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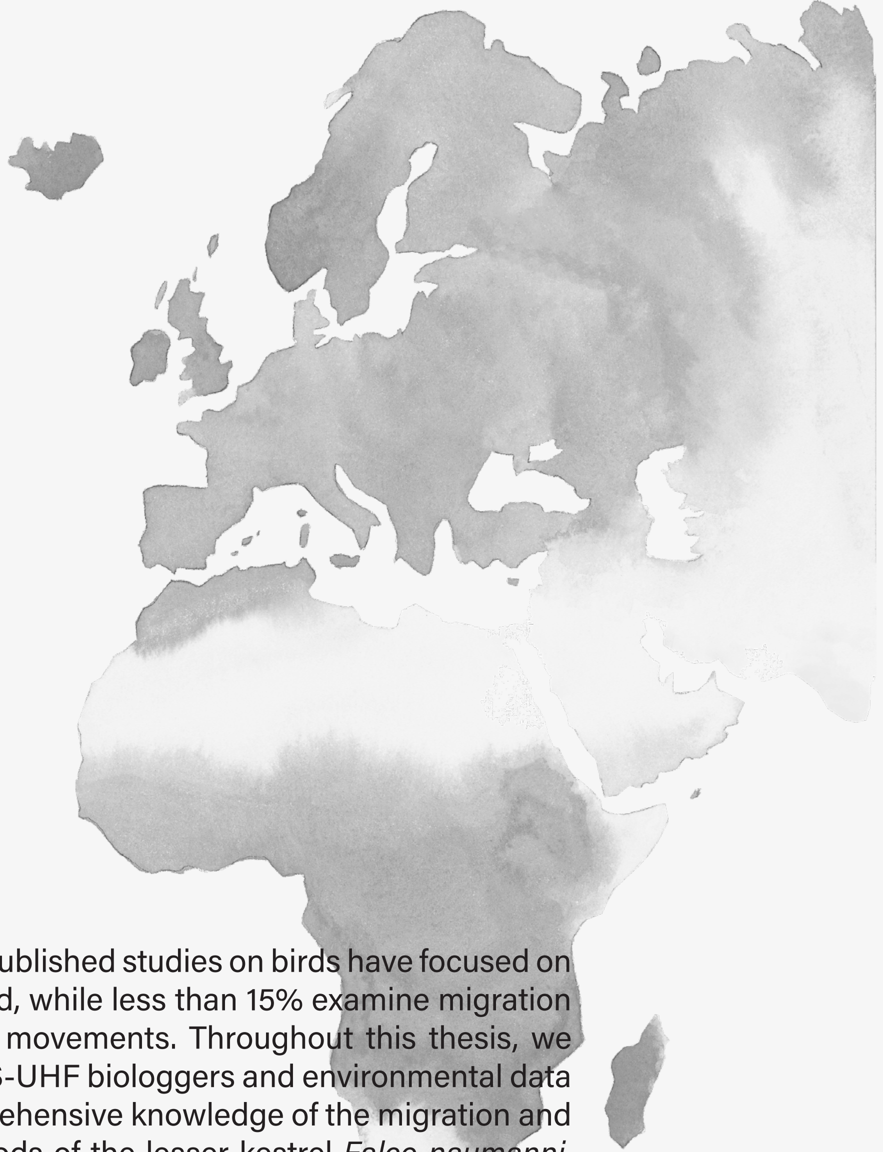

So far, 70% of the published studies on birds have focused on the breeding period, while less than 15% examine migration and non-breeding movements. Throughout this thesis, we combine solar GPS-UHF biologgers and environmental data to provide a comprehensive knowledge of the migration and non-breeding periods of the lesser kestrel *Falco naumanni*. Besides confirming previous findings and providing further insights on where and when the lesser kestrels migrate, we conclude that they exhibited great behavioural plasticity in migration. Lesser kestrels showed an effective barrier crossing by travelling through the night in addition to the day. Furthermore, we confirmed an itinerary lifestyle in West Africa, including either westward or eastward movements through intermediate sites to converge at their last staging sites in wetlands. Finally, we found a large interindividual variation in migration schedule driven by the breeding site phenology.

LINA LÓPEZ RICAURTE
PHD THESIS 2022

MIGRATORY BEHAVIOUR AND NON-BREEDING MOVEMENTS OF THE LESSER KESTREL REVEALED THROUGH GPS TECHNOLOGY

LINA LÓPEZ RICAURTE
PHD THESIS 2022

Migratory behaviour and non-breeding movements of the lesser kestrel revealed through GPS technology

Lina López Ricaurte
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Thesis:
Migratory behaviour and non-breeding
movements of the lesser kestrel revealed through
GPS technology

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Migratory behaviour and non-breeding movements of the lesser kestrel revealed through GPS technology

A thesis presented for the degree
of Doctor at the University of Pablo de Olavide
by **Lina López Ricaurte**

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Estación Biológica de Doñana CSIC

UNIVERSIDAD PABLO DE OLAVIDE SEVILLA

Dr. Javier Bustamante Díaz, Investigador Científico en la Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (EBD-CSIC) como director y tutor, y Dr. Jesús Hernández Pliego como investigador miembro del equipo científico del proyecto: KESTRELS-MOVE (2017-2020, CGL2016-79249-P), como co-director

CERTIFICAN:

Que los trabajos de investigación desarrollados en la Memoria de Tesis Doctoral "Migratory behaviour and non-breeding movements of the lesser kestrel revealed through GPS technology" son aptos para ser presentados por la Licenciada Lina López Ricaurte ante el Tribunal que en su día se designe, para aspirar al grado de Doctora por la Universidad Pablo de Olavide.

Y para que así conste, y en cumplimiento de las disposiciones legales vigentes, firman el presente documento en Sevilla, a 8 de junio de 2022.

Javier Bustamante

DIRECTOR Y TUTOR

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FDO. DR. JESÚS HERNÁNDEZ PLIEGO

A Laïa

CONTENTS

RESUMEN

Multitud de especies de animales se ven obligadas a desplazarse miles de kilómetros cada año en respuesta a cambios en las condiciones ambientales, para así sobrevivir y reproducirse. De entre los distintos grupos que migran, las aves llevan a cabo los desplazamientos más complejos y sus rutas migratorias abarcan la práctica totalidad de la superficie terrestre. Este fenómeno está presente en miles de especies de aves y alrededor de 200 son aves rapaces.

Hasta el momento, el 70% de los trabajos relacionados con aves se han enfocado en el periodo reproductor y menos del 15% se centra en el período no reproductor, que comprende la migración e invernada. Esta falta de conocimiento es especialmente importante, teniendo en cuenta que ciertas especies migradoras, por ejemplo, de larga distancia, pueden llegar a pasar hasta el 80% del ciclo anual en sus áreas de invernada.

Los avances tecnológicos recientes en el seguimiento a distancia de animales, tales como la miniaturización de dispositivos de GPS (Global Positioning System), han permitido seguir en detalle a números representativos de aves de pequeño a mediano tamaño durante todo su ciclo anual. De este modo, se ha incrementado el conocimiento sobre el comportamiento de las aves y sus movimientos migratorios. Además, dichos avances tecnológicos, junto con la mayor disponibilidad de datos de teledetección, han permitido estudiar la ecología de especies migratorias que se desplazan hasta latitudes tropicales y los peligros potenciales a los que se enfrentan en estos lugares, a veces remotos y de difícil acceso

En esta tesis hemos utilizado dispositivos GPS solares que descargan sus datos vía radio UHF (ultra alta frecuencia) y datos ambientales para profundizar en el conocimiento del período no reproductor de un halcón insectívoro de pequeño tamaño. Utilizamos un migrador Afro-Paleártico – el cernícalo primilla *Falco naumanni* – como especie modelo. Sus movimientos migratorios y de invernada han sido estudiados previamente mediante lecturas de anillas, el trabajo de campo *in situ* y el marcaje con geolocalizadores y emisores vía satélite (PTT). Dichos estudios han aportado información valiosa como la identificación de sus áreas de invernada en África y descrito sus rutas migratorias.

Gracias a la colaboración entre distintos grupos de investigación de España e Italia, el presente estudio cuenta con información de 73 cernícalos primilla adultos marcados en distintas colonias entre 2014 y 2021. En el **capítulo 1**, analizamos los factores que modulan los itinerarios de viaje y las velocidades de migración de una especie de vuelo generalista. Utilizamos datos de GPS de 70 adultos provenientes de 33 colonias diferentes de cría de España e Italia. En primer lugar, corroboramos los resultados de trabajos anteriores en relación a una migración pos-nupcial más rápida que la pre-nupcial. En segundo lugar, y contrario a nuestras expectativas, los vientos de cola a lo largo de las rutas migratorias resultaron en mayores distancias diarias recorridas y mayores velocidades de viaje durante la migración post-nupcial respecto a la pre-nupcial. No encontramos evidencias para apoyar la hipótesis de que los cernícalos migren con más urgencia durante el viaje pre-nupcial. Además, los factores geográficos modularon los itinerarios de viaje y se observó una tendencia de los primillas a hacer *sprints,* tanto de día como de noche, mientras atravesaban barreras geográficas como el Desierto del Sahara y el Mar Mediterráneo. Por el resto de zonas migraron más despacio y particularmente de día. En conclusión, mostramos que los factores externos (los vientos y factores geográficos) son más importantes que los internos (sexo) y la motivación estacional a la hora de explicar la variación en el comportamiento migratorio de este pequeño halcón de vuelo generalista, a pesar de su capacidad para alternar entre distintos modos de vuelo.

En el **capítulo 2** analizamos los factores que influencian la secuencia temporal de la migración pre-nupcial en el cernícalo primilla de diferentes colonias de cría ubicadas en un gradiente de latitud y longitud. Nuestros resultados demuestran que existe una gran variación interindividual, con una ventana de migración que se extiende a lo largo de tres meses. La ubicación de la colonia de cría es la principal fuente de variación que afecta al momento de la migración pre-nupcial, y no existen diferencias significativas entre sexos. Los cernícalos primilla procedentes de colonias ubicadas más hacia el suroeste salen antes de sus áreas de invernada en África y llegan antes a sus colonias de cría en el Mediterráneo en comparación con los individuos que se reproducen en colonias más hacia el noreste. Así mismo, la temperatura de la colonia de cría en primavera es un factor determinante de la fecha de llegada, con los primillas llegando antes a las colonias en

zonas más cálidas. También demostramos que la fecha de salida de los sitios de invernada en África es más importante que la velocidad de viaje o la duración de las paradas a la hora de explicar la variación interindividual en las fechas de llegada. Finalmente, los cernícalos primilla tienden a realizar un mayor número de paradas cuando los vientos en ruta son desfavorables o cruzan zonas con mayor productividad de vegetación, especialmente tras superar el Desierto del Sahara.

En el **capítulo 3** nos trasladamos al periodo de invernada en África Occidental para estudiar en detalle la estrategia de movimiento y las diferencias entre sexos. Además, investigamos el uso de hábitat a escala regional. Para ello, analizamos datos de movimiento de 61 cernícalos procedentes de España. Los resultados muestran que la mayoría de individuos, tanto machos como hembras, realizan movimientos itinerantes entre dos o tres áreas durante el período invernal. Observamos que los cernícalos llegan dispersos al interior de África Occidental –desde la frontera de Senegal hasta la parte más al este de la frontera entre Mauritania y Mali. Sin embargo, en contra de nuestra hipótesis de partida y de otras especies insectívoras, no se desplazan a lo largo de un eje norte-sur en el Sahel. Por el contrario, realizan movimientos longitudinales hacia el oeste o el este utilizando zonas intermedias para congregarse finalmente en áreas cercanas a humedales en las costas de Senegal o al este de Mauritania en la frontera con Mali. Aunque las causas de estos patrones espaciales están pendientes de estudiar, una posible hipótesis es que estas zonas húmedas tengan una mayor disponibilidad de alimento.

ABSTRACT

Every year, animals move hundreds to thousands of kilometres in response to seasonal changes in resource availability and abundance to which they must adapt if they are to survive and reproduce. More than any other group of animals, birds carry out the most complex journeys, and their migration routes encompass most of the Earth's surface. Among thousands of migratory birds, 200 species are raptors.

So far, 70% of the published studies on birds have focused on the breeding period, while less than 15 % examine migration and non-breeding movements. Importantly, long-distance migrants may spend the majority of their annual cycle at their non-breeding areas. This means that we still know relatively little about the migration and non-breeding period, which comprise up to 80% of the total annual cycle for some long-distance migrants.

Recent advances in tracking technology, such as miniaturised GPS tracking devices, have enabled us to follow representative number of small to medium-sized migrant birds in great detail and across their annual cycle. This has improved our understanding of bird migratory movements and behaviour considerably. Furthermore, these technological advances combined with remote sensing environmental data allow us to study the non-breeding ecology of migrants moving into tropical latitudes and the potential threats they face in such distant, often hard to access non-breeding areas.

In this research, we use a combination of solar GPS-UHF biologgers and environmental data to provide a comprehensive knowledge of the migration and non-breeding periods of a small-sized migratory falcon. We use an Afro-Palearctic migratory bird – the lesser kestrel *Falco naumanni* – as model species. The migration and non-breeding movements of the lesser kestrel have been mainly studied through ringing, field-based studies, light-level geolocators and satellite tracking. Such studies have provided valuable information on migration routes and non-breeding locations of west European breeding lesser kestrel. A great collaborative effort among environemental and research groups in Spain and Italy has allowed us to gather an impressive dataset of movement data of 73 adult lesser kestrels from different European colonies tracked between 2014 and 2021.

In **chapter 1**, we study the migration period by disentangling the influence of external factors (wind, geography), internal factors (sex) and season in shaping the daily travel schedules and flight speeds of a flight-generalist raptor. We used GPS-tracking data from 70 adults from 33 breeding colonies from Spain and Italy. We confirmed previous findings of a faster post than pre-breeding migration. We show that, due to the southern component of Trade winds, lesser kestrel experience more favourable winds along their realised travel direction during the post-breeding migration resulting in longer daily distances and faster travel speeds. We did not find any evidence that pre-breeding migration is more time-constrained than post-breeding migration in the lesser kestrel. Furthermore, geographical barriers mould regional differences in daily distances by shaping daily travel time budgets, with a propensity for sprinting across barriers. In both seasons, lesser kestrels sprinted across ecological barriers (the Sahara Desert and the Mediterranean Sea) and frequently migrated during the day and night. Conversely, they travelled at a slower pace and mainly during the day over non-barriers. We show that external factors have a greater influence than internal factors and season in explaining variation in migratory behaviour of a flight generalist, despite its ability to switch between flight modes.

In **chapter 2,** we take a closer look at the pre-breeding migration timing of lesser kestrels from different breeding locations spanning across a gradient of latitude and longitude. Lesser kestrels show a large variation in migration timing that extend over a three-month period. We found that the location of the breeding colony (latitude and longitude) explained most of interindividual variation in migration timing, whereas sex had no effect. The birds breeding in more southwestern colonies departed earlier from west African non-breeding grounds and arrived earlier to their Mediterranean colonies relative to birds breeding in more northeastern sites. We show that spring temperature at the breeding colony is an important factor in determining arrival date, with lesser kestrels arriving earlier to locations with warmer spring temperatures. Our results confirm that departure date from the non-breeding areas plays a more important role in early arrival than travel speed or duration of stopovers. When birds compromised in stopovers, they did so under adverse wind conditions or over areas with higher vegetation productivity, usually after crossings barriers.

In **chapter 3**, we move from the migration to the non-breeding period in West Africa and look into the non-breeding movement strategy and test for differences between sexes. Furthermore, we investigate habitat use at a

broad scale. Using GPS-tracking data from 61 adults breeding across Spain, we showed that male and female kestrels make itinerary movements between 2-3 consecutive staging sites in West Africa. We observed that at arrival kestrels spread out over the interior of West Africa – from the northeast Senegalese border to the easternmost part of the Mauritania-Mali border. Contrary to our expectations and to other locust-eating steppe birds, however, kestrels did not move along a north-south axis in the Sahel. Instead, they moved either westward or eastward through intermediate sites to converge at their last staging sites at coastal wetlands in Senegal or inland wetlands in eastern Mauritania at the border with Mali, respectively. Although the factors driving these movement patterns need further study, we suggest that the longitudinal movements are caused by a search for wetlands where food availability is expected to be higher.

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Understanding how animals respond and adapt to changes in their environment is a major area of research for ecologists. For example, a common response to the Earth's seasonal shifts in the amount of light, temperature and food availability is migration. It occurs in almost all forms of life – from bacteria to vertebrates. The American Monarch butterfly (*Danaus plexippus*) migrates up to 4000 km from its northernmost resident places in Canada to its wintering grounds in Mexico. The green turtle (*Chelonia mydas*) covers 3000 km to reach an specific beach to lay its eggs. Several gregarious terrestrial species, such as the reindeer *(Rangifer tarandus)* and wildebeest *(Connochaetes taurinus)*, cover up to 1500 km annually (Baker, 1991). Nevertheless, more than any other group of organisms, birds carry out the most complex and extensive migrations. Their ability to fly, the size, the homeothermy, and the morphological diversity coupled with a great ecological differentiation make them well adapted to a migratory lifestyle (Berthold, 2001).

Migratory species encounter varying environmental conditions in different stages of their journeys. Particularly, migratory birds will be affected by environmental conditions in their breeding grounds, wintering quarters and stopovers sites, sometimes thousands of kilometres apart, making them remarkably challenging to study. Moreover, they should optimise their migration routes and schedules according to the different environmental factors *en route*, like weather and food availability. Long-distance migrants have to cross harsh environments like deserts and seas with few or no resting, feeding, or drinking opportunities.

While over 70% of the published studies on birds have focused on the breeding period, less than 15% of the studies examine migration and non-breeding movements (Marra et al., 2015). This is an important gap in knowledge, considering that long-distance migratory birds often spend 9-10 months of the year outside their breeding grounds (Newton, 2004; Studds et al., 2005; Salewski & Jones, 2006). However, the rapid advancement of lighter and cheaper technologies has opened new horizons to study the movement patterns of increasingly smaller species and across the complete annual cycle

(Kays et al., 2015). In this research, we used a combination of GPS tracking and environmental data to provide a comprehensive knowledge of the migration and non-breeding movements in Africa of a small-sized raptor species.

Internal and external factors shaping migratory behaviour

The way migrants undertake their complex journeys often shows great spatio-temporal flexibility in behaviour (Akesson & Helm, 2020). This flexibility is governed by an interplay between (1) internal drivers, such as motion capacity (dependent on, for example, wing morphology), orientation ability (e.g. age), and the individuals' age, sex and/or reproductive state that shape the internal motivation to move. For example, reproductive advantages associated with early arrivals of adult males to establish territories during the pre-breeding migration (Kokko et al., 1999; Nilsson et al., 2013); and (2) environmental drivers such as weather conditions and geographical barriers that influence connectivity (Nathan et al., 2008; Alerstam, 2011). Finally, the daily cycle along the four seasons, with their characteristic features, bring with them constant changes in weather conditions influencing migratory behaviour, e.g. flight mode (soaring, flapping) or foraging patterns (Mueller et al., 2013; Miller et al., 2016).

Flight modes during migration

The adaptation of migratory birds to a particular flight mode is determined mainly by atmospheric currents, weather and biometrical constraints (Bildstein, 2005). Soaring flight results from such adaptation in large birds with high wing loading (calculated by dividing body mass by wing surface area), such as pelicans, storks and vultures (Nourani et al., 2017 and references there). Because the energetic cost of flight increases with body size (Pennycuick, 2008), flapping in such birds is highly costly. Conversely, their wings have evolved in such a way as to use atmospheric currents such as wind, updrafts and thermals to subsidise the energy required for flight (Hedenström, 1993).

Lighter migratory birds can be well adapted for flapping flight as well as for both flapping and soaring flight, the so-called 'flight generalist'). On the one hand, flapping flight is typically use by smaller birds, including obligate-flapping passerines and waders, for which the energetic cost of flapping flight is relatively smaller compared to larger and heavier species. On the other hand, flight generalists, such as bee-eaters, falcons and harriers, have intermediate body size and long slender wings; they can sustain flapping or soaring-gliding flight for long-distance/periods depending on environmental conditions. Thus, these birds are potentially less constrained by suitable atmospheric conditions compared to obligate-soaring migrants. Birds using flapping flight are assisted by winds that blow along the migratory route (tailwinds) to the same extent as soaring birds but are less affected by crosswinds, in contrast to larger birds which inevitably drift from their intended direction with every thermal ascent (Vansteelant et al., 2015).

Geography-effects on migratory behaviour

The flight mode may constrain the routes that migratory birds can use. For instance, soaring migrants, are usually restricted to fly over land and during the day, concentrate at bottlenecks, such as the Strait of Gibraltar (Martín et al., 2016), Eliat in Israel (Lott, 2002) and South-west Georgia (Verhelst et al., 2011) in order to avoid long energy-demanding sea-crossings (Mackrill, 2017). Such soaring migrants make long detours during migration to pass through these locations rather than taking a more direct route across the water (e.g. short-toed eagles, *Circaetus gallicus*, Panuccio et al. 2012). However, birds that show the ability to migrate long distances by flapping flight also can migrate by night when thermal updrafts are weaker. Furthermore, birds typically achieve higher speeds during nocturnal than diurnal migration, enabling them to cross barriers in non-stop flights (“sprints”). For example, curlews (*Numenius madagascariensis*) undertake a long, non-stop water crossing, taking 3 - 5 days to cross the Pacific Ocean between Australia and China (ca. 6500 km), flying day and night (Driscoll and Ueta 2002). Nocturnal travellers include species that have to undertake long journeys across the water, such as the Chinese sparrowhawks (*Accipiter soloensis*) and grey-faced buzzards *(Butastur indicus*) migrating between Japan and the Philippines through Ryukyu Islands and Taiwan or Amur falcons crossing the Indian Ocean between India and East Africa. Such extreme flights require birds to deposit sufficient fuel to power the entire migratory flight, which they may do prior to completing the migration, and often also during migration by (a) making re-fuelling stops, often referred to as stopovers (Alerstam, 2011) or (b) intermittent diurnal fly-forage, i.e. combination of foraging and flying in the migratory direction (Strandberg et al., 2007).

Migration timing

Migrating birds set off on long journeys from their non-breeding areas so as to arrive at their nesting areas not only synchronised with the most appropriate conditions for breeding but also to what their conspecifics are doing (Berthold, 2001; Newton, 2008). An early arrival allows them to secure better territories and mates and gain additional time to restore their body condition or renest if the first attempt fails (Marra et al., 1998; Halupka et al., 2008). However, arriving too early might expose birds to scarce food resources, thereby decreasing survival. Potential factors affecting migration timing include sex, age (Rubolini et al., 2004; Bildstein, 2006), differences in the timing of the life cycle events (Briedis et al., 2016), flexible responses to the phenology of the environment along the migratory route (Akesson & Helm 2020), the location of the breeding site (Conklin et al., 2010) or post-glacial colonisation patterns of the species (Hewitt, 2000; Perez-Tris et al., 2004).

Migration timing is under strong endogenous control (Gwinner, 1996; Gwinner & Helm, 2003) in response to external cues such as photoperiod (Burnside et al., 2021). However, weather could also trigger the onset of migration (Liechti & Bruderer, 1998). For example, large obligate-soaring raptors aggregated on the eastern Black Sea coast avoided taking off when clouds developed over interior mountains limiting thermal formation (Vansteelant et al., 2014). Climatic conditions also influence migration timing. For example, Filippi-Codaccioni et al. (2010) used a dataset comprising 28 years of migration counts (1981-2008) to show that long-distance migratory raptors have advanced their autumn migration passage dates over the Pyrénées-Atlantiques (south-west France), likely due to climate change.

Non-breeding period

After breeding, seasonal migrants travel to a site or sites to spend the boreal winter (Newton, 2008). These sites may be small, defined places where they could be resident throughout the whole period between the post and the pre-breeding migration. For example, the Whooping crane (*Grus americana*) flies from North America to a wetland in the Gulf of Mexico near Corpus Christi each year. Increasing numbers of northern European whooper swan (*Cygnus cygnus*) spend the winter confined at Lake Constance every year (Berthold, 2001). Passerines such as the Robin (*Erithacus rubecula*) and the marsh warbler (*Acrocephalus palustris*) move to one permanent resident area where they often establish territories, mark them by singing and defend them in some cases longer time than they defend their breeding territories (Berthold, 1996). Other species, however, overwinter in vast regions, exhibiting a nomadic behaviour (e.g. the blackcap, *Sylvia atricapilla*, wintering in the Mediterranean) (Cuadrado et al., 1995). An intermediate strategy to residency and nomadic lifestyles is itinerancy, occupying two or more residence areas during the course of the non-breeding season in succession and repeating destinations over consecutive years (Moreau, 1972). This behaviour seems to be a commonly used strategy among Palearctic birds (Trierweiler et al., 2013). For example, tawny pipits (*Anthus campestris*) use an itinerant strategy while in Western Sahel, with individuals moving westwards from the arrival site in mid-December, thus using two core wintering sites (Briedis et al., 2016). Even species thought to be nomadic migrants (Newton, 2008) have been proved to be itinerant. For example, Meyburg et al. (2015) revealed that the lesser spotted eagle (*Clanga pomarina*), concentrates and rotates its activity in certain core areas in the Sahel. Similarly, Montagu's Harrier (*Circus pygargus*), a presumed nomadic migrant by García & Arroyo moves through three to four core wintering sites in a north-south direction within the Sahel (García & Arroyo, 1998; Schlaich, 2019).

Advances in tracking technology

In recent years significant advances in tracking technology have greatly aided the study of bird migration (López-López, 2016). Of particular importance was the development of the first generation of satellite transmitters in the 1980s (Meyburg & Meyburg, 2007). At that time, the transmitters weighed 1 kg and were fitted to large migratory mammals such as polar bears (*Ursus maritimus*) and caribous (*Rangifer tarandus*). From 1984 onwards, when the weight of the transmitters had fallen to below 200 g, scientists were able to carry out pioneering experiments on large bird species such as bald eagles (*Haliaeetus leucocephalus*), swans (*Cygnus buccinator* and *C. columbianus)* and giant petrels (*Macronectes giganteus*) (Berthold, 2001). This technique was still at an experimental stage until 1990, when sufficiently small (185 g including batteries), light and solar-powered PTTs (Platform Transmitter Terminal) linked to the Argos Satellite System came on the market (Meyburg & Meyburg, 2009). Despite the limited accuracy (range from 250 m to 1500 m) of the Argos-based devices, researchers were able to record birds' daily movements during complete migratory journeys, thereby yielding new information on the route, winter range, and migration speed (Börger et al., 2016). The incorporation of GPS (Global Position System) and the increase of data storage and battery capacity (from on-board batteries to solar-powered rechargeable panels) have increased location accuracy to ±20 m and improved data ever since (López-López, 2016).

At the start of the millennium, small light-level geolocators were developed. Such loggers include a light sensor to measure solar irradiance and a real-time clock to calculate local sunrise and sunset times. In short, the day length is used to calculate latitude, while the time of solar noon is used to calculate longitude (López-López, 2016). Geolocators were first used on small-body songbirds in 2007 (Stutchbury et al., 2009). Since then, these devices have become more popular to study the migration and wintering ecology of small and medium-sized birds. In recent years, data loggers have grown in importance mainly due to their capability of integrating GPS positions with other sensors such as accelerometers (Brown et al., 2012) and heart rate (Bowlin et al., 2005), among others. The device is attached or implanted in animals and can register and store information in an on-board memory. Usually, dataloggers must be recovered for data download. Although in more recent devices, data can be remotely downloaded via satellite, Global System for Mobile Communication (GSM network) or through a base station connected with an antenna (López-López, 2016). Improvements in the frequency of data collection (up to 1 Hz), location estimation accuracy, memory storage capacity and the possibility of duty cycle reconfiguration remotely make it possible to undertake a detailed analysis of flight behaviour across entire migratory journeys (López-López 2016).

The rapid development of tracking technology offers new perspectives to study migration, foraging, bioenergetics and physiology in many animal species (López-López, 2016). However, critical questions surround the ethics of obtaining such data and the soundness of estimates derived from it. Several studies have shown that the behaviours of birds can be altered by the attached device (Barron et al., 2010). Others have identified negative impacts on breeding success, survival and flight performance (Constantini & Moller, 2013; Bodey et al., 2018), while others have found no adverse effect on demographic parameters or feeding ecology (Igual et al., 2005). The consensus is that the correct choice of the transmitter (i.e., PTTs, dataloggers, geolocators, etc.) and method of attachment (backpack harness, collar, glue, leg rings, leg-loop backpack harness, implantable transmitters etc.) are keys to reducing potential detrimental effects on birds (Vandenabeele et al., 2013; Blackburn et al., 2016). Most tracking studies follow the recommendation that the weight of the transmitter should not exceed 3-5% of the bird's body mass (López-López, 2016). Although some review studies claim that there is no empirical support for this rule (Barron et al., 2010) and others have found negative effects on survival, reproduction, and parental care even when tags weighed more than 1% of the species' body mass (Browlin et al., 2018). López-López et al. (2016) suggest that the precautionary principle should be respected (tracking should not be carried out if the effects of tagging are unknown or are suspected of detrimental effects in morphologically similar species). It is necessary therefore to further investigate the most appropriate tracking methods, not only the effect of tag mass but also how it affects aerodynamics in flight (López-López, 2016). Trapping, handling and attaching tracking devices requires a set of skills that must be taught and constantly re-evaluated. Sergio et al. (2015) suggest several recommendations to minimise tagging impact, including more rigorous licensing criteria and enforcing attendance at training courses for tagging. Finally, sharing of information and experiences among users should be fostered through blogs, workshops and open symposia.

The lesser kestrel *Falco naumanni*

The lesser kestrel (*Falco naumanni*) is a small insectivorous migratory falcon with a reversed sexual size dimorphism (females being ~15% larger in body mass) (Cramp & Simmons, 1980). It breeds in colonies across southern Europe, northern Africa to China and winters in the Sahel and up to South Africa, although some Mediterranean populations also contain resident individuals (Negro et al., 1991). The Lesser Kestrel is a species of European conservation priority and protected under the Bern convention and Bonn Convention (BirdLife, 2017), which has suffered steep population declines in the second half of the 20th century (Iñigo & Barov, 2010). Currently, the lesser kestrel is now declining in Spain, with the last census indicating that 43% of the population has been lost over the last seven years (Bustamante et al., 2020).

There is a vast knowledge on lesser kestrels' ecology during the breeding period (e.g. foraging and habitat preference, nest-site selection, reproductive biology), but its behaviour during migration and non-breeding period has been little studied. The migration of this species has been studied mostly using geolocators (Rodríguez et al., 2009; Catry et al., 2011), and satellite telemetry (Limiñana et al., 2012 & 2013), shedding light on routes, timing and wintering areas. Sarà et al. (2019) used GPS tracking to assess the migration connectivity (the mixing of individuals from different breeding areas during the non-breeding period) between three European lesser kestrel populations (Iberian, Italian, and Balkan).

MATERIALS AND METHODS

MATERIALS AND METHODS

GPS-UHF biologgers and data collection

We used GPS-tracking data collected between 2014-2020 from 73 adult lesser kestrels using three models of solar GPS-UHF biologgers (Pica, Ecotone, Gdynia, Poland; Microsensory LS, Córdoba, Spain; and NanoFix GEO+RF, Pathtrack Ltd., Leeds, UK., weighing 4-5 g). Lesser kestrels were tagged at 33 breeding colonies in Spain and Italy by different organisations (GREFA; The Spanish Society of Ornithology, SEO/BirdLife; Terra Naturalis, and Doñana Biological Station, EBD; Italian Institute for Environmental Protection and Research, ISPRA). The GPS-UHF biologgers weighted less than 4% of the birds' total mass and were attached as backpacks with a Teflon harness. As GPS-UHF biologgers were deployed for different projects by different teams, they were programmed with different schedules (see Supplementary Methods for details). Locations were stored on-board and later downloaded via a UHF base station placed near the breeding colony.

Environmental data annotation during migration

Underlying geographies

We assigned each GPS fix to one of three geographical categories, flying over the desert or over the sea (barriers) and flying outside these two regions (non-barriers) using the Global Biomes map (Olson et al., 2001). We used the 'join-attribute-by-location' tool in QGIS to join all the tracks to the corresponding position within the Global Biomes map.

Weather

Each GPS fix was annotated with environmental data of wind and boundary layer height using the Env-DATA track annotation tool of Movebank (Dodge et al., 2013). For each GPS point, we obtained: the boundary layer height (BLH) (in km), an estimate for thermal updraft formation at a spatial resolution of 0.75 degrees and temporal resolution of 3 hours; and the U (west-east) and V (north-south) wind components (km/h) at a spatial resolution of 0.75 degrees and temporal resolution of 6 hours from the ECMWF (European Center for Medium-Range Weather Forecast). To compute hourly tailwind and absolute crosswind, V- wind and U-wind components were combined in a single vector adding hourly flight direction in degrees to the north and wind strength (Vansteelant et al., 2015). We determined tailwind strength and absolute crosswind strength relative to the realised hourly travel direction of migration. We used weather data from the 925 hPa pressure level, corresponding to a mean flight altitude between 445 and 1,145 m a.s.l., which has been used extensively throughout migratory raptor studies (Schmaljohann et al., 2012; Limiñana et al., 2013). We selected the bilinear interpolation method for all wind variables.

Food availability

To determine the relative influence of food availability on stopover decisions, we used the Normalised Difference Vegetation Index (NDVI) as a proxy for food abundance . The NDVI is a vegetation index indicative of vegetation cover and photosynthetic activity in an area and also a proxy for food/insect abundance for insectivorous birds (Schlaich et al., 2016; Morganti et al., 2019). We annotated each GPS fix using the Env-DATA track annotation tool of Movebank (Dodge et al., 2013). We obtained NDVI from MODIS (NASA's Moderate Resolution Imaging Spectroradiometer) provided every 16 days at 250 m spatial resolution).

OBJECTIVES

OBJECTIVES

This thesis aims to provide a comprehensive knowledge of the migration patterns and non-breeding movement strategy of the lesser kestrels using a combination of solar GPS-UHF biologgers and environmental data. More specifically, our key aims are:

1. To disentangle the compounding effects of external factors (wind, geography), internal factors (sex) and season in shaping migratory behaviour.

2. To study the mechanisms shaping the spatio-temporal organisation of the pre-breeding migration in a trans-Saharan migrant.

3. To describe the movement strategy and schedules of lesser kestrels from the Spanish breeding population at their non-breeding quarters in West Africa, analysing potential differences between sexes.

CHAPTER 1

BARRIER CROSSINGS AND WINDS SHAPE DAILY TRAVEL SCHEDULES AND SPEEDS OF A FLIGHT GENERALIST

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ABSTRACT

External factors such as geography and weather strongly affect bird migration influencing daily travel schedules and flight speeds. For strictly thermal-soaring migrants, weather explains most seasonal and regional differences in speed. Flight generalists, which alternate between soaring and flapping flight, are expected to be less dependent on weather, and daily travel schedules are likely to be strongly influenced by geography and internal factors such as sex. We GPS-tracked the migration of 70 lesser kestrels (*Falco naumanni*) to estimate the relative importance of external factors (wind, geography), internal factors (sex) and season, and the extent to which they explain variation in travel speed, distance, and duration. Our results show that geography and tailwind are important factors in explaining variation in daily travel schedules and speeds. We found that wind explained most of the seasonal differences in travel speed. In both seasons, lesser kestrels sprinted across ecological barriers and frequently migrated during the day and night. Conversely, they travelled at a slower pace and mainly during the day over

non-barriers. Our results highlighted that external factors far outweighed internal factors and season in explaining variation in migratory behaviour of a flight generalist, despite its ability to switch between flight modes.

INTRODUCTION

The ability to fly gives birds the unique capacity to perform fast seasonal movements up to thousands of kilometres a year across multiple and often inhospitable habitats (Newton, 2008). Migrants often show great spatio-temporal flexibility in migratory behaviour throughout these challenging journeys (Akesson & Helm 2020). That flexibility is governed by an interplay between (1) external factors such as weather conditions and geography that influences connectivity and creates so-called ecological barriers (Nathan et al., 2008; Alerstam, 2011; Mellone et al., 2013) and (2) internal factors such as motion capacity (dependent on, for example, wing morphology), orientation ability, and the individual's age, sex, and/or reproductive state that shape the internal motivation to move (Nathan et al., 2008). However, understanding the relative contributions of such external and internal factors influencing migratory behaviour is often hampered by the lack of high-resolution tracking data for a diverse sample of individuals (Sur et al., 2020; Nilsson et al., 2013).

Studies that take into account the interplay of external and internal factors in shaping migratory behaviour (commonly measured via metrics such as ground speed, travel distance, duration of stopovers, and route straightness Vansteelant et al., 2015; Mueller et al., 2013; Miller et al., 2016) present a bias towards large soaring birds. Studies on these species have demonstrated that variation in weather (e.g., winds, thermals, and orographic updrafts) is often the prevailing factor explaining migration patterns, such as seasonal and regional differences in hourly and daily speeds (Vansteelant et al., 2015; Shamoun-Baranes et al., 2003). For example, turkey vultures (*Cathartes aura)* achieve faster speeds and travel more hours each day during the pre-breeding compared to the post-breeding migration because thermal uplift is stronger during the former (Dodge et al., 2014) . Oriental honey buzzards (*Pernis ptilorhynchus*) traverse ecological barriers (the East China Sea) during post-breeding migration when tailwinds are available and circumvent them during pre-breeding migration when wind conditions are less favourable for sea-crossing (Nourani et al., 2016). Considering internal factors, age and experience are important factors mediating the response to weather conditions (e.g., golden eagles, *Aquila chrysaetos*, Rus et al., 2017; ospreys, *Pandion haliaetus*, Thorup et al., 2003; black kites, *Milvus migrans*, Sergio et al., 2014; and honey buzzards, *Pernis* apivorus, Vansteelant et al., 2017), whereas sex typically has a small effect on travel speed of soaring migrants (Mellone et al., 2015b, Rotics et al., 2018).

We still know little about the relative importance of external and internal factors in shaping the migratory movements of species that can switch between flight modes, the so-called flight generalists (Shamoun-Baranes et al., 2016), such as bee-eaters, falcons, and harriers (Bildstein, 2006; Klaassen et al., 2012; Klaassen et al., 2017). Due to their wing morphology and intermediate body size, flight generalists can use a range of flight modes in response to environmental variability (Shamoun-Baranes et al., 2016). Although atmospheric conditions, especially wind, significantly impact flight speeds and costs in all flying animals (Bildstein, 2006; Shamoun-Baranes et al., 2017b), flight generalists are highly manoeuvrable and may be less constrained by suitable atmospheric conditions than obligate-soaring birds (Spaar & Bruderer, 1997). Thus, we might expect internal factors and the underlying geography to have a dominant role in shaping their migratory behaviour (Shamoun-Baranes et al., 2016).

Flight generalist migrants are capable of long-distance flapping, allowing them to extend their daily travel schedule into the night when thermals are weak or rare (Klaassen et al., 2017). Similarly, they are capable of long sea-crossings that are generally avoided by large soaring birds (but see Duriez et al., 2018; Nourani et al., 2021). Flight generalists typically also achieve higher travel speed during nocturnal than diurnal migration, enabling them to cross ecological barriers in non-stop flights ("sprints" Alerstam, 2009). For example, Amur falcons (*Falco amurensis*) undertake the longest non-stop water crossing of any bird of prey studied so far, taking 3-4 days to cross the Indian Ocean, from India to East Africa (ca. 3000-4000 km) flying day and night (Bildstein, 2006). Nevertheless, birds that invest energy in flapping flight at some point have to refuel by foraging. They may do this before or after migration, but they often do it during migration by making stopovers (Alerstam, 2011) or by intermittent diurnal fly-forage behaviour (a combination of foraging and flying in the migratory direction Strandberg & Alerstam, 2007; Strandberg et al., 2009). Studies on migrants such as Eurasian hobbies (*Falco subbuteo*) and Eleonora's falcons (*Falco eleonorae*) revealed significant seasonal variation in travel speed between regions, with fast and long flights over barriers and slower and shorter daily flights over non-barrier areas (Strandberg & Alerstam, 2007). For the latter species, geography was found to have a greater influence on flight speed relative to wind and age (Hadjikyriakou et al., 2020; Mellone et al., 2015a).

We focus on a flight generalist raptor, the lesser kestrel (*Falco naumanni*), a small-sized falcon with reverse size dimorphism (females being ca. 15% heavier than males) (Cramp & Simmons, 1980). We investigate which are the most influential factors driving differences in travel speed, distance and duration as proxies to measure migratory behaviour at coarse (trip) and fine (daily, hourly) temporal scales. European-breeding lesser kestrels regularly perform seasonal migrations to and from sub-Saharan Africa. We describe migration patterns by investigating differences between geographies (barriers such as sea and desert and non-barrier areas), during diurnal and nocturnal flights, accounting for season and sex. Crossing the sea and desert poses different challenges for migrants (e.g., extreme temperatures over the desert vs. few landing opportunities over the sea López-López et al., 2010) to which birds likely respond in different ways. Moreover, seasonal differences in travel speed are affected not only by different external conditions between seasons (e.g., wind regimes, food resources, daily cycle) while travelling over different geographies (Nilsson et al., 2013; Kemp et al., 2010) but also by seasonal differences in individual motivation (Kokko, 1999). For example, during pre-breeding migration, early arrivals can confer a reproductive advantage to adult males that compete to establish territories (Sur et al., 2020; Karlsson et al., 2012).

We aim to disentangle the compounding effects of external factors (wind, geography), internal factors (sex) and season in shaping migratory behaviour. We expect tailwinds along the kestrels' routes to explain a large part of the seasonal variation in travel speed. We further hypothesise that sex and season have a greater influence in moulding migratory behaviour compared to external factors in this flight generalist species. We predict that after accounting for wind effects, (1) kestrels will have shorter duration during pre-breeding migration than post-breeding migration because of the greater selective pressure for early arrival to the breeding grounds. As such, we expect kestrels to have fewer non-travelling days, straighter routes, faster travel speed, longer daily distance, and more travel hours per day during pre- than post-breeding migration. We also predict (2) significantly higher travel speed for the smaller males than for the larger females because flapping is theoretically less costly for the former (Pennycuick, 2008), and competition for securing a high-quality territory is weaker in the latter (Morbey &

Ydenberg, 2001). Finally, we hypothesise that lesser kestrels will sprint over barriers (such as the Mediterranean Sea or the Sahara Desert) where there are few or no resting/drinking/feeding opportunities (Klaassen et al., 2017; Strandberg & Alerstam, 2007; López-López et al., 2010). We thereby predict (3) that individuals will show geography-dependent differences in daily travel schedules and speeds by travelling faster, covering larger distances, and migrating at night when flying over barriers.

METHODS

Ethical statement

All experimental protocols were approved by Estación Biológica de Doñana Ethical Committee, Consejo Superior de Investigaciones Científicas Ethical Committee, and Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible de la Junta de Andalucía and carried out in accordance with relevant regulations approved by the Spanish Law on Animal Experimentation (RD53/2013 from 1st February https://www.boe.es/eli/es/rd/2013/02/01/53). In Italy, procedures were approved by the regional authorities (Regione Sicilia n. 1616/2014 and Regione Puglia n. 475/20169) following the guidelines approved by the Law 157/1992 [Art.4(1) and Art 7(5)], which regulates research on wild bird species conducted mainly by the Italian Institute for Environmental Protection and Research (ISPRA). Capture and device deployment were carried out by experienced ornithologists only in accordance with approved guidelines aimed at ensuring animal welfare throughout the operations (Whitworth et al., 2007). Handling time was kept to a minimum to reduce the potential for stress. No individual was injured during the capturing/handling procedure. When applicable, the design and reporting of the study were in accordance with ARRIVE Essential 10 international guidelines (Percie et al., 2020).

Study species and data collection

The lesser kestrel is a small insectivorous raptor, breeding in colonies across southern Europe, northern Africa to China, and with non-breeding areas in Africa, especially south of the Sahel to South Africa. However, some Mediterranean populations also contain resident individuals. From 2014 to 2019, we trapped 211 adult lesser kestrels (101 females and 110 males) at 33 breeding colonies in Spain and Italy. We fitted them with different solar GPS-UHF biologgers (Pica, Ecotone, Gdynia, Poland; Microsensory LS, Córdoba, Spain; and NanoFix GEO+RF, Pathtrack Ltd., Leeds, UK., weighing 4-5 g) attached as backpacks with a Teflon harness. Loggers plus harness did not exceed 4% of the average lesser kestrel's weight, which is within the accepted standards for animal welfare in research (Barron et al., 2010). Loggers were programmed with different schedules (i.e. device's duty cycle varied from 8 h to 24 h) and recorded GPS-locations day and night (65% of the tags had 24 h duty cycle). Over the whole migration, tracks were sampled with GPS fixes every 30 min to 1 h, depending on solar battery recharge and satellite geometry (≥4 satellites must be detected for a reliable fix). Data were stored on-board the device and downloaded the following year from successfully migrating individuals that returned to the breeding area via UHF base stations placed at the vicinity of the colony.

Tracking data set

We included 70 adults in our analyses (40 females and 30 males) who completed a migration from Spain (n = 58) and Italy (n=12) to Africa and back, either along the East Atlantic or the Central Mediterranean migration flyways. These birds provided 75 post-breeding and 66 pre-breeding migration trips. Of these kestrels (16/70) 23% had two and three repeated migration cycles. Of the birds that did not yield any migration track, 40 had confirmed technical failure of the tag (i.e. 23 tagged birds were seen in the colony but did not send data and 17 tags stopped providing GPS coordinates soon after deployment). Seven dispersed from the core study area, 4 were reported dead, and 2 with partial migration strategies were excluded from the analysis because their behaviour differed substantially. In the rest of the cases, we do not know the fate of the birds, but it is likely that they either died, dispersed, tags failed or were missed. One bird was seen again in 2021 after being missed during 2019 and 2020. As a consequence of all these factors, we are unable to estimate the actual impact of GPS tags on the return rate in this specific study but we cannot discount the inevitable impact of tagging.

Identifying migratory trips

The onset and end of migration were identified based on marked shifts in daily distance histograms (Vansteelant et al., 2015) . We calculated the distance between the current position to the previous one using the deg.dist function in the R package 'fossil' (Vavrk, 2011). For each migratory trip, we searched for a group of first and last three consecutive days with an average daily distance of at least 150 km, preceded (if onset) or followed (if end) by a stationary phase of five consecutive days with daily mean travel distance <70 km (Rotics et al., 2018). We assigned as the migration start day the first day of the first three-day period and as the migration end day the last day of the last three-day period. We confirmed those dates visually using QGIS (QGIS Development Team, 2020). We excluded tracks in which we could not precisely determine the onset or the end of migration due to the lack of GPS fixes (four cases during the post-breeding and thirteen cases during the pre-breeding migration).

Estimating travel metrics and their scales

At the trip scale, we defined a migratory trip as the set of data between the first position on migration start day and the last position on migration end day. We computed: (a) the migration duration as the period between the migration start and end dates; (b) the trip straight-line distance (i.e., the shortest orthodromic path) as the distance between the first position on migration start day and the last position on migration end day; (c) the cumulative distance as the sum of the successive daily travel distances between the start and end of migration dates; (d) trip straightness index as the ratio between the trip straight-line distance and the cumulative distance, ranging between 0 (corresponding to tortuous routes) and 1 (corresponding to straight-line routes); (e) the number of non-travelling days by summing days with a daily distance <50 km (see below); (f) travel speed was defined as the ratio between the straight-line distance and the migration duration in days (excluding non-travelling days). Means are given with standard errors throughout the paper.

At the daily scale, we defined each migration day of a kestrel from sunrise to sunrise of the next day (in our dataset lesser kestrels were frequently travelling during the night), thus capturing a complete day-night cycle. Partially due to low battery power (e.g., reduced amount of solar energy that reached the telemetry unit solar panel) and different working schedules (i.e., within a range of 8h-24h, as outlined above), some data gaps within migratory travel days were detected. We selected only those days with a minimum of 75% of daily coverage for this analysis. This was done to avoid bias in the calculation of daily metrics due to significant data gaps. The number of fixes per day was 22.72 ± 2.00. We computed the following travel metrics: (a) daily straight-line distance between the first and the last position of each unit day; (b) the daily travel duration, which is the cumulative sum of hourly travel segments (excluding foraging and resting events, see below); and (c) the daily mean travel speed as the daily straight-line distance divided by the travel duration. Flying for more hours per day or night determines a lot of the variation in daily distance (Klaassen et al., 2008). Since we aimed at quantifying what factors explain migratory behaviour during travel events, we calculated metrics during travel hours only and computed daily mean travel speed accounting for the effect of travel duration. Travelling days were defined as those in which a kestrel's displacement in the direction of migration was at least 50 km (Limiñana et al., 2013; Klaassen et al., 2010). Non-travelling days defined as complete days (sunrise to sunrise) in which less than 50 km of travel in the direction of migration was observed, were excluded from further analysis.

At the hourly scale, all data were resampled to a 1-hour interval, allowing deviations up to 20 minutes to maximise the number of observations. By resampling, we also avoided bias in our calculations of migratory parameters due to the variability in sampling frequencies (Vansteelan et al., 2015; Shamoun-Baranes et al., 2017a). After resampling, we analysed 31,153 hourly segments, from which 12,252 were annotated as travel segments. We calculated the travel distance and ground speed from each resampled location to the previous. We classified as travel segments those in which speed was ≥5 km/h (Strandber et al., 2007; Limiñana et al., 2012).

Annotating environmental variables

At the hourly scale, to examine possible changes in migratory behaviour of birds over different geographies, we first identified when GPS fixes were located over ecological barriers, specifically over the Mediterranean Sea or the Sahara Desert and over non-barriers (see Supplementary Methods for details) using the Global Biomes map (Olson et al., 2001). We used the 'join-attribute-by-location' tool in QGIS to join all the tracks to the corresponding position within the Global Biomes map. To identify possible changes in the behaviour of kestrels in relation to the time of day (i.e., day and night), we used the sunrise.set function in R package 'StreamMetabolism' (Sefick, 2016). We classified as diurnal all locations detected between sunrise and sunset, with the rest being nocturnal. To account for the influence of atmospheric conditions on migratory behaviour, we annotated each GPS fix with environmental data, namely boundary layer height (BLH) and wind using the Env-Data annotation service of Movebank (Dodge et al., 2013) (see Supplementary Methods for details). We identified daily travel schedules in relation to the hour of the day. For every migration day, the number of hourly segments was annotated according to two behaviours: travelling or non-travelling (López-López et al., 2010).

At the daily scale, to examine how geography influences migratory behaviour, we classified migration days as desert, sea and non-barrier days based on the proportion of time kestrels spent over the same geography (≥ 60% of day). We computed the amount of diurnal and nocturnal travelling time by summing diurnal and nocturnal travel segments. As we expected distance to increase linearly with travel duration, we used those segments directly as control variables to account for differences in travel duration in the weather models. We also calculated the nocturnal travel fraction (nocturnal travelling hours/total travelling hours) and included it in the daily speed models. We calculated mean daily tailwind, absolute crosswind, and mean daily BLH by averaging across the day, using only travel segments.

Statistical analysis

Trip scale

For our first and second prediction, we tested for differences in migratory behaviour between seasons and sexes using univariate statistics. After testing for normality, we used the parametric t-test for speed and non-parametric Wilcoxon rank-sum test for mean trip duration (days), mean number of travelling days, mean number of non-travelling days, and straightness index. Analyses were conducted using the ‘stats’ (R development core Team, 2020) package in R. For pairwise comparisons we used Tukey’s HSD (honestly significant differences) tests, considering an effect to be significant if p R 0.05, conducted with the ‘emmeans’(Russell, 2020) package.

Daily scale

For our third prediction, we identified whether there was a significant difference in mean daily migratory behaviour (i.e., travel speed, straight-line distance, and duration) among geographies (three level factor: sea, desert and non-barrier), using Generalised Linear Mixed Models (GLMMs) with bird identity as a random effect. After visual inspection of residual plots, we fitted models with Gaussian error distribution for travel speed, daily straight-line distance, and Poisson error and log link function for daily travel duration, which is appropriate for count data (Zeileis & Jackman, 2008). We conducted a Tukey's honest significance test, using the package 'multcomp' (Hothorn et al., 2014).

To disentangle the most influential factors driving differences in migratory behaviour, we modelled the relationship between daily metrics when flying over barriers (pooling data for sea and desert) vs. non-barriers, when differences between sea and desert proved to be non-significant, accounting for the interaction between season and sex. We also included as predictors the weather variables (mean daily tailwinds, absolute crosswinds, and BLH) and the proportion of diurnal and nocturnal travelling hours. We first computed full models including all predictors. We used the 'dredge' function in the R package 'MuMIn' (Bartoń, 2019), which uses Akaike's information criterion (AIC) to rank all possible subsets of reduced models from each full model. We selected the models if they had fjAIC R 2 units of the highest ranked-model and we retained the most parsimonious model (with the fewest parameters) because model averaging could not handle models with interaction effects (Cade, 2015; Buchan et al., 2021). We used the Satterthwaite's method to estimate degrees of freedom and to obtain p-values using the 'lmerTest' (Kuznetsova et al., 2017) R package. The proportion of variance explained by the fixed effects (Rmarginal) and by both fixed and random effects (Rconditional) was assessed using methods in Nakagawa & Schielzeth, 2013.

Before fitting the GLMMs, all continuous predictors and response variables were transformed to z-scores, to compare the relative importance among predictors (Schielzeth, 2010; Eager, 2017). We checked for multicollinearity of weather variables and season and included only variables that were not highly correlated (r<60). Multicollinearity was also tested by calculating variance inflation factors (VIF) for all our predictors using the 'car' (Fox, 2011) R package. Values of these were in all cases below 2.8. All the mixed model analyses were performed in the 'lme4'(Bates et al., 2014) package.

Hourly scale

To examine how ground speeds differed between diurnal and nocturnal travel when flying over different geographies, we used GLMMs (following the methods outlined above), using speed as a response variable and geography type and diurnal and nocturnal travel segments as fixed effects. We modelled the relationship between ground speeds when flying over barriers vs. non-barriers and during diurnal and nocturnal travel and included the interaction between season and sex and weather variables in our models, again using the approach outlined above.

To analyse the daily travel schedules, hourly travel speeds were plotted in relation to the time of the day for each season and over the sea, desert, and non-barriers. In addition, we used the classification mentioned earlier to obtain the distribution of travelling and non-travelling segments across all 24 hours of the day, which is a reasonable description of daily travel schedules (Klaassen et al., 2008). We compared the proportion of travelling and non-travelling segments between seasons, sexes, over barriers, and non-barriers using the Pearson's Chi-squared test using the 'vcd'(Meyer, 2017) R package.

RESULTS

Trip scale: season and sex patterns in travel duration

We obtained GPS data for 141 (75 post-breeding and 66 pre-breeding) complete migratory trips from 70 adults (Fig. 1). Contrary to theoretical predictions, but consistent with previous findings (Sarà et al., 2019), our data showed that birds progressed significantly faster during the post-breeding than during the pre-breeding migration (405 ± 14.33 km/day vs. 331.03 ± 12.21 km/day, respectively, excluding non-travelling days, p R 0.05—see Supplementary Table S1 and Fig. 2). Migration was significantly shorter during the post-breeding than during the pre-breeding migration (trip duration in days: 8.62 ± 0.44 vs. 15.62 ± 1.04, p R 0.05). They showed significantly fewer non-travelling days and followed straighter paths during the post-breeding than during the pre-breeding migration (non-travelling days: 1.00 ± 0.23 vs. 6.00 ± 0.78; straightness index: 0.86 ± 0.01 vs. 0.76 ± 0.01, respectively, p R 0.05). Seasonal migratory behaviour was similar between sexes.

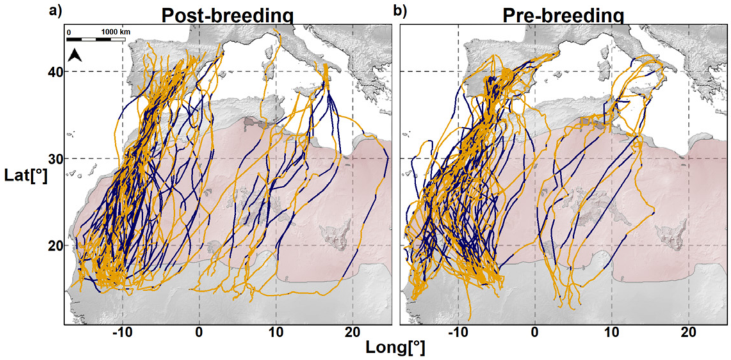


Figure 1. Migration routes of lesser kestrel tracked with GPS between 2014-2019. (a) Post-breeding and (b) pre-breeding migration. Colours indicate nocturnal migration (blue segments) and diurnal migration (orange segments) when flying over non-barriers (grey) or barriers (desert = red, sea= white). One position per hour was plotted.

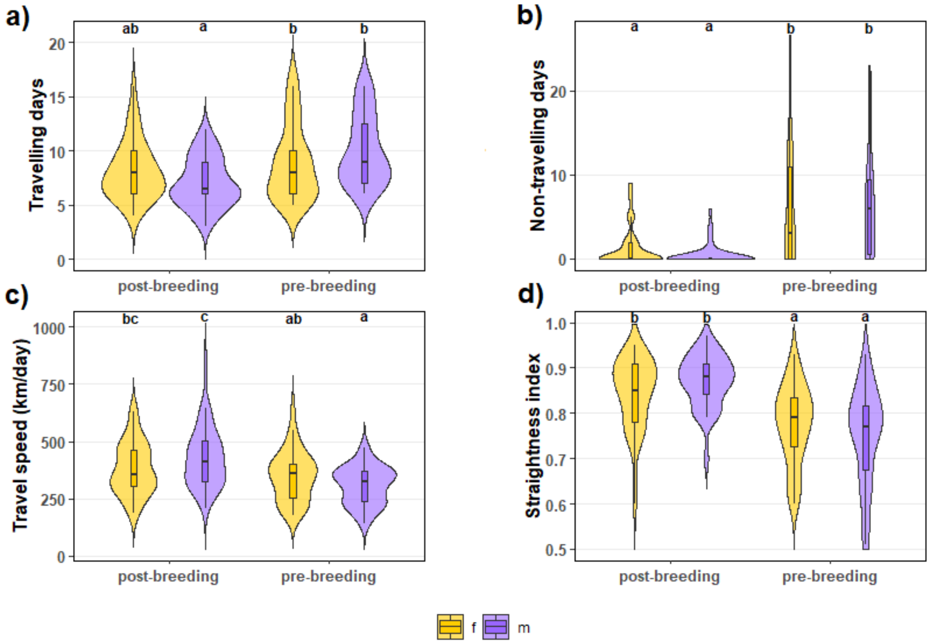
Daily scale: geographical patterns in migratory behaviour

In agreement with predictions on geography-dependent behaviour, we observed substantial differences in migratory behaviour between barriers and non-barriers. (Supplementary Table S2a). Lesser kestrels travelled faster, covered longer straight-line distances and travelled more hours per day over barriers. Travel speed and straight-line distance were not significantly different over the sea and the desert ($p \geq 0.05$). However, daily travel duration was significantly higher over the sea (20.00 ± 1.63 h) compared to the desert (12.72 ± 0.45 h) (sample size = 783 bird-migration days from sunrise to sunrise of the next day) (Supplementary Table S2b).

Daily scale: season, sex and external factors

Contrary to our hypothesis, season and sex had a limited role in modulating daily migratory behaviour. Rather, external factors explained the largest amount of seasonal and daily variation in migratory behaviour. Neither sex nor the interaction effect between season and sex were significant in any of the models (Table 1 and Supplementary Table S3).

Figure 2. Distribution of travelling days.
(a), non-travelling days (b), travel speed (c) and straightness index (d) of lesser kestrels accounting for season and sex (females in yellow, males in purple). The letters above represent significant differences by Tukey HSD post-hoc tests at the 0.05 significance level. Groups sharing the same letter are not significantly different.



The most parsimonious model for mean travel speed when flying over barriers retained nocturnal travel fraction and tailwind, with positive effects and this was consistent in both seasons (see Supplementary Fig. S1a, S1b). Over non-barriers, the most influential variables determining speeds were nocturnal travel fraction and winds, with positive effects.

For straight-line distance, the most parsimonious model when flying over barriers and non-barriers retained nocturnal and diurnal travelling hours and tailwind, with a strong positive effect of nocturnal travelling. We found a positive effect of tailwind, with birds flying farther with stronger mean daily tailwind, and this effect was weaker over barriers during the pre-breeding migration (see Supplementary Fig. S1c, S1d).

For travel duration, the most parsimonious model when flying over barriers and non-barriers retained wind, boundary layer height (hereafter BLH) and season. Travel duration of lesser kestrels was negatively associated with mean BLH and positively associated with absolute crosswind and tailwind strength. Barrier type was retained, indicating more extended travel duration over the sea relative to the desert. We also found substantial seasonal effects with birds travelling fewer hours per day during pre-breeding relative to the post-breeding migration.

Table 1. Estimates for fixed effects on daily mean travel speed, travel straight-line distance and travel duration as estimated by the most parsimonious model when flying over barrier (sample size=183 travel days) or non-barrier (sample size= 600 travel days) areas. The models for travel duration included the factor barrier type with two levels: sea and desert. Boundary layer height (BLH) serves as a proxy for the availability and strength of thermal uplifts. Model estimates in units of standard deviation (SD) (organised from higher to lower relative importance), standard error (±SE), and the t-value and z-value (the ratio between the estimate and its SE) are given. All models included individual identity (ID) as a random effect. (* = p≤0.05, ** = p≤0.01, *** = p≤0.001).

Response	Model	Predictor	Estimate	SE	t/z
Speed (km/h)	**Over barriers**	Intercept	-0.07	0.08	-0.91
		Nocturnal trav. fraction	0.57	0.06	9.62***
		Tailwind	0.33	0.05	7.21***
	Over non-barriers	Intercept	-0.07	0.06	-1.25
		Nocturnal trav. fraction	0.40	0.03	11.76***
		Tailwind	0.33	0.04	8.82***
		Crosswind	0.25	0.05	5.31***
		Season(Pre-breeding)	-0.14	0.06	-2.19*
Straight-line distance (km)	**Over barriers**	Intercept	-0.02	0.05	-0.48
		Nocturnal trav. hours	0.68	0.04	18.25***
		Tailwind	0.27	0.03	9.33***
		Diurnal trav. hours	0.24	0.04	5.65***
	Over non-barriers	Intercept	-0.03	0.02	-1.21
		Nocturnal trav. hours	0.68	0.02	41.76***
		Diurnal trav. hours	0.30	0.01	21.03***
		Tailwind	0.21	0.02	12.26***
		Season(Pre-breeding)	0.06	0.03	2.29*
Travel duration (h)	**Over barriers**	Intercept	2.62	0.08	34.77***
		Season(Pre-breeding)	-0.27	0.06	-4.29***
		Barrier type (Sea)	0.23	0.10	2.33*
		BLH	-0.20	0.03	-6.18***
		Tailwind	0.12	0.02	6.50***
		Crosswind	0.10	0.03	3.38***
	Over non-barriers	Intercept	2.15	0.03	66.54***
		Season(Pre-breeding)	-0.30	0.03	-8.59***
		Crosswind	0.29	0.02	15.64***
		Tailwind	0.11	0.02	6.28***
		BLH	-0.09	0.02	-5.18***

Hourly scale: season, geography and travel schedules

Our analyses at the hourly scale matched the behavioural patterns we observed at the daily scale. The distribution of travelling and non-travelling segments was significantly different between seasons (post-breeding vs. pre-breeding: $\chi^2 = 840.63$; DF=1; p R 0.05) and between geographies (barrier vs. non-barrier: $\chi^2 = 658.41$; DF=1; p R 0.05—see Supplementary Fig. S2), but it was not significantly different between sexes (females vs. males: $\chi^2 = 2.79$; DF=1; p = 0.09) (Supplementary

Figure 3. Ground speed during the post-breeding migration over barriers **(a)** desert and **(b)** sea, and **(c)** non-barriers and during the pre-breeding migration over barriers **(d)** desert, **(e)** sea, and **(f)** non-barriers. Only travel segments for each hour of the day are included. The grey areas in the background indicate nocturnal hours, and the white area indicates diurnal hours. Points represent outliers. Speed patterns are more similar when flying over the desert and non-barriers than over the sea, although over the desert, speeds are higher during the post-breeding migration, likely due to supportive winds (see Fig. 4). Over the sea kestrels achieve more constant travel speeds between 25-50 km/h with no differences between diurnal and nocturnal flights. During diurnal travel over non-barriers travel speed typically falls below 25 km/h.

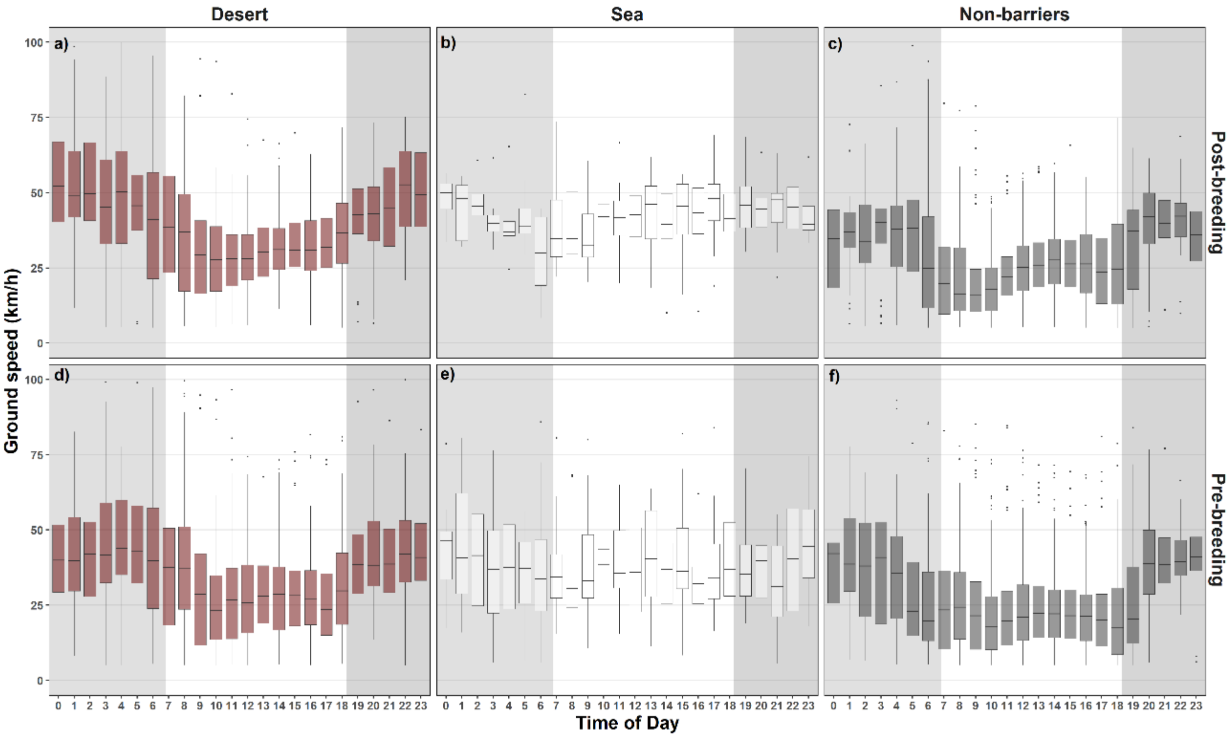


Table S4). Lesser kestrels attained faster travel speed during nocturnal vs. diurnal travel (Supplementary Table S4). A *post-hoc* multiple comparisons test showed the lowest speeds took place over non-barrier areas during the day (24.00 ± 0.43 km/h, p R 0.05) and the highest speeds over the desert and sea at night (45.20 ± 0.56 km/h vs. 42.1 km/h ± 0.98 respectively, p R 0.05) (Fig. 3 and Table 2). Over the sea, the difference in speed between diurnal and nocturnal flights was not significant (39.70 ± 0.77 vs. 42.10 ± 0.98, respectively, $p \geq 0.05$).

Hourly scale: season, sex and external factors

The variable that had the highest positive predictive importance on ground speed was tailwind strength (Fig. 4). Absolute crosswind had a negative effect on kestrel ground speed (Table 3 and Supplementary Table S5). During diurnal flights over non-barriers, season had a small and marginally significant impact on ground speed. The interaction between season and sex was significant, indicating that the speed difference between males and females during diurnal flights over non-barriers was significantly smaller during the pre-breeding relative to the post-breeding migration.

Table 2. Summary table showing the sample size (N) and the mean (±SE) hourly speed of lesser kestrels when flying over the desert, sea and non-barriers during diurnal and nocturnal flights. Multiple comparisons of means were performed using Tukey's post hoc tests at the 0.05 significance level. Means sharing the same group letter are not significantly different.

Pairwise comparison	N	Hourly speed (km/h)
Diurnal travel over non-barriers	6373	24.0 (0.43)^{a}
Diurnal travel over desert	2440	31.9 (0.50)^{b}
Nocturnal travel over non-barriers	1094	35.0 (0.60)^{c}
Diurnal travel over sea	526	39.7 (0.77)^{d}
Nocturnal travel over sea	287	42.1 (0.98)^{d}
Nocturnal travel over desert	1532	45.2 (0.55)^{e}

Figure 4. Ground speed in relation to tailwind along the kestrel's routes accounting for season and geography. We show the linear relationship between hourly speed and tailwind (including only travel segments) and the effects during the post-breeding migration over barriers **(a)** desert and **(b)** sea, and, **(c)** non-barriers and during the post-breeding migration over **(d)** desert, **(e)** sea and **(f)** non-barriers, accounting for diurnal (solid yellow line) and nocturnal migration (blue dashed line).

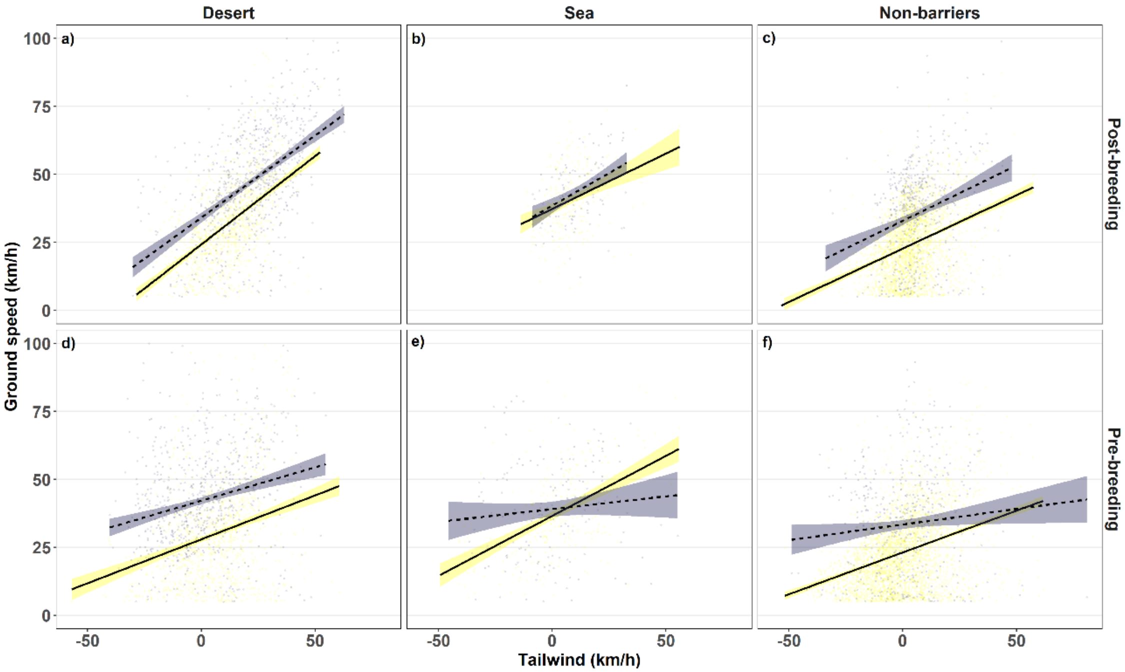


Table 3. Estimates for fixed effects at the hourly scale as estimated by the most parsimonious model during diurnal migration over barriers (sample size = 2,966), nocturnal migration over barriers (sample size = 1,819), diurnal migration over non-barriers (sample size = 6,373) and nocturnal migration over non-barriers (sample size = 1,094). Boundary layer height (BLH) serves as a proxy for the availability and strength of thermal uplifts; thus, we only included BLH in diurnal models. Model estimates in units of standard deviation (SD) (organised from higher to lower relative importance), standard errors (±SE) and the t-value (the ratio between the estimate and its SE) are given. All models included individual identity (ID) as a random effect. (* = p≤0.05, ** = p≤0.01, *** = p≤0.001).

Model	Predictor	Estimate	SE	t	p
Diurnal over barriers	Intercept	1.13	0.05	24.45	0.00
	Crosswind	-0.11	0.03	-4.22	0.00
	BLH	-0.10	0.01	-7.29	0.00
	Geography(Sea)	0.41	0.04	9.23	0.00
	Tailwind	0.43	0.02	25.04	0.00
Nocturnal over barriers	Intercept	1.64	0.06	25.89	0.00
	Crosswind	-0.13	0.04	-3.58	0.00
	Tailwind	0.36	0.02	15.69	0.00
Diurnal over non-barriers	Intercept	0.63	0.03	20.97	0.00
	Crosswind	-0.08	0.02	-5.27	0.00
	BLH	0.02	0.01	2.40	0.02
	Season(Spring)	0.14	0.03	5.61	0.05
	Sex(Male)	0.07	0.04	1.67	0.10
	Tailwind	0.32	0.01	29.03	0.00
	Season:sex	-0.18	0.04	-4.93	0.00
Nocturnal over non-barriers	Intercept	1.27	0.06	22.68	0.00
	Crosswind	-0.13	0.06	-2.24	0.03
	Tailwind	0.26	0.04	6.82	0.00

DISCUSSION

Contrary to our expectations for a flight generalist, our work suggests that migratory behaviour was only marginally influenced by sex and season. External drivers, in particular tailwinds experienced *en route*, were the main determinant of seasonal variation in travel speeds, whereas geography moulded differences in daily distances by shaping daily travel schedules, with a propensity for sprinting across barriers.

In accordance with previous tracking studies on the lesser kestrel, and contrary to our first prediction, individuals completed their migration faster during the post-breeding than during the pre-breeding migration (Sarà et al., 2019). Wind explained much of this seasonal variation, i.e., birds experienced more intense tailwinds along their realised travel direction during the post-breeding compared to the pre-breeding migration. By extending travel during the night, lesser kestrels could cover up to 1000 km per day in supportive autumn winds while only 500 km through opposing spring winds. Previous work on flight generalist birds in the African-Eurasian flyway pointed to the significance of tailwinds in determining travel speed and duration, whereby prevailing winds generally opposed northward migration during the pre-breeding migration, likely causing less straight routes compared to the post-breeding (Klaassen et al., 2017; Limiñana et al., 2013; Mellone et al., 2011). We also found that crosswind strength relative to the kestrels travel direction and boundary layer height were comparatively less influential than tailwind strength on daily and hourly speeds and daily distance. Such results were expected for a flight generalist, which is not so dependent on thermals that can alternate between flapping and soaring-gliding flight to efficiently overcome crosswinds, in contrast to larger birds that inevitably drift from their intended direction with every thermal ascent (Vansteelant et al., 2015). Although orientation behaviour (i.e., heading in relation to wind direction) is still to be investigated, kestrels seem rather prone to drifting in strong winds, especially above the desert (Limiñana et al., 2013).

During diurnal migration over non-barriers, kestrels appear to travel slightly faster during the pre- than post-breeding migration. We envisage two mechanisms: (1) seasonality in prey availability may favour different foraging strategies at different times of the year, and (2) lesser kestrels may accelerate flight when approaching the breeding grounds if there is an urgency to arrive early to secure breeding sites (Karlsson et al., 2012). Uncovering such time-selecting behaviour during the pre-breeding migration requires further study and a deeper understanding of the lesser kestrel's settlement phase (i.e. the time between territory establishment and the onset of the breeding period, Newton, 2008). Contrary to our second prediction of higher speeds for the smaller males, we did not find any sex differences in seasonal and daily migratory behaviour. Our hourly models did capture a marginal effect of the interaction between season and sex. We found that during the pre-breeding migration, males flew slower than females during diurnal migration over non-barriers relative to the post-breeding migration. However, it is important to consider that lesser kestrels reach their breeding grounds on average two months before the onset of breeding (Negro et al., 1991). Such a long establishment phase may well offset the need for early arrivals in pre-breeding migration and favour individuals that arrive in good condition to secure territories and prepare for reproduction (Hubner, 2006). In that case, one would indeed expect males and females to respond similarly to weather conditions and resource availability, as did they in our study.

Our predictive variables in the hourly scale models explained relatively little variation than those at the daily scale. There are several potential limitations to the interpretation of our results. Firstly, it is likely that other external factors that we did not measure directly in this study, such as seasonal peaks in food abundance, explain spatio-temporal variation in migratory behaviour (Nilsson et al., 2013; Shamoun-Baranes et al., 2003). It should be noted that the only pure internal factor we considered was sex, and it is therefore likely that we underestimated the effects of other biometric characteristics such as body mass, wing morphology, and other internal factors such as age and breeding status, that were not available in our data set. Secondly, wind speeds are estimated by models at a coarser temporal (6h), and spatial resolution (0.75 degrees) than kestrel tracking data, and kestrel flight altitude varies around the 925 mb pressure level more within than between days. It is possible therefore, that our weather variables are less suited to explain variation at such a fine temporal scale.

In agreement with our third prediction, lesser kestrels exhibited a propensity for sprinting when crossing barriers like the Sahara Desert or the Mediterranean Sea by travelling through the night as well as the day. When crossing barriers, birds thus showed a clear time-minimising behaviour in both seasons. We found higher mean travel speed over the sea and desert during nocturnal flights, almost twofold the travel speed over non-barriers during diurnal flights. During diurnal migration over non-barriers, travel speed typically falls below 25 km/h. We suggest that this can be due to differences in foraging opportunities and birds switching between flight-modes, as suggested for other flight generalists (gulls, Klaassen et al., 2012; falcons, Strandberg et al., 2007 and harriers, Klaassen et al., 2017). Thermal-soaring flight is thereby expected to dominate during diurnal migration Strandberg et al., 2007 and flapping flight during nocturnal migration, although kestrels may also resort to flapping flight during the day to reduce the time needed to cross inhospitable barriers Hadjikyriakou et al., 2020; Klaassen et al., 2008). Over the sea, no differences were found in travel speed between diurnal and nocturnal flights, with mean speeds between 42-45 km/h, which we believe is due to a consistent use of flapping flight over water. This pattern suggests that seas are a major ecological barrier not only for soaring birds (Bildstein, 2006) but also for flight generalists, even though we cannot exclude the possibility that kestrels exploit weak sea thermals (Duriez et al., 2018; Nourani et al., 2021).

CONCLUSION

We conclude that lesser kestrels exhibited great behavioural plasticity in migration, sprinting through the night across barriers, and possibly engaging in fly-forage behaviour elsewhere. In all cases, however, tailwind assistance significantly increases the hourly and daily travel speed of migration, and this accounts for the faster post- than pre-breeding migration. We suggest a long establishment phase likely buffers against an internal motivation for faster pre-breeding migration in lesser kestrel males. Our study generally emphasises the importance of accounting for external factors when interpreting complex spatiotemporal movement patterns and that season and sex play a limited role in modulating migratory behaviour even in flight generalist migrants.

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AUTHOR CONTRIBUTIONS

L.L.R., W.M.G.V., J.H.P., D.G.S and J.B. conceived the study. L.L.R., D.G.S., A.B., S.C., J.G.C., J.D.L.P., F.G.T., J.M.D., A.O., B.R.M., D.R., M.S. and J.B contributed to fieldwork and gathered the tracking data. L.L.R., W.M.G.V. and J.H.P. analysed the data. L.L.R., W.M.G.V., J.H.P., D.G.S. and J.B. led the writing of the manuscript with significant input from J.G.C., D.R., M.S and all co-authors. J.H.P and J.B. supervised the study.

SUPPLEMENTARY INFORMATION
CHAPTER 1

Supplementary Table S1. Season and sex patterns at the trip scale. Summary table showing sample size (N) and the mean (±SE) of the seasonal estimates for travelling days, non-travelling days, straightness index and travel speed for males and females lesser kestrels. Comparison of means performed using Tukey's post hoc tests at the 0.05 significance level.

	Sex	**Travelling days**		**Non-travelling days**	**Straightest index**	**Travel speed (km/days)**
		N	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Post-breeding	Male	34	7.05a (0.38)	0.50a (0.22)	0.87b (0.01)	431.40c (22.63)
	Females	41	8.17ab (0.42)	1.34a (0.37)	0.84b (0.01)	383.64bc (17.85)
Pre-breeding	Male	31	10.06b (0.57)	6.54b (1.16)	0.75a (0.01)	309.54a (14.89)
	Females	35	8.94b (0.58)	5.80b (1.08)	0.77a (0.01)	350.07ab (18.48)

Table S2a. Geographical patterns in migratory behaviour at the daily scale. Models for mean daily travel speed, straight-line distance and duration of lesser kestrel accounting for the effect of geography (desert, sea and non-barriers) as estimated by GLMMs, including ID as a random effect (n=783 travel days, individuals=45). Also shown the estimates, standard errors (±SE), the t-value, z-value and the $R^2_{mar,}$ which is the variation explained by fixed effects and R^2_{con}, the variation explained by the fixed and random effects. (* = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Response	Predictor	Estimate	SE	t/z	R^2_{mar}	R^2_{con}
Travel speed (km/h)	Intercept	28.89	1.20	24.08***	0.04	0.09
	Geography (Non-barriers)	-6.62	1.21	-5.45***		
	Geography (Sea)	3.06	4.45	0.69		
Travel straight-line distance (km)	Intercept	431.96	22.18	19.48***	0.09	0.13
	Geography (Non-barriers)	-180.89	22.89	-7.90***		
	Geography (Sea)	140.95	84.06	1.68		
Travel duration (h)	Intercept	2.54	0.04	71.36***	0.17	0.37
	Geography (Non-barriers)	-0.34	0.03	-12.43***		
	Geography (Sea)	0.45	0.08	5.62***		

Table S2b. Summary statistics for daily mean travel speed, travel straight-line distance and travel duration over different geographies (n = 783 travel days). We show the mean (±SE) for daily travel of lesser kestrels over the desert, sea and non-barriers. Groups sharing the same letter are not significantly different **(**GLMMs followed by Tukey HSD *post-hoc* test; $p \leq 0.05$).

Response	Speed (km/h)	Straight-line distance (km)	Travel duration (h)
Desert	28.9 (1.21)^{b}	432 (22.4)^{b}	12.72 (0.45)^{c}
Sea	31.9 (4.37)^{b}	573 (82.4)^{b}	20.00 (1.63)^{b}
Non-barriers	22.3 (0.77)^{a}	251 (14.0)^{a}	9.09 (0.27)^{a}

Supplementary Table S3. Best ranking models for season, sex and external factors at the daily scale. Selecting final GLMMs for daily mean travel speed, travel straight-line distance and travel duration as a function of the interaction between season and sex, nocturnal travel and external factors (mean daily tailwind, absolute crosswind and boundary layer height, BHL) when flying over barriers vs. non-barriers (n=783 travel days, individuals=45). All models included ID as a random effect. We show the best ranking models (ΔAIC ≤ 2), the models evaluating the effect of the interaction between season and sex, their AIC and the variation explained by fixed effects (R^2_{con}) and fixed and random effects (R^2_{mar}).

Response variable	**Model**
Daily speed (km/h)	**Over barriers**
	Over non-barriers
Daily straight-line distance (km)	**Over barriers**
	Over non-barriers
Daily travel duration (h)	**Over barriers**
	Over non-barriers

Fixed and random effects	df	AIC	ΔAIC	R^2_{con}	R^2_{mar}
~ Nocturnal trav. fraction + Season + Sex + Tailwind + (1 | ID)	7	459.6	0	0.53	0.53
~ Nocturnal trav. fraction + Season + Tailwind + (1 | ID)	6	460.6	0.90	0.52	0.53
~ Nocturnal trav. fraction + Sex + Tailwind + (1 | ID)	6	460.8	1.11	0.52	0.52
~ Crosswind + Nocturnal trav. fraction + Season + Sex + Tailwind + (1 | ID)	8	460.5	1.15	0.53	0.53
~ Crosswind + Nocturnal trav. fraction + Season + Sex + Tailwind + (1 | ID)	7	460.8	1.2	0.52	0.52
~ Crosswind + Nocturnal trav. fraction + Tailwind + (1 | ID)	6	461.2	1.5	0.51	0.53
~ Nocturnal trav. fraction + Tailwind + (1 | ID)	5	461.4	1.5	0.51	0.52
~ Nocturnal trav. fraction + Season * Sex + Tailwind + (1 | ID)	8	461.1	1.6	0.53	0.53
Crosswind + Nocturnal trav. fraction + Season + Tailwind + (1 | ID)	7	461.4	1.84	0.52	0.53
~ Season * Sex + (1 | ID)	6	579.4	119	0.03	0.13
~ Crosswind + Nocturnal trav. fraction + Season * Sex + Tailwind + (1 | ID)	6	1276	0	0.41	0.44
~ Crosswind + Nocturnal trav. fraction + Season + Tailwind + (1 | ID)	7	1277	1.20	0.40	0.43
~ Crosswind + Nocturnal trav. fraction + Season + Tailwind + BHL + (1 | ID)	10	1277	1.58	0.41	0.44
~ Season * Sex + (1 | ID)	6	1573	296	0.02	0.05
~ Diurnal trav. hours + Nocturnal trav. hours + Tailwind + (1 | ID)	6	274.1	0	0.84	0.85
~ Diurnal trav. hours + Nocturnal trav. hours +Season + Tailwind + (1 | ID)	7	247.4	0.50	0.84	0.85
~ Season * Sex + (1 | ID)	6	583.4	309	0.05	0.29
~ Diurnal trav. hours + Nocturnal trav. hours + Season + Sex + Tailwind + (1 | ID)	8	328.8	0	0.86	0.86
~ Crosswind + Diurnal trav. hours + Nocturnal trav. hours + Season + Sex + Tailwind + (1 | ID)	9	329.3	0.55	0.86	0.86
~ Diurnal trav. hours + Nocturnal trav. hours + Season + Tailwind + (1 | ID)	7	329.7	0.77	0.86	0.86
~ Crosswind + Diurnal trav. hours + Nocturnal trav. hours + Season + Tailwind + (1 | ID)	8	330.1	1.22	0.86	0.86
~ Diurnal trav. hours + Nocturnal trav. hours + Season * Sex + Tailwind + (1 | ID)	9	330.2	1.41	0.86	0.86
~ BLH + Diurnal trav. hours + Nocturnal trav. hours + Season + Sex + Tailwind + (1 | ID)	9	330.3	1.55	0.86	0.86
~ Crosswind + Diurnal trav. hours + Nocturnal trav. hours + Season * Sex + Tailwind + (1 | ID)	10	330.7	1.97	0.86	0.86
~ Season * Sex + (1 | ID)	6	1503	1174	0.02	0.02
~ BLH + Crosswind + Season + Tailwind + (1 | ID)	6	1252	0	0.30	0.68
~ BLH + Crosswind + Season + Sex + Tailwind + (1 | ID)	7	1254	1.78	0.31	0.69
~ Season * Sex + (1 | ID)	5	1365	112	0.05	0.67
~ BLH + Crosswind + Season + Tailwind + (1 | ID)	6	3764	0	0.33	0.44
~ BLH + Crosswind + Season + Sex + Tailwind + (1 | ID)	7	3765	1.22	0.33	0.44
~ Season * Sex + (1 | ID)	5	4097	333	0.07	0.30

Supplementary Table S4. Barriers and seasonal patterns in hourly speed of males and females kestrels. Summary table showing the mean (±SE) hourly speed of lesser kestrels for both post- and pre-breeding migration, specifically comparing barriers vs. non-barriers and diurnal and nocturnal flight segments. Comparison of means was performed using Tukey's *post hoc* tests at the 0.05 significance level. Means sharing the same group letter are not significantly different.

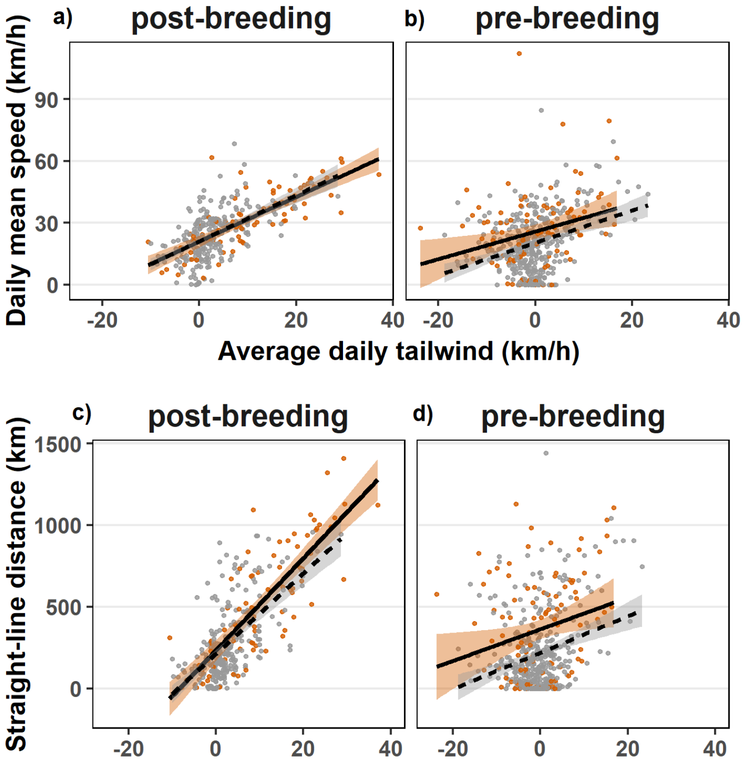
	Diurnal/ Nocturnal	Season	Sex	Hourly speed (km/h)
Barrier	Diurnal	post-breeding	f	35.01 (0.58)^{def}
	Diurnal	pre-breeding	f	28.95 (0.64)^{c}
	Diurnal	post-breeding	m	34.24 (0.74)^{de}
	Diurnal	pre-breeding	m	28.14 (0.69)^{c}
	Nocturnal	post-breeding	f	43.60 (0.81)^{i}
	Nocturnal	pre-breeding	f	39.09 (1.03)^{gh}
	Nocturnal	post-breeding	m	43.27 (0.93)^{hi}
	Nocturnal	pre-breeding	m	38.41 (0.90)^{efg}
Non-Barrier	Diurnal	post-breeding	f	24.43 (0.26)^{ab}
	Diurnal	pre-breeding	f	24.84 (0.30)^{ab}
	Diurnal	post-breeding	m	26.31 (0.33)^{bc}
	Diurnal	pre-breeding	m	22.38 (0.29)^{a}
	Nocturnal	post-breeding	f	36.26 (0.82)^{defg}
	Nocturnal	pre-breeding	f	35.04 (0.87)^{def}
	Nocturnal	post-breeding	m	38.98 (0.73)^{fg}
	Nocturnal	pre-breeding	m	34.60 (0.76)^{d}

Abbreviations: f, female; m, male

Supplementary Table S5. Best ranking models for season, sex and external factors at the hourly scale. Selecting final GLMMs for hourly speed as a function of season, sex and external factors (tailwind, crosswind and BLH). All models included ID as a random effect. Only the results of the best ranking models (**ΔAIC ≤ 2),** the models evaluating the effect of the interaction (season:sex), their AIC and the variation explained by fixed effects (**R^2_{con}**) and fixed and random effects (**R^2_{mar}**) are shown.

Model	Fixed and random effects	df	AIC	ΔAIC	R^2_{con}	R^2_{mar}
Diurnal over barriers	~ BLH + Crosswind + Geography + Season + Tailwind + (1 | ID)	8	7062	0	0.20	0.29
	~ BLH + Crosswind + Geography + Season + Sex + Tailwind + (1 | ID)	9	7064	1.34	0.20	0.29
	~ BLH + Crosswind + Geography + Tailwind + (1 | ID)	7	7064	1.65	0.20	0.29
	~ Season * Sex + (1 | ID)	6	7742	680	0.01	0.13
Nocturnal over barriers	~ Crosswind + Tailwind + (1 | ID)	5	4969	0	0.13	0.23
	~ Season * Sex + (1 | ID)	6	5189	231	0.02	0.15
Diurnal over non-barrier	~ BLH + Crosswind + Geography + Season * Sex + Tailwind + (1 | ID)	9	12869	0	0.12	0.16
	~ Season * Sex + (1 | ID)	6	13667	797	0.01	0.06
Nocturnal over non-barriers	~ Crosswind + Tailwind + (1 | ID)	5	3106	0	0.04	0.10
	~ Crosswind + Sex + Tailwind + (1 | ID)	6	3108	1.7	0.04	0.10
	~ Crosswind + Season + Tailwind + (1 | ID)	6	3108	1.9	0.04	0.10
	~ Season * Sex + (1 | ID)	6	3148	42.0	0.01	0.07

Supplementary Figure S1. Linear relationships between average daily tailwind strength along the falcons realised travel direction (km/h) and lesser kestrel daily mean travel speed and straight-line distance. (a) mean daily speed during the post-breeding migration, (b) mean daily speed during the pre-breeding migration, (c) daily straight-line distance during the post-breeding and (d) daily straight-line distance during the pre-breeding, when flying over barriers (orange and solid line) or non-barriers (grey and dashed line).



Supplementary Figure S2. Travel schedules for different geographies (barrier vs. non-barrier) and seasons. The distribution of travelling (blue) vs. non-travelling (pink) flight segments of the lesser kestrel per hour of the day during the post-breeding migration over (a) barriers and (b) non-barriers, and during the pre-breeding migration over (c) barrier and (d) non-barrier. Data over the sea and desert are pooled.

SUPPLEMENTARY METHODS

Geographies

During their migratory trip, lesser kestrels pass in broad fronts over two types of barriers, the Mediterranean Sea and the Sahara Desert[1]. These are barriers for lesser kestrel migration not only due to the lack of feeding opportunity but due to lack of landing opportunities (sea) and very hostile climate (desert). Although over the sea there is also a weaker formation of thermal updrafts compared to the desert. We assigned each GPS fix to three geography categories, flying over the desert, sea and flying outside these two regions to non-barriers.

Weather effects

Each GPS fix was annotated with environmental data of wind and boundary layer height using the Env-DATA track annotation tool of MoveBank2. For each GPS point, we obtained: the boundary layer height (in km) (BLH), an estimate for thermal updraft formation at a spatial resolution of 0.75 degrees and temporal resolution of 3 hours; and the U (west-east) and V (north-south) wind components (km/h) at a spatial resolution of 0.75 degrees and temporal resolution of 6 hours from the ECMWF (European Center for Medium-Range Weather Forecast). To compute hourly tailwind and absolute crosswind, V- wind and U-wind components were combined in a single vector adding hourly flight direction in degrees to the north and wind strength[3]. We determined tailwind strength and absolute crosswind strength relative to the realised hourly travel direction of migration. We used weather data from the 925 hPa pressure level, corresponding to a mean flight altitude between 445 and 1,145 m a.s.l., which has been used extensively throughout migratory raptor studies[4,5]. We selected the bilinear interpolation method for all wind variables.

CHAPTER 2

GEOGRAPHICAL CLIMATE GRADIENTS INFLUENCE PRE-BREEDING ARRIVAL PATTERNS IN A LONG-DISTANCE MIGRANT

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GEOGRAPHICAL CLIMATE GRADIENTS INFLUENCE PRE-BREEDING ARRIVAL PATTERNS IN A LONG-DISTANCE MIGRANT

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ABSTRACT

In migratory animals, there is strong pressure for timely arrival at the breeding grounds. This has been ultimately explained by natural selection shaping arrival date whereby early arrival can provide fitness benefits. For long-distance migratory birds, variation in arrival date might be proximately caused by differences in departure date, travel speed and duration of stopovers, which can be determined by weather conditions. We aim to study the factors influencing pre-breeding arrival dates in a trans-Saharan migrant, the lesser kestrel (*Falco naumanni*). We use GPS-tracking data to describe patterns in migration timing, accounting for geographical differences and sex-related effects. Lesser kestrels show a large interindividual variation in migration timing that extend over a three-month period. We found that the location of the breeding colony (latitude and longitude) explained most of interindividual variation in migration timing, whereas sex had no effect. The time of arrival at the breeding grounds was 6 days later for every degree increase in latitude and 2 days later for every degree increase in longitude, reflecting the later onset of spring at higher latitudes and eastern longitudes. We show that spring temperature at the breeding colony is an important factor in determining arrival date, with lesser kestrels arriving earlier to locations with warmer spring temperatures. Our results confirm that departure date from the non-breeding areas plays a more important role in early arrival than travel speed or duration of stopovers. When birds compromised in stopovers, they did so under adverse wind conditions or over areas with higher vegetation productivity, usually after barrier crossings.

Keywords: pre-breeding migration, movement ecology, migration timing, proximate factors, ultimate factors, spring green-up.

INTRODUCTION

Appropriate timing is considered essential in the migratory lifestyle (Berthold, 2001; Newton, 2008). Generally, there is an optimal time for migration that maximises successful reproduction and/or survival (Tökölyi et al., 2012; Bauer et al., 2020). In migratory birds, breeding success is typically maximised with an early arrival to the breeding grounds (Kokko, 1999). Early migrants could potentially acquire better territories and gain additional time to restore their body condition or renest if the first attempt fails (Marra et al., 1998; Halupka et al., 2008). In addition, early arriving individuals seem to perform better during the breeding season, including laying larger clutch size and raising more fledglings (Hötker 2003; Tryjanowski et al., 2004; Sergio et al., 2007). However, arriving too early might expose individuals to environments with food shortage, thereby decreasing survival (e.g. Lerche-Jørgensen et al., 2018). Moreover, reproductive success usually declines with the progression of the season (Verhulst & Nilsson, 2008), hence, late arriving individuals may suffer a lower reproductive success due to a decline in food and optimal environmental conditions for breeding associated with the progress of the season. There tends to be a relatively large variation in migration timing (i.e. arrival and departure dates) between and within populations (e.g. Lourenço et al., 2011; Gill et al., 2014; Rotics et al., 2018). Potential factors affecting migration timing include sex- and age-related differences (Moller, 1994; Rubolini et al., 2004; Bildstein, 2006), differences in the timing of the life cycle events (Briedis et al., 2016b), flexible responses to the phenology of the environment along the migratory route (Akesson & Helm 2020), the location of the breeding site (Conklin et al., 2010) or post-glacial colonisation patterns of the species (Hewitt, 2000; Perez-Tris et al., 2004). Elucidating the mechanisms driving interindividual temporal and geographic variation in seasonally migrating organisms remains a fundamental question in current bird migration research (Rotics et al., 2018; Smith et al., 2020; Burnside et al., 2021).

When investigating the mechanisms driving interindividual temporal and geographic variation in migratory birds, it may be helpful to distinguish between ultimate and proximate factors (Tinbergen, 1963; Bauer et al., 2011). While the former explains why a specific trait has evolved (why a specific migration pattern is reproductively advantageous), the latter explains how it is realised (how it happens) (Low, 2006; Schmaljohann, 2018). The ultimate cause for an early arrival to the breeding colony is natural selection, whereby early arriving individuals generally get access to better territories/mates/resources, increasing their breeding success (Kokko, 1999). Migrants could achieve this by departing earlier, increasing travel speed or reducing stopover duration (Nilsson et al., 2013). Studies that have jointly tested the relative contribution of these mutually non-exclusive proximate factors to the observed arrival date in a single species have frequently yielded different results. For example, recent biologging studies have revealed that an early departure from the non-breeding area, but not migration speed, significantly influences early arrival (Lemke et al., 2013; Ouwehand & Both, 2017; Rotics et al., 2018). However, other findings highlight that travel speed is an important proximate factor for an early arrival to the breeding grounds (McKinnon et al., 2016; Schmaljohann et al., 2016). Concerning the duration of stopovers, if migrants want to reduce overall migration time during the pre-breeding migration, they could achieve that most effectively by reducing stopover duration (Nilsson et al., 2013). Previous tracking studies have reported different migratory behaviours across and even within populations (Carneiro et al., 2020). For example, some Icelandic-breeding whimbrels (*Numenius phaeopus islandicus*) performing seasonal migrations to and from West Africa undertook a direct migration (fly non-stop to Iceland), while others made stopovers during their pre-breeding migration (Alves et al., 2016). Undertaking a direct flight may guarantee an early arrival, whereas prolonged stopovers may help individuals arrive in better body conditions to their breeding areas. Furthermore, it has been previously shown that the territorial sex (males in most bird species) arrive to the breeding grounds earlier than females (Marra et al., 1998; Rubolini et al., 2004; Tøttrup & Thorup, 2008). The ultimate cause for this difference in behaviour has been attributed to the high competitiveness of males for securing a high-quality territory, which results in gains in individual fitness (Kokko, 1999; Morbey &

Ydenberg, 2001). Knowledge of the relative importance of proximate factors to the observed sex-specific differences in arrival date remains undescribed for many species (but see: Schmaljohann et al., 2016; Rotics et al., 2018; Briedis et al., 2019).

Optimal migration timing is ultimately determined by the benefit that birds achieve when timing their migration with the temporal and spatial availability of ephemeral food sources along their routes and at their breeding grounds (Kolzsch et al., 2015; Armstrong et al., 2016). Synchronising their migration timing with the local phenology of the environment is key for individual survival and reproductive success (Marra et al., 1998; Alerstam et al., 2003; Visser et al., 2015). Long-distance (e.g. trans-Saharan) migrants mainly rely on endogenous biological clocks and fixed cues, such as photoperiod, for timing departure decisions from the non-breeding areas (Berthold, 2001; Ramenofsky & Wingfield, 2007; Bossu et al., 2022), but local environmental conditions could also modulate the migration departure (Haest et al., 2018; Burnside et al., 2021). Once migration is started, birds are expected to adjust their migration progress (e.g. travel speed and stopovers) in response to environmental conditions related to, for example, food availability or wind conditions encountered *en route* (Drent et al., 1978; Van der Graaf et al., 2006; Kölzsch et al., 2015). As birds approach to their breeding destinations, decisions on arrival timing can be made based on expected environmental conditions at their breeding areas (Rakhimberdiev et al., 2018; Briedis et al., 2020). Climatic variables, in particular temperature, which correlates with latitude, are related to spring green-up onset (Newton 2008; Briedis et al., 2019). Because of the strong relationship between the phenology of plants and insects, this factor serves to time the migration of herbivores and insectivorous birds (Sorte et al., 2014; Usui et al., 2017). Among conventional expectations for the pre-breeding arrival date of birds in relation to climate and latitude are that: birds shall arrive earlier when they experience high temperatures along their route and subsequently at their breeding areas (Sokolov & Kosarev 2003; Tottrup et al., 2010; Vaitkuvienë et al., 2015); birds shall depart earlier and arrive earlier in years with higher winter rain (McKellar et al., 2013; Haest et al., 2020) and individuals breeding at lower latitudes shall arrive earlier (Conklin et al.. 2010; Briedis et al. 2016b). Furthermore, the arrival date may vary with longitudinal gradients in climate (Briedis et al., 2020). In Europe, the climate varies along a west to east gradient ranging from a more oceanic climate with relatively small temperature fluctuations in the western part and a more continental climate in the eastern part with more substantial fluctuations (Metzger et al., 2005;

Metzger et al., 2013). If populations are capable of tracking spring at the breeding grounds, we may expect arrival dates to be timed with longitudinal climatic gradients from west to east (Briedis et al., 2020). Wind direction and strength may also generate differences in migration timing by influencing departure and stopover decisions (Thorup et al., 2006), with more favourable wind conditions allowing birds to arrive earlier (Haest et al., 2020).

This paper studies the pre-breeding migration timing of the lesser kestrel (*Falco naumanni*) from sub-Saharan Africa to different breeding locations in Spain and Italy. Our aims are (1) to describe spatiotemporal patterns in pre-breeding migration (i.e., the relation between the geographical location of breeding sites, departure location from non-breeding sites and migration timing) in addition to sex-related differences. We expected birds breeding at southern latitudes and western longitudes to arrive earlier to the colonies, owing to climatic gradients (Briedis et al., 2020). Based on the general sex-specific migratory timing pattern of males returning earlier than females (Morbey et al., 2001; Rubolini et al., 2004; Coppack et al., 2009), and the observed territorial behaviour of male lesser kestrels defending a nest hole within their breeding colonies at arrival from pre-breeding migration (Serrano & Tella, 2007), we also expected the former to depart from the wintering sites and arrive at the breeding colonies significantly earlier than the latter. (2) To evaluate the relative importance of proximate factors (departure date, travel speed and duration of stopovers) as drivers of early arrival, accounting for sexual differences. We expected departure date to play a major role, as it has been demonstrated for long-distance migrants (Bildstein, 2006; Schmaljohann et al., 2016; Rotics et al., 2018). In addition, if there are sexual differences in migration timing, we expected males to depart earlier, make fewer stopovers, and travel faster. (3) To assess the relative contribution of expected spring temperature and winter rain at the breeding colony (as proxies for the onset of spring) and departure and arrival location in explaining temporal variation in arrival date. We hypothesised that lesser kestrels are capable of tracking a “green wave” (the increase in plant productivity with spring arrival) at the breeding location (but see Wang et al., 2019). Therefore, if the timing of migration is ultimately explained by foreseen local phenology, we expected spring temperature and winter rain at arrival sites to explain a large part of the temporal variation in the arrival date. Birds breeding at warmer locations (southwestern sites) should arrive earlier relative to those breeding at colder locations (northeastern sites). Finally, (4) to explore geographic patterns in stopover behaviour and whether lesser kestrels adjust their migration progress (i.e. stopover duration) to the phenology and wind conditions along their migratory routes. Birds are expected to prolong stopover duration when they find areas with suitable drinking/fuelling conditions or under strong adverse winds (Thorup et al., 2006).

METHODS

Study species tagging and tracking

The lesser kestrel is a small insectivorous raptor with a reversed sexual size dimorphism (females being ~15% larger in body mass) (Cramp & Simmons 1980). It breeds in colonies across southern Europe, northern Africa to China and winters in Africa south of the Sahel and up to South Africa, although some Mediterranean populations also contain resident individuals. From 2014 to 2020, birds were tagged with three different types of solar GPS-UHF loggers (Pica, Ecotone, Gdynia, Poland; Microsensory LS, Córdoba, Spain; and NanoFix GEO+RF, Pathtrack Ltd., Leeds, UK). The GPS-UHF loggers weighing 5.5 g (including harness, ~3.8 % of the mean weight at capture, males = 146.0 g ± 35 SD; females = 148.0 g ± 29 SD) were attached as backpacks with a Teflon harness. Locations were stored on-board and downloaded via a UHF base station placed in the vicinity of the colony. Details on loggers programming are described in the supplementary material.

We analysed 84 pre-breeding migratory trips of 61 adults breeding in Spain (53 individuals) and Italy (8 individuals) from 24 locations (Fig. 1a, b). There were 21 individuals with 2 and 1 individual with 3 migratory trips from different years (Supplementary Table S1).

Identifying the pre-breeding migration trip

GPS locations were mapped and examined visually using QGIS. We identified pre-breeding trips based on evident long directional flights towards the north (breeding range). Having identified visually the segment of data occurring between the Sahel and the breeding range, where individuals were undoubtedly migrating, we calculated the distance between the current position to the previous one using the deg.dist function in R package 'fossil' (Vavrek, 2011). The onset and end of migration were identified based on marked shifts in daily accumulated distance histograms. For each migratory trip, we searched for a group of first and last three consecutive days with an average daily distance of at least 150 km, preceded (if onset) or followed (if end) by a stationary phase of five consecutive days with mean daily travelled distance <70 km (cf. Rotics et al., 2018). We assigned as the start of migration day to the first of the three-day set and the end of migration day to the last of the three-day set. We confirmed those dates visually, again using QGIS.

Movement metrics

We re-sampled all data to one-hour intervals to have a uniform temporal resolution (with deviations of 20 minutes). After re-sampling, we analysed 24,335 hourly segments corresponding to the pre-breeding migration. We calculated the daily straight-line distance (i.e., the shortest orthodromic path) between the first and last daily position for each bird (for 24-h intervals, sunrise to sunrise, Lopez-Ricaurte et al., 2021). Next, we differentiated between travel days and stopover days using a threshold of the total travelled distance of 50 km day^{-1} (Klaassen et al., 2011; Limiñana et al., 2013). We segmented each pre-breeding migratory trip into travel vs stopover segments and calculated for each stopover event the total duration (in days) and the median latitude and longitude for the stopover location (n =125 events, ranging from 1 to 17 days). Finally, travel speed (km/day) was calculated as the ratio between the total migration distance and the migration duration (excluding stopover days).

Environmental data

For all breeding colonies, we extracted a monthly average of minimum air temperature (°C), maximum air temperature (°C) and precipitation (mm) from WorldClim at 0° 2.5" (~21 km^2) resolution (www.worldclim.org; Hijmans et al., 2005). We extracted the average minimum and maximum temperatures (Tmin and Tmax respectively) from February to March, (the months in which lesser kestrels arrived from the pre-breeding migration) and averaged values across years (2010-2018). We computed the temperature range as the difference between Tmax and Tmin (we considered these as measures for expected spring temperature). We also calculated the cumulative average monthly precipitation from December to March (a measure of winter rain) and averaged values across years (2010-2018) since accumulated winter rain has a known influence on lesser kestrel breeding success (Rodriguez & Bustamante 2003).

To determine the relative influence of food availability and wind conditions on stopover decisions, we used the Normalized Difference Vegetation Index (NDVI) as a proxy for food abundance and wind direction and strength in relation to migratory direction. The NDVI is a vegetation index indicative of vegetation cover and photosynthetic activity in an area and a proxy for food/insect abundance for insectivorous birds (Schlaich et al., 2016; Morganti et al., 2019). We annotated each GPS fix using the Env-DATA track annotation tool of Movebank (Dodge et al., 2013). We obtained NDVI from MODIS (NASA's Moderate Resolution Imaging Spectroradiometer) provided every 16 days at 250 m spatial resolution). Wind direction and strength come as U (west-east) and V (north-south) wind components (km/h) at a spatial resolution of 0.75 degrees and temporal resolution of 6 hours from the ECMWF (European Center for Medium-Range Weather Forecast). We interpolated wind components from the 925 mb pressure level (approx. 750 m.a.s.l.) (Schmaljohann et al., 2012; Limiñana et al., 2013). We averaged those per day and computed daily wind speed and direction. We calculated tailwind strength relative to the realised travel direction of migration (Vansteelant et al., 2015). We selected the bilinear interpolation method for all variables (Dodge et al., 2013).

Statistical analyses

Geographic and sex-related patterns in migration timing

We first describe the patterns in pre-breeding migration timing by computing the range and mean (± SE) departure and arrival date. We analysed spatiotemporal variation in migration timing (i.e. departure and arrival date) in relation to sex by means of Generalised Linear Mixed Models (GLMMs). To account for the geographic influence, we added departure latitude, departure longitude, arrival latitude, arrival longitude and an interaction term for sex and breeding location (continuous variables: departure latitude, departure longitude, arrival latitude and longitude) as fixed factors. After inspecting residual plots, we fitted a Gaussian error distribution. We included bird identity as a random effect to account for 23 repeated migratory trips corresponding to the same individual in different years in all models. We computed a full model and used the 'dredge' function in the R package 'MuMIn' that uses Akaike weights (AICw) to rank all possible subsets of reduced models from the full model based on Aikaike's Information Criterion corrected for small sample sizes (AICc) (Barton, 2019). We selected the models if they had fjAICc R 2 units of the highest-ranked model. Where we had multiple models within fjAICc R 2 units, we selected the most parsimonious model (i.e., with fewer predictors) (Burnham & Anderson, 2002). Estimates of parameters whose 95% confidence interval (CI) do not overlap zero were considered significant. We used 'lmerTest' R package to estimate degrees of freedom using the Satterthwaite's method and obtain p-values for fixed effects (Kuznetsova et al., 2017). We calculated marginal ($R_{marginal}$) and conditional ($R_{conditional}$) values following Nakagawa & Schielzeth (2013) using the R package 'MuMIn' (Barton, 2019).

Proximate factors affecting arrival date

We analysed the relative contribution of each proximate factor (departure date, duration of stopovers and travel speed) to the observed variation on arrival date. Since we aimed at determining which of these primarily characterised early-arriving birds, we first fitted separated LMMs to arrival date as a response variable, including individual identity as a random effect. We compared $AIC_{C,}$ and the proportion of variance explained by each predictor. Marginal ($R_{marginal}$) and conditional ($R_{conditional}$) values were calculated. We investigated the effect of departure date, duration of stopovers and travel speed altogether in a single model, accounting for sex effect, by means of Generalised Linear Mixed Models (GLMMs). Before fitting the GLMMs, all continuous predictors and response variables were transformed to z-scores.

Climatic and geographic gradients at breeding locations

We aimed at testing whether the expected onset of spring at the breeding location ultimately explained temporal variation in the arrival date. The effect of the mean maximum temperature from February (TmaxFeb), the minimum temperature from February (TminFeb), the maximum temperature from March (TmaxMarch), the minimum temperature from March (TminMarch), the temperature range (Trange) and the cumulative precipitation from December, January, February and March (CumPrec) were analysed separately using LMMs. To investigate the relative importance of climate versus geographic variables on the arrival date, we used GLMMs.

Geography and environmental conditions at stopovers

We used LMMs to compare the duration of stopovers in relation to departure latitude, departure longitude, arrival latitude, and arrival longitude, accounting for sex differences, with individual identity as a random effect. We fitted models with Poisson error and log link function for stopover duration, appropriate for count data (Zeileis & Jackman, 2008). To identify whether NDVI and wind conditions influence stopover decisions, we compared NDVI and daily tailwind strength between stopover and travelling days. We fitted LMMs of daily tailwind conditions and NDVI. We included ID as a random effect and added the variable 'travel' (with two levels: travel, stopover) as a fixed factor. To estimate differences between travel vs stopover days, we used the 'emmeans' function from the emmeans package and the Kenward–Rogers method to estimate degrees of freedom (Russell, 2020).

All data analyses were conducted in R (v.3.5.3., R Core Development Team, 2020), and all figures were produced with ggplot2 (Wickham, 2009). We checked for multicollinearity and only included variables that were not highly correlated ($R < 0.60$) (Hinkle et al., 2003) (Supplementary Table S2).

RESULTS

Geographic and sex-related patterns in migration timing

Lesser kestrels' departure dates from sub-Saharan non-breeding areas spanned across a three-month period between 25 January and 24 April (mean: 28 February ± 17 days) (Fig. 1c). Arrival dates to the breeding colonies ranged from 2 February to 13 May (mean: 14 March ± 20 days).

Our models identified arrival latitude and longitude as important predictors for migration timing (Table 1). Neither departure latitude, departure longitude and sex, nor the interaction effects of sex with the breeding location were selected in the most parsimonious model (Supplementary Table S3-S4). The model for departure date retained arrival latitude and arrival longitude with a positive relationship. Birds breeding at more northern and eastern locations departed increasingly later, at a rate of c. 5 days delay per 1° increase in arrival latitude and c. 1 day delay per 1° increase in arrival longitude. Similarly, the model for arrival date retained arrival latitude and arrival longitude with a positive relationship. Most northeastern breeding migrants reached their breeding grounds later, at a rate of c. 6 days delay per 1° increase in arrival latitude and c. 2 days delay per 1° increase in arrival longitude.

Figure 1. Pre-breeding migration trips (n= 84) of lesser kestrels and stopover duration (legend). For visualization, we show two subsets of data that correspond to the location of the breeding colony relative to an arbitrary reference latitudinal boundary used: (a) northernmost breeders (> 40° N, red colour) and (b) southernmost breeders (< 40° N, blue colour) (c) individuals variation in the timing of the pre-breeding migration. The geographic extent of our breeding sites stretched between 37 – 42° N latitude and between -6.5 – 16.5° E longitude, which falls in a climatic transition among the hot-summer Mediterranean, continental Mediterranean, steppe to warm temperate climate (according to the Köppen-Geiger climate classification and orographic conditions Koppen,1936). Yellow circles indicate clusters of breeding colonies near each other and included in our study (maximum distance between colonies in a cluster = 60 km).

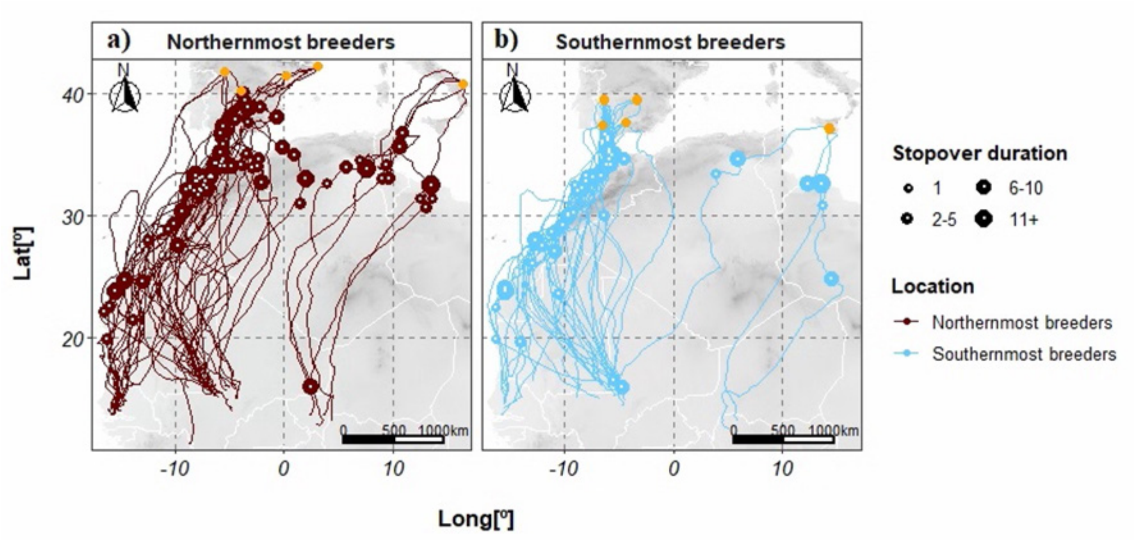


Table 1. Estimates for fixed effects on departure and arrival dates as estimated by the most parsimonious model. Model estimates, standard error (± SE), and the t-value (the ratio between the estimate and its SE) are given, as well as the variance for the random effects. All models included individual identity (ID) as a random effect. (*p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001).

Response variable	**Fixed effects**				**Random effects**			
		Esti-mate	**SE**	**t**		**Variance**	**R^2_{mar}**	**R^2_{con}**
Departure date	Intercept	-147.90	38.15	-3.87***	ID	40.20 ± 6.10	0.50	0.59
	Arrival latitude	5.27	0.95	5.50***	Residual	170.87 ± 13.07		
	Arrival longitude	1.25	0.21	5.79***				
Arrival date	Intercept	-151.70	44.29	-3.43**	ID	1.26 ± 1.12	0.51	0.51
	Arrival latitude	5.76	1.11	5.18***	Residual	212 ± 14.59		
	Arrival longitude	1.71	0.26	6.59***				

Observations = 84 migratory trips, ID = 61 individuals

Proximate factors influencing arrival date

As expected, departure date explained the largest amount of variation in arrival date of lesser kestrels ($R^2_{mar} = 0.84$), with a positive effect (Fig. 2a and Table 2). The duration of stopovers days and travel speed also influenced arrival date, although to a lesser extent (Fig. 2b, c). The variance in arrival date explained by these variables was lower compared to departure date (R^2_{mar} = 0.31 and 0.15, respectively). Both departure date and stopover duration were consistently selected ahead of travel speed as predictors of arrival date (Supplementary Table S5-S6), indicating that they explain more variation than travel speed. We found no evidence for sex-related differences in arrival date.

Table 2. Results of separate LMMs (with ID as a random effect) of proximate factors influencing arrival date. (*p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001).

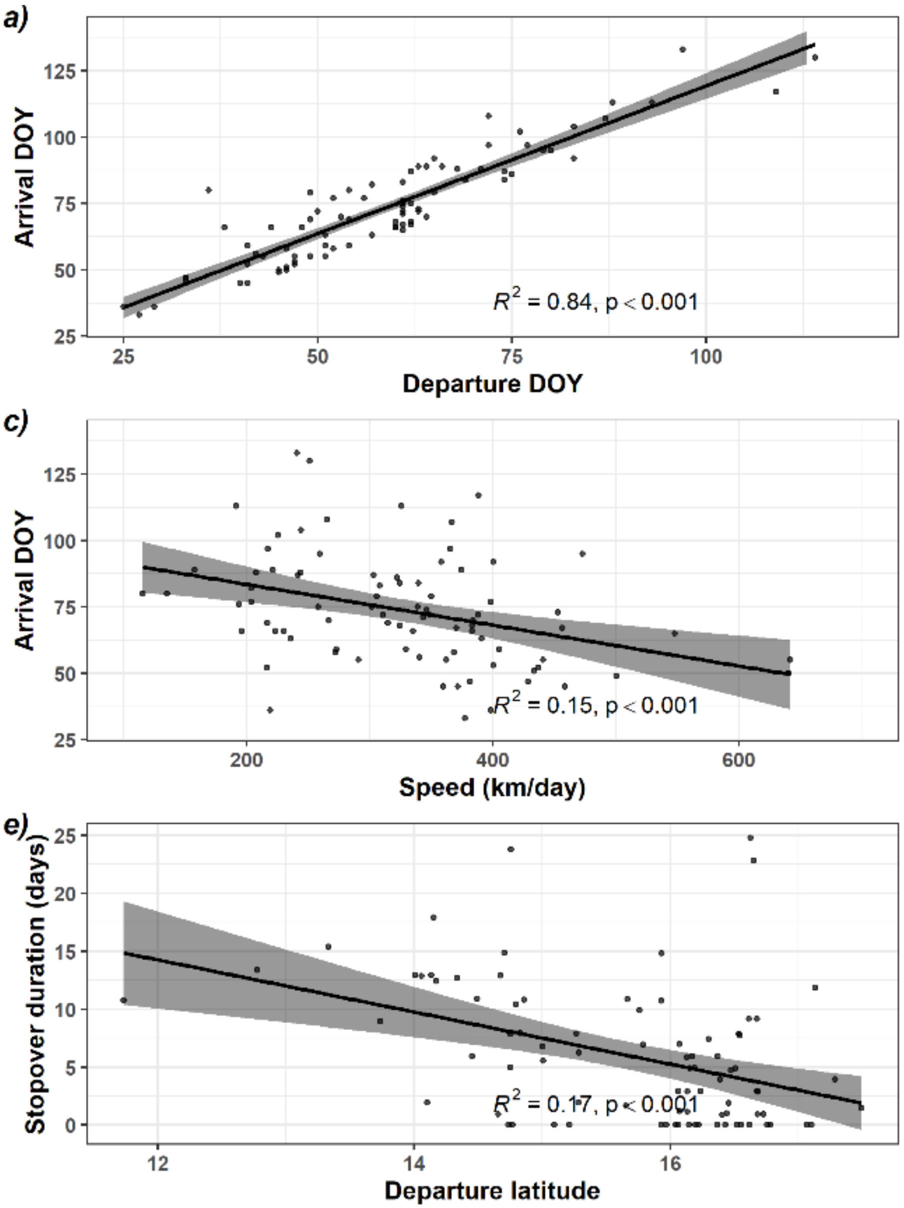
Variable	Estimate	Std. Error	t	LCI, UCI	AICc	R^2_{mar}	R^2_{con}
Departure date	0.92	0.04	20.46***	0.83,1.09	91.9	0.84	0.88
Stopovers (days)	0.55	0.08	6.81***	0.39,0.71	203.8	0.31	0.74
Speed (km/day)	-0.38	0.10	-4.01***	-0.57,-0.19	225.5	0.15	0.59

Sample size = 84 migratory trips from 61 individuals.

Geographic and climatic factors influencing arrival date

Examining variables with separate LMMs revealed that the climatic factor that explained most of the variance in arrival date was spring temperature at the breeding colony (TmaxMarch: $R^2 = 0.30$, *p* R 0.001; Table 3, Fig. 2d) with lesser kestrels arriving earlier to locations with warmer spring temperatures. The winter rain and the temperature range were also identified as important predictors and were used in the subsequent models. The most parsimonious climatic model for arrival date retained spring temperature and temperature range and explained 32% (R^2mar) (Table 4). When including geographic variables in the model, the effect of winter rain and spring temperature became negligible (Table 5). The most parsimonious model explained 48 % (R^2_{mar}) of the variation in arrival date and retained arrival latitude and longitude with positive effects, suggesting that they are probably surrogates for combinations of climatic factors (Supplementary Table S7).

Figure 2. Correlation between arrival date and (a) departure date (day-of-year, DOY), (b) stopover duration (days), (c) travel speed (km/day). Also showing (d) correlation between arrival date and spring temperature at the breeding colony, (e) correlation between stopover duration (days) and departure latitude and (f) correlation between stopover duration (days) and arrival longitude. Each dot represents one pre-breeding migration trip.



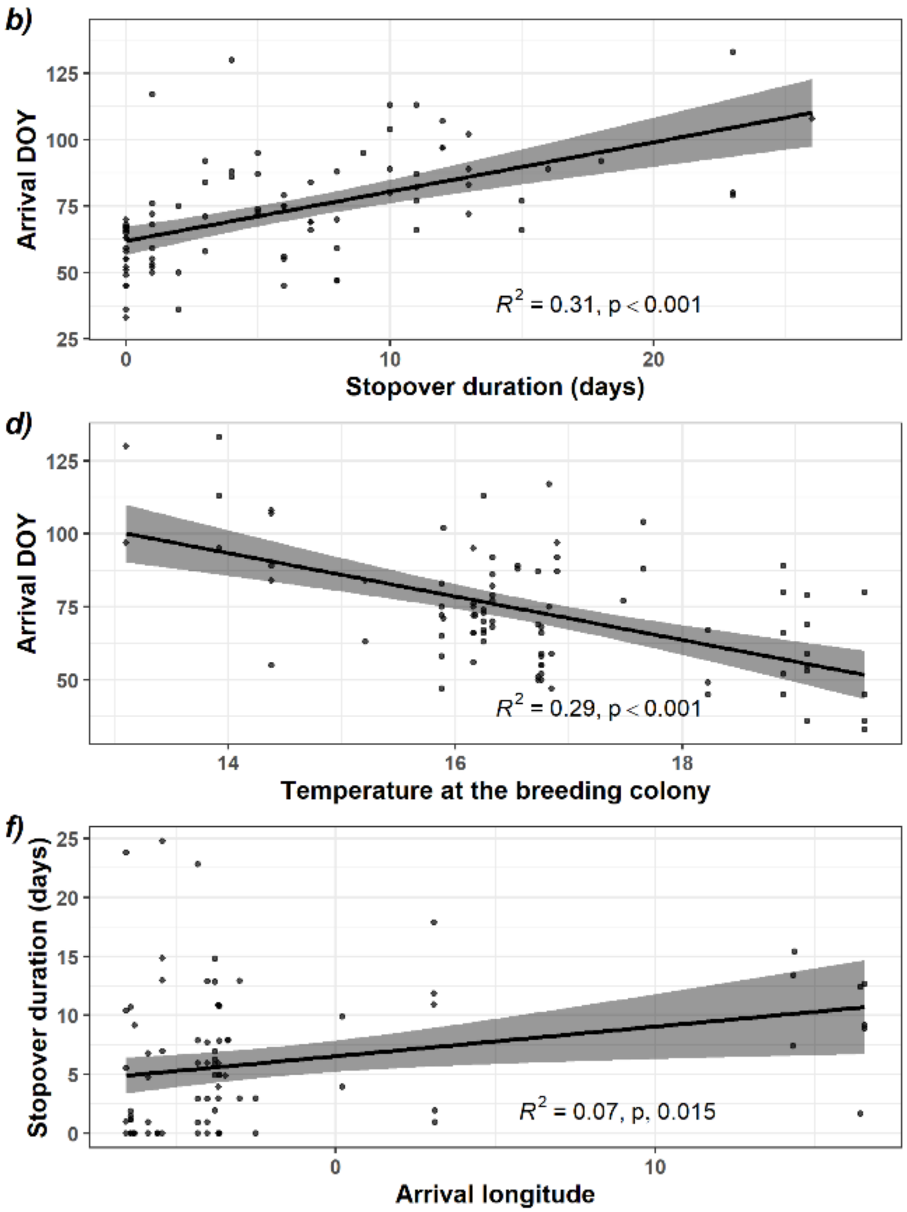

b)
Arrival DOY
125
100
75
50
25
0
10
20
Stopover duration (days)
$R^2 = 0.31, p < 0.001$
d)
Arrival DOY
125
100
75
50
14
16
18
Temperature at the breeding colony
$R^2 = 0.29, p < 0.001$
f)
Stopover duration (days)
25
20
15
10
5
0
0
10
Arrival longitude
$R^2 = 0.07, p, 0.015$

Table 3. Results of separate linear mixed models (with ID as a random effect) associating arrival date (day-of-year, DOY) with different climatic variables at the breeding location averaged for the period (2010–2018). Significant differences are shown in bold. (*p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001).

	Climate variable	Estimate	SE	t	LCI, UCI	R^2_{mar}	R^2_{con}
Arrival date	TmaxFeb	-5.43	1.19	-4.56***	-7.80, -3.06	0.22	0.51
	Tmin Feb	-2.28	1.22	-1.87	-4.71, 1.17	0.05	0.48
	TmaxMarch	-7.52	1.33	-5.67***	-10.15, -4.88	0.30	0.53
	Tmin March	-1.88	1.43	-1.31	-4.71, 0.98	0.02	0.50
	CumPrec	-0.15	0.05	-3.04***	-0.24, -0.05	0.12	0.48
	Trange	-6.24	1.57	-3.97****	-9.37, -3.12	0.17	0.53

Abbreviations: TmaxFeb = Mean maximum temperature from February, **Tmin Feb =** Mean minimum temperature from February, **TmaxMarch =** Mean maximum temperature from March, **Tmin March =** Mean minimum temperature from March, **CumPrec =** Mean cumulative precipitation from December, January, February and March, **Trange** = temperature range.

Table 4. Table of top-ranked models for the effect of climate at the breeding colony on arrival date. Models are ranked according to increasing AIC values, with the best performing model on top. Highly correlated predictor variables (r < 0.6) were omitted (i.e. Tmax Feb was excluded due to close a correlation with Tmin Feb and Tmin Feb was also excluded due to a correlation with Tmax Mar) . Grey boxes indicate that a given variable is included in the model.

CumPrec	TmaxMarch	Trange	df	logLik	AICc	delta	weight	R^2_{mar}	R^2_{con}
■	■	■	6	-99.44	211.96	0.00	0.61	0.36	0.53
	■	■	5	-101.51	213.79	1.83	0.24	0.32	0.54
■		■	5	-102.62	216.02	4.05	0.08	0.30	0.52
	■		4	-104.50	217.51	5.55	0.04	0.27	0.52
■	■		5	-103.74	218.25	6.29	0.03	0.28	0.51
		■	4	-108.65	225.80	13.83	0.00	0.17	0.53
■			4	-111.55	231.60	19.63	0.00	0.12	0.48
			3	-115.79	237.88	25.92	0.00	0.00	0.50

Abbreviations: CumPrec = Mean cumulative precipitation from December, January, February and March, **TmaxMarch =** Mean maximum temperature from March, **Trange** = temperature range.

Table 5. Table of top-ranked models for the effect of climate at the breeding colony and geographic location on arrival date. Models are ranked according to increasing AIC values, with the best performing model on top. Highly correlated predictor variables ($R < 0.6$) were omitted. Grey boxes indicate that a given variable is included in the model.

Departure latitude	Departure longitude	Arrival latitude	Arrival longitude	CumPrec	TmaxMarch	Trange	df	logLik	AICc	delta	weight	R^2_{mar}	R^2_{con}
		▨	▨				5	-90.81	192.39	0.00	0.17	0.48	0.55
▨		▨	▨				6	-90.04	193.18	0.79	0.12	0.49	0.55
	▨	▨	▨				6	-90.43	193.96	1.57	0.08	0.49	0.58
		▨	▨			▨	6	-90.49	194.06	1.67	0.07	0.49	0.53
		▨	▨	▨			6	-90.78	194.65	2.26	0.06	0.49	0.55
		▨	▨		▨		6	-90.79	194.67	2.29	0.06	0.48	0.55
▨		▨	▨			▨	7	-89.73	194.93	2.55	0.05	0.50	0.53
▨	▨	▨	▨				7	-89.98	195.43	3.04	0.04	0.49	0.56

Abbreviations: CumPrec = Mean cumulative precipitation from December, January, February and March, **TmaxMarch =** Mean maximum temperature from March, **Trange** = temperature range.

Geographic patterns and environmental conditions shaping stopover behaviour

Based on LMMs, departure latitude had a significant negative impact on stopover duration (Table 6, Fig. 2e). Birds departing from northern latitudes (covering shorter total migration distances) spent shorter periods at stopovers. Moreover, arrival longitude had a significant positive impact on stopover duration (Fig. 2f). Birds breeding at more eastern locations spent longer periods at stopovers. We did not find a significant impact of departure longitude, arrival latitude and sex on stopover duration. Stopover days corresponded to locations with higher NDVI values than travel days, and stopover days had significantly stronger headwinds than travel days (Fig. 3 and Supplementary Table S8).

Figure 3. Comparing conditions found on stopovers (grey) and travel days (orange). **(a)** Mean NDVI comparisons and (b) mean daily tailwind speed comparison. The asterisks above represent significant differences between stopover and travel days by Tukey HSD post-hoc test at the 0.05 significance level.

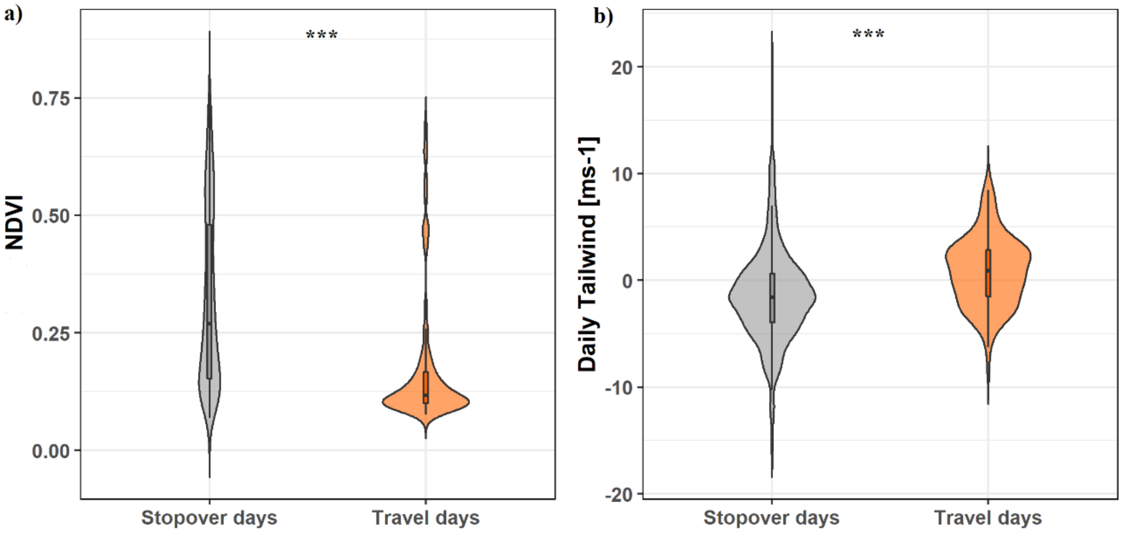


Table 6. Results of separate linear mixed models (with ID as a random effect) associating stopover duration (days) with geographic variables and sex. Significant differences are shown in bold. (*p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001).

Response variable	Fixed effects	Estimate	SE	z-value	R^2_{mar}
Stopover duration	Sex	0.05	0.29	0.6	0.00
Stopover duration	Departure Latitude	-0.27	0.07	-3.62***	0.08
Stopover duration	Departure Longitude	-0.03	0.02	-1.27	0.02
Stopover duration	Arrival Latitude	0.13	0.10	1.32	0.03
Stopover duration	Arrival Longitude	0.05	0.02	2.67*	0.08

Observations = 84 migratory trips, ID = 61 individuals.

DISCUSSION

Our work shows a large variation in the pre-breeding migration timing of lesser kestrels, mainly driven by the location of the breeding colony in association with a climatic gradient, with no sex-related differences. Generally, birds breeding at more southwestern colonies departed earlier from west African non-breeding grounds and arrived earlier to their Mediterranean colonies relative to birds breeding in more northeastern sites. This is likely due to climatic gradients between S-N and W-E European breeding colonies. Our results confirm previous findings that birds ultimately aim to synchronise their arrival to match the expected onset of spring (Briedis et al., 2020), with likely downstream consequences on lesser kestrel reproductive success (Rodriguez & Bustamante, 2003).

In accordance with previous tracking studies on the lesser kestrel (Sarà et al., 2019), and contrary to our expectations, our results show no sex effects in arrival date. Sex differences in pre-breeding migration schedules in general and males preceding females, in particular, have been shown in many migratory species (Schmaljohann et al., 2015; Briedis et al., 2019), including raptors (e.g. bald eagle, *Haliaeetus leucocephalus*; red kite, *Milvus milvus*; northern harrier, *Circus hudsonius*, American kestrel, *Falco sparverius*; merlin, *Falco columbarius*, Bildstein, 2006). We envision two possible reasons for our results: (1) the long establishment phase of the lesser kestrel, arriving two months before the onset of breeding (Negro et al., 1991), may well offset the need for an early arrival and favour individuals that arrive in good shape to acquire the best nesting holes. (2) Coloniality offsets the need to arrive earlier than "competitors" due to the advantage of being there at the same time to benefit from the fitness gains of colonial breeding (Maggio et al., 2013).

In agreement with our expectations and consistent with previous studies (Jahn et al., 2013; Schmaljohann et al., 2016; Ouwehand & Both, 2017), the departure date from the West African non-breeding area explained much of the variation in arrival date ($R_{marginal}$=0.86, Fig. 2a and Table 2). Departure date could be triggered by a mixture of endogenous cues, photoperiod and local environmental factors such as wind, temperature, rain and food supplies (Newton, 2008, Burnside et al., 2021). For example, a study on the long-distance migrant Swainson's thrush (*Catharus ustulatus*), migrating from Canada to the Gulf Coast and back, revealed that departure decisions were best explained by a mixture of high daily temperatures (>21 °C) and low wind speed (< 10 km/h) at the time of take-off (Bowlin et al., 2005). However, lesser kestrels tracked in this study are known to aggregate in communal areas before the onset of the pre-breeding migration (Pilard et al., 2011 and unpublished data), experiencing similar environmental cues. We found that birds had varying departure dates corresponding to the latitude and longitude of their breeding colony. We speculate that endogenous biological clocks play a more important role in kestrels' departure decisions than local conditions. The existence of timekeeping mechanisms or the use of biological clocks to time migration has been recently described in closely related species such as the peregrine falcon (*Falco peregrinus*) and the American kestrel (*Falco sparverius*) (Gu et al., 2021; Bossu et al., 2022). In addition, environmental cues indicating the onset of suitable phenological conditions at the breeding sites 3000 km away and in 1 month in the future may be unlikely (Åkesson et al., 2017; but see Saino & Ambrosini, 2008). We also found that stopover duration and travel speed had a significant effect on arrival date but were comparatively less influential than the departure date. Birds that departed later did not compensate for their delay by increasing migration progress (reduce stopover, see Supplementary Fig. S1), which contrasts other studies (White storks, *Ciconia ciconia,* Rotics et al., 2018; Western Marsh Harriers, *Circus aeruginosus*, Vansteelant et al., 2020), where late departing birds migrated faster to overtake their conspecifics.

We aimed to understand the relative importance of climatic and geographic variables commonly used to explain variation in arrival date (Conklin et al., 2010; Knudsenet al., 2011; Briedis et al., 2016b; Cadahía et al., 2017). The location of the breeding colony explained a good proportion of this variation, although it is hard to disentangle climatic and geographic effects because there exists a strong correlation between latitude and temperature (r=73 supplementary Table S2) and precipitation of the study sites (r=0.58, supplementary Table S2). We found a positive relationship between the latitude and the longitude of the breeding sites and arrival date, i.e. with each additional 1° latitude delaying arrival by c. 6 days and with each additional 1° longitude delaying arrival by c. 2 days. This revealed an earlier migration among the southwest relative to the northeast Mediterranean colonies, which we believe is due to a spatiotemporal gradient in habitat phenology. Indeed, spring temperature and winter rain, although the last one with a relatively minor effect, showed such gradients, with earlier onset of spring (warmer spring temperatures and more rainy winters) in the more southwestern colonies. This is ultimately explained by individuals adjusting their arrival date at their breeding locations to match expected spring temperatures or associated factors that promote the emergence of insects (Marra, 2005).

Birds departing from southern latitudes (covering longer total migration distances) showed longer stopovers, mainly after crossing ecological barriers: the Mediterranean Sea or the Sahara Desert (Lopez-Ricaurte et al., 2021) (or at the western and the northern edges of the Sahara Desert) (Map 1 and Fig. 2.e). We suggest this could be due to birds recovering the energy invested after barrier crossings, as suggested for other trans-Saharan migrants (e.g. ospreys, Monti et al., 2018; marsh harriers, Vansteelant et al., 2020). Another non-exclusive alternative may be that birds engage in stopovers at shorter distances from the breeding areas to track the phenology at their breeding grounds since conditions are temporally correlated at shorter distances (Usui et al., 2017; Burnside et al., 2021). Birds might delay their arrival to breeding areas by remaining at stopover sites until conditions become appropriate at their colonies (e.g. White-Crowned Sparrows, *Zonotrichia leucophrys orianthi*, Morton 2002; Icelandic whimbrels, *Numenius phaeopus islandicus*, Carneiro et al., 2020). In addition, easternmost breeding kestrels often engaged in stopovers in North Africa just after crossing the Sahara Desert (Fig. 1 and Fig 2f). The influence of ecological barriers running from the east to the west (e.g. Sahara desert) possibly explain this pattern. Birds departing from more eastern locations traverse the central part of the Sahara, where the distance over inhospitable habitats is larger relative to the western edges of the barrier, to which birds likely respond by making long stopovers after prolonged flights over the desert (Adamik et al., 2016). Lesser kestrels stopped in areas with higher vegetation productivity and when experiencing stronger headwinds compared to days when they travelled, suggesting that food availability and winds may be important factors mediating stopover decisions. Limitations that could be raised about this interpretation are that we do not analyse other environmental variables *en route* that could also affect the progress (i.e. stopover duration, travel speed) of lesser kestrels (e.g. rainfall, sandstorms) (Haest et al., 2018; Haest et al., 2020). Thus, we can't discount the effect of other environmental variables in mediating stopovers decisions. However, given the location of the stopovers, it is likely that birds are recovering energy or tracking environmental phenology at their breeding grounds.

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“LIFE ZEPAURBAN), and in Andalucía by “KESTRELS MOVE” project (ref: CGL2016 79249 P) (AEI/FEDER, UE). We are thankful for funding provided by MIUR (PRIN 2010-2011/20180-TZKHC). Logistic and technical support in Doñana, Spain, was provided by ICTS-RBD. GPS-tagging activity in Apulia (Southern Italy) was done within LIFE+Natura project “Un falco per amico” (LIFE11/NAT/IT000068). Finally, we thank Ciampanella D. (LIFE project manager), Lorusso M. (Comune di Altamura), Parisi F. (Comune di Gravina in Puglia), Giglio P. and Pellegrino S.C. (LIPU-BirdLife), and Frassanito A. (Parco Nazionale dell’Alta Murgia) for assistance and support.

SUPPLEMENTARY INFORMATION
CHAPTER 2

Supplementary Table S1. Summary table of adult lesser kestrels tagged during the breeding season of 2014-2019. The table summarizes the period of one year after tagging (when data download could take place).

[1] Kestrels that could not be located one year after tagging. They either died, dispersed, tags failed or were missed.

[3] Visual observation of tagged bird in the colony for which we were unable to download data or tags sent back to the manufacturer because they failed soon after deployment.

Counts	**Adults**
Total kestrels tagged	228
Completed pre-breeding migration (included in the analyses)	61
Did not migrate (excluded from the analyses)	2
Dispersed or changed of colony	7
Missing[1]	105
Tag malfunction[2]	40
Journeys that were partially recorded	12

Supplementary Table S2. Correlations between continuous predictor variables. We excluded variables from analysis if they showed high correlation (Pearson R > 0.60, < -0.60), retaining whichever variable of the correlated pair was deemed to explain more variance in migratory timing patterns. Tmax Feb was excluded due to close a correlation with Tmin Feb (R = -0.81), Tmin Mar (R = 0.93) and Tmax Mar (R = 0.95), respectively. Tmin Feb was also excluded due to a correlation with Tmax Mar (R = 0.67).

	Location long	**Location lat**	**Tmin Feb**	**Tmin Mar**	**Tmax Feb**	**Tmax Mar**	**Cumulative Precipitation**	**Trange**
Location long	1							
Location lat	0.17	1						
Tmin Feb	0.16	-0.74	1					
Tmin Mar	0.19	-0.58	0.93	1				
Tmax Feb	-0.29	-0.81	0.81	0.75	1			
Tmax Mar	-0.45	-0.73	0.67	0.58	0.95	1		
Cumulative Precipitation	-0.22	-0.58	0.58	0.41	0.47	0.42	1	
Trange	-0.75	-0.14	-0.3	-0.45	0.25	0.46	-0.05	1

Supplementary Table S3. Table of top-ranked models including departure location, arrival location and an interaction effect for sex and breeding location on departure date. Models are ranked according to increasing AIC values, with the best performing model on top. Grey boxes indicate that a given variable is included in the model.

Daparture Latitude	Departure Longitude	Arrrival Latitude	Arrival Longitude	Sex	Arrival Latitude:Sex	Arrival Longitude:Sex	df	logLik	AICc	delta	weight	R^2_{mar}	R^2_{con}
		▨	▨				5	-96.32	203.42	0.00	0.26	0.41	0.51
	▨	▨	▨				6	-95.91	204.92	1.50	0.12	0.41	0.49
		▨	▨	▨			6	-96.11	205.31	1.89	0.10	0.40	0.51
▨		▨	▨				6	-96.13	205.36	1.94	0.10	0.40	0.53
▨	▨	▨	▨				7	-95.38	206.23	2.82	0.06	0.41	0.51
	▨	▨	▨	▨			7	-95.56	206.59	3.18	0.05	0.42	0.48
		▨	▨	▨		▨	7	-95.91	207.30	3.88	0.04	0.41	0.51
▨		▨	▨	▨			7	-95.98	207.43	4.01	0.04	0.40	0.52

Supplementary Table S4. Table of top-ranked models including departure location, arrival location and an interaction effect for sex and breeding location on arrival date. Models are ranked according to increasing AIC values, with the best performing model on top. Grey boxes indicate that a given variable is included in the model.

Daparture Latitude	Departure Longitude	Arrrival Latitude	Arrival Longitude	Sex	Arrival Latitude:Sex	Arrival Longitude:Sex	df	logLik	AICc	delta	weight	R^2_{mar}	R^2_{con}
		▨	▨				5	-90.81	192.39	0.00	0.21	0.48	0.55
▨		▨	▨				6	-90.04	193.18	0.79	0.14	0.49	0.55
		▨	▨	▨	▨		7	-89.06	193.60	1.21	0.11	0.51	0.57
	▨	▨	▨				6	-90.43	193.96	1.57	0.09	0.49	0.58
		▨	▨	▨			6	-90.65	194.39	2.01	0.08	0.49	0.55
▨		▨	▨	▨	▨		8	-88.42	194.75	2.36	0.06	0.51	0.57
▨		▨	▨	▨			7	-89.97	195.41	3.02	0.05	0.5	0.55
▨	▨	▨	▨				7	-89.98	195.43	3.04	0.05	0.49	0.57

Supplementary Table S5. Table of top-ranked models for the effect of proximate causes on arrival date. We tested a set of models, including stopover days, travel speed and departure date. We included individuals as random effects. Models are ranked according to the increasing AICc values, with the best performing model on top. Grey boxes indicate that a given variable is included in the model.

Stopover duration	Sex	Travel speed	Departure date	df	logLik	AICc	delta	weight	R^2_{mar}	R^2_{con}
▨		▨	▨	6.00	104.43	-195.77	0.00	0.76	0.99	0.99
▨	▨	▨	▨	7.00	104.45	-193.42	2.35	0.24	0.99	0.99
▨	▨		▨	6.00	46.82	-80.54	115.23	0.00	0.98	0.98
▨			▨	5.00	45.56	-80.36	115.41	0.00	0.98	0.98
		▨	▨	5.00	-15.02	40.81	236.58	0.00	0.91	0.94
	▨	▨	▨	6.00	-14.91	42.91	238.68	0.00	0.91	0.94
			▨	4.00	-41.72	91.95	287.72	0.00	0.84	0.88
	▨		▨	5.00	-41.34	93.46	289.23	0.00	0.84	0.88

Supplementary Table S6. Coefficients estimates from GLMMs for the effect of proximate causes on arrival date. Estimates for fixed effects as estimated by the most parsimonious model. Model estimates are shown in units of standard deviation (SD). Bold indicates significant predictors as confidence intervals excluded zero—all variables were z transformed.

Variable	Estimate	Std. Error	t	LCI, UCI
Intercept	-0.01	0.007	0.00	-0.01, 0.01
Departure date	0.83	0.01	106.72	0.81, 0.84
Stopover duration (days)	0.33	0.01	37.76	0.30, 0.34
Speed (km/day)	-0.14	0.01	-16.19	-0.15, -0.12

Sample size = 84 migratory trips from 61 individuals.

Supplementary Table S7. Coefficients estimates from GLMMs as estimated by the most parsimonious model on arrival date. Estimates for fixed effects as estimated by the most parsimonious model. Model estimates are shown in units of standard deviation (SD). Bold indicates significant predictors as confidence intervals excluded zero.

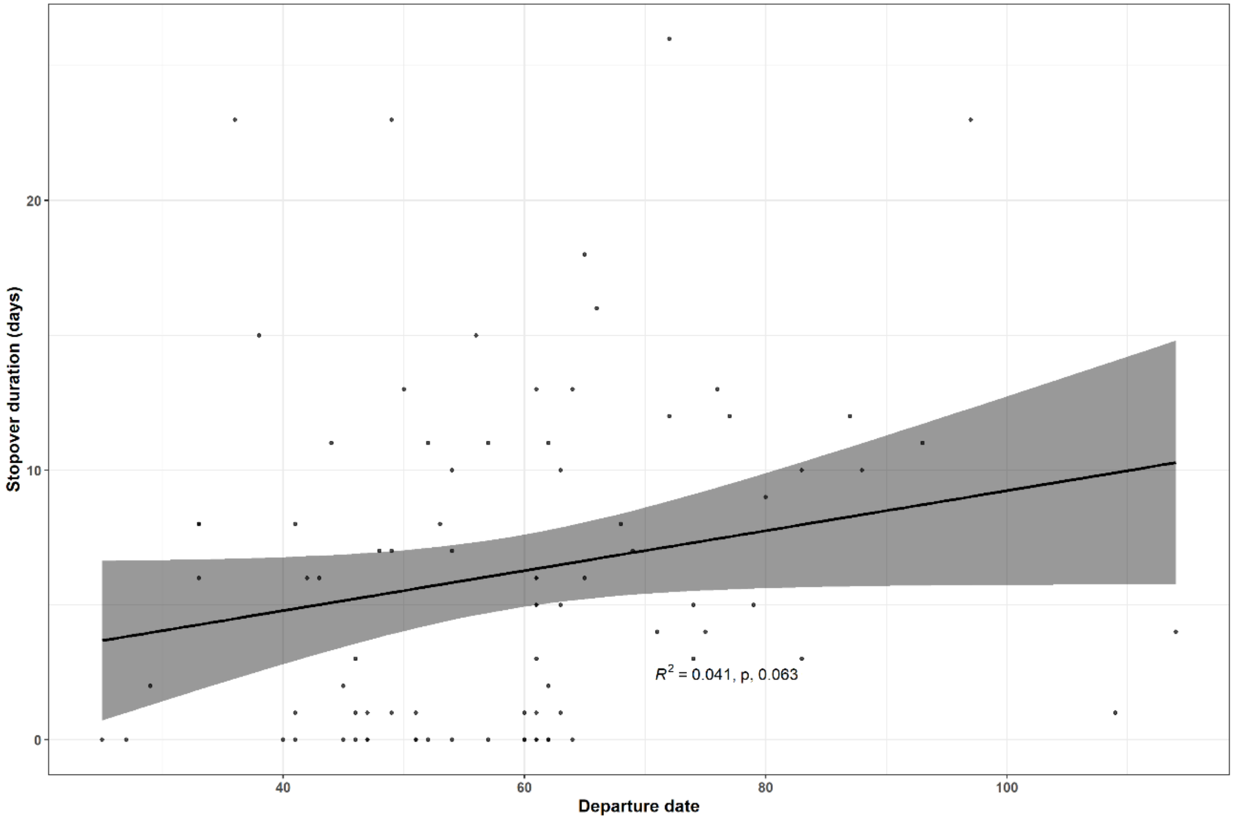
	Estimate	SE	t	LCI, UCI
(Intercept)	0.01	0.08	0.09	-0.15, 0.17
Arrival latitude	0.41	0.08	4.93	0.24, 0.56
Arrival longitude	0.50	0.08	6.20	0.33, 0.65

Supplementary Table S8. Results of separate LMMs (with ID as a random effect) comparing NDVI and wind conditions on travel days and rest days. Estimates from LMMs of NDVI and daily tailwind conditions and fixed effects of the categorical term 'travel' (two levels: travel and stopover days).

Response variable	Predictor	Estimate	SE	t	LCI, UCI
NDVI	Travel (travel)	-0.17	0.01	-12.04	-0.20, -0.14
Tailwind	Travel (travel)	2.10	0.36	5.82	1.39, 2.81

Sample size = 84 migratory trips from 61 individuals.

Figure S1. Correlation between departure date and stopover duration (days). Each dot represents one pre-breeding migration trip. Birds that departed later do not seem to compensate for their delay by decreasing stopover duration.



CHAPTER 3

AN ITINERANT LIFESTYLE OF LESSER KESTRELS IN THEIR WEST AFRICAN NON-BREEDING GROUNDS

CHAPTER 3

AN ITINERANT LIFESTYLE OF LESSER KESTRELS IN THEIR WEST AFRICAN NON-BREEDING GROUNDS

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ABSTRACT

Migratory birds often spend large proportion of their annual cycle in their non-breeding areas. We know relatively little about the non-breeding strategies of migrants at tropical latitudes. While some species are highly sedentary after arriving in their non-breeding areas, others engage in itinerary or nomadic movements to track seasonally shifting or unpredictable resources. We used GPS-tracking to confirm that lesser kestrel (*Falco naumanni*) -an insectivorous falcon- employs an itinerant lifestyle during their non-breeding season in sub-Saharan Africa. We investigate timing and habitat use during their non-breeding movements and test for differences between sexes. Tracking data of 61 individuals revealed that kestrels on average use 2-3 successive staging sites. Only in 3 individual tracks out of 78 analysed, the individuals remained the whole non-breeding period resident at a single staging site. Kestrels behaved as sedentary 89% of the days while only 4% of the days were devoted to exploratory flights. Male and female lesser kestrels showed similar non-breeing areas and timing of itinerant movements. Upon arrival to West Africa at the end of September kestrels dispersed throughout the Sahel, but converged at two clearly delineated areas in Senegal and along the Malinese-

Mauritanian border during the second half of the non-breeding season. The birds stayed longer and showed greater daily activity in those areas, which were situated close to wetlands, compared to their first and intermediate ones. Overall, lesser kestrels used mosaics of habitat types (grassland, shrubland, cropland, and sparse vegetation) and increasingly used bare, urban and moister habitats. Rather than tracking suitable climatic conditions southward, we observed that lesser kestrels survived the West African dry season by moving westward or eastward. We discuss what resources may drive these movement patterns. Our findings match reports of lesser kestrel super-roosts in West Africa and stress the conservation value of the wetlands of the Senegal River and the Inner Niger Delta in West Africa for the Spanish lesser kestrel population, as these are areas where they concentrate for 20% of their annual cycle. Environmental changes there could affect survival and have population-level consequences.

INTRODUCTION

The ecology of migratory animals is shaped by conditions in more than one part of the world: their breeding grounds, non-breeding quarters and migratory routes (Bildstein, 2006; Schofield et al., 2010; Cherry et al., 2016). Owing to their reliance on multiple areas across their annual cycle, they are in ‘multiple jeopardy’ (Sanderson et al., 2006; Gilroy et al., 2016). Importantly, long-distance migrants may spend the majority of their annual cycle in their non-breeding areas (Newton, 2004; Salewski & Jones, 2006; Studds & Marra, 2005), and conditions in those areas can have carry-over effects on survival and reproduction (Marra et al., 1998; Newton, 2004; Norris et al., 2004). Despite this, many aspects of the non-breeding ecology, and in particular for migrants moving into tropical latitudes, and the potential threats they face in such distant, often hard to access non-breeding areas, remain to be learned (reviewed in Wilcove & Wikelski, 2008; Stanley et al., 2021).

Several billion land birds of about 200 species from the Palearctic spend the boreal winter in sub-Saharan Africa (Dean, 2004; Salewski & Jones, 2006). The first comprehensive evidence of their non-breeding ecology comes from long-term migration counts, ringing and field-based studies, suggesting that long-distance movements within their their non-breeding areas are widespread (Moreau, 1952, 1972; Pearson & Backhurst, 1976). It has been suggested that an increased mobility during non-breeding is needed for birds to track seasonally shifting resources across large areas (Lack, 1986; Sinclair, 1978; Salewski et al., 2002). In addition, and contrary to the breeding period, birds have more freedom to move during the non-breeding season, when they are not tied to a nest site. This freedom to move historically hampered our ability to study such species for an extended period (Bildstein, 2006). Nowadays, however, advanced tracking technology allows the study of a wide range of Palearctic-African migrants, including those with highly mobile lifestyles (Smith et al., 2011; Vickery et al., 2014; Norevik et al., 2019).

Bio-logging has confirmed different movement strategies and great interspecific behavioural flexibility during the non-breeding period (Bildstein, 2006; Salewski & Jones, 2006; Norevik et al., 2019). Some species, like pied flycatchers *Ficedula hypoleuca* (Ouwehand et al., 2016) and common redstarts *Phoenicurus phoenicurus* (Kristensen et al., 2013) remain on a single territory -often covering smaller areas than their breeding home ranges- during the whole non-breeding period, a strategy known as winter residency (Newton, 2008). Conversely, species could be highly mobile, performing nomadic movements in their non-breeding grounds and visiting different destinations year after year (Dean, 2004; Newton, 2008; van Wijk et al., 2016). A nomadic lifestyle may be prevalent in semi-arid heterogeneous environments (e.g. deserts) where resources are patchy in space and time and determined by fluctuations in rainfall (Jensen, 1972; Dean, 2004). Species presumed to perform nomadic movements in the non-breeding season include black kites *Milvus migrants,* steppe eagles *Aquila nipalensis,* red-footed falcons *Falco vespertinus* Amur falcons, *Falco amurensis* and black-winged pratincoles *Glareola nordimanni* (Newton, 2008). An intermediate strategy to residency and nomadic lifestyles is itinerancy, occupying two or more residence areas during the course of the non-breeding season in succession and repeating destinations over consecutive years (Moreau, 1972). Itinerancy is thought to be associated with declining resources as aridity increases in areas north of the equator as the season progresses, such that birds follow the seasonal shifts of food abundance southwards to more benign habitats (Trierweiler et al., 2013; Thorup et al., 2017). This strategy has been reported in both the Nearctic-Neotropical (e.g. veeries *Catharus fuscescens*, Heckscher et al., 2011; Swainson's thrushes *Catharus ustulatus*, Delmore et al., 2012; bobolinks *Dolichonyx oryzivorus,* Renfrew, 2013) and Palearctic-African bird migration systems (e.g. reed warblers *Acrocephalus arundinaceus*, Lemke et al., 2013; lesser spotted eagles *Clanga pomarina* Meyburg et al., 2015; willow warblers *Phylloscopus trochilus*, Lerche-

Jørgensen et al., 2017; pallid swifts *Apus pallidus*, Norevik et al., 2018; Montagu's harriers *Circus pygargus*, Trierweiler et al., 2013; Schlaich, 2019).

Nevertheless, it seems to be some interindividual variation of these strategies within species. Studies considering individual differences in non-breeding movements have revealed mixed strategies in which some individuals are winter residents and others are itinerants within the same species. For example, 3 individual turtle doves *Streptopelia turtur* used one residency site, while 2 were itinerant (Eraud et al., 2013). The same pattern was also shown by 1 out of 6 tawny pipits *Anthus campestris* (Briedis et al., 2016a), by 4 out 129 Montagu's harriers *Circus pygargus* (Schlaich, 2019) and by 2 out of 10 marsh harriers *Circus aeruginosus* (Vansteelant et al., 2020). Furthermore, age and sex differences in non-breeding schedules and habitat use have been reported. For example, female American kestrels *Falco sparverius* arrive first in South Florida's non-breeding territories and occupy better habitats than males (Smallwood, 1988; Ardia & Bildstein, 1997). Evidence from ringing indicates that males yellow wagtails *Motacilla flava* winter further north than females (Wood, 1992). Yet, assessing individual differences in non-breeding strategies is often challenging due to the technological inaccessibility of sufficient and accurate tracking data for multiple individuals across long periods.

There is evidence that a wide range of Afro-Palearctic migrant populations have declined in recent decades (Sanderson et al., 2006; Zwarts et al., 2009; Vickery et al., 2014). In particular, for birds wintering in the Sahel, the causes of such decline are likely linked to a combination of several known threats both on their breeding grounds, such as agricultural intensification (Benton et al., 2003; Newton, 2004), and on their non-breeding grounds, such as the cultivation of natural habitats, overgrazing, excessive woodcutting, heavy use of pesticides and climate causes, e.g. droughts (Thiollay, 2007; Zwarts et al., 2009; Vickery et al., 2014). However, trends in decline have not been homogenous across migratory species (Sanderson et al., 2006; Vickery et al., 2014), meaning that some traits associated with migration may confer particular sensitivity to environmental change (Gilroy et al., 2016). For example, long-distance migrants may be more prone to population declines than short-distance migrants (Sanderson et al., 2006; Oppel et al., 2015), owing to their reliance on multiple sites across the annual cycle. Similarly, populations with strong migration connectivity may be more sensitive than those with low connectivity, as the former breed and winter together and are aggregated in the same area at both times of the year (Rubenstein et al., 2002; Webster et al., 2002). Understanding how conditions in African staging sites could affect the population dynamics of Palearctic migrants requires identifying non-breeding locations and unravelling the non-breeding ecology, such as movement strategy, schedules, habitat use, and site fidelity.

The lesser kestrel is a small trans-Saharan migratory raptor that breeds in colonies from southern Europe and northern Africa to China. During the boreal winter, it has an Afrotropical distribution (Ferguson-Lees & Christie, 2001), although some populations in the Mediterranean exhibit partial migration, with some individuals being migrants and others non-migrants (Negro et al., 1991). Previous studies using geolocators (Rodríguez et al., 2009; Catry et al., 2011) and satellite telemetry (Limiñana et al., 2012) identified non-breeding areas of lesser kestrels from the western breeding range. Moreover, Catry et al. showed interindividual variation in non-breeding movements with 1 lesser kestrel female using one residency site while 3 used two or more sites (Catry et al., 2011). Recent tracking studies have revealed that lesser kestrels from Mediterranean populations migrate in a broad front across ecological barriers (e.g., the Mediterranean Sea and Sahara desert) and that there is strong connectivity between breeding and non-breeding areas (Sarà et al., 2019; López-Ricaurte et al., 2021). In addition, field studies in the South of Spain indicated that a higher proportion of males spend the northern winter in Spain, thus staying closer to the breeding colonies to return before females in spring (Negro et al., 1991). Furthermore, during the non-breeding season, lesser kestrels are known to aggregate in super roost wetlands within western Senegal (e.g. Kaolac and Khelkom) that can hold tens of thousands of individuals (Pilard et al., 2011; Augiron et al., 2015). Analysis of regurgitated pellets collected at such super roosts revealed that lesser kestrels are insectivorous also at these non-breeding sites (Pilard et al., 2011). Individuals mainly used arable land, shrub savannah and grassy savannah (Augiron et al., 2015). However, we still know relatively little about lesser kestrel's non-breeding ecology outside these areas and whether they also form such super roosts elsewhere.

This study aims to describe the movement strategy of lesser kestrels from the Spanish breeding population at their non-breeding quarters in West Africa, and to test for potential differences in the mobility and timing of intra-African movements between sexes. Lesser kestrels have a high movement ability (McCann, 1997; Bildstein, 2017), thus we expect lesser kestrels to be highly mobile within West Africa, moving progressively further south over the season to follow the seasonal shifts in insect abundance (c.f., other locust-eating steppe birds, Berthold 2002, 2004; Trierweiler et al., 2013; Schlaich et al., 2016). Finally, we draw some interpretations of habitat uses in their non-breeding range using the GlobCover land use map (2009) (resolution 300m) in a similar way to previous studies (Trierweiler et al., 2013; Schlaich, 2019).

METHODS

Tagging and tracking

Lesser kestrels were tagged using two models of solar GPS-UHF biologgers (GPSminiDatalogger, Microsensory LS, Córdoba, Spain; and NanoFix GEO+RF, Pathtrack Ltd., Leeds, UK.). Birds were tagged at 20 breeding sites across Spain by different organizations (GREFA; The Spanish Society of Ornithology, SEO/BirdLife; Terra Naturalis, and Doñana Biological Station, EBD). The GPS-UHF biologgers weighing ca. 5.5 g (including harness, ~3.8 % of weight at capture, males = 146.0 g ± 35 SD; females = 148.0 g ± 29 SD) were attached as backpacks with a Teflon harness. As GPS-UHF biologgers were deployed for different projects by different teams, they were programmed with different schedules (see Supplementary Methods for details). Locations were stored on-board and later downloaded via a UHF base station placed near the breeding colony.

We relied on 78 non-breeding tracks of 54 adult birds (25 males and 29 females) (Supplementary Fig. S1). 23 individuals provided tracks for two consecutive non-breeding seasons and one individual for three non-breeding seasons.

Annotating non-breeding movements

All data were resampled to a 1-h interval, allowing deviations up to 20 min. By resampling, we also avoided bias in our calculations of movement parameters due to the variability in sampling rates (Shamoun-Baranes et al., 2017a). After resampling, we analysed 167,793 hourly segments, from which 108,792 were recorded by day, and 59,001 by night. We determined arrival and departure to and from the non-breeding grounds based on daily movement metrics (See Methods sections for full details). We studied non-breeding movements within Africa by interpreting the tracks using QGIS (cf. Trierweiler et al., 2010; Schlaich, 2019). We annotated as (1) 'resident days', each day in a group of ≥ 3 days in which the bird stayed stationary at a site (using roosts less than 10 km apart on consecutive nights), (2) "transit days", when the individual performed a directional flight away from a site without returning, and (3) "exploratory days", when birds performed non-directed movements away from a site but returned to the previous roost (could last one or several days) (Supplementary Fig. 2).

For mapping, we determined the centroid of each site where the bird was resident as the median latitude and longitude of all positions at this site (hereafter staging sites). The staging sites were subdivided into three categories: the 'first' staging site south of 17° N used upon arrival from the post-breeding migration, 'last' as the last staging site used before the onset of the pre-breeding migration, and 'intermediate' all other consecutive sites used between first and last staging sites (could be one or several). Sometimes individuals remained highly mobile for 1 – 2 days upon arriving to West Africa and before moving into their first staging site (5 individuals). Such movements were classed as 'exploratory days'. The arrival date to the non-breeding grounds in such birds was determined as the date on which the individual moved into the first staging site. Three individuals stayed the whole non-breeding period at a single staging site; and these were classified as last staging sites (because birds using more than one site tended to spend the most time at the last site).

Non-breeding schedules and movement metrics

We computed the total duration within West Africa (in days), the total number of resident, transit and exploratory days per individual and the daily distance covered (mean of the sum of successive distances between the first and the last GPS fix of a day). For each first, intermediate, and last staging site we quantified the (1) arrival and departure dates to each staging site (2) the staging duration per site (3) mean cumulative daily distance, (4) mean trajectory ground speeds from each GPS fix to the previous (i.e., the speed between consecutive fixes), (5) the daily time spent flying/sitting and (6) the daily proportion of daylight period spent flying/sitting. To calculate (5) and (6) we determined 'flying' segments as hourly segments with a ground speed ≥ 5 km/h.

Statistical analyses

We tested for sex differences in arrival, departure dates, and duration of the stay in West Africa using Linear Mixed Models (LMMs), allowing for random intercepts per bird. Visual inspection of residual plots indicated that a Gaussian error distribution and identity link function provided the best model fit.

Differences in the daily distance covered among types of days (resident, transit, exploratory) and between sexes were investigated using Generalized Linear Mixed-effect Models (GLMMs). We also tested for differences in timing of itinerary movements (arrival and departure dates) and mobility (daily distance, duration of the stay and % of time spent flying) between consecutive staging sites and sexes using GLMMs. The percentage of time spent flying was arcsine-square-root transformed to get a proper fitting of the models. We added the variable 'staging site' (with three levels: first, intermediate, last) and 'sex' as fixed factors, and bird identity and non-breeding cycle (i.e. 2018-2019,2019-2020,2020-2021) as random effects in all models. For pairwise comparisons, we used Tukey's HSD (honestly significant differences) tests, conducted with the 'emmeans' package (Russell, 2020), whereby we considered an effect to be statistically significant if p R 0.05.

Habitat composition and use

We estimated the overall non-breeding home range for the Spanish lesser kestrel population as the 100% minimum convex polygon (MCP) across the centroid of all staging sites. We excluded one site that was situated far south of all kestrel staging sites in Guinea, resulting in a final sample of 196 staging sites. To examine lesser kestrels' broad habitat selection across West Africa, we used the GlobCover 2009 V2.3 land use map at 300 m resolution (Bontemps et al., 2009). First, we calculated the percentage of available land cover types within the MCP non-breeding area. Then, the habitat types used by lesser kestrels were determined by projecting 1-h GPS daylight fixes onto the GlobCover map and extracting habitat type for each hourly location using the *raster* and *extract* functions in the R package 'raster' (Hijmans, 2015). Transit and exploratory days were excluded from the habitat use analyses.

RESULTS

General description of non-breeding movements

The average arrival date to West Africa was September 30 ± 12 days, and the average departure date was February 24 ± 14 days (Table 1). The number of days spent in the non-breeding range was 147 ± 17, corresponding to 40% of the total annual cycle (Supplementary Table S1). We did not find any significant sex differences in arrival, departure dates and duration of the stay in West Africa (Table 2). From the time spent in Africa, 131 ± 25 days were resident (sedentary at a staging site, 89% of the non-breeding period), 11 ± 10 days were transit (moving between sites, 7% of the non-breeding period), and 6 ± 5 days were exploratory (4% of the non-breeding period). The mean daily distance covered during resident days was 40.41 ± 36.60 km, during transit days was 80.89 ±71.01 km, and that of exploratory days was 98.03 ± 73.96 km, and these differences were significant (GLMM: $F = 7825.90$, P R 0.001; Fig. 1A). Mean daily distance across all days did not differ significantly between males and females (GLMM: $F = 1.31$, $P = 0.25$).

Table 1. Arrival and departure dates of lesser kestrels at the non-breeding grounds.

Variable	N (tracks/individuals)	Mean (± SD)	Min	Max	Range
Arrival	78/54	Sep 30 ± 12 days	Sep 9	Nov 9	61
Departure	78/54	Feb 24 ± 14 days	Jan 24	Apr 18	100
Duration (days)	78/54	147 ± 17 days	92	200	108

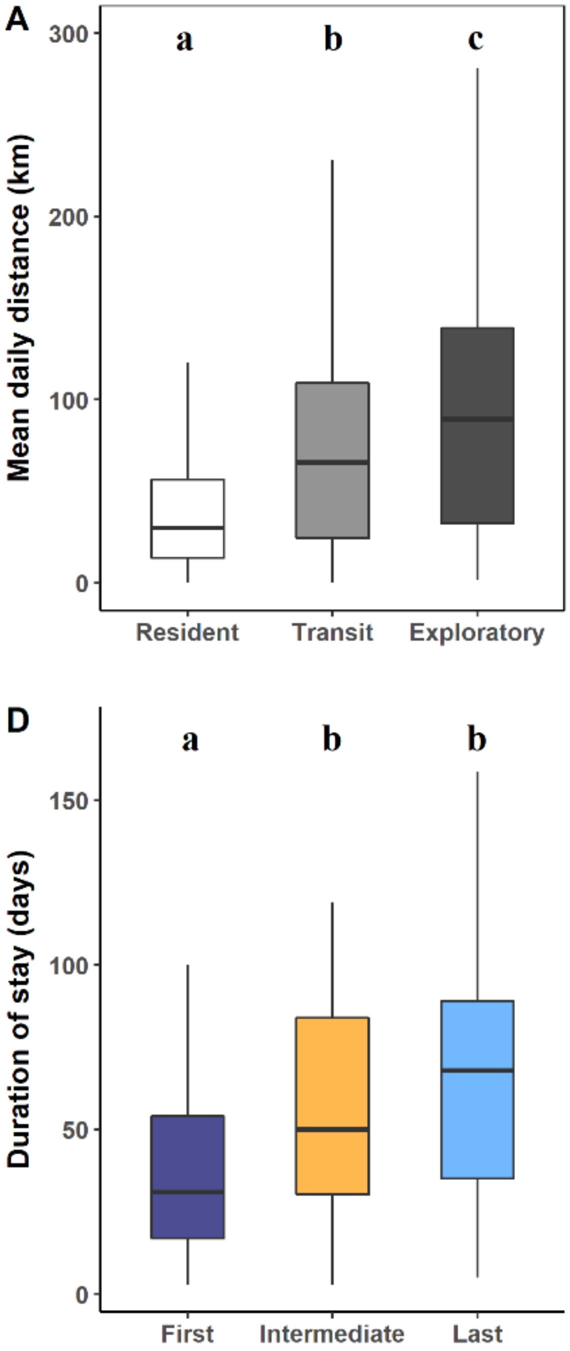
Table 2. Linear mixed models to test for sexual differences in arrival date, departure date and duration. Individual identity (ID) was included as a random factor in the models.

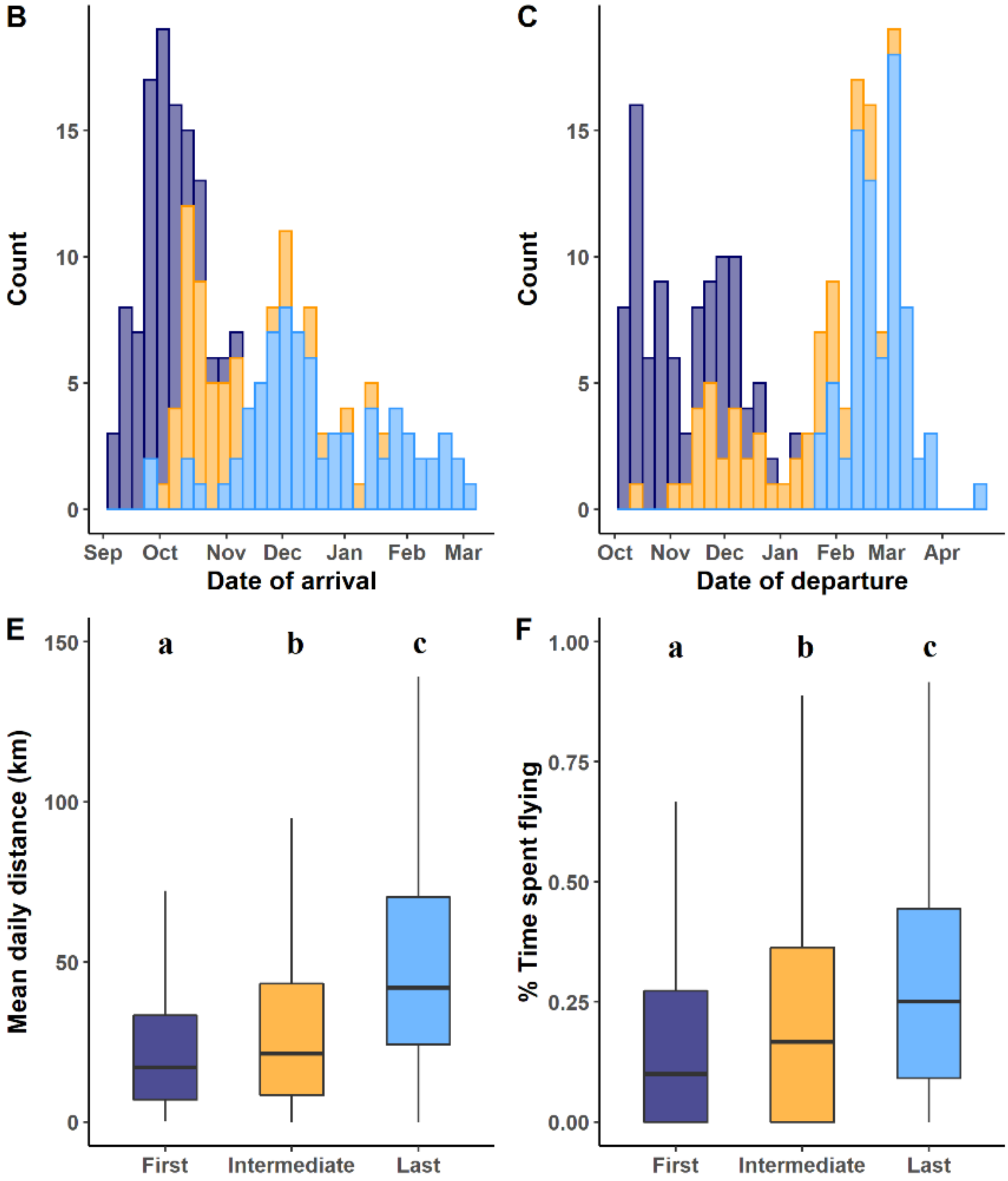
Response variable	Fixed effects	Estimate	SE	t	P
Arrival date	Intercept Sex (male)	272.14 2.73	2.03 2.86	133.63 0.95	≤ 0.001 0.34
Departure date	Intercept Sex (male)	56.73 -2.33	2.61 3.74	21.72 -0.62	≤ 0.001 0.53
Duration (days)	Intercept Sex (male)	149.18 -4.75	3.26 4.58	45.67 -1.03	≤ 0.001 0.30

N = 78 observations, ID =54 individuals

Temporal and movements patterns at staging sites

Figure 1. (A) Mean daily cumulative distance during resident, transit and exploratory days, **(B)** arrival dates, **(C)** departure dates, **(D)** total days spent per staging site type, **(E)** Mean daily distance covered per site, and **(F)** percentage of daylight hours with flight activity (segments with ground speed ≥ 5 km/h). Colours indicate the type of staging site: first sites in purple, intermediate sites in yellow, and last sites in blue. The letters above represent significant differences by Tukey HSD post-hoc tests at the 0.05 significance level. Groups sharing the same letter are not significantly different.




B
Count
0
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Sep
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Date of arrival
C
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Oct
Nov
Dec
Jan
Feb
Mar
Apr
Date of departure
E
Mean daily distance (km)
0
50
100
150
a
b
c
First
Intermediate
Last
F
% Time spent flying
0.00
0.25
0.50
0.75
1.00
a
b
c
First
Intermediate
Last

The staging sites of tracked birds were located across West Africa (Senegal, Mauritania and western Mali) between ca. 13.5° and 17.5° N and -16° and -4° W (Fig. 2A). We observed either a westward or an eastward individual movement pattern from the first to last staging site as the non-breeding period progressed (Fig. 2B, 2C). First staging sites were mainly distributed at central longitudes, intermediate sites were more spread out, and the last sites fell in two distinct eastern and western clusters. On average, individual kestrels used 2.5 ± 0.71 staging sites, ranging from 1 (3 of 78 tracks, 3.84%) to 4 (5 of 78 tracks, 6.41%) (Fig. 2D). The median arrival date at the first sites was September 29, at the intermediate sites October 20, and at the last sites November 20 (Fig. 1B). The number of staging sites used did not differ significantly between sexes (GLMM: $F = 1.05$, $P = 0.31$; Fig. 3A). The median departure date from the first site was October 26, from the intermediate site November 1, and from the last site February 23 (Fig. 1C) with no differences between sexes (GLMM: $F = 0.96$, $P = 0.33$; Fig. 3B).

The mean duration of the stay was significantly different among consecutive staging sites (GLMM: F 41.38, $P < 0.001$). Kestrels spent on average 36 ± 21 days on the first staging site, 52 ± 32 days at intermediate sites, 68 ± 36 days at their last staging site, corresponding to 10%, 14% and 20% of the total annual cycle, respectively (Supplementary Table S1), with no differences between sexes (GLMM: F=0.007, P = 0.93; Fig. 3D). Birds spent significantly longer time at intermediate and last sites than at first sites (Fig. 1D). The daily distance covered and the percentage of time spent flying were significantly different between sites (mean daily distance GLMM: F=10927.77, $P < 0.001$; percentage of time spent flying: GLMM =9720.97, $P < 0.001$). Birds covered significantly longer daily distances and spent more time flying at the last site relative to the first and intermediate sites (Fig. 1E and F) with no sex differences (mean daily distance GLMM: F=0.22, P = 0.63; percentage of time spent flying GLMM: F=0.94, P = 0.33) (Fig. 3C, E).

Figure 2. (A) Map showing the location of lesser kestrel staging sites in West Africa. Colours indicate the type of staging site: first sites in purple, intermediate sites in yellow, and last sites in blue. The black dot represents the centroid of each site (i.e. median latitude and longitude of all positions at a site). The 100% MCP representing the tracked kestrels' non-breeding range is also depicted. **(B)** Example of three individual tracks representing the typical movements of lesser kestrels during the 2018-2019 non-breeding period, i.e. birds arriving within central West Africa and then dispersing into the west or east staging sites. Large circles represent staging sites (first in purple, intermediate in yellow, last in blue), and symbols represent different individuals: female 4178696 RVFN (diamond), female 4170460 4JT (square) and male 4173803 RJA1 (triangle). Red arrows connect subsequent staging sites of the same individual. **(C)** First, intermediate and last staging sites used by each individual related to their mean longitude. **(D)** Histogram of the mean number of staging sites used by each individual.

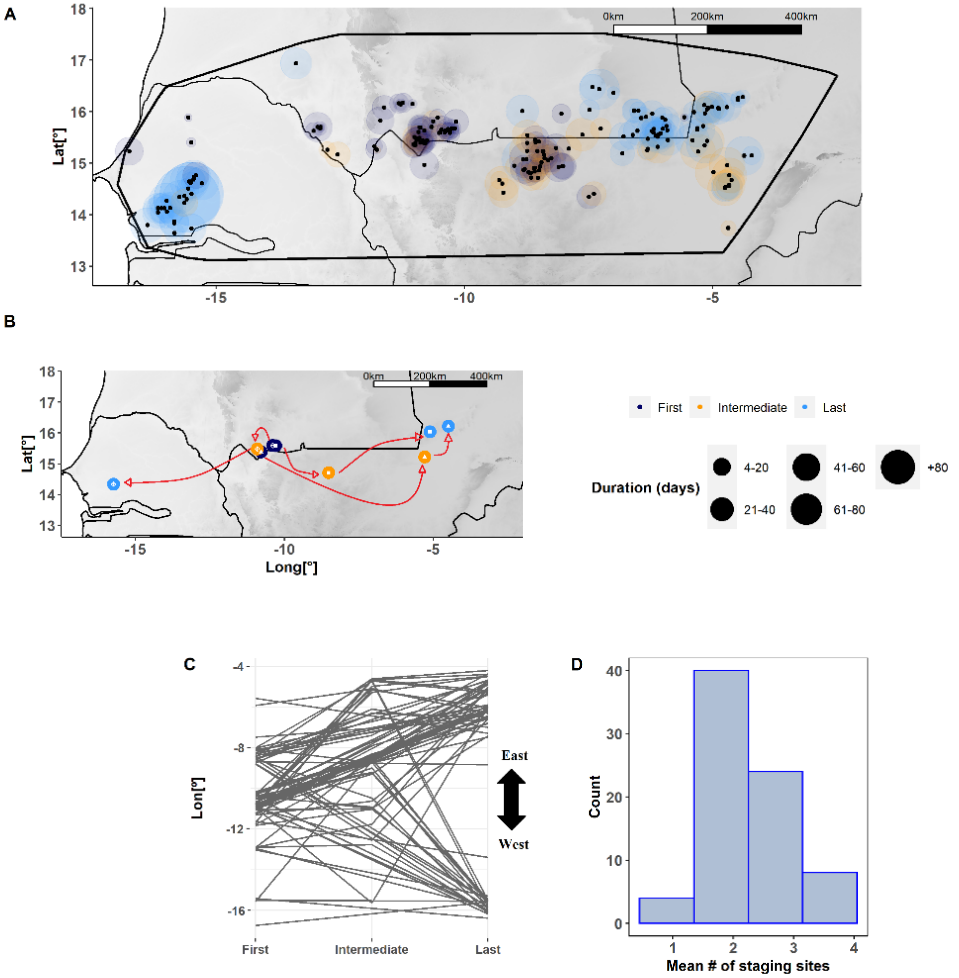
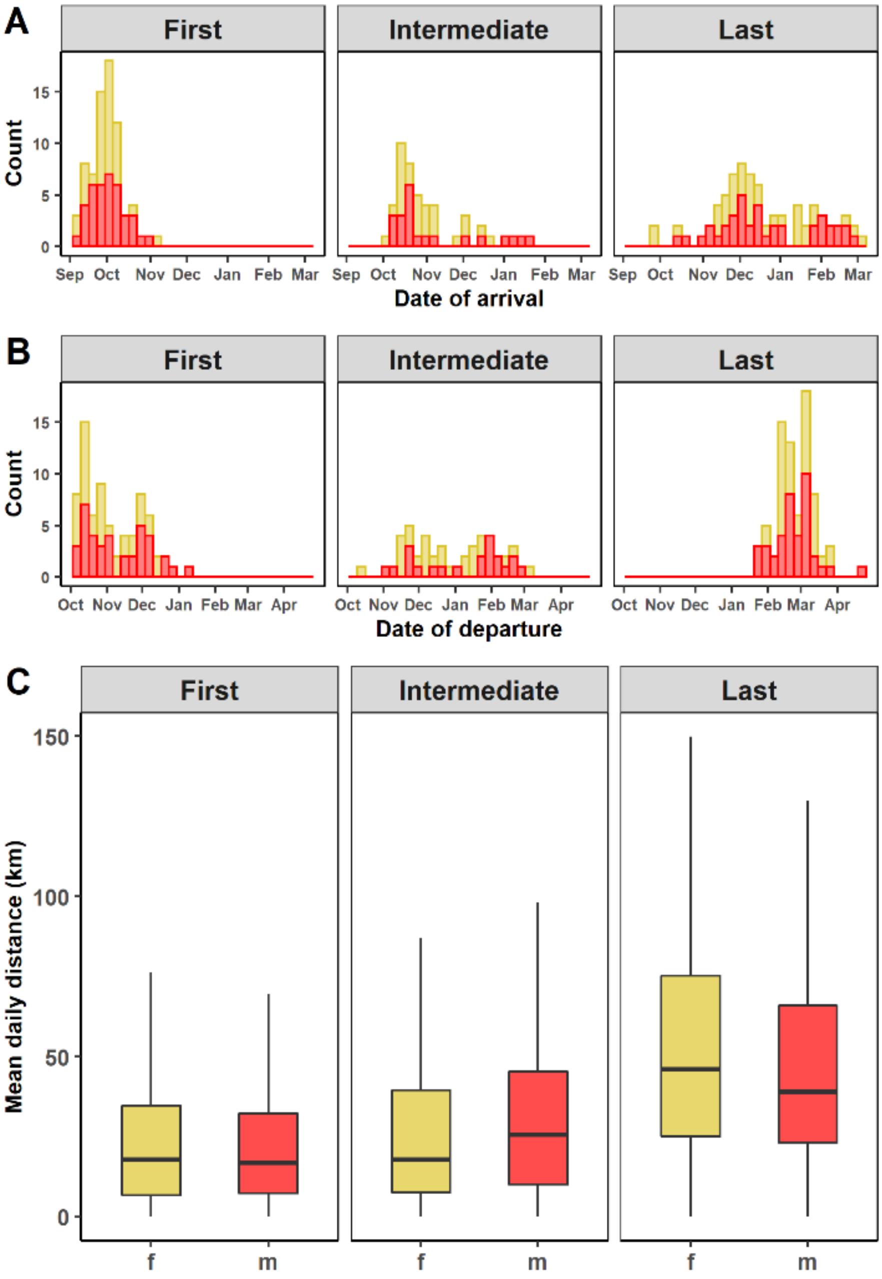
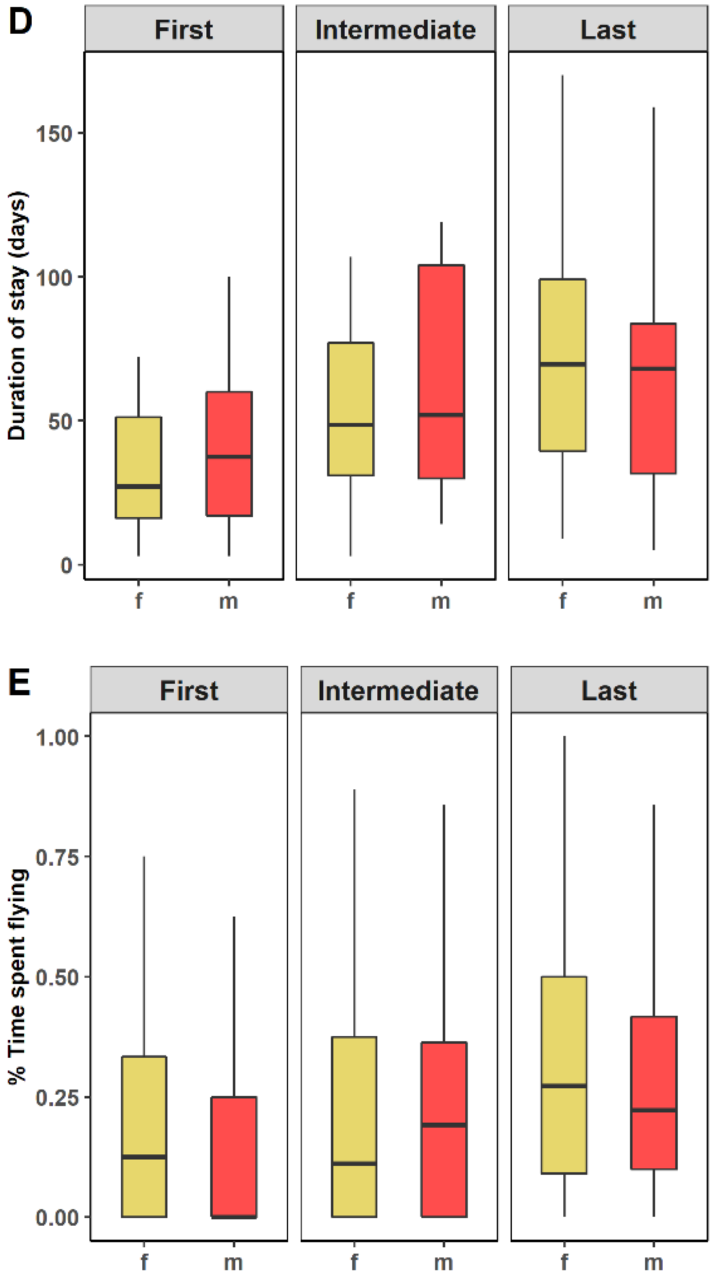


Figure 3 (A) Histogram of arrival dates of lesser kestrel males and females at first, intermediate and last staging sites, (females in yellow, males in red). **(B)** Histogram of departure dates. **(C)** Histogram of mean daily distance per site.

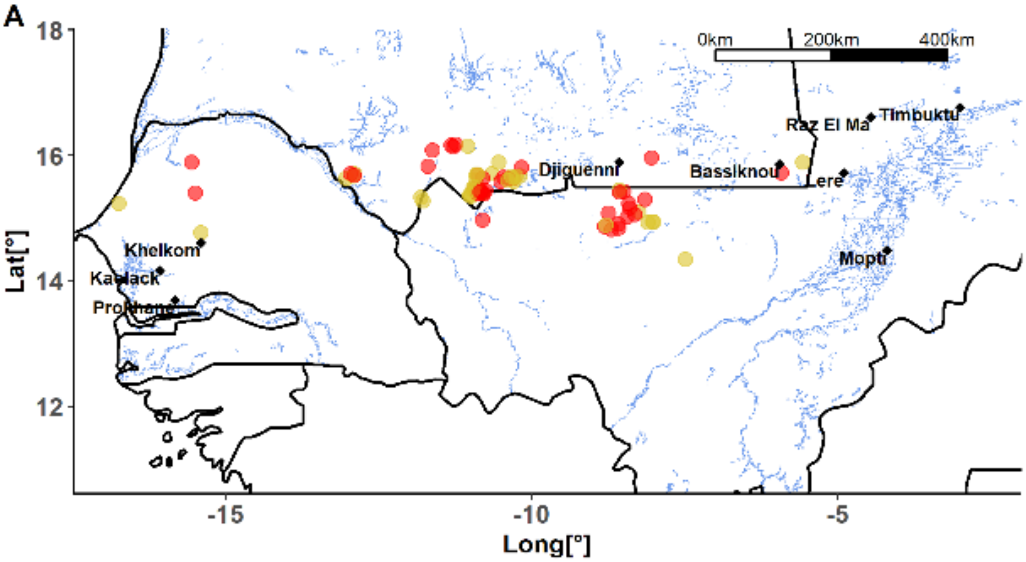


(D) Mean duration of stay according to sex at first, intermediate and last staging sites, and **(E)** Mean percentage of daylight hours with flight activity (segments with ground speed ≥ 5 km/h) in relation to sex.



At the end of the non-breeding period, lesser kestrels typically congregated in two clearly delineated clusters, one in Senegal, on the western side of the non-breeding range, and another on the Mauritania-Mali border eastern side. Out of 78 tracks, 32% converged close to Kaolack, Khelkom and Prokhane (west Senegal), including 26% of all females and 35% of all males. In addition, 49% congregated in Bassiknou and Djiguenni (Mauritania), including 59% of all females, and 44 % of all males. Furthermore, 19% converged in Lere and Mopti (Mali), including 15% of all females and 21% of all males (Fig. 4).

Figure 4. Map showing (**A**) first and (**B**) last staging sites according to sex (females yellow and males in red dots). Blue coloured lines indicate the inland water present in Senegal, Gambia, Mauritania and Mali. Black diamonds indicate the region closer to lesser kestrels staging sites. In central Senegal: Khelkom (also known as Mbégué), Kaolack and Prokhane (near the border with Gambia); in southwestern Mauritania: Bassikounou and Djiguenni in the region of Hodh Ech Chargui, and in northeastern Mali: Mopti, Timbuktu, Raz El Ma and Lere. A notable cluster of sites closer to floodplains (Inner Niger Delta), wetlands in eastern Mauritania, and coastal wetlands, notably Sine Saloum in Senegal and the Gambia, can be observed at the end of the non-breeding period.



Of the birds tracked during two consecutive years (n=23) and three consecutive years (n=1) 33% (8 out of 24 tracks) consistently revisited the same last site (maximum distance between sites < 20 km) in consecutive years. In addition, 50% (12 out of 24 tracks) of lesser kestrels used sites near the one visited in an earlier non-breeding period (< 200 km apart). Most of these birds (83%, 20 out of 24 tracks) used the same general non-breeding area in consecutive non-breeding cycles (Senegal vs Mauritania-Mali border). Finally, 16% (4 out of 24 tracks, all adult males) changed the last staging site (> 300 km apart) (Fig. 5).

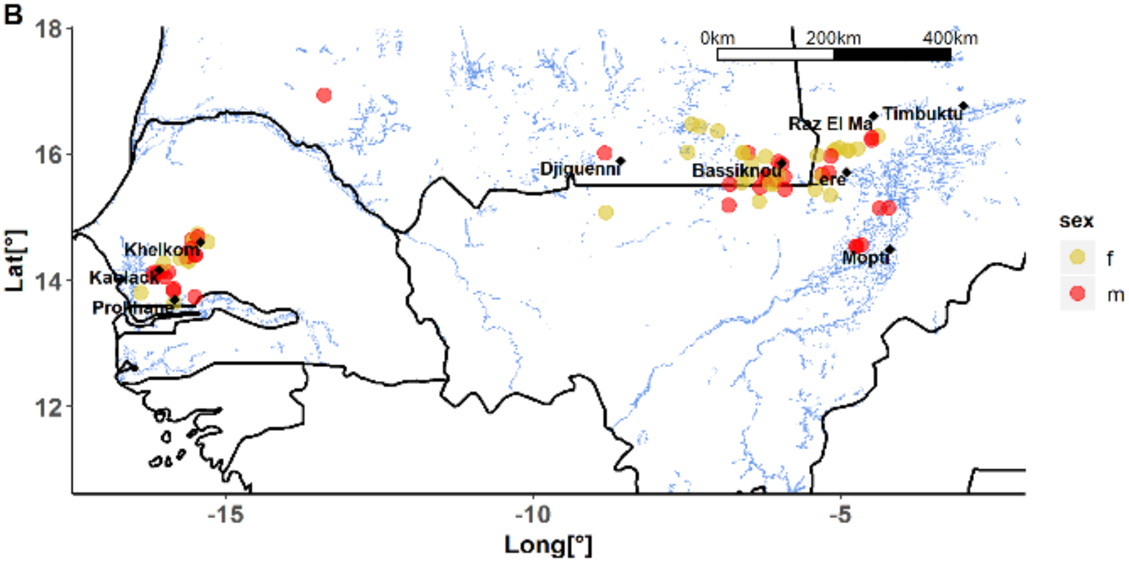
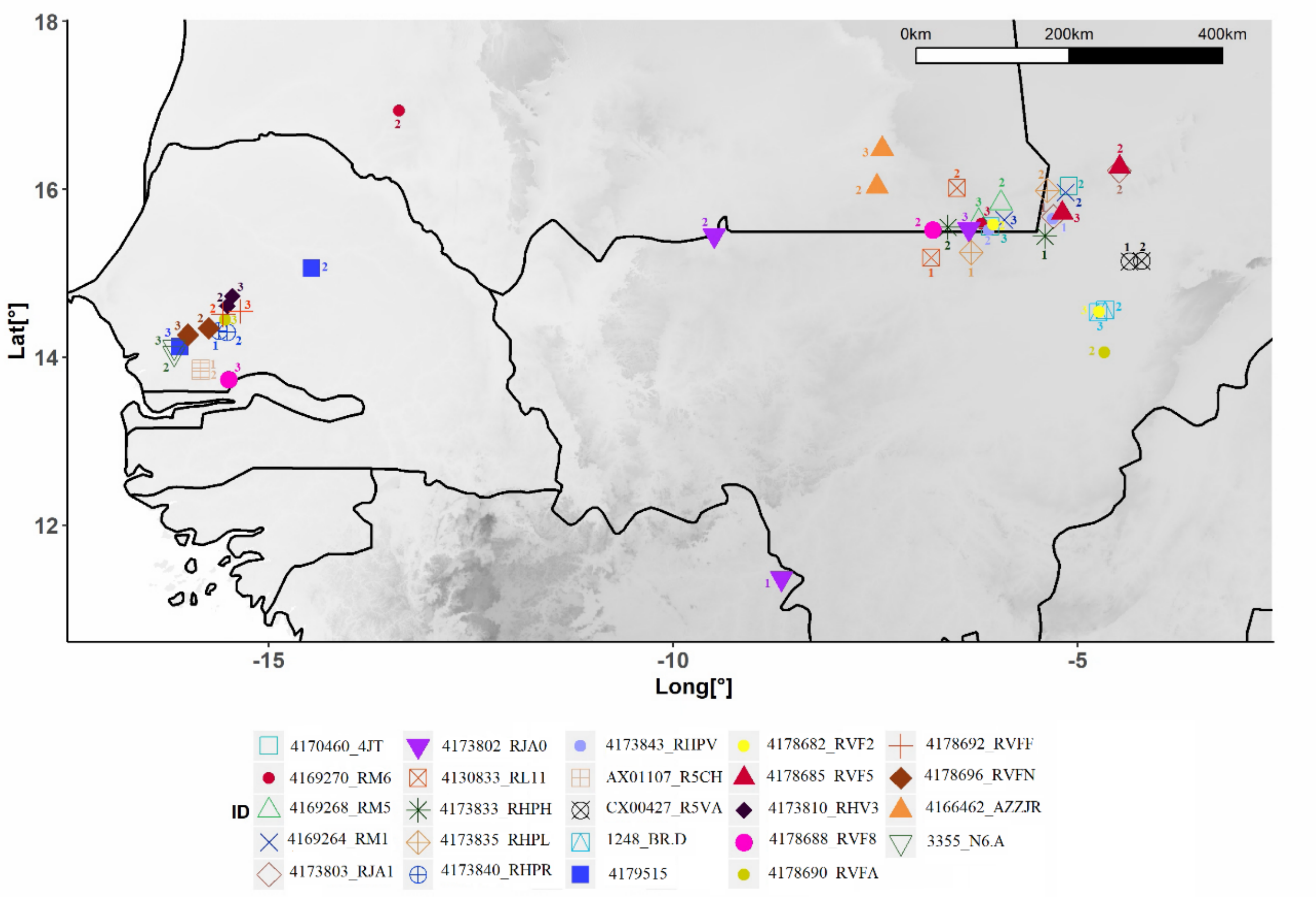


Figure 5. Last staging sites in West Africa of 24 adult lesser kestrels (represented with different colours and symbols) tracked during consecutive years. 83 % of these kestrels consistently spent the last period of their stay in West Africa in the same or near the same area as the previous year. Numbers correspond to the year cycle: 1 to 2017-2018, 2 to 2018-2019 and 3 to 2019-2020. Bird 4169270_RM6 moved from western Mauritania in the first non-breeding period to the Mauritania-Mali border in the second non-breeding period; bird 4173802_RJA0 moved from Guinea in the first non-breeding period to western Mauritania in the second non-breeding period and to the Mauritania-Mali border in the third non-breeding period; bird 4178688_RVF8 moved from the Mauritania-Mali border in the first non-breeding period to Gambia in the second non-breeding period, and bird 4178690_RVFA moved from Mali in the first non-breeding period to Senegal in the second non-breeding period.

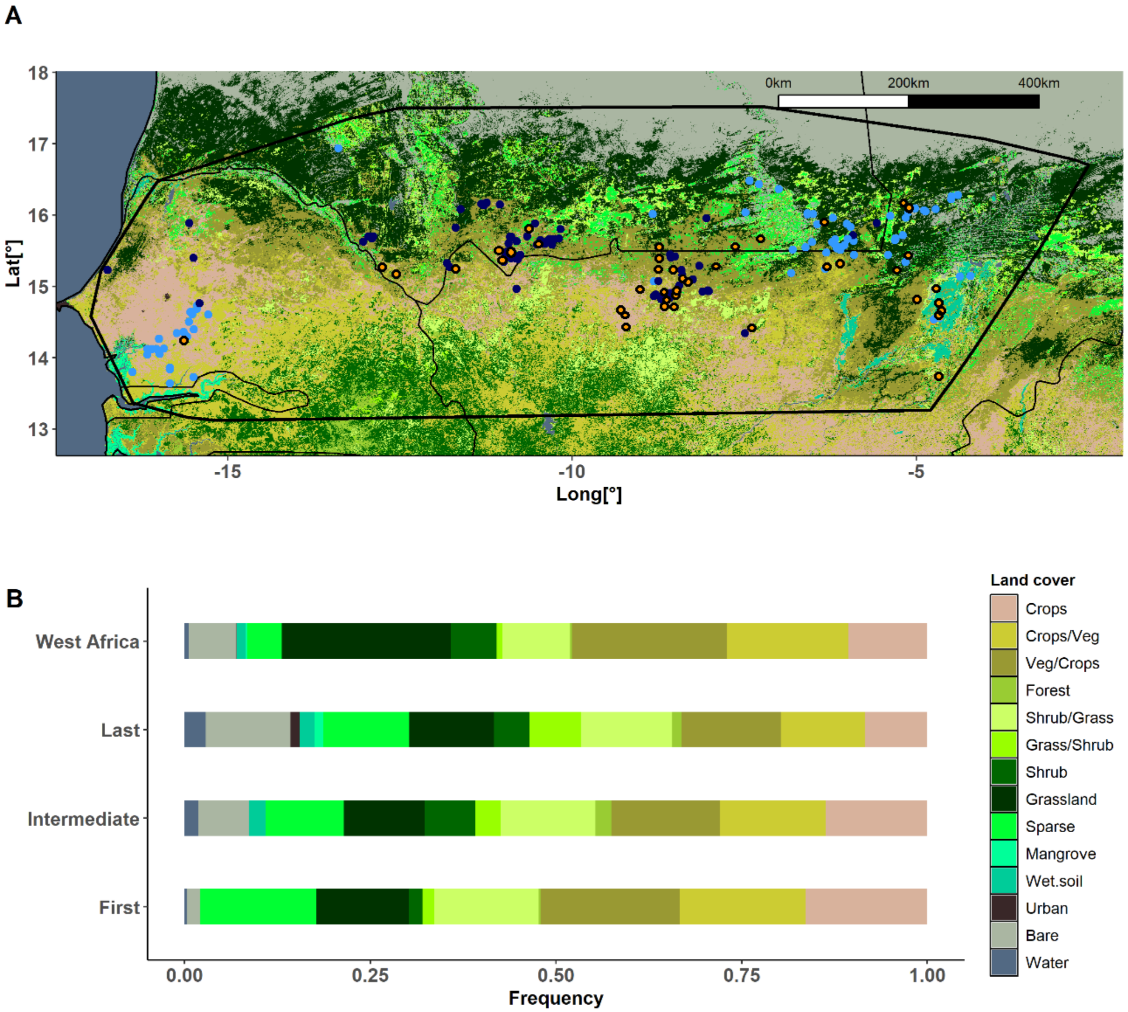


Habitat use

Fourteen out of 23 GlobCov categories were available across the potential non-breeding range of lesser kestrels. Grassland, mosaics of vegetation (veg/crop), mosaics of cropland (crop/veg) and crops were the most frequent categories in the region (23%, 21%, 16%, 10%, respectively) (Fig. 6A; a description of the GlobCover categories is included in Supplementary Table 2).

Our results for habitat suggested some shifts in habitat used along successive staging sites. In the first sites, 11 GlobCov categories were used. We found that relative to the habitats available in West Africa, kestrels used veg/crops, crops/veg, crops, sparse vegetation, followed by mosaics of shrubland (shrub/grass) and grassland. The least used habitat types relative to what is available were water, bare, shrub, mosaics of grassland (grass/shrub) and forest. 12 GlobCov categories were used at intermediate, and 14 categories at last sites. At intermediate sites, they primarily used veg/crops and crops/veg, followed by crops, shrub/grass, grassland and sparse. At last sites, they primarily used veg/crops, crops/veg, shrub/grass and also, grassland, sparse and bare habitats. We observed that the use of mosaics of vegetation (veg/crops), mosaics of cropland (crops/veg) and crops decreased gradually from the first to last sites. Conversely, the proportion of time spent by kestrels in bare, urban and moister habitats (water, wet soil and mangrove) increased from first to last sites (Fig 6b).

Figure 6. (A) Habitat composition available in the non-breeding area in West Africa according to the GlobCover land use map. The dots represent the centroids of each staging site: purple dots indicate first sites, orange dots with black border intermediate sites and blue dots last sites. The black polygon indicates 100% MCP for the first, intermediate and last sites. (**B**) Bar graph showing the availability of each land use category in the MCP West African non-breeding range (black-line polygon on map) and the proportion of land cover types used by kestrels (i.e., the proportion of GPS fixes within each land cover category) in the first, intermediate and last staging sites. Fourteen out of 23 GlobCov categories are used by kestrels. Kestrels use crops and mosaics of crops/veg habitats in the first months of their stay in Africa and a shift towards more varied habitat use, including also wetter, urban and bare habitats at last staging sites.



DISCUSSION

We found that lesser kestrels have an itinerant lifestyle during the non-breeding period in West Africa. This is an intermediate strategy between residency at a single site and a nomadic lifestyle. Lesser kestrels used a small number of staging sites (two or three) in one non-breeding season, to which they showed fidelity in consecutive years, particularly to the last staging sites. Kestrels allocated extended periods of their non-breeding time (89%) in those sites. Conversely, they spent a relatively small proportion of time moving between sites (7%) or engaging in seemingly exploratory movements (4%). Lesser kestrels arrived to their non-breeding staging sites at the end of September and they spent 147 days in their non-breeding area before departing north, typically in the last week of February. Moreover, males and females followed a similar non-breeding strategy, with no significant differences in the timing of itinerary movements or movement metrics at successive staging sites. We also observed that kestrels spread out over the interior of West Africa at arrival – from the northeast Senegalese border to the easternmost part of the Mauritania-Mali border. Contrary to our expectations and to other locust-eating steppe birds, however, kestrels did not move along a north-south axis in the Sahel (Trierweiler et al., 2013; Schlaich et al., 2016). Instead, they moved either westward or eastward through intermediate sites to converge at their last staging sites at coastal wetlands in Senegal or inland wetlands in eastern Mauritania at the border with Mali, respectively (Fig. 1 A, B, C; Fig 4B).

In agreement with previous studies on the non-breeding movement patterns of Afro-Palearctic insectivorous migrants (swifts, Akesson et al., 2012; swallows, Norevik et al., 2019, harriers, Trierweiler et al., 2013; Schlaich et al., 2016), we found that lesser kestrels spent the boreal winter in the Sahel by adopting an itinerant strategy (Moreau's Paradox, Moreau, 1972). Lesser kestrels used on average 2.5 staging sites. The minimum number of days used to define a site as a staging site influences the final number of staging sites per individual. Our classification of staging sites is reliable because we found that repeatedly tracked birds were faithful to sites identified based on the '3-day rule'. However, lesser kestrels arrived at the northern part, where they settled for 1 month. Then, they showed directional westward or eastward movements until reaching their last staging sites. Such east-west movements within the Sahel have been reported for other species (e.g. tawny pipits *Anthus campestris*, Briedis et al., 2016a; turtle doves *Streptopelia turtur*, Eraud et al., 2013). We suggest these movements can be due to kestrels tracking resource fluxes in the Sahel wetlands. We suspect that after traversing ecological barriers (the Mediterranean sea and the Sahara desert) with limited possibilities for fuelling during the post-breeding migration, birds may stop at the first suitable place they encounter (i.e. north of the Sahel during the rainy season, Trierweiler et al., 2010; Vansteelant et al., 2020). We can assume that lesser kestrels remain there until the region becomes too inhospitable due to increased aridity as the season progresses (Salewski et al., 2002). During the transition from the wet to the dry season, kestrels move out of the most arid regions into areas with more abundant and larger water bodies within the Sahel (e.g. coastal wetlands, Inner Niger delta, wetlands in eastern Mauritania), which dry out later and may suppress the adverse effects of the dry season for several months (Studds & Marra, 2005). Such 'wet havens' might keep suitable conditions for Afro-Palearctic birds, e.g. there are more insects in wetlands than in drylands, enabling them to spend a large part of their non-breeding period at these sites (Zwartz et al., 2009; Vafidis et al., 2014).

Lesser kestrels exhibited little individual variation in non-breeding strategy with no sex differences in schedules or movement metrics. We found that only 3 tracks out of 78 (3.84 %) showed a strategy of winter residency, staying the whole non-breeding period at the same staging site, while the great majority were itinerant. Lesser kestrels are food specialists (eating namely flying insects, e.g. grasshoppers during the non-breeding period, Pilard et al., 2011). Therefore they may rely on an itinerant strategy to track the fluxes of their prey, in contrast to food generalists who could feed on a diversity of prey items available in the same site (Salewski et al., 2002). Furthermore, we did not find any sex differences related to schedules or movement metrics. Sex-related differences in non-breeding schedules, movements and habitat use have been reported, particularly in species with size dimorphism. Males ruffs (*Philomachus pugnax*), the larger sex, winter further to the north than females, and their migration phenology is more advanced (van Rhijn 1991). Based on field observations, males wintering in the Senegal Delta started to fatten before embarking on northward migration three weeks earlier than females (Zwarts et al., 2009). Field-based studies on Marsh harriers wintering in the Inner Niger Delta showed that females use wetlands, likely due to their ability to hunt larger waterbird prey, while males focus more on small prey such as small mammals and grasshoppers in dryer areas (Bijlsma et al., 2001). The lesser kestrel has a reversed size dimorphism, with females being 15% heavier than males (Cramp, S. & Simmons, 1980). However, such a size difference may not be enough to give females access to alternative resources than males, so they respond similarly to conditions in the Sahel.

Our tracked lesser kestrels spent the longest time (two months on average), covered longer mean daily distances, and spent more daylight hours flying in the last staging sites than at first and intermediate ones. We speculate three non-exclusive explanations: (1) the necessity of depositing fat during the last weeks prior to the return migration (Newton 2008). (2) The high intraspecific competition derived from the massive individual aggregation in the last staging sites may explain the larger daily distances covered in such sites relatively to intermediate and first sites. And (3) birds feeding on slightly larger prey species or within a species the larger sex at the last sites (e.g. grasshoppers species such as *Ornithacris cavroisi* or the larger desert locusts *Schistocerca gregaria* females, Mullié, 2021), requiring more time on the wing (more time flying vs. perch hunting smaller prey at first sites).

Lesser kestrels are insectivorous steppe birds using open grasslands and croplands at their breeding areas in the Mediterranean (Ursúa et al., 2005; Franco et al., 2004). In general, birds used to winter in mosaics of habitats types: grassy vegetation, shrubland, cropland, and sparse. Additionally, our results suggested some shifts in habitat use over the non-breeding period. Lesser Kestrels first stopped in crops and mosaics of habitat types along the Mauritania and Mali border. The most important non-breeding habitats at intermediate and last sites were mosaic habitat types (e.g. vegetation, cropland, shrubland) and more natural habitats such as grassland and sparse vegetation. This is in accordance with previous studies, which suggested that Palearctic migrants typically used heterogeneous rather than homogenous landscapes in their wintering grounds (Salewski & Jones, 2006). For example, Khelkom (Senegal) was protected under Senegalese law until 1991. Since then, the area was gradually cleared as rangeland and for groundnut development until 2004. The resulting mosaic of cropped areas, arable land and regenerating natural savannah has become an ideal habitat for grasshoppers. In turn, the area has attracted massive numbers of insectivorous bird species such as white storks *Ciconia ciconia* (3.500 individuals; representing 1.75% of the flyway population), Montagu's harriers *Circus pygargus* (5.000-6000; 16%) and lesser kestrels (5.000; 10%) (Mullié & Guèye, 2010).

There are potential caveats to the interpretation of the habitat use data in the study. It should be noted that the map consists only of 22 classes and that the study region features numerous other habitat types that are likely to be important for lesser kestrels because large concentrations of locusts may occur there (e.g. laterite plateaus, estuaries, Schlaich, 2019). Therefore, it is likely that our interpretation of habitat use may underestimate the importance of other habitats used by lesser kestrels, and in any case, it is hard to translate land use to ecologically relevant parameters such as prey availability. We are confident that some patterns revealed from GlobCover data are robust, such the apparent avoidance of widely available grassland at the start of non-breeding period and the increasing diversity of habitat use from first to last staging sites. However, further investigation of habitat preferences and land cover change would require other more detailed habitat maps to match better relevant resources for kestrels (e.g. insect distribution, fires) in West Africa and, ideally, ground-truth such products in the field to improve accuracy (Vickery et al., 2014).

CONSERVATION IMPLICATION

In the late 1960s and early 1970s, numerous Afro-Palearctic migrants –including the lesser kestrel – showed a sharp population decline (Sanderson et al., 2006; Iñigo & Barov, 2010). During the first decade of the 21st century, there have been several years of higher rainfall in the Sahel which may have led to population recovery of Afro-Palearctic migrants (Nevoux et al., 2008), including probably the lesser kestrel. However, this positive trend has not been maintained in subsequent years, and like numerous steppe and grassland birds, the lesser kestrel is now declining in Spain (Bustamante et al., 2020). While land-use change in the breeding areas is certainly part of the reason for this decline, the need for more accurate knowledge of the areas used by wintering migrants for conservation action has been highlighted by numerous authors (Newton, 2008; Morrison et al., 2013; Vickery et al., 2014). Here we show that the average annual time allocated for the non-breeding period was 40%, and the average annual time spent at first, intermediate and last sites was 10%, 14% and 20%, respectively. Our work emphasises the conservation value of west Africa for lesser kestrels and of last staging sites in particular, as an area where they aggregate in large numbers close to wetlands. Our results confirms previous findings of staging sites in central Senegal, hosting c. 30.000 birds annually, that represent 45% of the population breeding in Western Europe (Pilard et al., 2011; Augiron et al., 2015). The aggregation of birds in large super-roosts at potentially vulnerable habitats in the Sahel (e.g. wetlands, natural savannahs, mosaics) makes the species more sensitive to land use change. Its seeming dependence on insect prey suggests that pesticide use, combined with the continuous conversion of wetlands and grasslands into cropland and excessive forest clearing for firewood by a growing rural population in West Africa, may pose a significant risk to the species (Thiollay 2007, Zwarts et al., 2009).

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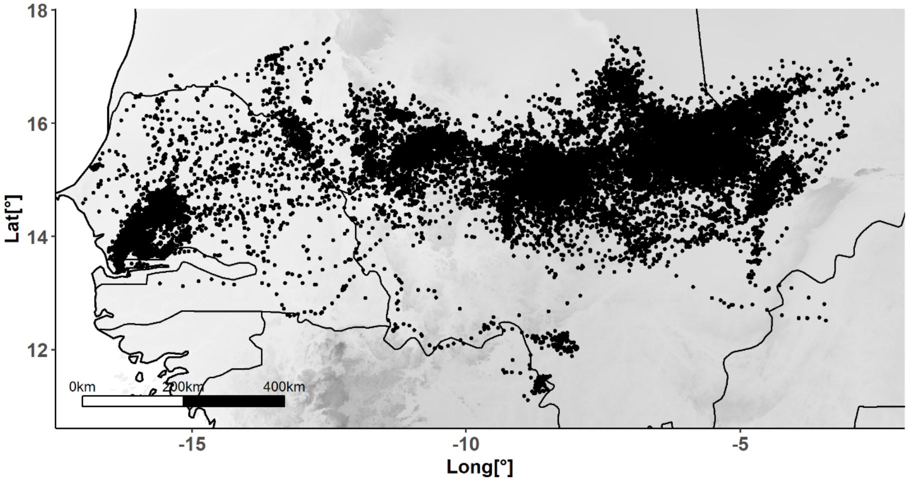
SUPPLEMENTARY INFORMATION CHAPTER 3

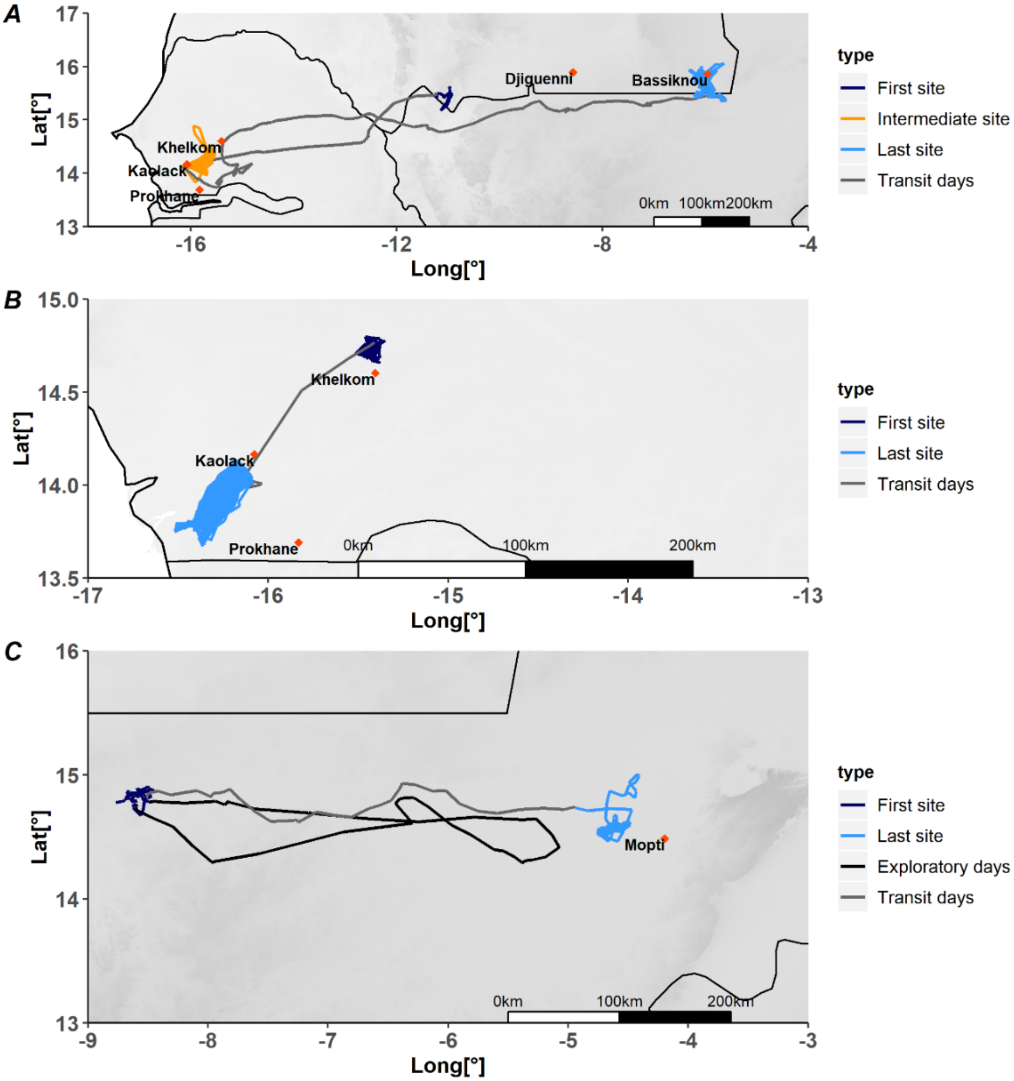
Supplementary Figure S1. Map showing all GPS fixes of the 54 lesser kestrels tracked during winter (2016-2020).

Supplementary Figure 2. Example of annotation of GPS tracked adults and movements within the West African wintering area. (A) Female lesser kestrel (4170933_R8J4) during the northern winter 2018-2019 used three wintering sites (first site in purple, intermediate in yellow and last in



blue). Transit days or days when she flew between sites without returning to the previous site are shown in grey. (B) Female (4179802_RU00) arrived at Khelkom (first site) on 2 October 2018. On 27 November, she flew 80 km southward, where she spent most of her winter close to a salt lake near Kaolack, a typical daytime roost known to hold several tens of thousands of raptors (Pilard et al., 2011; Zwarts et al., 2009). She stayed on this wetland until the onset of migration on 17 March 2019. (C) Track of a male lesser kestrel (BR.D) during the northern winter (2018-2019) showing exploratory days in black (lasted six days).

Supplementary Table S1. Wintering summary statistics for 54 lesser kestrels showing: the first year of tracking, sex, numbers of winters tracked, number of staging sites, the average duration of



the stay in West Africa, average duration spent at the first, intermediate and last sites, the average number of resident, transit and exploratory days. Average values for birds with 2 or 3 tracks are shown.

Bird identity	First tracking year	Sex	N of winters tracked	N of staging sites	Mean duration winter period (days)	Mean duration at first sites	Mean duration at intermediate sites	Mean duration at last sites	Resident days	Transit days	Exploratory days
B00300	2018	f	2	4	144	27.5	46.5	63.5	130.5	6	4
B00309	2018	f	1	2	141	65	6	66	134	2	2
B00316	2018	f	1	2	136	18		96	81	21	24
B00323	2018	f	1	3	151	23	107	12	138	13	
B00324	2018	f	1	2	144	54		80	121	9	
B00331	2018	f	1	1	170			170	102		
B00336	2018	f	1	3	130	19	43	64	120	3	
B00338	2018	m	1	3	152	26	17	31	69	49	
B00342	2018	m	2	3	144	35.5	34	75.5	123	14	
B00347	2018	f	1	2	130	3	3	83	63	24	
B00348	2018	m	2	3	149	53.5		68.5	97.5	12.5	
B00349	2018	m	2	3	139	23		93	115.5	18.5	
B16127	2017	m	2	4	149	26.5	104	18.5	147.5	9.5	9
B16137	2017	m	3	2	140.5	64.5		68.5	127	10	
B16212	2016	m	1	2	156	61		92	148	2	
B16228	2017	m	1	2	154	44	20	84	151	4	
B16275	2017	f	1	3	175	4	41	113	160	16	
B16584	2017	f	1	2	199	54	107	27	191	10	
B16611	2017	m	2	2.5	177	62.5		33	170.5	6	
B16639	2017	m	1	2	149	66		81	148	1	
B16643	2017	f	2	2	132.5	45		85.5	131	1	3
B16645	2017	f	2	3	138	19.5	78.5	27.5	121	16	
B16661	2017	f	2	1.5	158	65		124.5	140.5	1	2
B16679	2017	f	2	2	171.5	21.5	36	99	154	14	2
B16687	2017	f	1	2	154	3		149	154	1	
B16688	2017	m	2	2.5	139	66.5		70	137	1.5	3
B16690	2017	m	2	3.5	165.5	24	50	81.5	154.5	10.5	3
B17199	2018	f	1	3	126	3	77	40	121	6	
B17210	2018	m	2	2	105	19.5	30	61.5	95.5	7.5	6
B17214	2018	f	1	4	139	17	94	24	133	8	
B17215	2018	f	1	2	147	11	26	89	129	19	
B17218	2018	m	1	4	135	5	106	20	121	15	
B17219	2018	m	1	2	142	5		135	142	8	
B17230	2018	m	2	2.5	108	10	17	77	94.5	13.5	2
B17235	2018	m	2	2	143.5	63.5		73	135.5	6	6
B17237	2018	m	2	3.5	153	35	102.5	8.5	141	13.5	
B17239	2018	f	2	2	146	11.5	22.5	91.5	128.5	16.5	7
B17240	2018	m	1	2	151	51		90	129	9	14
B17241	2018	f	1	4	171	65	92	9	164	8	
B17245	2018	f	1	2	132	66		24	92	41	
B17250	2018	m	2	2.5	146.5	42.5	62	67	141	5.5	
B17251	2018	m	1	3	129	26	52	47	127	3	
B17253	2018	m	2	1.5	145.5	67	14	93.5	130	12.5	
B17254	2018	m	2	3	146	17	88	35	140	9	1
B17256	2018	f	1	2	114	31	31	39	104	11	
B17261	2018	m	1	2	156	48	38	19	108	49	
B17262	2018	f	1	3	151	49	50	46	134	18	
B17278	2018	f	2	2.5	160	27.5	51	103	155	5.5	
B17280	2018	f	1	2	154	39	58	41	141	14	
B17281	2018	f	1	2	150	24	42	80	149	2	
B17282	2018	f	2	3	136.5	29	62.5	41	128	4	11
B17288	2018	f	1	2	166	72	33	54	161	10	1
B17292	2018	f	1	2	165	55		108	165	1	
B40128	2018	m	2	2	134	40	20	80	132.5	2.5	

Supplementary Table S2. GlobCover legend description

Glob-Cover value	GlobCover label	Description	Abreviation
14	Rainfed croplands	Rainfed shrub crops/ rainfed tree crops / rainfed herbaceous crops	Crops
20	Mosaic cropland: 50-70% cropland / 20-50% vegetation (grassland, shrubland, forest)	Cultivated and managed terrestrial areas / natural and semi-natural, primarily terrestrial vegetation	Crops/Veg
30	Mosaic vegetation: 50-70% vegetation (grassland, shrubland, forest) / 20-50% cropland	Natural and semi-natural, primarily terrestrial vegetation / cultivated and managed terrestrial areas	Veg/Crops
40	>15% closed to open broadleaved evergreen and/or > 5m semi-deciduous forest	Broadleaved evergreen closed to open trees / semi-deciduous closed to open trees	Forest
60	15-40% open broadleaved deciduous forest/ >5m woodland	Broadleaved deciduous (40-(20-10)%) woodland	
110	Mosaic shrubland: 50-70% shrubland / 20-50% grassland	Closed to open trees / closed to open shrubland (thicket) / herbaceous closed to open vegetation	Shrub/Grass
120	Mosaic grassland: 50-70% grassland / 20-50% forest or shrubland	Closed to open shrubland (thicket) / herbaceous closed to open vegetation / closed to open trees	Grass/Shrub
130	>15% closed to open (broadleaved or needleleaved, evergreen or deciduous) <5m shrubland	Broadleaved closed to open shrubland (thicket)	Shrub
140	>15% closed to open herbaceous vegetation (grassland, savannas or lichens/ mosses)	Herbaceous closed to very open vegetation / Closed to open lichens/mosses	Grassland
150	<15% sparse vegetation	Sparse trees / herbaceous sparse vegetation / sparse shrubs	Sparse
170	>40% closed broadleaved forest or shrubland permanently flooded - saline or brackish water	Closed to open (100-40%) broadleaved trees on permanently flooded land (with daily variations), water quality: saline water / closed to open (100-40%) broadleaved trees on permanently flooded land (with daily variations), water quality: brackish water / closed to open (100-40%) semi-deciduous shrubland on permanently flooded land (with daily variations), water quality: saline water / closed to open (100-40%) semi-deciduous shrubland on permanently flooded land (with daily variations), water quality: brackish water	Mangrove
180	>15% closed to open grassland or woody vegetation on regularly flooded or waterlogged soil - fresh, brackish or saline water	Closed to open shrubs / closed to open herbaceous vegetation	Wet.soil
190	>50% urban areas	Artificial surfaces and associated areas	Urban
200	Bare areas	Bare areas	Bare
210	Water bodies	Natural water bodies / artificial water bodies	Water

SUPPLEMENTARY METHODS

Logger programming

Loggers were programmed with different duty cycles: 50 NanoFix GEO+RF tags had a double schedule. From these, 43 tags collected GPS positions at an interval of 15 min on a 14 h ON/10 h OFF cycle between 6:00 and 20:00 during Jan, May, June, July, Nov, Dec, and at an interval of 30 min on a 24 h ON cycle during Feb, March, April, Aug, Sept, and Oct. Three tags collected GPS positions at an interval of 15 min on a 12 h ON/12 h OFF cycle between 8:00 and 20:00 during May, June, July and at an interval 1 h on a 24 h ON cycle during Jan, Feb, Mar, Apr, Aug, Sep, Oct, Nov, Dec. Four tags collected GPS positions at an interval of 10 min on a 13 h ON/13 h OFF cycle between 8:00 and 21:00 during Mar, Apr, Jun, Jul, Aug, Sep and at an interval of 30 min on a 24 h ON cycle during Jan, Feb, May, Oct, Nov, Dec. Eleven Microsensory tags collected positions at an interval of 15 min on a 15 h ON/9 h OFF cycle between 6:00 and 20:00 and 1 nocturnal position at 1 am. Intervals differed depending on solar battery recharge and satellite geometry (≥ 4 satellites must be detected for a reliable fix).

GENERAL DISCUSSION

GENERAL DISCUSSION

Throughout this thesis, we have studied the migratory and non-breeding movements of the lesser kestrel *Falco naumanni*, a well-studied falcon species in its breeding grounds. We used GPS tracking data from 73 adults of this trans-Saharan migrant falcon species breeding in Spain and Italy. When we started this PhD, migration and non-breeding movements of the lesser kestrel were mainly studied through ringing, field-based studies, light-level geolocators and satellite-tracking (Rodríguez et al., 2009; Catry et al., 2011; Pilard et al., 2011; Limiñana et al., 2012; Augiron et al., 2015). Such studies have provided valuable information on migratory routes, migration speed, ability to undertake nocturnal migration, and non-breeding locations. This PhD's great collaborative research effort allowed us to pool an impressive dataset with a balanced sampling of females and males from different breeding colonies tracked between 2014 and 2021. This is indeed a valuable dataset since most tracking studies for birds this size have used smaller sample sizes and lower spatial resolution devices such as geolocators or PTTs.

The reversed sexual size dimorphism, with females being 15% heavier than males (Cramp & Simmons, 1980), makes the lesser kestrel a pertinent species to study sex-specific differences in migratory behaviour and non-breeding movements. In addition, its ability to migrate using a combination of flapping and soaring-gliding flight (so-called flight generalists) gives them more flexibility to cope with weather conditions according to internal motivation (sex and season) (Shamoun-Baranes et al., 2016). This thesis addresses a timely question in current migration research about what factors drive variation in migratory behaviour of a small-sized flight generalist bird at multiple scales (chapter 1). Furthermore, we contribute to a deeper understanding of the movement strategy of lesser kestrels at their non-breeding quarters in West Africa, and test for potential differences in the mobility and timing of non-breeding movements between sexes (chapter 3). Finally, we focus on the main factors driving interindividual variation in migration timing during pre-breeding migration (chapter 2).

Seasonal variation in migratory behaviour

Every year lesser kestrels travel thousands of kilometres from their temperate breeding grounds in southern Europe to their African non-breeding grounds and back. The way migrants undertake this complex journey often shows a great flexibility in migratory behaviour. But what are the most important factors driving spatio-temporal variation in migratory behaviour of this flight generalists bird? To answer this question, we first studied seasonal variation in migratory behaviour accounting for sex differences.

According to previous studies on Icelandic whimbrels (Carneiro et al., 2019), marsh harriers (Vansteelant et al., 2020) and also lesser kestrels (Rodríguez et al., 2009; Limiñana et al., 2012; Sarà et al., 2020), birds complete their migration faster during the post than the pre-breeding migration. Our results show that lesser kestrels migrated faster, showed significantly fewer non-travelling days and followed straighter paths during post-breeding migration, with no differences between sexes (chapter 1). Previous studies have suggested that some species may minimise the time during the post-breeding migration due to competition for non-breeding territories (Mellone et al., 2015; Panuccio et al., 2014). For example, adult ospreys that are sedentary on their non-breeding grounds and that show inter-year wintering site fidelity are expected to compete for such territories (Alerstam et al., 2006, Washburn et al., 2014). However, as we showed in chapter 3, lesser kestrels make itinerary movements between 2-3 consecutive staging sites in West Africa, so it seems unlikely that competition for non-breeding territories drives migratory behaviour during the post-breeding migration.

However, seasonal differences in migration duration or speed do not necessarily indicate time constraints as there is a strong difference in environmental conditions between seasons (Carneiro et al., 2019). We found that post-breeding migration was shorter than pre-breeding migration, as individuals spent 1.00 ± 0.23 days non-travelling in the former and 6.00 ± 0.78 days non-travelling in the latter (chapter 1). Lesser kestrels spent those non-travelling days in areas with higher vegetation productivity during the pre-breeding migration and mainly north of the Sahara (chapter 2). There have been proposed several non-mutually exclusive explanations for making more stopovers during the pre-breeding migration. First, the seasonal differences in food availability along the migration route. During the post-breeding migration, as birds depart to their wintering grounds in the Sahel from the Iberian and Italian peninsula, they initially migrate fast due to the shortage of food and unsuitable habitats in North Africa (Shamoun-Baranes, et al., 2003). During the pre-breeding migration, when lesser kestrels reach the north of Africa, conditions are favourable for refuelling and resting compared to post-breeding migration, as a result of winter rains (Trierweiler et al., 2014; Vansteelant et al., 2020). Second, the possibility of remaining at stopover sites until conditions become appropriate at their breeding colonies since conditions are temporally correlated at shorter distances (Usui et al., 2017; Burnside et al., 2021) (chapter 2). Finally, the seasonal wind regimes are likely more supportive during the post than the pre-breeding season. We found that lesser kestrels stopped when experiencing stronger headwinds along their migration routes compared to days when they travelled, suggesting that winds may be important factors mediating stopover decisions.

Drivers influencing the migratory behaviour of a flight generalist species

When looking deeper into the external and internal factors driving variation in migratory behaviour at daily and hourly time scales, we found that migratory behaviour was only marginally influenced by sex and season. Contrary to our expectations for a flight generalist, external factors, in particular tailwinds experienced *en route,* were the main determinant of seasonal variation in daily distance and hourly speeds. As a result, the more supportive tailwinds encountered during the post-breeding migration enabled lesser kestrels to cover up to 1000 km per day while only 500 km through opposing winds encountered during the pre-breeding migration (chapter 1).

This seasonal wind regime could be masking the common pattern found for birds to migrate faster during the pre than the post-breeding migration (Nilson et al., 2013). It has been suggested that there is a strong pressure for an early arrival at the breeding grounds to get access to better territories, mates and resources, and this might motivate many species to migrate faster in the pre- than the post-breeding migration (Kokko, 1999; Morbey & Ydenberg, 2001). This selection pressure might be stronger for the territorial sex (males in most bird species) (Marra et al., 1998; Rubolini et al., 2004; Tøttrup & Thorup, 2008). However, we found that sex differences explain relatively little variation in migration timing (chapter 2) and in migratory behaviour compared to the effect of geographical barriers and wind encountered by falcons along their migration routes (chapter 1). Again this was not expected, assuming that flight generalists species are less restricted by environmental (and especially weather) conditions compared to obligate soaring-gliding migrants.

We did not find any evidence that pre-breeding migration is more time-constrained than post-breeding migration in the lesser kestrel. We envision two possible reasons for our results: (1) the long establishment phase of the lesser kestrel, arriving two months before the onset of breeding (Negro et al., 1991), may well offset the need for an early arrival and favour individuals that arrive in good shape to acquire the best nesting holes. In that case, one would indeed expect males and females to respond similarly to weather conditions and resource availability, as they did in our study. (2) Coloniality offsets the need to arrive earlier than "competitors" due to the advantage of being there at the same time to benefit from the fitness gains of colonial breeding (Maggio et al., 2013).

Geographical barriers shape daily travel schedules

When lesser kestrels migrate to Africa across African-Eurasian flyways, they have to cross geographical barriers like the Mediterranean Sea and the Sahara Desert, where food, landing opportunities, shelter and other vital resources are scarce or completely lack. Crossing the sea or desert pose different challenges for migrants (e.g., extreme temperatures over the desert vs fewer landing opportunities over the sea), to which birds likely respond in different ways (López-López et al., 2010). Flight-generalist migrants are capable of flapping flights that extend daily travel schedules into the night when thermal updrafts are rare or weak (Klaassen et al., 2017). They typically also achieve higher speeds during nocturnal than diurnal migration, enabling them to cross ecological barriers in non-stop flights ("sprints") (Alerstam, 2009). We expected that individuals would show geography-dependent differences in daily travel schedules and speeds by travelling faster, covering larger distances, and migrating at night when flying over barriers. Accordingly, we found that geography moulded regional differences in daily distances by shaping daily travel time budgets, with a propensity for sprinting across barriers. In both seasons, lesser kestrels sprinted across ecological barriers and frequently extended migration time into the. Conversely, they travelled at a slower pace and mainly during the day while over non-barriers (chapter 1). When crossing barriers, birds thus showed a clear time-minimising behaviour in both seasons.

We found the hourly scale models explained relatively little variation compared to those at the daily scale. This is probably due to the fact that wind speeds are estimated by models at a coarser temporal (6 h) and spatial resolution (0.75°) than lesser kestrels tracking data, which could led to our inability to capture the importance of weather variables at such a fine temporal scale.

Non-breeding movements in their West African non-breeding quarters

Prior to this thesis, ringing and tracking data provided some important information on the non-breeding range of lesser kestrels from populations across Southern Europe. Lesser kestrels from this region spend the non-breeding period in different areas of the Sahel. In particular, Spanish birds spend the non-breeding period along the Malinese-Mauritanian border and Senegal (Rodríguez et al., 2009; Limiñana et al., 2012; Pilard et al., 2017), whereas Italian birds non-breeding distribution extend from eastern Mali to Niger and Nigeria (Sarà et al., 2019). During the non-breeding season, lesser kestrels are known to aggregate in super roost in wetlands within western Senegal (e.g. Kaolac and Khelkom) that can hold tens of thousands of individuals (Pilard et al., 2011; Augiron et al., 2015). Catry et al. (2009) and Limiñana et al. (2012) suspected large longitudinal movements within West Africa along the non-breeding season. Beyond the spatial distribution of their non-breeding range, relatively little is known about their non-breeding ecology.

Using GPS tracking data from the Spanish lesser kestrel population over three consecutive annual cycles (2018-2019,2019-2020,2020-2021) enabled us to confirm the location of non-breeding areas of the Spanish population (chapter 3). Lesser kestrels spread out over the interior of West Africa at arrival – from the northeast Senegalese border to the easternmost part of the Mauritania-Mali border. Then they moved either westward or eastward to converge at staging sites at coastal wetlands in Senegal or inland wetlands in eastern Mauritania at the border with Mali or in floodplains (Inner Niger Delta), respectively. We revealed an itinerant lifestyle during their non-breeding season in West Africa. Lesser kestrels used a small number of staging sites (on average two or three) that they visited in subsequent years, particularly the last site. Contrary to other locust-eating steppe birds (Trierweiler et al., 2013; Schlaich et al., 2016), kestrels did not move along a north-south axis in the Sahel, as individuals undertook either westward or eastward movements through intermediate sites to converge at their last staging sites. Such east-west movements within the Sahel have been reported for other species (e.g. tawny pipits *Anthus campestris*, Briedis et al., 2016; turtle doves *Streptopelia turtur*, Eraud et al., 2013). We suggest these movements can be due to kestrels tracking resource fluxes in the Sahel wetlands.

During the last part of the wintering period, birds typically congregated in certain regions in western Senegal and eastern Mauritania in the border with Mali. Such aggregation of birds may increase the vulnerability of this already declining species as local habitat disturbance at these staging sites may affect survival and subsequent breeding performance. We show that birds spend the longest time (two months on average) at the last staging site, covering longer mean daily distances, and spending more daylight hours flying compared to the first and intermediate staging sites. The need to deposit fat during the last weeks prior to the pre-breeding migration and the likely high intraspecific competition derived from the massive individual aggregation in those places could explain the increase in the daily foraging activity. Another explanation could be that birds feed on slightly larger prey species or within a species, the larger sex at the last sites (e.g. grasshoppers species such as *Ornithacris cavroisi* or the larger desert locusts *Schistocerca gregaria* females, Mullié, 2021), requiring more time on the wing (more time flying vs perch hunting smaller prey at first sites). Finally, the tracked individuals spent about 147 days in West Africa, corresponding to 40% of the total annual cycle. We found little interindividual variation in movement strategy with no sex differences in schedules or movement metrics. Size differences between males and females may not be enough to give females access to alternative resources than males, so they respond similarly to conditions in the Sahel. It is also likely that energetic demands during the non-breeding period are similar for both sexes.

On their way back to their breeding grounds

After the non-breeding period in the Sahel, adult lesser kestrels return to their previous breeding colony. Birds have to time their arrival to the breeding grounds not only with respect to what their conspecifics are doing but also with the temporal and spatial availability of ephemeral food resources along their routes and at their breeding grounds (Kolzsch et al., 2015; Armstrong et al., 2016). Synchronising their migration timing with the local phenology of the environment is key for individual survival and reproductive success (Marra et al., 1998; Alerstam et al., 2003; Visser et al., 2015). Previous tracking studies of long-distance migrants have shown different migration schedules of individuals breeding in different locations (Conklin et al., 2010; Briedis et al. 2016; Vansteelant et al., 2020). For example, and similar to our findings, bar-tailed godwit (*Limosa lapponica baueri*) of different breeding locations spend the non-breeding period in the same area experiencing similar environmental conditions (chapter 3). However, departure dates during the pre-breeding migration differed among individuals, with southern breeders departing first and arriving earlier relative to more northerly breeding individuals. We found a large interindividual variation in pre-breeding migration timing that spreads over a three-month period. Kestrels depart from sub-Saharan Africa between 25 January and 24 April and arrive at the breeding sites between 2 February and 13 May. We found different temporal schedules in which birds breeding at more northern latitudes and more eastern longitudes depart always later than those breeding at southern latitudes and western longitudes. The temporal differences in arrival dates between Mediterranean breeding colonies are likely due to a spatiotemporal gradient in habitat phenology (Chapter 2). Briedis et al. (2020) demonstrated this in 23 passerine and near-passerine Afro-Palaearctic bird species of 55 European breeding populations, where individuals from the Western and Eastern migratory flyways were tracked back and forth to their breeding grounds. Similar to our findings, birds breeding in more southwestern locations departed earlier and arrived earlier at their breeding sites in Europe relative to birds breeding in more northeastern sites reflecting the later spring green-up at higher latitudes and more eastern longitudes.

If migratory birds want to arrive on time to their breeding colonies, they can achieve that by departing earlier from the non-breeding grounds, reducing the number or duration of stopovers, and/or increasing flight speed (Nilsson et al., 2013). Our results from chapter 2 reveal that the departure date from the non-breeding area explains much of the variation in arrival date. We also found that stopover duration and travel speed had a significant effect on arrival date but were comparatively less influential than the departure date. We found that birds had varying departure dates corresponding to the latitude and longitude of their breeding colony and with little influence of the non-breeding locality. Such spatiotemporal pattern of departure dates suggests that departure decisions of the lesser kestrel are predominantly under endogenous control. However, future studies should aim to disentangle endogenous mechanisms from external cues such as photoperiod and local environmental factors (e.g. wind, temperature, rain and food supplies) in shaping departure decisions.

Conservation implications

The lesser kestrel is a species of European conservation priority and protected under the Bern convention and Bonn Convention (BirdLife, 2004; BirdLife International, 2017), which has suffered steep population declines in the second half of the 20th century (Iñigo & Barov, 2010). Currently, the lesser kestrel is now declining in Spain, with the last census indicating that 43% of the population has been lost over the last seven years (Bustamante et al., 2020). While land-use change in the breeding areas is certainly part of the reason for this decline, the need for more accurate knowledge of when and where populations reside during migration and during the non-breeding period in Africa is crucial for developing appropriate conservation measures.

To avoid significant negative impacts of land-use change to migratory species, policies concerning the protection of staging sites during migration and in their non-breeding grounds could be strengthened and extended to other areas where other species are known to aggregate in very high densities in their wintering grounds: Amur and the Red-footed falcon (Bildstein, 2005; Alexander & Symes, 2016), marsh harriers (Zwards et al., 2009), barn swallows (Bijlsma & Brink, 2005) and starlings (Newton, 2008), among others. In addition, detailed mapping of fine scale-habitat variation of these core sites, combined with ground-truthing tracking data, would also help identify key areas (roosts and foraging hotspots) for environmental protection.

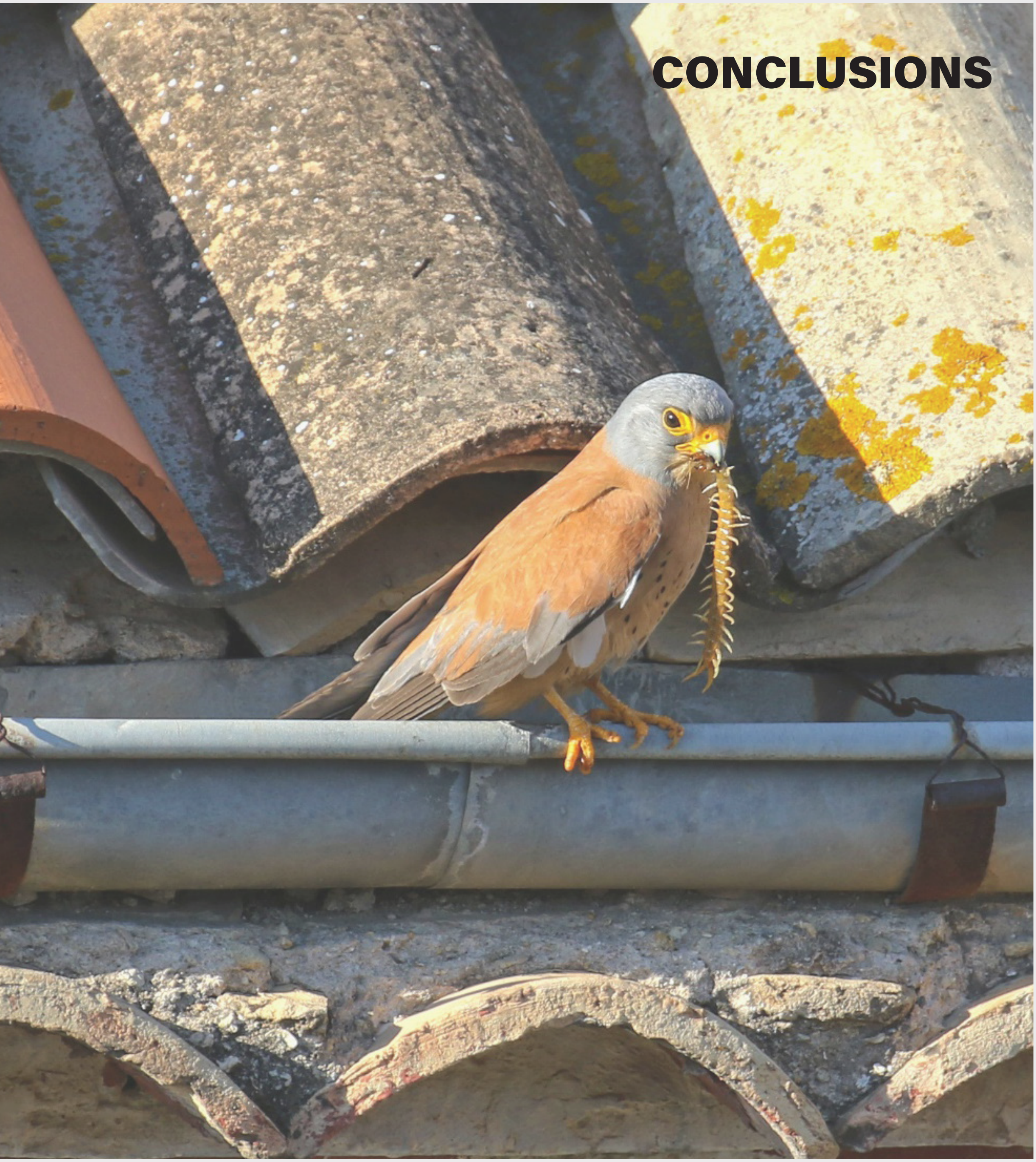
Future perspectives

We have described lesser kestrels' broad habitat use during their non-breeding period in West Africa using the GlobCover land cover map based on remote sensing. Investigation of fine-scale habitat selection would require more detailed habitat maps, hopefully, created on the field within individual home ranges. This would improve our knowledge of habitat preferences and possibly help to identify key habitats for conservation. Although remotely sensed products such as Normalized Difference Vegetation Index (NDVI) or weather data (e.g. precipitation, temperature) could be used to gain more insights into the ecology of lesser kestrels over the whole non-breeding period, these are not direct measures of insects abundance. Thus, ground-truthing such products in the field to improve accuracy is highly recommended (Vickery et al., 2014).

In this thesis, we gained knowledge of the large-scale movement patterns of lesser kestrels in West Africa. We speculated that the longitudinal movements we observed are due to a search for wetlands where food availability (e.g. flying insects such as grasshoppers) is expected to be higher. Our knowledge of lesser kestrel's diet during the non-breeding period comes from previous studies on regurgitated pellets collected during the non-breeding period at few locations (Pilard et al., 2011). To gain a deeper knowledge of their diet during the non-breeding period on a broader spatial scale, fieldwork studies should collect pellets on roosts in Senegal and along the Malinese-Mauritanian border (see chapter 3 for more details on location). Fieldwork in such places should consider the remoteness and long-term political instability of the Sahel. Finally, field observations of hunting behaviour in key foraging hotspots may provide valuable information of intake rates and of key habitats for lesser kestrels in West Africa. Remotely reprogrammable GPS-loggers with accelerometers will allow researchers to collect movement data in great detail to further investigate how lesser kestrels use their non-breeding sites.

On their way back to their breeding grounds in Europe we found that lesser kestrels stopped in the North of Africa during the pre-breeding migration. We found that lesser kestrels stopped in areas with higher vegetation productivity (chapter 2). A combination of GPS tracking data and fieldwork studies in such sites could be useful to gain further knowledge on lesser kestrel's stopover ecology. For example, to collect data on prey abundance through transect counts and identification of communal roosts and pellet collection to get information on prey choice. Finally, fine-scale habitat use analysis in such sites could provide information on habitat preferences and hopefully guide conservation action.

CONCLUSIONS



CONCLUSIONS

This thesis dives into the migration and non-breeding movements in Africa of a small insectivorous raptor. Besides confirming previous findings and providing further insights on where and when the lesser kestrels migrate, we conclude that they exhibited great behavioural plasticity in migration. It is one of the few attempts at considering the influence of internal and external factors driving variation in the migratory behaviour of a small species. We show that external factors far outweighed internal factors in explaining variation in migratory behaviour of both sexes, despite lesser kestrels' capability to switch between flight modes.

Among the most interesting findings were:

1 **A faster post-breeding than pre-breeding migration due to seasonal wind regimes with no differences between sexes. We suggest a long establishment phase likely buffers against an internal motivation for faster pre-breeding migration in lesser kestrel males.**

Una migración pos-nupcial más rápida que la pre-nupcial debido a los vientos en ruta, y sin diferencias significativas entre sexos. Sugerimos que el largo periodo de establecimiento en la colonia de cría (alrededor de dos meses) puede amortiguar en contra de la urgencia por llegar de los machos durante el viaje pre-nupcial.

2 **The effective barrier crossing by travelling through the night in addition to the day. When crossing barriers, falcons thus showed a clear time-minimising behaviour in both seasons.**

Los cernícalos mostraron una eficaz forma de cruzar barreras viajando tanto de día como de noche. Cuando cruzan barreras buscaron minimizar el tiempo de viaje tanto en la migración pos-nupcial como en la pre-nupcial.

3 **We confirmed an itinerary lifestyle in West Africa, including either westward or eastward movements through intermediate sites to converge at their last staging sites in wetlands.**

Confirmamos un comportamiento itinerante en África Occidental incluyendo movimientos longitudinales hacia el oeste o el este utilizando zonas intermedias para congregarse finalmente en áreas cercanas a humedales.

4 **The large interindividual variation in migration schedule is driven by the breeding site phenology.**

Una larga variación interindividual en los tiempos de migración causada por la fenología de la colonia de cría.

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> *Sólo un exceso*
> *es recomendable en el mundo:*
> *el exceso de gratitud*
>
> JEAN DE LA BRUYERE

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