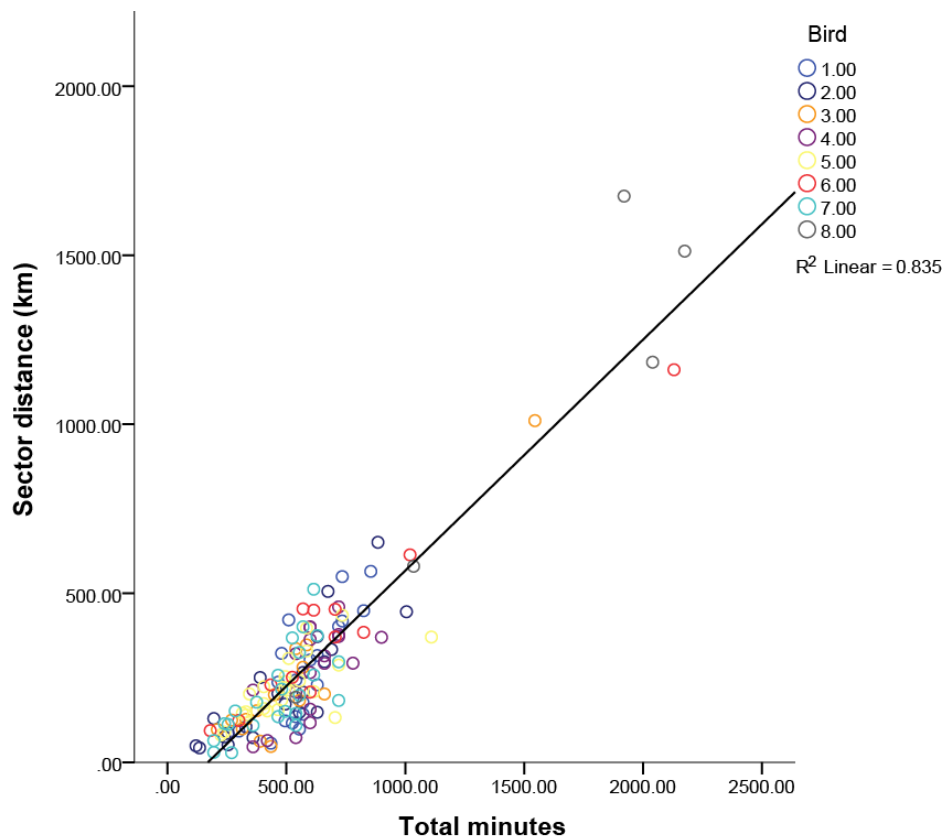


Figure 4.6. Scatterplot showing correlation between total minutes and sector distance. *The longest flight sectors involved long ocean crossings.*

4.4.2.3. Hourly groundspeeds

Groundspeed (mean 9.86 ms^{-1} , SD = 3.57 ms^{-1}) on travelling days varied significantly between birds ($p < 0.001$). Bird 8 achieved faster groundspeeds than all birds except bird 6 (all $p < 0.001$); while bird 6 was faster than birds 1, 3, 5 and 7 (all $p < 0.05$). There were no other additional differences between individuals. These data are shown in Figure 4.7.

4.4.2.4. Effect of environmental factors

Overall ospreys experienced weak tailwinds (mean -2.96 ms^{-1} , SD = 4.0 ms^{-1}) and weak absolute crosswinds (mean = 3.84 ms^{-1} , SD = 3.16 ms^{-1}) during travelling days on the eight completed migrations. Opposing winds (i.e. headwind component $> 2.5 \text{ m s}^{-1}$) were experienced during 8 % of 139 migration sectors analysed compared to 38 %

weak winds and 54 % following winds (tailwind component $< 2.5 \text{ m s}^{-1}$). Mean boundary layer height was 1830 m (SD = 1075 m).

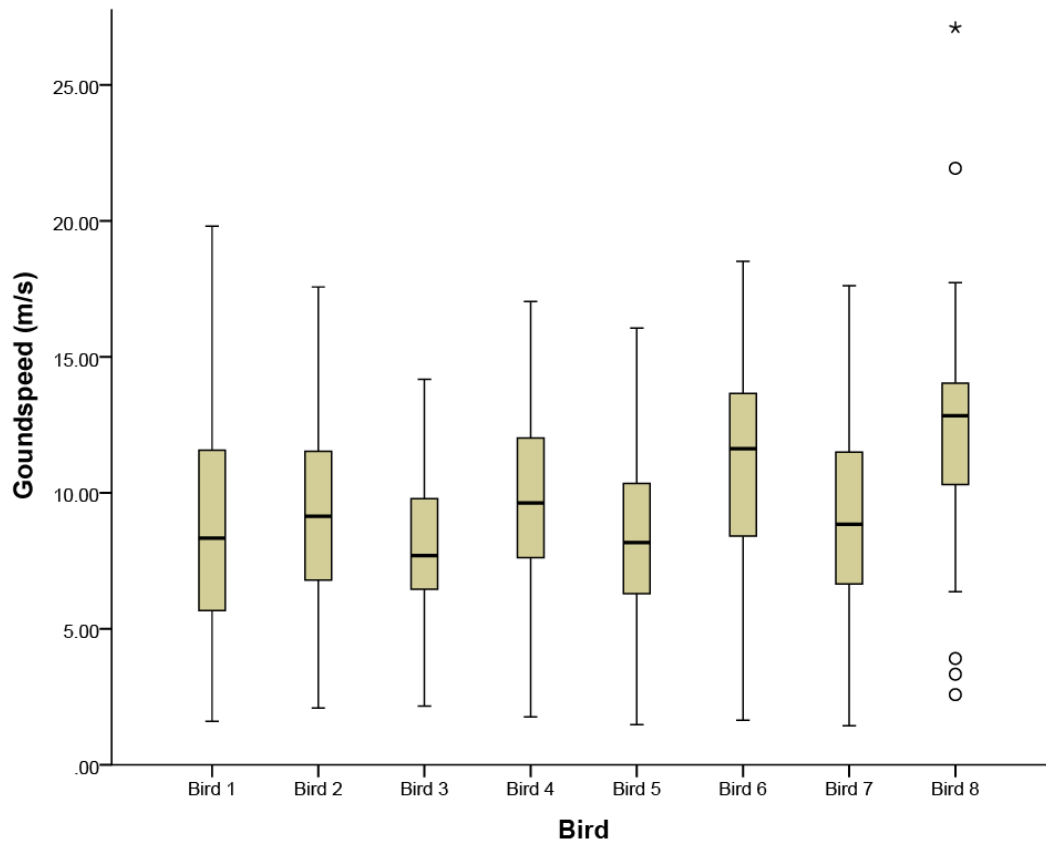


Figure 4.7. Boxplot showing mean hourly groundspeeds of ospreys that completed migration. Outliers are indicated by a circle and extreme outliers by a star.

A LMM with bird ID as a random factor indicated that head/tailwind and boundary layer had a significant effect on hourly groundspeeds but that crosswind did not (Table 4.4). Estimated marginal means showed that hourly groundspeeds were faster with following winds than in either weak wind ($p < 0.001$) or opposing winds ($p = 0.002$) and also faster when boundary layer was high ($> 2500 \text{ m}$) as opposed to low ($< 1250 \text{ m}$) ($p = 0.020$) or medium ($1250 \text{ m} - 2500 \text{ m}$) ($p < 0.001$).

A second LMM with log transformed sector distance as the dependent variable, bird ID as a random factor and day length, head/tailwind, crosswind and boundary layer as explanatory variables, indicated that only boundary layer height had a significant effect on sector distance ($F = 5.934$, $p = 0.003$), with ospreys flying furthest when boundary layer was high. It is notable, however that on occasions ospreys achieved very long sector distances when boundary layer was low. As a result the increase in log sector distance estimated marginal means was significant between medium and high boundary layer ($p = 0.01$) but marginally not significant between low and high ($p = 0.068$).

Table 4.4. LMM showing effects of meteorological variables on hourly groundspeed.

Explanatory variables	Denominator df	F	Sig.
Intercept	9.629	488.792	< 0.001
Head/tailwind	826.886	19.582	<0.001
Crosswind	823.485	2.262	0.105
Boundary Layer	829.516	7.855	<0.001

4.4.2.5. Effect of crosswinds on migration routes

Although crosswinds did not have a significant impact on either hourly speeds or sector distance, they did have a profound influence on the routes used by the juvenile ospreys. In order to determine whether individual flight sectors were the result of wind drift, compensation or over-compensation for crosswinds, the heading of sectors where crosswind component (relative to the mean heading for all birds) exceeded 2 ms^{-1} were compared to the mean heading for all birds. These sector headings were classified as being the result of wind drift if sector heading varied by more than 15° with the wind, over-compensation if heading varied by more than 15° against the

wind, and compensation if heading varied by less than 15°. In this case there was no significant difference between individuals in deviation from the mean heading ($p > 0.05$) and so all birds were analysed together. Of 60 flight sectors over 100 km (median distance 250.5 km) that qualified for the analysis the subsequent flight sector headings were the result of wind drift on 24 occasions, compensation on 29 occasions and over-compensation on 7 occasions (Figure 4.9). The clearest indication of the effect of wind drift on sector length and heading were very long sea crossings made by bird 8 between Spain and the Canary Islands and the Canary Islands and Cape Verde due to strong north-easterly winds. Wind drift also resulted in bird 6 missing the northern coast of Spain, necessitating a compensatory change of heading in order to reach the Portuguese coast (Figure 4.9). It is also notable that there was a tendency for wind drift to occur at the beginning of migration.

4.4.2.6. *Sea crossings and nocturnal flight*

Nocturnal flight was undertaken by seven birds on a total of 12 occasions. Five involved continuous overnight flight, each during long crossings of the Atlantic Ocean. Four of the remaining seven flights were extended after sunset in order to complete sea crossings and the remaining three instances of night-time flight were recorded in France (233 mins after sunset), Spain (125 minutes after sunset) and Mali (125 minutes after sunset during a crossing of the Sahara). Thus nocturnal flight was predominantly associated with sea crossings and, as such, necessitated by an inability to land, rather than a technique to intentionally increase daily flying times.

The longest sea crossings involved birds flying direct between the UK and the Iberian Peninsula over the Bay of Biscay, and also across the Atlantic between Europe and Africa. Such flights were undertaken by bird 1, bird 3, bird 6 and bird 8. Table 4.5 summarises these flights. All flights were supported by tailwinds, other than during bird 6's compensatory flight to the Portuguese coast. The three longest flights were all the result of wind drift (even though bird 6's flight is categorised as compensation due to its subsequent change of heading).

The mean groundspeed during ocean crossings (12.64 m s^{-1} , $SD = 2.71$) was faster than the corresponding figure over land (8.93 , $SD = 3.50$), even though mean boundary

layer (580 m, SD = 296 m) was significantly lower (Mann-Whitney U test: $p < 0.001$) than the corresponding figure over land (mean = 2128 m, SD = 1214 m). It was also notable that ospreys regulated airspeed according to wind conditions over the ocean, reducing airspeeds with an increasing tailwind component (Figure 4.8).

Table 4.5. Sea crossings (> 375 km) undertaken by juvenile ospreys.

Bird	Date	Location	Distance flown (km)	Total time (mins)	Mean groundspeed (ms^{-1})
1	28/8/11	Bay of Biscay	431	735	9.8
1	19/9/11	Atlantic	444	480	15.4
3	13/9/12	Bay of Biscay	485	930	8.7
6	10/9/09	Bay of Biscay	1302	1995	10.9
6	18/10/09	Atlantic	397	510	13.0
8	13/9/13	Bay of Biscay	456	540	14.1
8	15/9/13	Atlantic	1013	1515	11.1
8	18/9/13	Atlantic	1524	1905	13.3

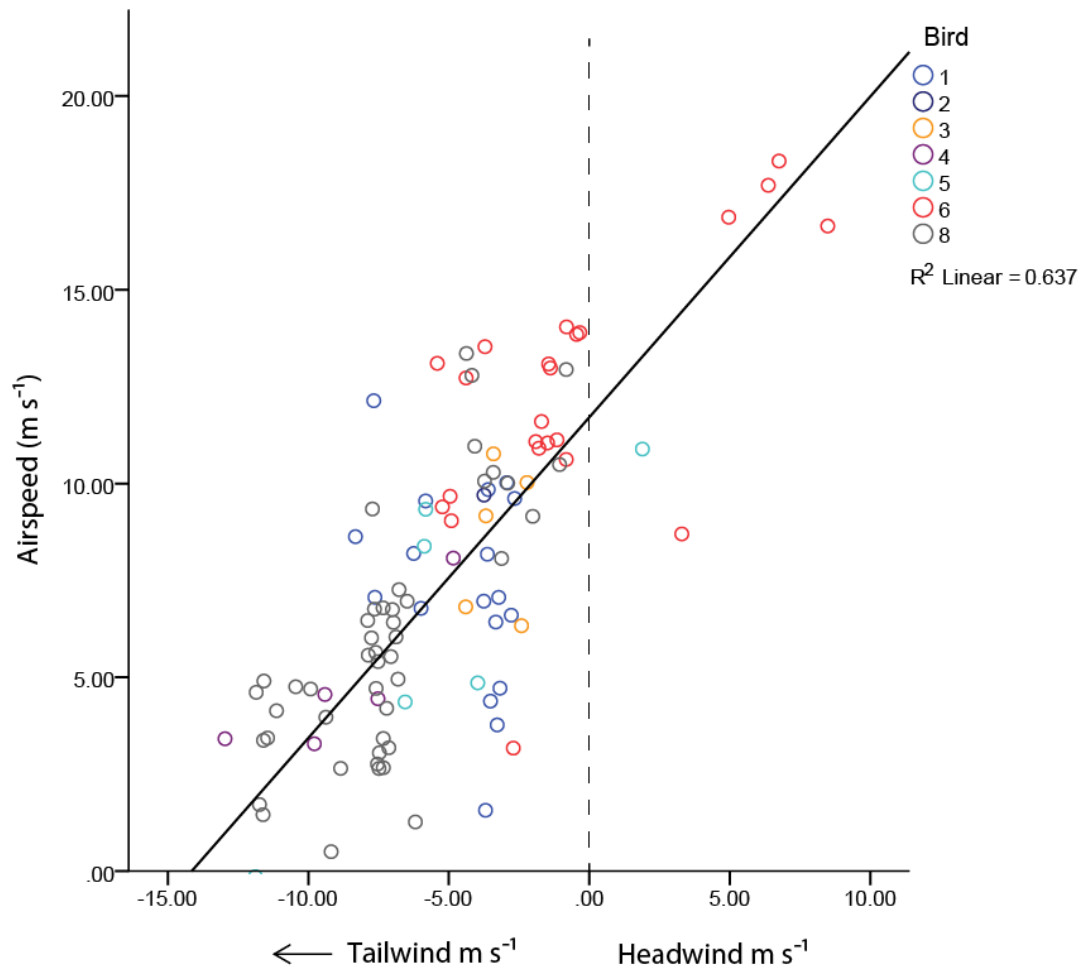


Figure 4.8. Scatterplot showing the relationship between hourly airspeeds and head/tailwind component experienced by ospreys during sea crossings.

The fastest airspeeds were achieved by bird 6 after it made a compensatory change of heading over the Bay of Biscay/Atlantic, forcing it to fly into a headwind.

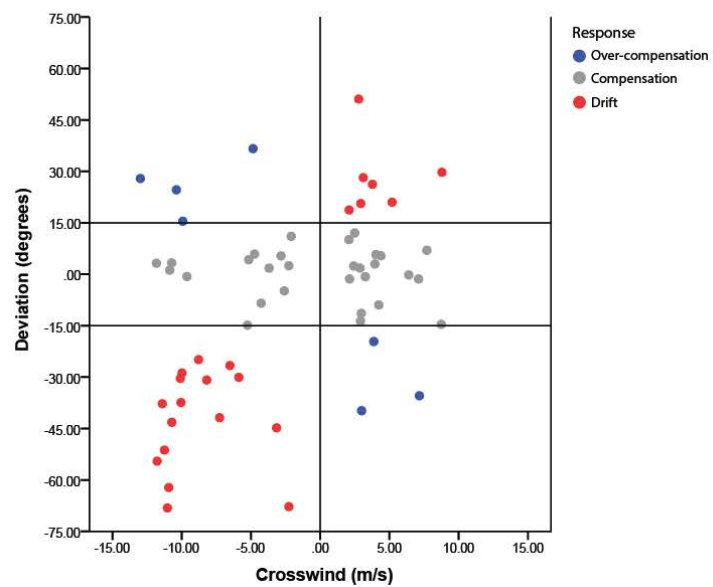
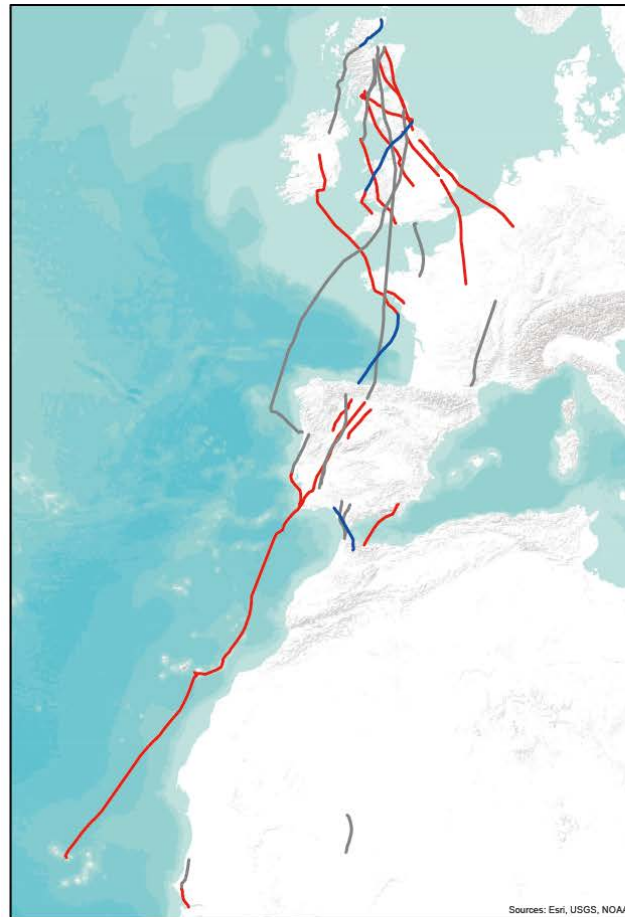


Figure 4.9. The response of ospreys to crosswinds experienced during different migration sectors where crosswinds exceeded 2 ms⁻¹. Instances of wind drift are indicated by red lines, compensation by grey lines and over-compensation by blue lines.

4.4.2.7. Comparison with adult birds

The migrations of the juvenile ospreys in this study were broadly similar to the autumn migrations of adult birds analysed in chapter 2, but with some key differences. The juveniles migrated to the same region of West Africa as the adult birds, although wintering sites among both age classes were widely dispersed.

At the journey scale GLMMs with bird ID as a random factor showed that adult birds completed their migrations in fewer days than juveniles ($F = 107.869$, $p < 0.001$). This was predominantly due to the fact that they incorporated fewer stop-over days ($F = 176.870$, $p < 0.001$, but also because they required less travelling days ($F = 4.959$, $p = 0.032$). A LMM with logit transformed journey straightness as the dependent variable and bird ID as a random factor showed that the routes used by adult birds (mean straightness = 0.90, SD = 0.06) were also more direct than those of juveniles (mean straightness = 0.94, SD = 0.03) ($F = 4.904$, $p = 0.033$). Summary statistics from all of the autumn migrations are shown in Table 4.6 and Table 4.7.

At the daily scale, LMMs with bird ID as a random factor and log transformed daily/sector distance as the dependent variable showed that there was no significant difference in daily/sector distance flown between adult and juveniles in either Europe ($F = 0.291$, $p = 0.597$) or in Africa ($F = 1.401$, $p = 0.251$). Summary statistics of daily/sector flights in these two regions are shown in Table 4.8 and Figure 4.10 shows individual variability in daily/sector distance.

Table 4.6. Summary of autumn migrations by adult ospreys (from chapter 2) and juvenile ospreys (chapter 4). Mean figures shown where appropriate for adult birds.

Adults							Juveniles					
ID	Sex	N	Winter site	Total days	Distance flown	Straightness	ID	Sex	Winter site	Distance flown	Total days	Straightness
1	M	1	Senegal	16	4656	0.94	1	M	Senegal	5391	37	0.928
2	F	3	Senegal	12 (SD = 1)	4433 (SD = 37)	0.98 (SD = 0.01)	2	M	Mauritania	5672	90	0.761
3	M	1	Guinea	14	5048	0.96	3	F	Senegal	5147	22	0.918
4	F	1	Guinea-Bissau	47	5406	0.97	4	M	Mali	5415	22	0.877
5	M	3	Senegal	30 (SD = 9)	5601 (SD = 114)	0.94 (SD = 0.02)	5	F	Senegal	5516	51	0.919
6	F	1	Mauritania	21	4985	0.89	6	M	Senegal	4791	47	0.972
7	M	4	Senegal	20 (SD = 5)	5378 (SD = 88)	0.94 (SD = 0.02)	7	F	Senegal	5046	79	0.912
8	M	2	Guinea-Bissau	25 (SD = 0)	5531 (SD = 113)	0.95 (SD = 0.02)	8	M	Cape Verde	5142	8	0.949
9	M	3	Senegal	40 (SD = 9)	5301 (SD = 142)	0.91 (SD = 0.01)						
10	F	8	Spain	18 (SD = 5)	2473 (SD = 33)	0.95 (SD = 0.01)						
11	F	2	Spain	17 (SD = 7)	2071 (SD = 3)	0.90 (SD = 0.01)						
12	M	3	Senegal	16 (SD = 2)	5253 (SD = 96)	0.97 (SD = 0.02)						
13	M	1	Senegal	19	5274	0.95						
14	M	1	Senegal	23	5515	0.92						

Table 4.7. Comparison of complete migrations by adult and juvenile ospreys during autumn. Travelling fraction is calculated by dividing total days by number of travelling days.

Age	N	Total days		Travelling fraction		Straightness	
		Mean	SD	Mean	SD	Mean	SD
Adult	34	22	10	0.76	0.20	0.90	0.64
Juvenile	8	45	29	0.59	0.35	0.94	0.26

Table 4.8. Comparison of daily flights of adult and juvenile ospreys during autumn migration.

Age	Region	N	Day length (hh:mm)		Flying time (mins)		Daily distance (km)		Actual distance flown (km)		Daily straightness	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Adult	Europe	269	13:32	01:05	515	275	263.5	210.9	291.0	265.2	0.941	0.067
Juv.	Europe	77	12:30	01:20	534	333	250.7	259.0	266.9	275.9	0.923	0.109
Adult	Africa	171	12:11	00:20	577	119	307.0	123.1	317.3	119.0	0.951	0.075
Juv.	Africa	52	11:29	00:28	573	179	269.0	121.7	285.3	129.1	0.940	0.082

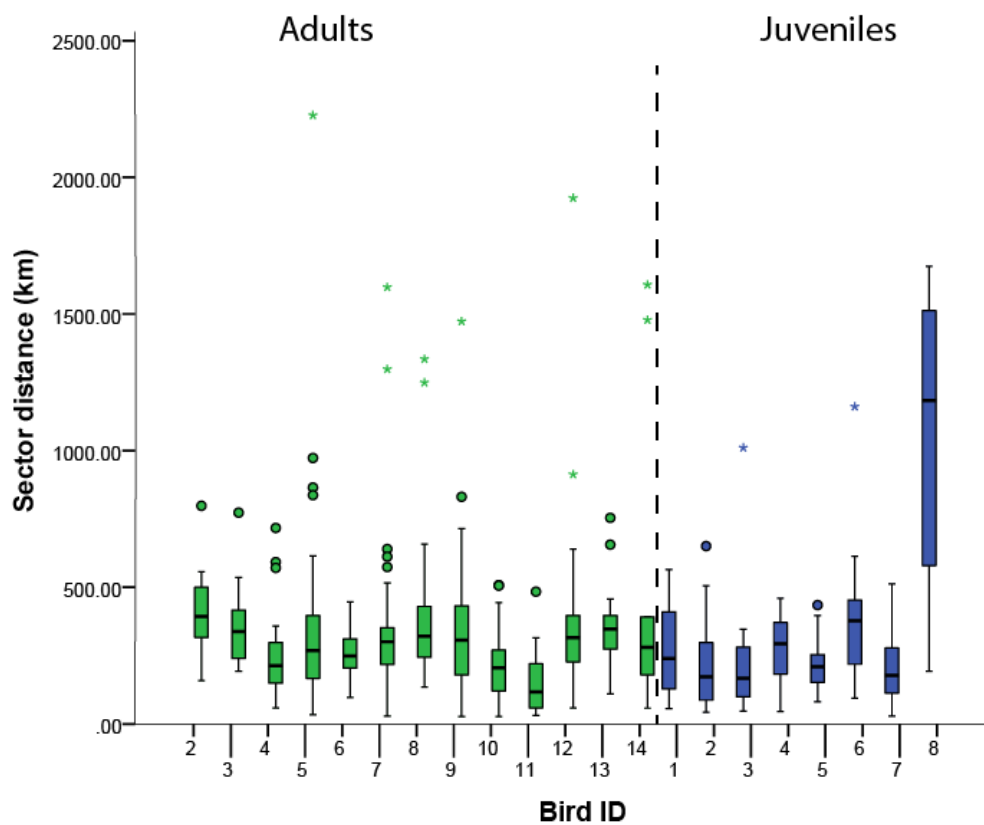


Figure 4.10. Box plot showing individual variation in daily/sector distance flown.

There was no significant difference in mean sector distance flown by juveniles (blue) compared to adults (green) but juvenile bird 8 flew considerably further than all other birds as a result of its very unusual migration to Cape Verde.

4.5. Discussion

The results of this study indicate that there is considerable individual variation in both post-fledging and migratory behaviour of juvenile ospreys. Dispersal from the nest during the post-fledging period followed a fairly predictable pattern, but the extent of exploratory behaviour prior to migration and timing of subsequent departure varied considerably. Meteorological variables had a clear impact on migration, most notably the role of crosswinds in shaping migration routes. The finding that birds with the longest post-fledging phase migrated fastest appears to emphasise the importance of the post-fledging phase in influencing migratory behaviour.

4.5.1. Post-fledging

The mean duration of the post-fledging period was a week longer than the corresponding figure recorded by Bustamante (1995), but there was considerable individual variation. The general trend for birds to fly further from the nest two-three weeks after fledging is comparable to the findings of Monti et al. (2012), and meant that the earliest-departing individuals made few exploratory flights. These flights are thought to be important in the development of flight skills (Bustamante 1993, Bustamante 1994a), making it a risky strategy for juvenile ospreys to depart early. This was exemplified by the fact that bird 10 died soon after setting out on migration after a short post fledging period. It is notable that this individual and two other birds that departed less than four weeks into the post-fledging period were the latest to fledge. This contrasts with the work of Bustamante (1995) who found that fledging date had no impact on the length of the post-fledging period among juvenile ospreys in a long-term study of a single nest in northern Scotland. However studies of other species have demonstrated a link: Catline and Rosenberg (2014) showed that burrowing owls that fledged later in the season dispersed more quickly than birds that fledged earlier, and Rahman et al. (2014) found that post-fledging range size was positively correlated to fledging date in saker falcon.

As expected there was a general trend for juvenile ospreys that remained in the natal area for longer to make lengthier and more frequent exploratory flights during the latter stages of the post fledging period, thereby corresponding with previous research

on raptors and owls (e.g. Delgado et al. 2009, Soutullo et al. 2006, Yamac and Bilgin 2012). Nevertheless there was considerable individual variation, best exemplified by bird 7. This bird was not recorded more than 1 km from the nest prior to migration, despite the fact that the duration of its post-fledging period exceeded the mean for all birds. Given that all birds were dependent on parental food provision until migration (as per Monti et al. 2012) it is possible that such a strategy may be employed by some individuals to ensure they deposit sufficient fuel prior to migration. During the post-fledging period adult ospreys deliver food to the nest (Bustamante 1995) and so by remaining nearby bird 7 may have been able to claim fish before its siblings.

4.5.2. Migration

4.5.2.1. Influence of energy minimisation

Like the post-fledging period, juvenile ospreys showed individual variation in migratory behaviour at all temporal scales measured. At the journey scale it was notable that some birds incorporated extended stop-overs into their journeys whereas others did not. Ospreys use the fly-and-forage strategy where birds exploit opportunities to feed before, during or after a day's flight (Strandberg and Alerstam 2007). Stop-overs provide a valuable opportunity for juveniles to replenish fuel reserves (Yosef et al. 2006) and, potentially, an additional chance to improve foraging skills (Mellone et al. 2013). This may explain why the juvenile ospreys in this study incorporated longer stop-overs into their migrations than the adult birds analysed in chapter 2. An increased number of stop-over days was the key factor in determining the total number of days required to complete migrations, particularly as juveniles covered similar daily distances to adult birds in both Europe and Africa on travelling days. This is in agreement with other studies of raptor migration which have also shown that juveniles tend to incorporate longer stop-overs than adults (Hake et al. 2003, Mellone et al. 2014). It is also notable therefore that the three birds that completed migrations without stop-overs were the individuals with the longest post-fledging period. In this case the extended post-fledging period may have better-prepared these individuals for migration and negated the necessity for stop-overs. This corresponds to Kjellén et al. (2001) who found that later departing ospreys incorporated fewer stop-overs, possibly

as a result of additional fuel deposition on the breeding grounds. All stop-overs were made in Europe, in agreement with Alerstam et al (2006) and Vali and Sellis (2016) that stop-overs are usually made at northerly latitudes during autumn migration.

The tendency to incorporate lengthy stop-overs indicates that energy minimisation plays a key role in shaping the migration speed of juvenile ospreys, whereas evidence from chapter 2 suggests adults are strongly influenced by time constraints even in autumn; as exemplified by the fact that adult birds incorporated fewer stop-over days than juveniles. Given that juveniles migrate according to an endogenous programme of distance and direction, there is little, if any, selective advantage to be gained from migrating faster, whereas the urge to reclaim a known wintering site is likely a strong behavioural driver in shaping adult migration speed. The more cautious approach adopted by most juvenile birds in this study may thus be indicative of an energy-minimisation strategy that reduces mortality risk during migration and facilitates individuals arriving at wintering sites in better condition (Newton 2008). Previous research has shown that juvenile ospreys wander widely after arriving in potential wintering areas (Hake et al. 2001), indicating that birds in optimal physical condition may have a competitive advantage when selecting wintering sites. Miller et al. (2016) reported similar behaviour during golden eagle migration, leading them to suggest that autumn migration is predominantly energy-selected.

A clear advantage of migrating according to the rules of energy-minimisation is that an individual may select optimal weather conditions for migration (Alerstam and Lindström 1990). Duerr et al. (2014) found that golden eagles selected environmental conditions favourable for flight during autumn migration by travelling on days with tailwinds and good thermals conditions. A notable feature of the migrations in this study, therefore, was that ospreys predominantly migrated on days classified as either following winds or weak winds. Although wind-selectivity was not explicitly tested, the fact that ospreys experienced a very low percentage of opposing winds (headwinds $> 2.5 \text{ m s}^{-1}$) on travelling days indicates that they may have preferentially migrated on days when winds were more favourable. Thorup et al. (2006) concluded that ospreys do not show wind selectivity during migration, but their study was limited to adult

birds only. A strategy of wind selectivity may be more important to juvenile birds, which have been shown to migrate less efficiently (Rotics et al. 2016).

The benefit of migrating when meteorological conditions are favourable is exemplified by the fact that hourly groundspeeds of juvenile ospreys were faster when they were supported by following winds (tailwind $> 2.5 \text{ m s}^{-1}$) and when boundary layer was high ($> 2500 \text{ m}$) and therefore indicative of good thermals conditions. This is in agreement with other raptor migration studies that have demonstrated the positive effects of tailwinds (Mellone et al. 2012, Vansteelant et al. 2015, Mellone et al. 2015) and thermal conditions (Borher et al. 2012, Vansteelant et al. 2015). The surprising lack of a significant effect of head/tailwind on sector distance is most likely the result of the fact that there were few instances of opposing winds on travelling days. The fact that juveniles generally migrated in favourable conditions may also explain why there was no significant difference in daily/sector distance flown by juvenile birds compared to the adults analysed in chapter 2, even though the cost of flight to these inexperienced birds is likely to have been higher (Rotics et al. 2016).

4.5.2.2. *Effect of wind on migration speeds and routes*

In general hourly groundspeeds and daily/sector distance varied less between individuals than overall duration of migration. Mean daily/sector distance was similar to the corresponding figure achieved by ospreys in other satellite tracking studies (e.g. Hake et al. 201, Martell et al. 2001) and the adult birds in chapter 2. Nevertheless some exceptionally long flight sectors were also recorded. The longest flights involved lengthy sea crossings, which sometimes necessitated nocturnal flight as has been recorded in other studies of osprey migration (DeCandido et al. 2006, Horton et al. 2014). In several cases these sea crossings were the result of wind drift, most notably bird 8 that migrated to Cape Verde. This bird was unable to re-orientate in order to reach the African mainland after drifting across the Atlantic in north-easterly winds. Instead it continued to submit to wind drift during flights between Spain and the Canary Islands and the Canary Islands and Cape Verde. This supports the 'clock-and-compass concept' (Gwinner 1996) whereby migration of juveniles is controlled by an

endogenous temporal/directional programme with limited or no elements of compensation for geographical displacement.

It was clear that wind had a profound effect on the variability in routes used by the juvenile ospreys, thereby concurring with Thorup et al (2003) who suggest that compensation for wind drift in ospreys and honey buzzards is age-dependent, with the superior navigational abilities of adult birds enabling them to compensate for the effects of crosswinds more efficiently than juveniles. The susceptibility of first-year birds to wind drift may explain the more indirect routes used by juveniles compared to adult birds, who migrate to a known wintering site and intermediary goal areas, rather than relying on vector summation in the manner of juveniles (Alerstam et al. 2006). Wind drift has particular implications for juvenile ospreys migrating south from the UK because of the close proximity of the Bay of Biscay, most pertinently when east or north-easterly winds have the potential to push migrating juveniles off course, especially at night when a lack of visual clues makes navigation even more difficult (Klaassen et al. 2011). This was borne out by bird 6, which missed the northern coast of Spain as a result of wind drift during a night-time crossing of the Bay of Biscay. This bird only reached land in Portugal after a compensatory change of direction after dawn. Previous research has indicated that such flights across the Bay of Biscay can result in mortality (Dennis 2002).

It is notable that there was a tendency for cases of wind drift to be most prevalent at the start of migration. This corresponds with the theoretical predictions of Alerstam and Lindström (1990) who suggested that under the rules of optimal bird migration an individual should submit to wind drift at the start of migration and then compensate to an increasing degree on approaching the goal. In the case of juvenile ospreys, which are thought to navigate by vector summation (Thorup et al. 2003) and thus rely on an inherited programme of direction and distance, submitting to wind drift at the start of migration has the potential to save them both time and energy (Alerstam 2000) particularly as birds on their first migration are unlikely to be navigating towards intermediate goals in the manner of adult birds (Alerstam et al. 2006). Instead they are migrating towards a distant goal consisting of many flight steps (Alerstam 2000). Interestingly, all of the juvenile ospreys in this study initiated migration when wind

was from the west or north/west. This resulted in south-easterly headings overland through the UK, thereby avoiding long sea crossings at the start of migration which would be the case if their initial heading was south-west. These results correspond with Maransky et al. (1997) who demonstrated that red-tailed hawks *Buteo jamaicensis* wait for supportive tailwinds before migrating south in autumn.

We also found evidence that in some cases juvenile ospreys are able to achieve some degree of compensation for the effects of crosswinds. The most notable example was the change of heading made by bird 6 over the Atlantic, although additional compensatory behaviour was also recorded in over half of flights affected by crosswinds. This supports the suggestion made by Horton et al. (2014) that juvenile ospreys do possess the ability to compensate for wind-drift, albeit to a lesser capacity than adult birds (Thorup et al. 2003).

In addition to their flight heading response to crosswinds, juvenile ospreys also displayed an ability to regulate airspeed according to wind conditions. This was evident during flights over the ocean when there was a significant correlation between airspeed and head/tailwind velocity. This conforms to the rules of optimal adjustment of airspeed described by Liechti et al. (1994) and reviewed by Alerstam (2000) that airspeed is expected to be reduced when the resulting groundspeed exceeds the airspeed and to be increased when groundspeed falls short of the airspeed. Our data supports the findings of Horton et al (2014) who found that juvenile ospreys regulated airspeed in the manner predicted by optimum bird migration theory during long flights across the western Atlantic Ocean. Airspeed regulation is likely to be particularly beneficial during very long ocean crossings when it would allow ospreys to make valuable energetic savings. This emphasises the advantages to migrating ospreys of undertaking long ocean crossings when supported by tailwinds.

Even accounting for the fact that ospreys regulated airspeed during sea crossings, groundspeeds recorded over the ocean were significantly faster than the corresponding speeds over land. This corroborates with Klaassen et al. (2008) who demonstrated the same trend in a study of Swedish ospreys. Similarly Vansteelant et al. (2015) reported that honey-buzzards *Pernis apivorus* and Montagu's harriers *Circus*

pygarrus travelled faster over the ocean than land. Hourly speeds were faster and sectors distances greater when boundary layer was high, but this did not apply to ocean crossings because boundary layer was always lower than the corresponding values over land. This lack of a correlation between boundary layer height and flight speeds over the ocean is likely because ocean crossings were undertaken predominantly by flapping flight, whereas ospreys preferentially migrate by soaring-gliding over land, and are thus much more constrained by thermal conditions as shown in chapter 2.

4.5.3. Conclusion

The post-fledging period and subsequent migration are challenging for inexperienced juvenile ospreys. Individual variation during the post-fledging phase appears to be driven by endogenous factors which result in differing strategies, but as with most satellite tracking studies this conclusion is limited by a restricted sample size. Analysis of the post-fledging behaviour of a larger number of individuals would help to determine the extent to which the results presented here are representative of the wider population. Nevertheless the post-fledging period appears to play a key role in shaping subsequent migratory behaviour, particularly given that the individuals that remained in the vicinity of the nest for longest migrated without stop-overs. Individual variation in migration speed and routes was also driven by meteorological factors - most notably crosswinds which resulted in very long ocean crossings - and by the apparent priority of conserving energy over saving time.

5. Discussion

In recent years, the study of avian migration has been revolutionised by advances in technology, most notably satellite tracking (López-López 2016). The ability to track birds on complete migratory journeys at high temporal resolution provides a unique insight into the challenges individuals face, and enables comparisons to be made between empirical data and theoretical predictions (López-López 2016). The results of this study demonstrate that even in a well-researched species such as the osprey, satellite tracking has the potential to provide new and valuable information that enhances our understanding of avian migration and aids conservation.

Prior to the advent of satellite tracking, ringing data provided evidence that ospreys migrated between Europe and sub-Saharan Africa (Saurola 1994), and North America and South America (Ewins and Houston 1992). Subsequent satellite tracking studies have provided valuable new data on the routes, speed, and duration of migration of both European (e.g. Hake et al. 2001, Alerstam et al. 2006, Vali and Sellis 2016) and North American ospreys (e.g. Martell et al. 2001, Martell et al. 2014) including the species' ability to undertake very long sea crossings, even at night (DeCandido et al. 2006, Horton et al. 2014). The results of this study provide further insights into flight method during migration, seasonal variation in migration speed and the potential hazards juvenile ospreys face when migrating south from the UK for the first time.

Prior to the development of GSM transmitter technology, research into flight method during migration was limited to hourly or daily scales (Kjellen et al. 2001, Klaassen et al. 2008, Mellone et al. 2012) or fixed locations using visual observations or radar (Meyer 2000, Kjellen et al. 2001). GSM technology facilitates analysis of flight method across complete journeys including location, altitude and orientation data. The ospreys' ability to migrate by a combination of flapping-gliding and soaring-gliding flight makes it a particularly pertinent species to study because tracking data can demonstrate how individual birds adapt to the different environmental conditions encountered during their long migrations.

5.1. Flight method during migration

The results of chapter 3 confirmed the expectation that ospreys preferentially migrate by soaring-gliding and only resort to flapping-gliding when updrafts do not provide sufficient energy to power soaring-gliding flight. Alerstam (2000) outlines that the mechanical power required for flapping flight is always higher than the corresponding curve for gliding flight, but that the ability of a given species to utilise these contrasting flight modes during migration is determined by its size, morphology and ability to optimally adjust its wings and tail at different speeds. In the case of the osprey its wing loading enables it to utilise thermal and orographic updrafts efficiently (Mellone et al. 2012), and its highly-adapted morphology – specifically long narrow wings (Agostini 2015) – is thought to make the shift to flapping flight far less energetically costly compared to larger species (Alerstam 2000, Horvitz et al. 2014). This ability to switch to flapping-gliding flight makes ospreys less constrained by thermal conditions than most other migratory raptors and, as a result, they are able to continue flying during the night (DeCandido et al. 2006) and across wide expanses of ocean (Horton et al. 2014). The results described in chapters 2, 3 and 4 agree with this previous research, with the additional important finding that on occasion ospreys exploit sufficient lift to support soaring-gliding flight over the sea; the first time that such behaviour has been described for this species. Climbing rates for the two flights across the ocean described in chapter 2 were within the range reported for migrating ospreys tracked by radar over land in southern Sweden (Kjellén et al. 2001) indicating that, given suitable environmental conditions, sea thermals strong enough to sustain soaring-gliding flight by ospreys develop at northerly latitudes. It is notable that each soaring-gliding flight was made during autumn when sea temperatures are warmer. This supports the suggestion that weak thermals can develop in the Northern Atlantic when cool air flows over the warm water surface (Elkins 1995). Soaring-gliding flights were also limited to days when tailwinds had the potential to improve flight performance by prolonging the gliding phase. Nevertheless ospreys are also likely to have incorporated sporadic flapping (Mellone et al. 2012).

The data presented in chapter 3 represents a small sample size - a frequent limitation of satellite tracking studies (López-López 2016) - but the trend for a greater number of

crossings of the Bay of Biscay undertaken in autumn was identified by the more extensive dataset in chapter 2, even though these data were not of sufficient resolution to identify cases of soaring-gliding flight. During autumn Bay of Biscay crossings were only undertaken when north-easterly winds provided tailwind support. In spring the predominance of north-westerly winds (Puillat et al. 2006) create headwind conditions that prohibit long ocean crossings, even though ospreys are under selection pressure to arrive back at their nest sites as early as possible (Alerstam 2006). These trends correspond with other studies that have identified contrasting raptor migration routes in autumn and spring according to seasonal differences in environmental conditions, often referred to as loop migrations (Mellone et al. 2013, Yamaguchi et al. 2013).

Autumn crossings of the Bay of Biscay often constituted significant sectors of the long non-stop flights from the UK to northern Spain. The distance achieved in such flights exceeded theoretical predictions of Alerstam (2000) based on the morphology of ospreys. These calculations, however, are based on energy-expenditure in flapping flight, and ospreys would significantly reduce energetic costs by soaring-gliding during sea crossings. Additional GSM tracking studies of a larger number of birds would help to confirm if the trends identified in this study are indicative of a general ability of ospreys to exploit thermal updrafts over the ocean, albeit to a lesser extent than highly-adapted seabird species such as frigatebirds (Brewer and Hertel 2007). The dataset analysed in chapter 3 was not always of sufficient resolution to determine flight method across complete ocean crossings. Nevertheless, these results are exciting and warrant further study, particularly if the novel flight classification method could be further validated by comparison with the method devised by Resheff et al. (2014) based on accelerometer data. A limitation of the GSM transmitter used in this study was that they do not log such data which has been used to categorise flight method in other studies (Rotics et al. 2016).

5.2. Season variation in migration and the influence of time and energy

A key finding of this study was that autumn migration speed was greater than spring at all temporal scales, as described in chapter 2. This contrasts with a general trend for

birds to migrate faster in spring than autumn (Nilsson et al. 2013) and exemplifies the challenge of extricating the relative importance of behavioural and meteorological factors in determining bird migration speed. One of the key behavioural drivers is thought to be selection pressure (Newton 2008) and it has been proposed that the urge to return to the breeding site as quickly as possible motivates many species to migrate faster in spring than autumn (Koko 1999, Alerstam 2006, Nilsson et al. 2013). However, there is a growing body of evidence that some species may be under additional selection pressure in autumn in relation to reclamation of winter territories (Mellone et al. 2015, Panuccio et al. 2014). Studies have shown that adult ospreys are faithful to the same wintering site each year and are highly sedentary on arrival (Alerstam et al. 2006, Washburn et al. 2014). It seems likely, therefore, that the reclamation of these winter territories plays a key role in shaping migratory behaviour during autumn (Alerstam et al. 2006). The challenge, however, is to determine the extent to which this behaviour is independent of contrasting meteorological factors.

The results of chapter 2 demonstrate that meteorological conditions were a key driver in determining daily distance flown and, as a result, the more favourable conditions encountered during autumn enabled ospreys to migrate further per day than in spring. This is in agreement with other raptor migration studies that have demonstrated the positive effects of tailwinds (Mellone et al. 2012, Vansteelant et al. 2015, Mellone et al. 2015) and thermal conditions (Borher et al. 2012, Vansteelant et al. 2015) on hourly speeds and daily distance, as well as the negative effect of strong crosswinds (Vansteelant et al. 2015). Nevertheless the fact that later departing ospreys incorporated more time minimisation techniques into migration during autumn – such as increased instances of nocturnal flight and long crossings of the Bay of Biscay - is indicative of the fact that they were migrating with increased urgency. Furthermore, there was no seasonal variation in stop-over duration is further evidence that time minimisation affects migration speed in autumn as well as spring (Alerstam 2006, Nilsson et al. 2013), but a more critical analysis requires pre-migratory periods to be taken into consideration, particularly as fuel deposition during this period has the potential to influence daily distance and the necessity for stop-overs (Kjellen et al. 2001, Alerstam et al. 2006). Pre-migratory fuelling is often over-looked in migration

studies (Alerstam et al. 2006), but the trend for both adult and juvenile ospreys to make long flights at the beginning of autumn migration indicates that it is of key importance (Kjellen et al. 2001). This is further supported by the results of chapter 4 which suggest that a longer post-fledging period negates the need for juvenile ospreys to incorporate stop-overs, possibly as a result of greater pre-migratory fuel deposition (Yosef et al. 2006) and the development of improved flying skills. The importance of pre-migratory fuelling is best exemplified by the remarkable non-stop flights of bar-tailed godwits between Alaska and New Zealand, a distance of over 10,000 km (Gill et al. 2008). Such flights are only achievable because the intertidal infauna of the central and southern Yukon-Kuskokwim - the principal autumn staging site, provides extremely rich foraging with few avian predators (Gill et al. 2008). The study of the pre-migratory periods of ospreys is thus warranted, particularly if satellite data could be combined with field-based observations in order to determine the pre-migratory fuelling rate of known individuals. The osprey would be an excellent species to study because regular foraging sites could be easily identified by satellite tracking data and individuals subsequently observed in-situ. It would be particularly interesting to study birds from different geographical areas given that food availability may limit the extent of pre-migratory fuelling at some northerly breeding latitudes (Alerstam 2006).

Another key finding was that both adult and juvenile ospreys appear to exhibit wind selectivity at the start of autumn migration. This is indicative of an energy minimisation strategy (Alerstam and Lindström 1990, Henderström 1993), and facilitates long flights at the start of autumn migration. However these longer flights, particularly those that involve nocturnal flight, are diagnostic of time-minimisation. Such confounding factors support the conclusions of Miller et al. (2016) who suggest that golden eagles appear to use a mix of both time- and energy minimisation strategies and that the balance between the two was affected by age, location and timing. The findings of Miller et al. (2016) are further supported by the results of chapter 4 which indicate that juvenile ospreys incorporate more energy minimisation strategies than adults during autumn migration. This is best exemplified by the lengthy stop-overs incorporated by some individuals and by the fact that very long flight sectors were the result of wind drift, rather than a concerted effort by the bird to save

time. This more cautious approach is indicative of the fact that, unlike adults, juvenile ospreys gain little or no selective advantage by arriving at potential wintering sites early. Furthermore they may actually gain fitness advantages by arriving in good physical condition (Newton 2008) given that juvenile ospreys often wander widely after arriving in over-wintering areas (Hake et al. 2001).

5.3. Airspeed regulation

Empirical studies have indicated that migrant birds generally do not generally fly at a fixed (wind-independent) minimum power speed and instead regulate their airspeed according to wind conditions and behavioural drivers (Alerstam 2011) as predicted by optimum migration theory (Alerstam and Lindström 1990). The results of this study indicate that both adult and juvenile ospreys regulate airspeed during migration and that this serves two contrasting functions. Decreasing airspeed in tailwind conditions reduces the energetic costs of flight (Alerstam 2000) and has the potential to increase daily flying time, and therefore range, as demonstrated by the very long flights undertaken by both adult and juvenile ospreys at the start of autumn migration. Conversely, increasing airspeed when flying into headwinds enables ospreys to increase groundspeeds in unfavourable conditions. This is particularly important when birds are under selection pressure to migrate quickly and, as such, airspeed is a useful attribute for establishing the relative influence of behavioural and meteorological factors on migration speed (Nilsson et al. 2013).

Horton et al. (2014) found that juvenile ospreys regulated airspeed during long flights across the western Atlantic Ocean and it has also been reported in species such as swifts (Henningsson et al. 2009) that migrate by flapping flight (Alerstam 2000). The rules of optimal airspeed adjustment relate to flapping flight only (Liechti et al. 1995) but the analysis of GSM data in chapter 3 indicates that ospreys have the ability to regulate airspeed in both flapping and gliding flight. This corroborates the findings of Spaar (1997) who reported gliding speed airspeed adjustments by six species of soaring-gliding raptors.

In addition to its benefits from an energy-minimisation perspective, regulation of airspeed enables birds to increase groundspeeds when wind conditions are unfavourable. This was most evident during spring migrations presented in chapter 3 when ospreys increased both flapping and gliding airspeeds in response to headwinds. Horvitz et al. (2014) suggest that soaring-gliding species achieve faster gliding airspeeds by flying closer to optimal glide speed (V_{opt}), which necessitates steeper glides and increased risk of grounding or swapping to flapping flight. Ospreys, however, are well-adapted to flying at V_{opt} because the switch to flapping flight is less energetically costly than for larger species with high wing loadings (Horvitz et al. 2014). The results of chapter 3 indicate that during spring migration, when ospreys are under selection pressure to reclaim nest sites, increasing gliding and flapping airspeeds is an effective time-minimisation technique.

5.4. Crosswinds and migration routes

The effect of wind was not limited to the forward movement of ospreys during migration, with crosswinds having a clear influence on perpendicular movement and routes used by both adult and juveniles. Juvenile birds are thought to be unable to correct for displacement during their first autumn migration, suggesting that true navigation is only possible among individuals with experience of previous migratory journeys (Guildford et al. 2011). Instead juvenile birds rely on an inherited programme of direction and distance, known as vector summation (Rabøl 1978) in order to reach their wintering site (Mourtsen 2003). Under this technique migration consists of a series of flight steps, with variations in orientation from the endogenous direction caused by limitations in the precision of the birds' navigational abilities and external variables such as wind drift (Alerstam 2000). This is exemplified by flights of juvenile birds described in chapter 4, most notably bird 8 that made a highly unusual migration to Cape Verde as a result of wind drift, and by bird 6 that missed the north coast of Spain as a result of strong north-easterly winds during a night-time crossing of the Bay of Biscay. The effects of wind drift resulted in exceptionally long flight sectors that included lengthy non-stop flights across the ocean in both instances. Additional cases of wind drift were identified in 40 % of flight sectors where juvenile ospreys

were migrating in crosswinds, confirming the supposition that wind drift plays a key role in determining the migratory heading and, ultimately, destination of juvenile ospreys (Thorup et al. 2003).

Cases of wind drift among juvenile ospreys were most prevalent at the start of migration. This conforms to theoretical predictions of Alerstam and Lindström (1990) who suggested that under the rules of optimal bird migration an individual should submit to wind drift at the start of migration and then compensate to an increasing degree on approaching the goal. It difficult to determine whether the observed trend was indicative of juveniles intentionally conceding to wind drift or symptomatic of inexperience, but given that juvenile ospreys migrate without the aid of experienced conspecifics (Alerstam et al. 2006), wind selectivity at the start of migration may be an endogenous adaptation to migration. This hypothesis is supported by the results of chapter 2 that adult birds also initiated migration when wind was from the north-west, thereby providing maximum tailwind support in the intended direction of migration. These results correspond with Maransky et al. (1997) who demonstrated that red-tailed hawks wait for supportive tailwinds before migrating south in autumn. These interesting findings merit further study and could be more robustly tested with a larger number of birds.

The differing ability of adult and juvenile birds to respond to the effects of crosswinds is a notable finding of satellite tracking research and one that continues to spark debate. Thorup et al. (2003) demonstrated that compensation for wind drift in ospreys and honey buzzards is age-dependent, with the superior navigational abilities of adult birds enabling them to compensate for the effects of crosswinds more efficiently than juveniles. In contrast Horton et al. (2014) propose that juvenile ospreys migrating over the western Atlantic Ocean are able to fully-compensate for wind drift, even during night-time flights. The results presented in chapter 4 do not fully corroborate with either study given that instances of both wind drift and compensation were identified, most significantly during crossings of the Bay of Biscay and Atlantic. The most notable example of compensatory behaviour was the change of heading made by bird 6 over the Atlantic after it missed the Spanish coast as a result of wind drift. However this change of heading was not made until after dawn emphasising the navigational

challenges of migrating at night (Liechti 1996, Klaassen et al. 2011). Further compensatory behaviour was recorded in over half of flights affected by crosswinds and this suggests that juvenile ospreys do possess some ability to compensate for wind-drift, albeit to a lesser degree than adult birds (Thorup et al. 2003). However, given that this study, as well as those of Thorup et al. (2003) and Horton et al. (2014) are limited in the number of birds tracked, there is a need for additional research into the response to crosswinds of migrating raptors, particularly juveniles (López-López 2016).

The superior navigational capabilities of adult ospreys are exemplified by their ability to adapt their response to crosswinds according to local conditions; drifting when favourable and compensating or overcompensating when approaching a goal or facing the risk of being blown into hazardous habitats (Klaassen et al. 2011). This suggests that adult birds develop enhanced map-based navigation over successive migrations enabling them to detect and correct for lateral displacement during migration (Klaassen et al. 2011, Thorup et al. 2003). This study did not explicitly test the effect of crosswinds on adult ospreys, but the results of chapter 2 indicate that during autumn migration adult ospreys only cross the Bay of Biscay when winds are from the north-east. Migrating south along the French coast under these wind conditions would involve a compensatory increase in airspeed and change of heading (Liechti 1995), and so ospreys are likely to save time by submitting to wind drift (Alerstam 2000). Under this scenario, utilising weak sea thermals and elements of the wind to achieve soaring-gliding flight over the sea has the potential to provide energetic savings as well. In addition, the migration routes used by adult ospreys across the Sahara appear to be indicative of 'adapted drift' (Alerstam 1979) given that autumn routes were more direct but there was no seasonal difference in crosswind strength. Under the theory of 'adapted drift' a bird should submit to wind drift in the initial flight steps, and then compensate to an increasing degree when approaching the goal (Alerstam 1979). The Sahara flights fit well with this given that the crossing occurs towards the latter end of autumn migration, but at the start of spring. Klassen et al. (2011) found that ospreys and marsh harriers often drifted with the wind at the start of spring migration,

however there was no clear case of dominance of drift during crossings of the Sahara and other geographic barriers.

5.5. Conservation implications

The ospreys remains a rare breeding species in the UK, but conservation initiatives such as provision of artificial nests (Dennis 2008, Schmidt et al. 2014) and translocation projects (Mackrill 2013) have aided a recent population increase and range expansion. However, as with all migratory species, an understanding of migration routes and timing, stop-over sites and wintering locations is necessary in order to identify natural and anthropogenic threats and to guide appropriate conservation action (Wilcove and Wikelski 2008). This is particularly relevant in the face of global environmental change resulting from factors such as climate change and habitat loss, both of which have been shown to result in declines in migratory species in recent years (Both et al. 2006, Møller et al. 2008, Flousek et al. 2015, Piersma et al. 2016).

Stop-overs were used by both the adult and juvenile ospreys tracked in this study, and are likely especially important for juveniles (Yosef et al. 2006, Mellone et al. 2013). It is difficult to identify priority sites for conservation of ospreys because both adult and juvenile birds migrate singly and on a broad front, but many of the individuals in this study migrated along the Atlantic coast of France in both spring and autumn. Furthermore most of the birds that made long flights across the Bay of Biscay set-out across the ocean from North-west France. The protection of estuarine habitat along the Atlantic coast of France would thus ensure that highly suitable habitat exists both for stop-overs and also for birds pausing for short periods in order to forage (Strandberg and Alerstam 2007). The same is true of estuarine sites in northern Spain. Indeed one of the sites used by bird 4 (chapter 2) for a prolonged stop-over in spring, was subsequently chosen as a site for a reintroduction of ospreys (Galarza and Zuberogoitia 2012).

The broad winter distribution of the ospreys in this study – which ranged from Mauritania to Guinea-Bissau in West Africa, and also included two individuals that

wintered in Spain, suggests that ospreys should be relatively resilient to environmental change (Gilroy et al. 2016). Nevertheless the fact that all of the adult birds that migrated to West Africa wintered in coastal areas and remained faithful to the same site each year emphasises the need for ongoing protection and monitoring of key coastal sites (e.g. Diop et al. 1999, Ecoutin et al. 2010).

Wind drift experienced by juvenile ospreys as detailed in chapter 4 is thought to contribute to the maintenance of genetic variation in the inherited orientation programme and is essential for the evolution of new migratory routes (Thorup et al. 2003). However, it may also have implications in relation to future climate change. There is broad consensus that the frequency and intensity of storms, cyclones, and high-impact wind speed will increase over Western Europe over the period 2020-2190 (Molter et al. 2016). This clearly has the potential to have a detrimental impact on inexperienced juveniles of ospreys and many species during their first migration and undoubtedly warrants further investigation. It is highly likely that global environmental change resulting from factors such as climate change will pose challenges to migratory species in years, decades and centuries to come and so the ongoing monitoring of migratory species using advanced techniques such as satellite tracking are key to monitoring the effects of any such change (López-López 2016).

5.6. The future

The osprey's cosmopolitan distribution and capacity for long-distance migration has made it a popular species for migration research, but the results presented in this thesis have identified several areas for future study, particularly now that GSM transmitters facilitate high temporal resolution data collection. The results of chapter 3 and those of other recent studies (e.g. Duerr et al. 2012, Harel et al. 2016, Miller et al. 2016) have demonstrated the value of GSM transmitters and other high-resolution technology in studies of flight method of migrant raptors, but there is considerable potential for the scope and range of this work to be extended. The technique devised in chapter 3 using location, altitude and orientation data to determine flight method requires further validation, but could be replicated across similar studies and thereby provide further insights into how ospreys – and other species – adapt flight mode

according to changing environmental conditions. High temporal resolution tracking data has the potential to facilitate analysis of specific elements of flight during migration, such as gliding airspeed regulation; another key finding of this study. These results corroborate with previous research (e.g. Spaar 1997) but are of added value because GSM data cover the complete migratory range, rather than being limited to a single site in the manner of radar studies (e.g. Horvitz et al. 2014). It would be interesting to compare the gliding airspeed of different species in relation to changing wind conditions, particularly according to season and the relative influence of time- and energy-minimisation on migration.

The advent of high temporal resolution tracking has created new opportunities in the field of avian migration research and in years to come it is likely that the miniaturisation of transmitters will enable a broader range of species to be tracked. The seasonal migration of birds is one of the great phenomena of the natural world and thanks to these advances in technology our understanding of it is improving at an unprecedented rate. Nevertheless numerous questions remain to be answered providing an exciting and extremely worthwhile challenge to researchers for many years to come.

Appendix 1

Fit of models described in chapter 2

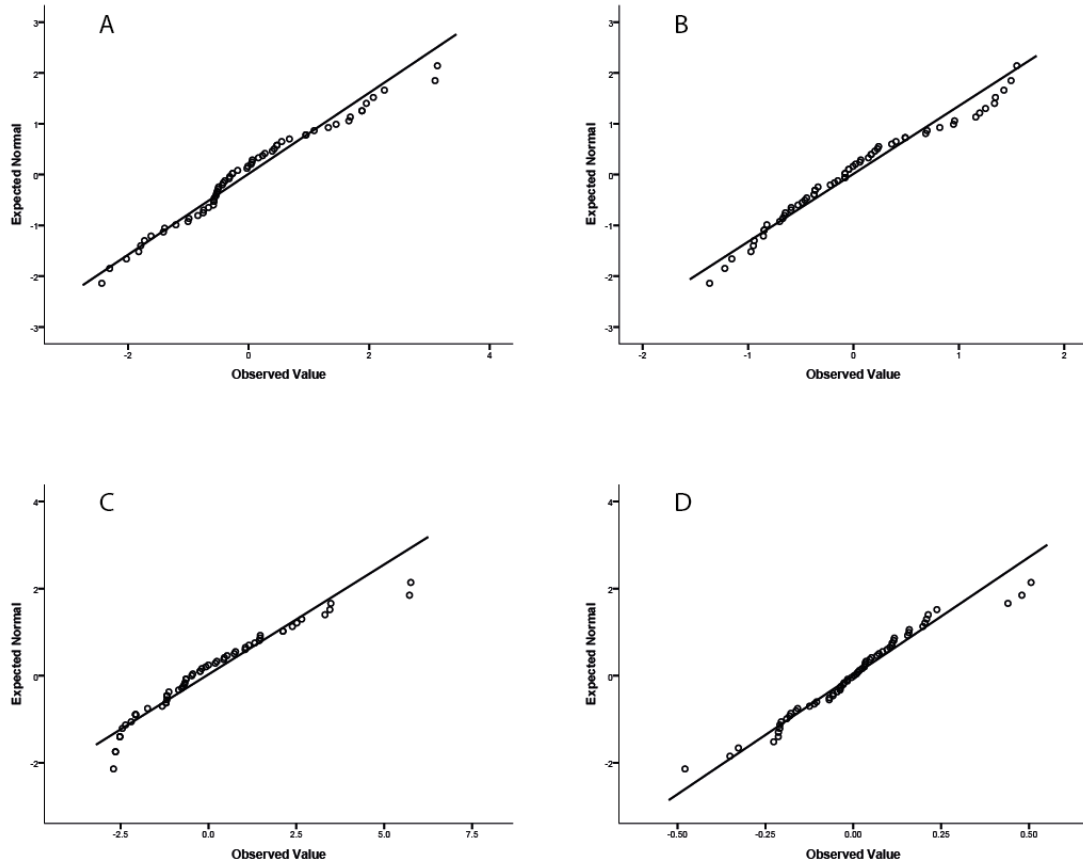


Figure A1.1. Q-Q plots showing model residuals plotted against expected normal distribution for GLMMs (season and bird sex explanatory variables, bird ID random factor) for (A) number of total days, (B) travelling days and (C) stop-over days of completed migrations. (D) LMM for logit transformed journey straightness (season and bird sex explanatory variables, bird ID random factor).

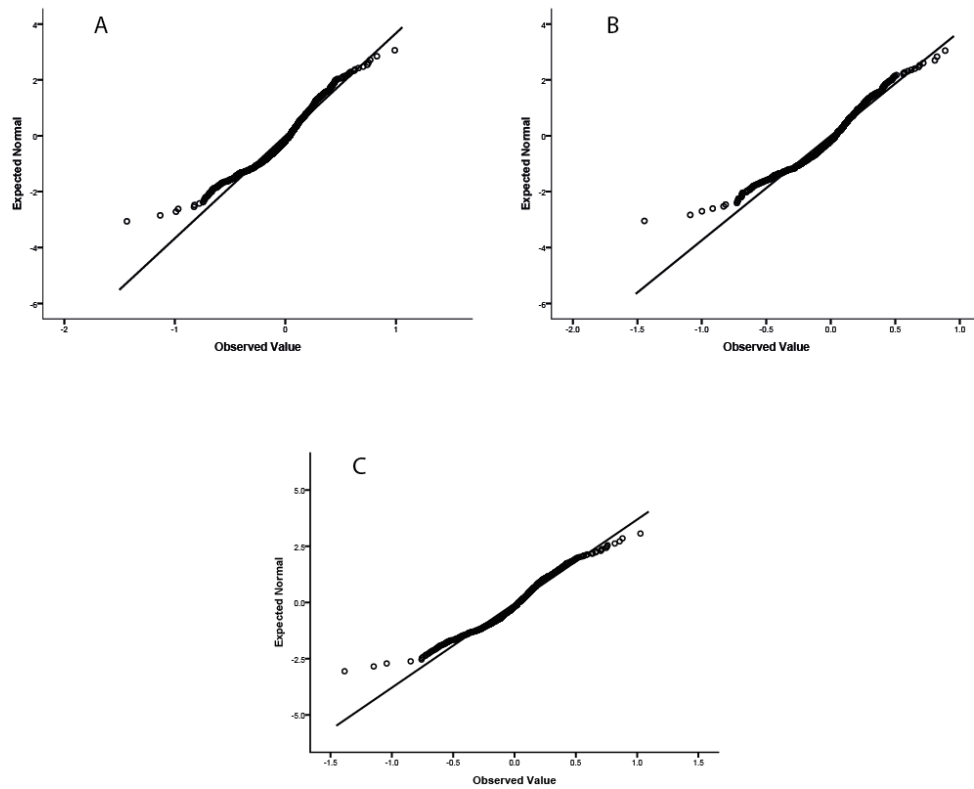


Figure A1.2. Q-Q plots showing model residuals plotted against expected normal distribution for LMMs with log transformed sector distance as the dependent variable, bird ID as a random factor and (A) season and bird sex (B) region/season and bird sex and (C) boundary layer height, head/tailwind, crosswind and departure date as explanatory variables.

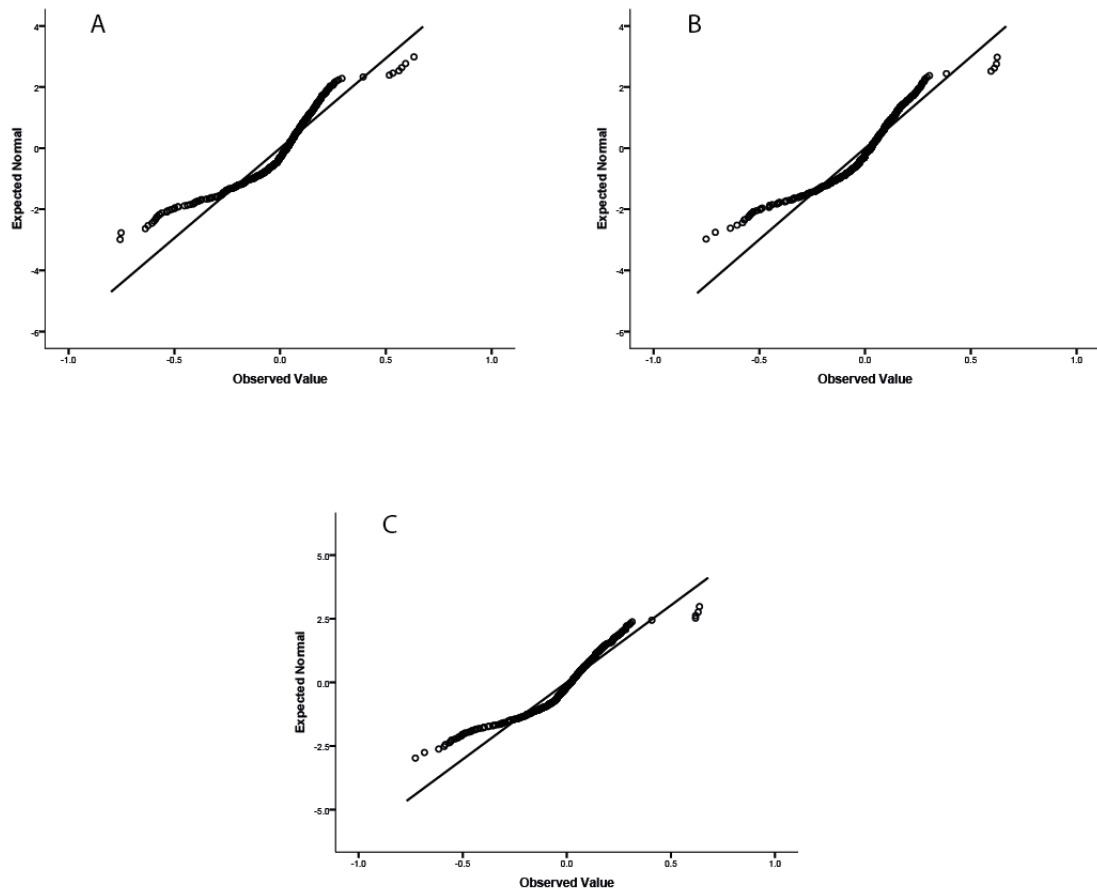


Figure A1.3. Q-Q plots showing model residuals plotted against expected normal distribution for LMMs with log transformed sector flying time as the dependent variable, bird ID as a random factor and (A) season and bird sex (B) region/season and bird sex and (C) region/season, bird sex, day length, headwind, crosswind and boundary layer height as explanatory variables.

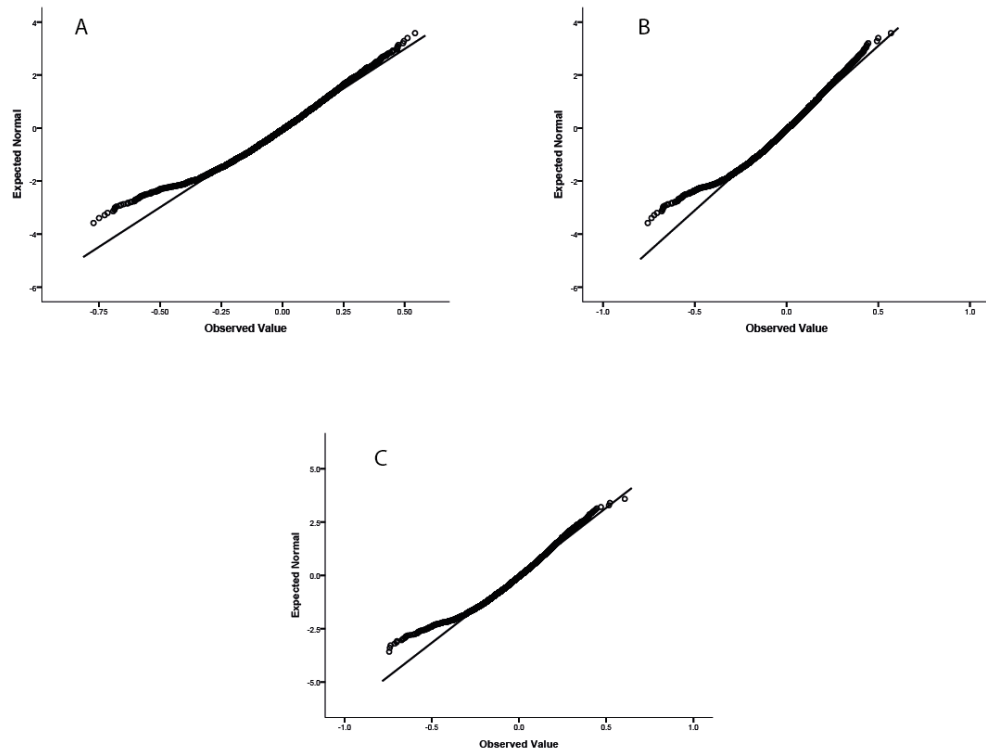


Figure A1.4. Q-Q plots showing model residuals plotted against expected normal distribution for LMMs with log transformed groundspeed as the dependent variable, bird ID as a random factor and (A) season and bird sex (B) region/season and bird sex and (C) region/season, headwind, crosswind, boundary layer height, departure date and departure date*season as explanatory variables.

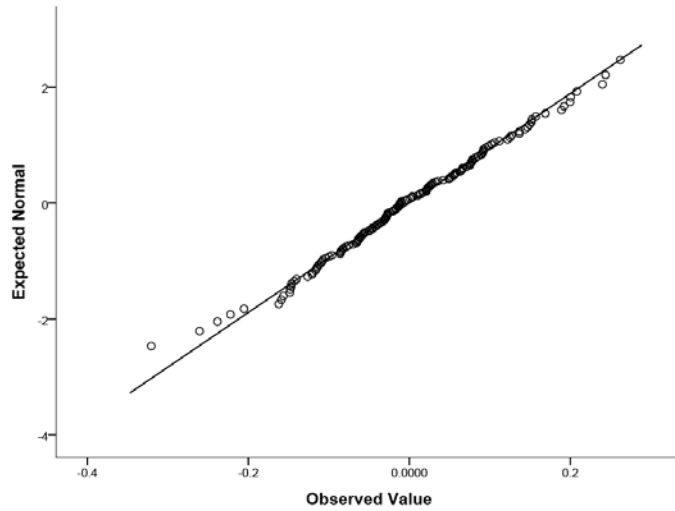


Figure A1.5. Q-Q plot showing model residuals plotted against expected normal distribution for LMM with log transformed groundspeed across the Bay of Biscay as the dependent variable, bird ID as a random factor and season and bird sex as explanatory variables.

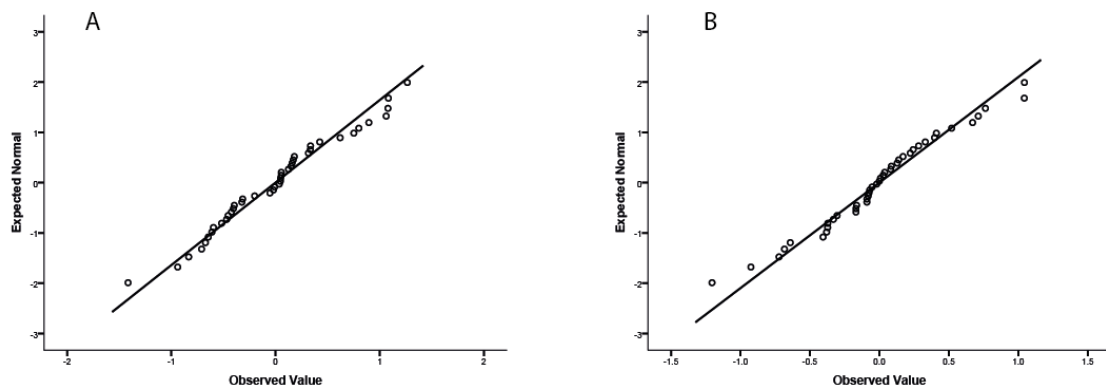


Figure A1.6. Q-Q plots showing model residuals plotted against expected normal distribution for LMMs with logit transformed journey straightness of flights across the Sahara as the dependent variable, bird ID as a random factor and (A) season and bird sex and (B) season, bird sex, day length, headwind, crosswind and boundary layer height as explanatory variables.

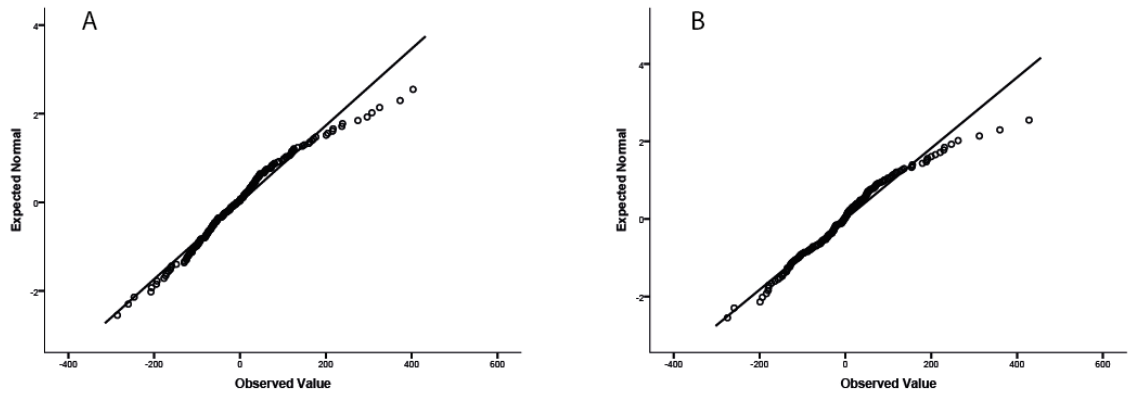


Figure A1.7. Q-Q plots showing model residuals plotted against expected normal distribution for LMMs with daily distance flown during flights across the Sahara as the dependent variable, bird ID as a random factor and (A) season and bird sex and (B) season, bird sex, day length, headwind, crosswind and boundary layer height as explanatory variables.

Appendix 2

Supplementary material – chapter 3.

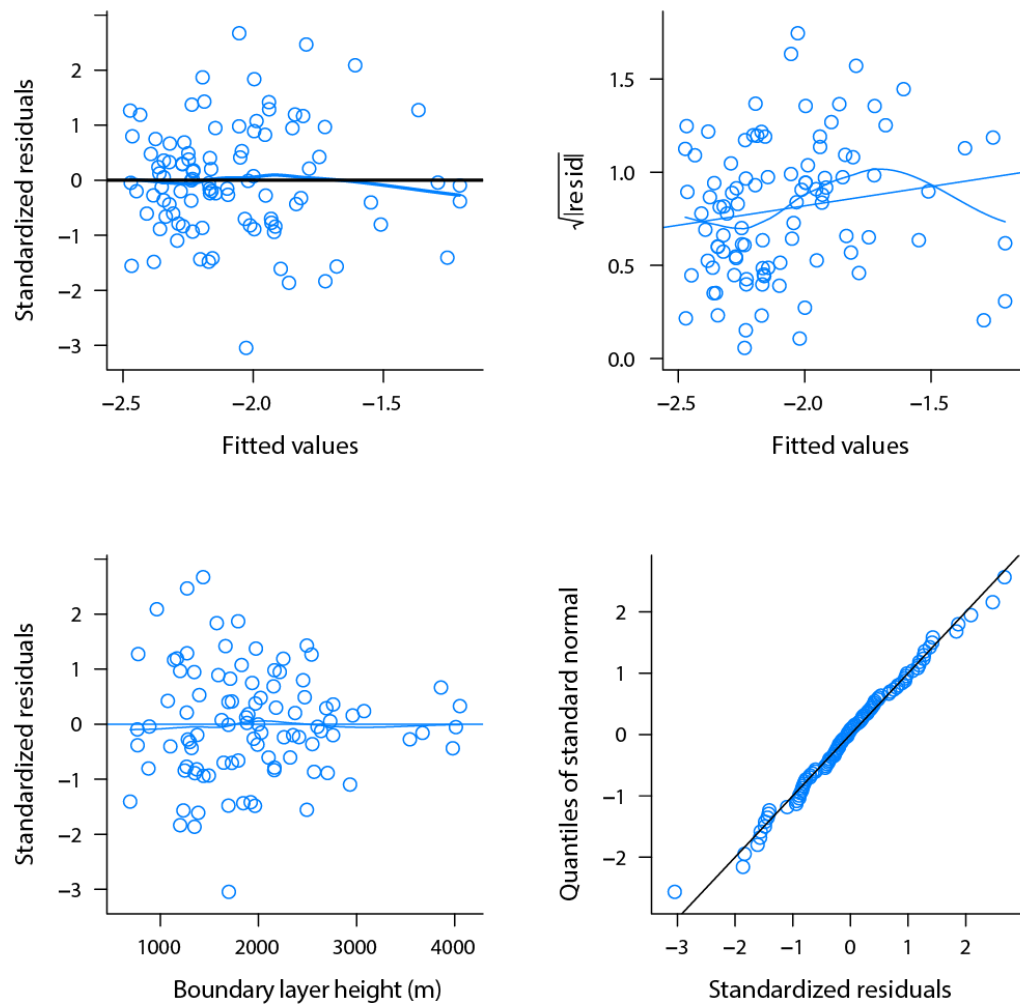


Figure A2.1. Diagnostic plots of model fit for model predicting flight method over land.

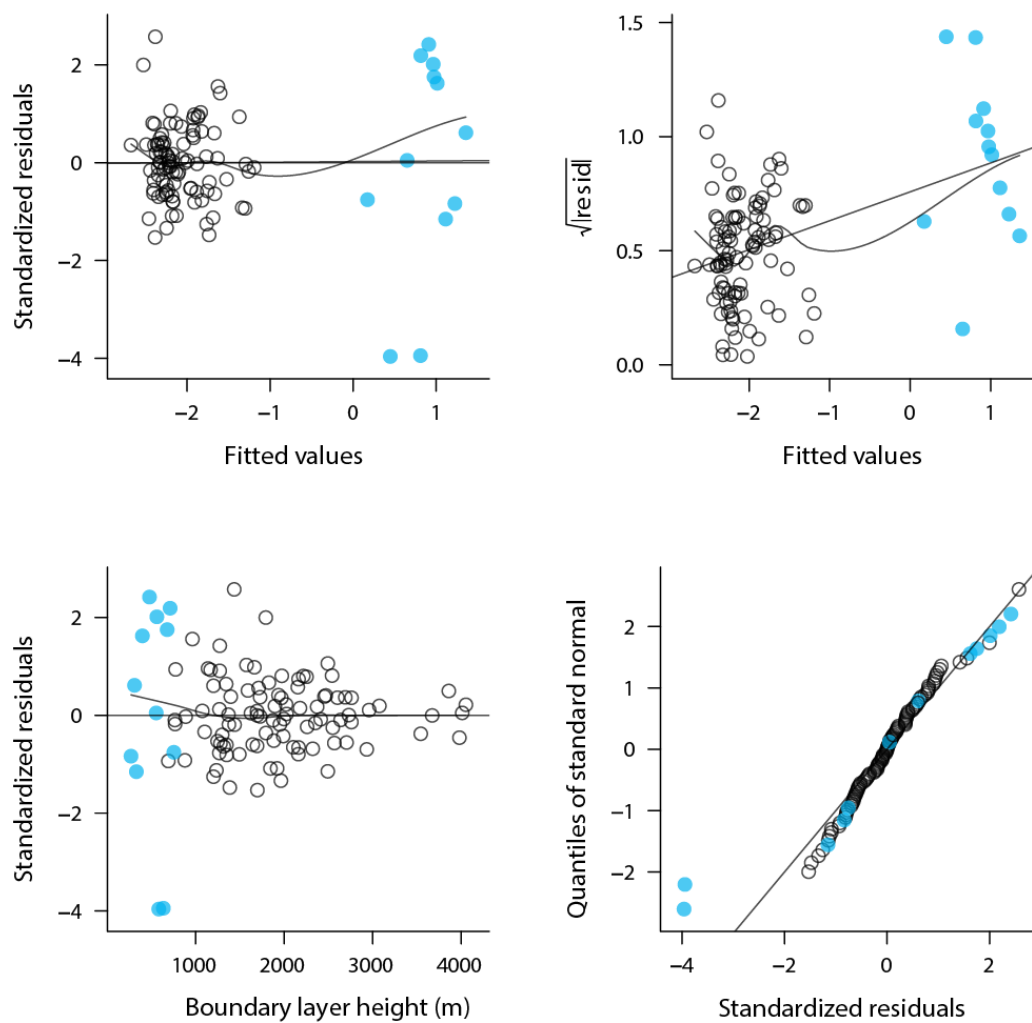


Figure A2.2. Diagnostic plots of model fit for the model predicting flight over land and ocean. *Flights over land are indicated by circles with a black border, ocean flights are indicated by blue circles.*

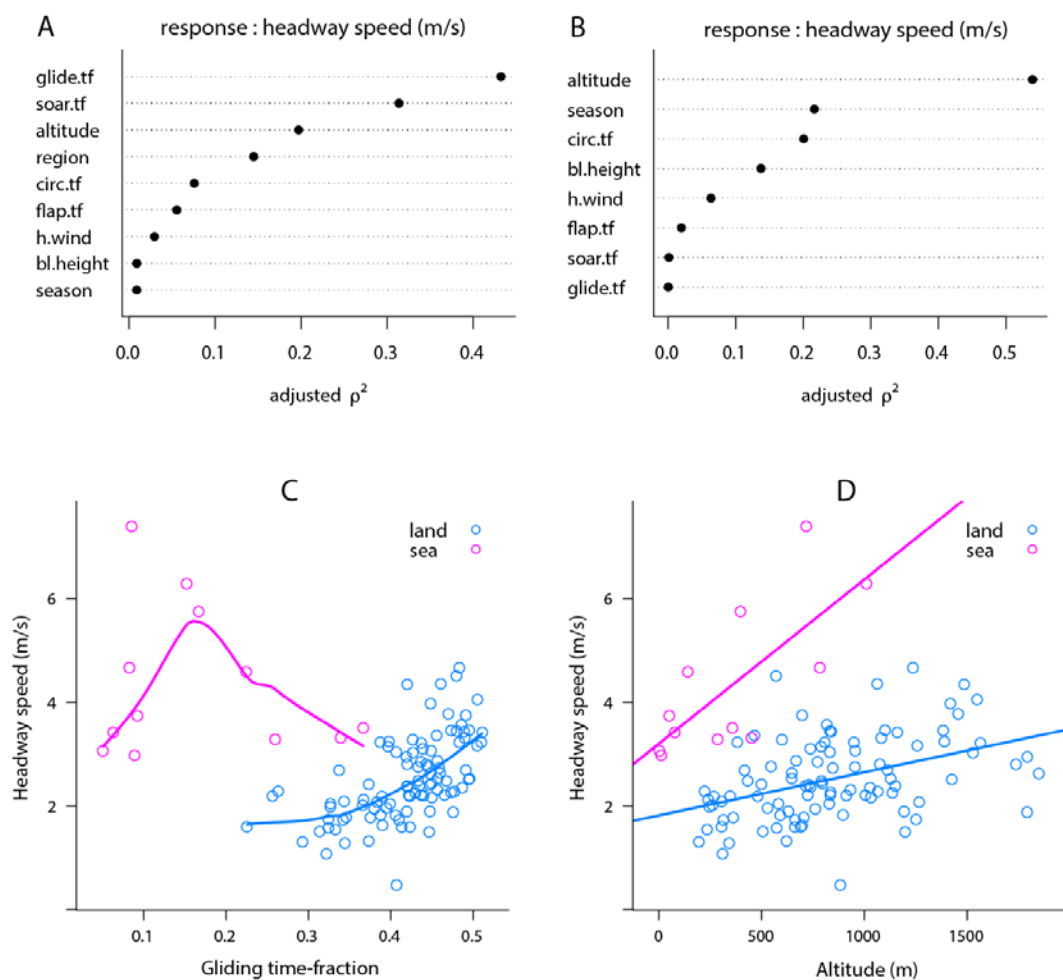


Figure A2.3. A,B: Univariate associations (Spearman's rank correlation ρ^2) between candidate explanatory variables and headway / time over land (A) and ocean (B). **C,D:** Relationships between headway speed / time and key explanatory variables: gliding over land (C) and altitude over ocean (D). In both C and D, land flights are shown in blue and ocean flights in pink. Abbreviated variable names: *bl.height*, boundary layer height; *circ.tf*, circling time-fraction (TF); *flap.tf*, flapping TF; *glide.tf*, gliding TF; *h.wind*, headwind; *soar.tf*, soaring TF.

Table A2.1. Spearman's rank correlations between headway speed / time over land and candidate explanatory variables. Abbreviated variable names: *bl.height*, boundary layer height; *circ.tf*, circling time fraction (TF); *flap.tf*, flapping TF; *glide.tf*, gliding TF; *h.wind*, headwind; *soar.tf*, soaring TF. *Adj. ρ^2* , adjusted ρ^2 .

Variable	ρ^2	<i>F</i>	<i>df</i> ₁	<i>df</i> ₂	<i>P</i>	Adj. ρ^2	<i>N</i>
<i>h.wind</i>	0.029	2.88	1	95	0.0928	0.019	97
<i>flap.tf</i>	0.055	5.57	1	95	0.0203	0.045	97
<i>bl.height</i>	0.009	0.86	1	95	0.3572	-0.002	97
<i>region</i>	0.145	3.89	4	92	0.0057	0.108	97
<i>season</i>	0.009	0.85	1	95	0.3583	-0.002	97
<i>soar.tf</i>	0.314	43.45	1	95	< 0.0001	0.307	97
<i>glide.tf</i>	0.432	72.36	1	95	< 0.0001	0.426	97
<i>circ.tf</i>	0.076	7.79	1	95	0.0064	0.066	97
<i>altitude</i>	0.197	23.32	1	95	< 0.0001	0.189	97

Table A2.2. Spearman's rank correlations for headway speed / time over ocean and candidate explanatory variables. Abbreviated variable names: *alt*, altitude; *bl.height*, boundary layer height; *circ.tf*, circling time fraction (TF); *flap.tf*, flapping TF; *glide.tf*, gliding TF; *h.wind*, headwind; *soar.tf*, soaring TF. *Adj. ρ^2* , adjusted ρ^2 .

Variable	ρ^2	<i>F</i>	df ₁	df ₂	<i>P</i>	Adj. ρ^2	<i>N</i>
<i>h.wind</i>	0.063	0.68	1	10	0.4299	-0.030	12
<i>flap.tf</i>	0.020	0.20	1	10	0.6646	-0.078	12
<i>bl.height</i>	0.137	1.59	1	10	0.2356	0.051	12
<i>season</i>	0.216	2.76	1	10	0.1275	0.138	12
<i>soar.tf</i>	0.001	0.01	1	10	0.9141	-0.099	12
<i>glide.tf</i>	0.000	0.00	1	10	0.9656	-0.100	12
<i>circ.tf</i>	0.201	2.51	1	10	0.1443	0.121	12
<i>alt</i>	0.539	11.70	1	10	0.0065	0.493	12

Appendix 3.

Fit of models described in chapter 4

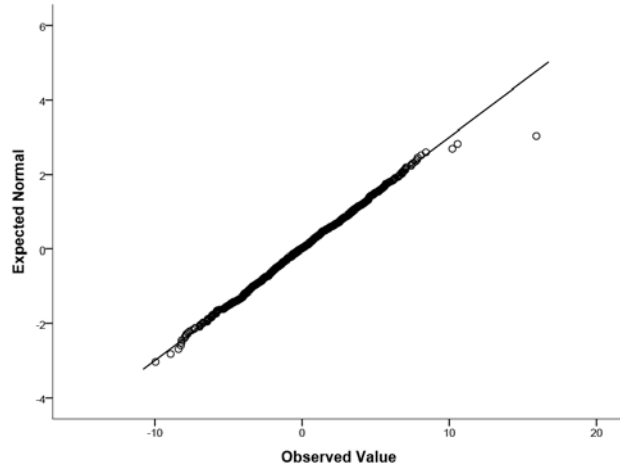


Figure A3.1. Q-Q plot showing model residuals plotted against expected normal distribution for LMM with groundspeed as the dependent variable, bird ID as a random factor and headwind, crosswind and boundary layer height as explanatory variables.

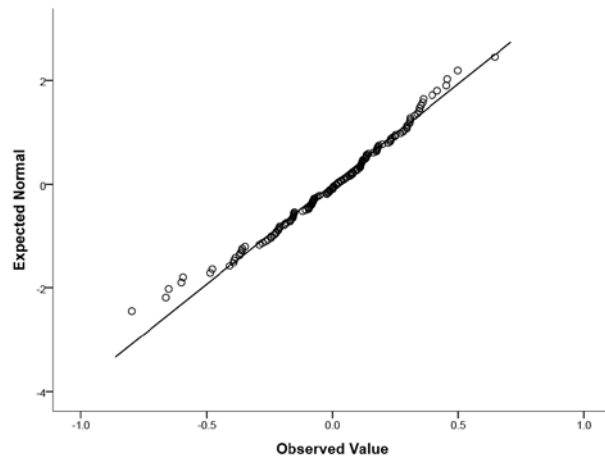


Figure A3.2. Q-Q plot showing model residuals plotted against expected normal distribution for LMM with log transformed sector distance as the dependent variable, bird ID as a random factor and day length, headwind, crosswind and boundary layer height as explanatory variables.

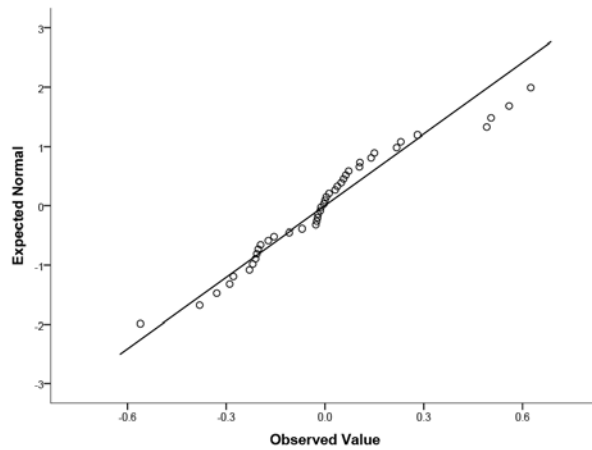


Figure A3.3. Q-Q plot showing model residuals plotted against expected normal distribution for LMM with logit transformed journey straightness as the dependent variable, bird ID as a random factor and bird age as the explanatory variable.

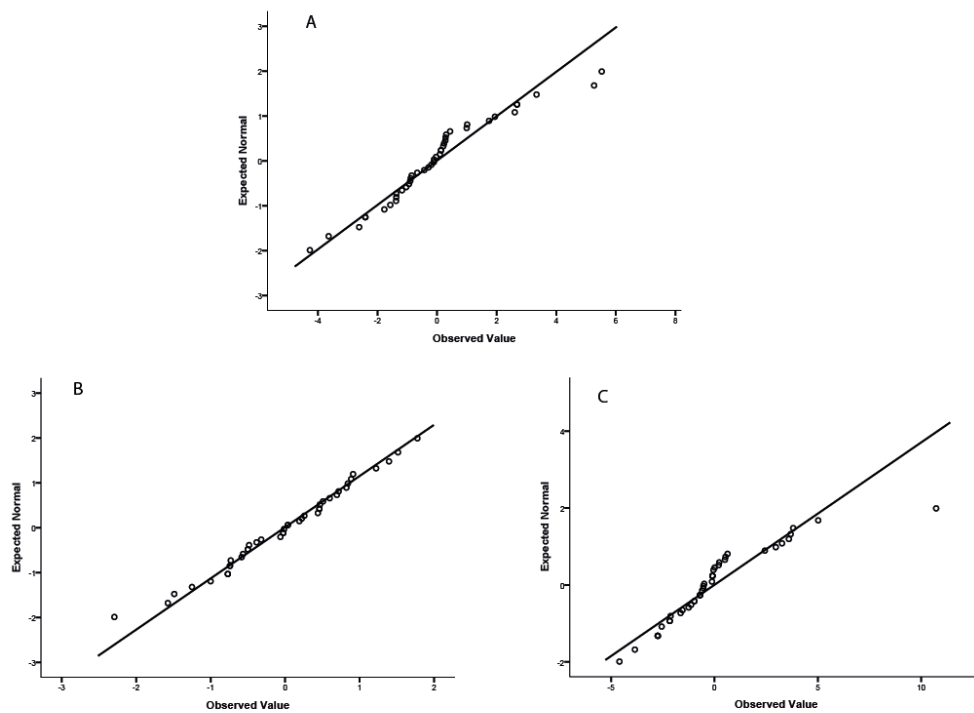


Figure A3.4. Q-Q plot showing model residuals plotted against expected normal distribution for GLMM with A) total days, B) travel days and C) stop-over days as the dependent variable, bird ID as a random factor and bird age as the explanatory variable.

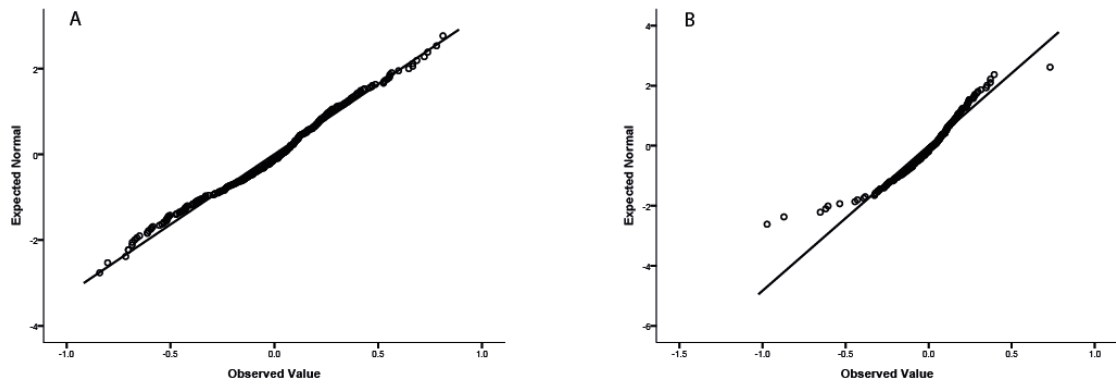


Figure A3.5. Q-Q plot showing model residuals plotted against expected normal distribution for LMM with A) log transformed daily/sector distance in Europe, B) log transformed daily/sector distance in Africa as the dependent variable, bird ID as a random factor and bird age as the explanatory variable.

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