Foraging Behavior of the **Lesser Kestrel** under the **Movement Ecology** Paradigm Revealed using **Biologgers**

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Ph.D. Thesis

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Foraging behavior of the lesser kestrel under the Movement Ecology paradigm revealed using biologgers.

Memoria presentada por el Licenciado en Biología Jesús Hernández Pliego para optar al título de Doctor por la Universidad de Pablo de Olavide.

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CERTIFICAN

Que los trabajos de investigación desarrollados en la Memoria de Tesis Doctoral "Foraging behavior of the lesser kestrel under the Movement Ecology paradigm revealed using biologgers" son aptos para ser presentados por el Ldo. Jesús Hernández Pliego ante el Tribunal que en su día se designe, para aspirar al Grado de Doctor por la Universidad Pablo de Olavide.

Y para que así conste, y en cumplimiento de las disposiciones legales vigentes, extendemos el presente certificado a 15 de Julio de 2016.

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JUNTA DE ANDALUCIA CSIC CONSEJO SUPERIOR DE INVESTIGACIONES CIENTÍFICAS HORUS

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A mi familia
A mis amigos

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SUMMARY

The recent revolution of biologging technology has provided novel insights into free-ranging animal ecology with an unprecedented spatiotemporal resolution. As a consequence, literature on animal movement has vastly increased. This is the breeding ground over which Movement Ecology has arisen as a new discipline to unify all movement research under a common framework. Accordingly, Movement Ecology states that individual movement results from the interaction between four elements: individual state or motivation (why to move), motion abilities (how to move), navigation capacities (when and where to move), and external factors (both biotic and abiotic). This paradigm stresses the necessity to evaluate these elements in order to get a comprehensive understanding of the movement path. Thus, the Movement Ecology aims to answer old ecological questions and also to generate new ones thanks to the application of the latest technological advances to research on movement.

The lesser kestrel (*Falco naumanni*) is a small insectivorous falcon that breeds in colonies across the Palearctic and winters in Africa. This species suffered a severe world population decline during the second half of the 20th century because of the agricultural intensification. The lesser kestrel has been well-studied during the breeding period, especially in its foraging ecology and mainly focusing on habitat selection and diet. In this PhD thesis, we investigated the foraging ecology of the lesser kestrel from the perspective of Movement Ecology by deploying high-frequency GPS and tri-axial accelerometers dataloggers on 35 individual lesser kestrels at two breeding colonies during four consecutive breeding seasons in southern Spain.

Among external factors influencing movement, wind has been reported as one of the most important for flying animals. For this reason, we evaluated the influence of both wind speed and direction on lesser kestrel decisions about which direction to head when leaving the breeding colony to forage throughout the breeding season (**Chapter One**). We did not find any strong effect of wind

conditions on lesser kestrel flights probably due to the prevailing winds registered in the study area that were weak and constant in direction. However, we found that kestrels show a uniform distribution of foraging trip departure directions when foraging early in the breeding season, which seems to be related to more exploratory flights when prey abundance is low and individuals have little knowledge about prey spatial distribution. Meanwhile, at the end of the breeding season kestrels concentrate their departure directions towards high-quality foraging areas when preferred prey abundance, individual experience, and energy demand derived from rearing the offspring are higher. Therefore, individual internal factors (mostly navigation capacities) appear to guide kestrel decision about departure directions of foraging trips, with little effect of external factors like wind.

In some species with biparental care each member of the breeding pair cooperates by assisting its partner in every reproductive task, whereas in others each parent specializes in different tasks. The latter case is known as reproductive role specialization. In role-specialized species, such as the lesser kestrel, it is expected that sex will be an important motivational element that influence movement behavior in order to satisfy the temporally dynamic requirements during reproduction. We analyzed the effect of role specialization of the lesser kestrel on its foraging movement patterns throughout the breeding season (**Chapter Two**). Overall, we found differences in foraging movements between sexes in accordance with the general trend of raptor role specialization. Males fly larger daily distances and perform higher number of shorter foraging trips per day than females being the main responsible for provisioning tasks. Meanwhile, lesser kestrel females tend to stay longer than males at the colony through the day, which agrees with being the main responsible for nest protection, egg incubation and chick brooding. Furthermore, the lesser kestrel shows a sexual spatial segregation, with females constantly flying towards foraging areas located farther from the colony than males. This might be the result from an adaptive foraging strategy based on role specialization in order to avoid prey depletion in the surroundings of the colony and reduce intersexual competition between members of the breeding pair to be successful in reproduction.

Most avian species move by flying and they can do it either through flapping, which requires muscles to convert chemical energy into work, or through soaring-gliding, which harvests kinetic energy from moving air masses to replace muscle work. We studied the flight strategy of the lesser kestrel during foraging trips and the effect of solar radiation (as a proxy for thermal updrafts) on several foraging trip parameters during the breeding season (**Chapter Three**). Surprisingly, we found that the lesser kestrel, which has been traditionally considered as a flapping raptor, relies heavily on thermal soaring during foraging trips, especially at higher values of solar radiation. Individuals fly at slower speeds at higher altitudes and reach farther distances from the colony during foraging trips with thermal soaring events in comparison to those without them. This guides to a circadian pattern of lesser kestrel foraging behavior: individuals fly by flapping their wings towards foraging areas located closer to the colony when thermals are weak or absent, whereas they fly towards foraging areas farther away by soaring on thermals as soon as they are formed. Theoretical flight models indicate that, given the lesser kestrel preference for feeding on large grasshoppers and considering the average distance traveled along the trips, foraging by flapping their wings would result in a negative energy balance for the family group.

Apart from tracking devices, a series of animal-borne biological sensors has been developed to help fully understand individual movement, perhaps being accelerometers the most widely used devices nowadays. Tri-axial accelerometers measure body acceleration across three spatial axes at high temporal resolutions (typically 10 Hz or more). On the one hand, tri-axial accelerometry helps inferring animal behavior with no need of direct observation and, on the other hand, it has been also proved to be an effective methodology to measure animal energy expenditure. In **Chapter Four**, we built a behavioral classification model based on

tri-axial accelerometer and GPS data for the lesser kestrel. Then, we investigated the effect of internal (breeding phenology, role specialization) and external factors (prey availability, weather conditions) on the behavioral time and energy budget of the lesser kestrel during the day in general and when foraging in particular. Our behavioral classification model performs well when classifying free-ranging lesser kestrel behaviors. Flapping and hovering flights require more energy than soaring-gliding flights, and these flight behaviors consume more energy than stationary (incubating/brooding and perching) behaviors. The daily time and energy budget of the lesser kestrel is mostly determined by behavior-specific costs and the role specialization between sexes. Lesser kestrels gradually replace flapping with soaring-gliding during commuting flights as solar radiation increases, that is, as thermal updraft gets stronger. Lesser kestrels also progressively substitute perching (i.e., sit-and-wait hunting strategy) with hovering flights (i.e., active hunting strategy) at the foraging patch as wind speed increases, that is, as they experience stronger lifts to be aloft. However, kestrels seem to decide which hunt strategy to use regarding the activity level of the preferred prey, which is influenced by air temperature. Thus, individuals increase the use of hovering flights as air temperature, and prey activity level, also increase.

Overall, our results support predictions derived from the optimal foraging theory and suggest that the lesser kestrel prioritizes saving energy than time when foraging throughout the breeding season. This PhD thesis fills a gap of knowledge about the foraging behavior of the lesser kestrel through using the newest biologging technology, and so it has helped to understand better the lesser kestrel ecology during the breeding period.

RESUMEN

La reciente revolución tecnológica de los sistemas de seguimiento ha aportado perspectivas muy novedosas al estudio de la ecología animal gracias a la resolución espaciotemporal obtenida sin precedentes. Como consecuencia, la bibliografía sobre movimiento animal se ha incrementado en gran medida. Esto ha supuesto el caldo de cultivo sobre el cual ha nacido la Ecología del Movimiento como una nueva disciplina cuyo objetivo es unificar los estudios sobre movimiento bajo un marco conceptual común. Así, la Ecología del Movimiento afirma que el movimiento de los individuos es el resultado de la interacción entre cuatro elementos: el estado o motivación del individuo (¿por qué moverse?), la motilidad (¿cómo moverse?), las capacidades de orientación (¿cuándo y hacia dónde moverse?) y factores externos (bióticos y abióticos). Este paradigma resalta la necesidad de evaluar estos elementos para entender completamente el movimiento observado. De este modo, la Ecología del Movimiento se centra en responder antiguas cuestiones ecológicas a la vez que genera otras nuevas gracias a la aplicación de los últimos avances tecnológicos en los estudios de movimiento.

El cernícalo primilla (*Falco naumanni*) es un pequeño halcón insectívoro que cría en colonias a lo largo del Paleártico, y pasa los inviernos en África. Esta especie sufrió un grave declive poblacional a nivel mundial debido a la intensificación agrícola durante la segunda mitad del siglo XX. El cernícalo primilla ha sido objeto de multitud de estudios, en especial de aquéllos con el objetivo de investigar su ecología de alimentación basada en dieta y selección de hábitat durante la temporada de cría. En esta tesis doctoral, investigamos la ecología de alimentación del cernícalo primilla desde la perspectiva de la Ecología del Movimiento mediante el uso de dispositivos GPS y acelerómetros tri-axiales dataloggers de alta frecuencia en 35 individuos de cernícalo primilla procedentes de dos colonias de cría durante cuatro temporadas reproductivas consecutivas en el sur de España.

Entre los factores externos que afectan al movimiento, el viento ha sido descrito como uno de los más influyentes en animales voladores. Por esta razón, evaluamos la influencia de la velocidad y dirección del viento en la toma de decisiones del cernícalo primilla relacionadas con la dirección en la que abandonan la colonia para dirigirse hacia las áreas de caza a lo largo de la época de cría (**Capítulo Uno**). No encontramos un efecto marcado de las condiciones de viento en los vuelos de los cernícalos primilla probablemente debido a que los vientos dominantes en el área de estudio fueron débiles y constantes en dirección. Sin embargo, encontramos que los cernícalos muestran una distribución uniforme en las direcciones de salida de los vuelos de alimentación a principio de la temporada de cría, lo que parece estar relacionado con un mayor componente exploratorio de los vuelos cuando la abundancia de presas es baja y los individuos tienen aún poco conocimiento sobre cómo se distribuyen las mismas en el espacio. Mientras tanto, al final de la época de cría, los cernícalos concentran las direcciones de salida de los vuelos de alimentación hacia áreas de caza de gran calidad cuando la abundancia de presas, la experiencia de los individuos, y la demanda energética asociada a la cría de pollos son altas. Por lo tanto, factores endógenos del individuo (principalmente las capacidades de orientación) parecen determinar la decisión sobre las direcciones de salida de los vuelos de alimentación en el cernícalo primilla, con poco efecto de factores externos como el viento.

En algunas especies con cuidado biparental cada miembro de la pareja coopera asistiendo a su compañero en cada tarea reproductiva, mientras que en otras cada miembro de la pareja se especializa en tareas diferentes. Este último caso es conocido como especialización de roles. En especies con especialización de roles, se espera que el sexo sea un elemento importante que influya en los patrones de movimiento con el fin de satisfacer los requerimientos dinámicos que varían a lo largo de la temporada de cría. Analizamos el efecto de la especialización de roles del cernícalo primilla en los movimientos de alimentación a lo largo de la época de cría (**Capítulo Dos**). En general, encontramos diferencias en los movimientos de alimentación entre los dos sexos de acuerdo con la tendencia general de la especialización de roles en el grupo de las rapaces. Los machos vuelan distancias diarias acumuladas más largas y completan un mayor número de vuelos de alimentación por día, que además son más cortos, que las hembras al ser los principales responsables de las tareas de aprovisionamiento de alimento. Por otro lado, las hembras tienden a quedarse en la colonia durante períodos más largos de tiempo diarios que los machos, lo cual coincide con que este sexo es el principal responsable de la protección del nido, la incubación de los huevos y el cuidado de pollos en rapaces. Además, el cernícalo primilla muestra una segregación espacial entre sexos, con las hembras volando hacia áreas de caza más alejadas de la colonia que los machos. Esto puede ser el resultado de una estrategia adaptativa de alimentación basada en la especialización de roles de la especie con el objetivo de evitar agotamiento de presas en los alrededores de la colonia y reducir la competencia intersexual entre miembros de la pareja para tener éxito en la reproducción.

La mayoría de especies de aves se desplazan volando y lo pueden hacer a través del vuelo aleteado, que requiere actividad muscular para convertir energía química en trabajo, o a través del vuelo planeado, que extrae energía cinética de masas de aire en movimiento para reemplazar la actividad muscular. Estudiamos las estrategias de vuelo del cernícalo primilla durante los vuelos de alimentación y el efecto de la radiación solar (como proxy del desarrollo de corrientes térmicas ascendentes) en diferentes parámetros de los vuelos a lo largo la temporada de cría (**Capítulo Tres**). Sorprendentemente, encontramos que el cernícalo primilla, que ha sido considerado tradicionalmente como una rapaz de vuelo aleteado, recurre frecuentemente al vuelo planeado durante los vuelos de alimentación, especialmente cuando la radiación solar es intensa. Los individuos vuelan con velocidades más lentas, a mayores altitudes y alcanzan distancias más alejadas de la colonia en vuelos de alimentación en los que se identificaron eventos de cicleos en térmicas en comparación con aquellos vuelos sin dichos eventos. Esto conlleva la aparición de un patrón circadiano en el comportamiento de alimentación del cernícalo primilla: los individuos vuelan con vuelo aleteado hacia áreas de caza localizadas cerca de la colonia cuando las térmicas son débiles o inexistentes, mientras que vuelan hacia áreas de caza ubicadas lejos de la colonia mediante el vuelo planeado dependiente de térmicas tan pronto como éstas se forman. Modelos teóricos de vuelo indican que, dada la preferencia del cernícalo primilla por alimentarse de grandes saltamontes y considerando la distancia media recorrida durante los vuelos de alimentación, desplazarse mediante vuelo aleteado resultaría en un balance energético negativo para el grupo familiar.

Además de los dispositivos de seguimiento, se ha desarrollado una batería de sensores biológicos con el fin de ofrecer una visión más completa del movimiento individual, siendo quizás los acelerómetros los sensores más utilizados en la actualidad. Los acelerómetros tri-axiales registran la aceleración del cuerpo a lo largo de los tres ejes del espacio a alta resolución temporal (normalmente 10 Hz o más). Por un lado, la acelerometría tri-axial permite inferir el comportamiento del individuo sin necesidad de realizar observaciones directas y, por otro lado, ha demostrado ser una metodología eficaz para medir el gasto energético animal. En el **Capítulo Cuatro**, construimos un modelo de clasificación de comportamientos basados en los datos registrados por los acelerómetros tri-axiales y los dispositivos GPS colocados en los cernícalos primilla. Después, investigamos los efectos de los factores internos (fenología de cría, especialización de roles) y externos (disponibilidad de presas, variables meteorológicas) en el presupuesto energético y de tiempo del cernícalo primilla durante el día en general y durante los vuelos de alimentación en particular. El modelo de clasificación desarrolló correctamente su cometido a la hora de clasificar de forma automática el comportamiento de los cernícalos primilla. El vuelo aleteado y cernido requiere más energía que el vuelo planeado, y a su vez estos comportamientos consumen más energía que los comportamientos estacionarios (incubación/cría de pollos y posado). El presupuesto energético y de tiempo diario del cernícalo primilla está determinado en gran medida por los costes específicos de los comportamientos y la especialización de roles entre los sexos. Los cernícalos primilla reemplazan de forma gradual el vuelo aleteado por el planeado durante los vuelos de alimentación a medida que la radiación solar se incrementa, esto es, a medida que las corrientes térmicas se hacen más potentes. Los cernícalos primilla también sustituyen de forma progresiva la caza desde posadero por la caza mediante vuelo cernido en las áreas de caza a medida que la velocidad del viento aumenta, esto es, a medida que experimentan fuerzas de elevación más potentes para mantenerlos en el aire. Sin embargo, los cernícalos parecen decidir la estrategia de caza en relación al nivel de actividad de la presa preferida, lo cual está influido por la temperatura del aire. Así, los individuos incrementan el uso relativo de la caza cernida a medida que la temperatura del aire, y el nivel de actividad de las presas, aumentan.

De forma general, nuestros resultados apoyan las predicciones derivadas de la teoría del aprovisionamiento óptimo y sugieren que el cernícalo primilla prioriza el ahorro energético sobre el de tiempo cuando se desplaza en busca de alimento a lo largo de la temporada de cría. Esta tesis doctoral llena un vacío de conocimiento sobre el comportamiento de alimentación del cernícalo primilla gracias a la aplicación de los sensores biológicos más novedosos y, en consecuencia, ha ayudado a comprender mejor la ecología de esta especie durante el período reproductor.

GENERAL INTRODUCTION

Movement can be defined as "the process by which individual organisms are displaced in space over time" (Turchin 1998), and hence it may be affected by mechanisms operating at different spatial and temporal scales (Johnson et al. 2002, Fryxell et al. 2008, Avgar et al. 2013). Movement reflects an indispensable response of individuals to a spatially heterogeneous and temporally dynamic environment in order to maximize fitness (Kokko & López-Sepulcre 2006). Therefore, movement strongly determines individual reproduction and survival that in turn condition processes at higher levels of organization, from population dynamics to ecosystem functioning, and even species evolutionary history (Revilla et al. 2004, Damschen et al. 2008, Jeltsch et al. 2013). For that reason, studying animal movement has become paramount to develop appropriate species conservation management especially in the current scenario of global change (Allen & Singh 2016).

The rise of Movement Ecology

Long time has passed since the first bird ringing programs were carried out in the United Kingdom during the first half of the 20th century (Landsborough Thomson 1937). Individual birds were marked, and still are in the present day, with metal rings including a unique numeric code to be unequivocally identified. Analogously, other kinds of marks were later adopted to individualize members of a wide range of animal taxa populations, from sea snails to elephants, during the last century. Paints and dyes, plastic eartags, pit tags, mutilations or even natural body peculiarities are some examples of marks used to distinguish individuals for scientific purposes nowadays (Powell & Proulx 2003, and references therein). Mark-recapture procedures are based on those marks and allow researchers to know individual displacement between the marking site and the recovery sites but they have as primarily objective the study of population dynamics (Hestbeck et al. 1991, Turchin & Thoeny 1993, Sillett et al. 2000). This technique provides scientists with a snapshot of independent locations where the marked individuals are captured and later recaptured but it informs nothing about the timing or the route followed during the displacements, which are reduced to the unreal Euclidean distance between locations. Another drawback of the mark-recapture method is the necessity of an enormous human effort to mark a high number of individuals and also to survey across different locations in order to increase the recapture probability, in this way limiting the study of animal movement (Lindberg 2012). In spite of the mentioned constraints, these studies defined the origin of the movement ecology that still had a long way to go until what we know at present comes into existence.

The next important step for movement study was the use of very-high-frequency radio technology (VHF) to track free-ranging terrestrial animals since the 1970s (Amlaner & MacDonald 1980). VHF transmitters emit radio wave signals that may be detected by receiver antennas within a short or medium distance range. Since each VHF transmitter can be programmed to produce radio waves at different frequencies, this methodology allows to track simultaneously several individuals within a study area without confounding the received signals (e.g. Aebischer et al. 1993). The application of radio-tracking supposed a milestone for the movement ecology because of a change of perspective: from the Eulerian approach focused on population relocations to the Lagrangian approach based on individual movements (Turchin 1998). However, a triangulation of the radio signal is needed to reveal the spatial location of the marked individuals, which are susceptible to bias and errors associated to such treatment (Tucker 1979). Furthermore, this tracking system still requires a huge human effort since a battery of field assistants holding receiver antennas, or alternatively non-mobile receiver towers, is needed to follow the radio wave signals as marked individuals move across the landscape during long study periods in order to get a proper dataset (Harris et al. 1990).

Later in the 1980s, satellite transmitters started to be deployed on wild animals and led a shift in the spatial scale of individual tracking from local movements to a global range. These transmitters communicate with satellites orbiting Earth by ultra-high-frequency (UHF) radio waves so as to register the spatial position across the globe through the Doppler Effect in transmission frequency. Argos system was pioneer in the application of satellite technology to animal movement studies and provides locations with acceptable spatial resolution (> ± 100 m) (e.g. Rutz & Hays 2009). Nevertheless, a disadvantage of this tracking system is the fact that researchers must periodically pay taxes in order to access the data collected (Robinson et al. 2010). Furthermore, the relatively heavy transmitters prevent tracking the majority of animal species, which would explain why they were initially used to mostly study movement of large marine species (Kays et al. 2015). A lighter alternative to Argos transmitters was found in geolocators, which are currently the only devices suitable to track smaller songbirds (up to 0.3 g) (Bridge et al. 2013). Geolocators carry a light sensor able to measure solar irradiance levels that, together with information about daylight period duration and sunrise and sunset timing, estimate the spatial positions of tracked individuals on Earth. However, the spatial resolution of geolocators is lower (hundreds of kilometers) than that obtained from Argos transmitters, especially around the equinoxes when the duration of day and night are similar in all latitudes (Rakhimberdiev et al. 2016). Another downside of this tracking system is that the recapture of tracked individuals is needed since spatial information is stored in a logger, so a high number of animals should be deployed with geolocators in order to increase the recovery rates.

It was not until the 1990-2000s when the study of animal movement experienced a real revolution with the application of the Global Positioning System (GPS) to ecological research. GPS consists of 24 satellites orbiting Earth created by the United States of America with military purposes in origin, although it is now freely accessible to anyone with GPS receivers. These devices communicate with the satellites and provide users with high temporal (up to one fix per second) and spatial (> 3-5 m) resolution locations by a process of trilateration, which is analogous to the traditional triangulation but including references of known spatial coordinates (Bridge et al. 2011). Therefore, GPS devices have allowed researchers to study animal movement with high accuracy from a local range to a global scale, in this way multiplying the possibilities of animal tracking. As a consequence of such flexibility in animal tracking scale, different methods have been developed in order to recover the data from the GPS devices. Devices may include a datalogger, so tracked individuals have to be recaptured or, alternatively, data can be downloaded by a short-range wireless communication with a ground station when tracking at local scales. On the other hand, when individuals are tracked across the globe, GPS devices are typically associated to the Argos system, although researchers should periodically pay for retrieving the data, or they can send the data to a ground station by taking advantage of the world mobile communication network (GSM or GPRS). Thus, both the high spatiotemporal resolution and the flexibility in methods to recover the spatial data have helped GPS to rapidly establish as an effective alternative to track free-ranging animals (Tomkiewicz et al. 2010). Furthermore, the gradually decreasing economic cost together with the ongoing sophistication (battery life, logger memory) and miniaturization experienced by GPS devices in the last years have expanded the application of GPS to study animal movement of a range of increasingly smaller species (Kays et al. 2015).

In addition to tracking devices, new animal-borne devices have emerged in order to fully understand individual movements in the last years: tri-axial accelerometers, micro-video cameras, physiological sensors such as heart-rate, stomach temperature or blood chemistry, magnetometers, or depth and salinity sensors, among others (Robinson et al. 2010, Wilmers et al. 2015, Wilson et al. 2015). As a consequence, the application of the latest technological advances has expanded the frontiers of ecological knowledge and has also opened new perspectives in the study of animal movement. The unprecedented spatiotemporal resolution and the wider range of studied species have guided the tracking data to enter the so-called era of big data accompanied by its most fundamental problems, the challenge of managing and analyzing such large databases (Rutz & Hays 2009, Bridge et al. 2011). The development of powerful and efficient tools to analyze tracking data has subsequently become a matter of overwhelming importance. Major tasks for these analytical tools might well be the interpretation of movement from the spatial locations provided by tracking devices and the inference of the mechanisms underlying the observed movement patterns (Patterson et al. 2008, Demšar et al. 2015). In this context, the number of studies on animal movement has risen and, with it, the need to create a framework to encompass all of them (Holyoak et al. 2008). That has been the breeding ground for the enhancement of Movement Ecology as a new paradigm (Nathan et al. 2008).

The Movement Ecology discipline advocates that individual movement results from the interaction between four endogenous and exogenous factors. First, the individual internal state that includes the motivation to move. Males and females of a single animal species can have different nutritional requirements, so the motivation varies between sexes and that may influence individual movements (Lewis et al. 2002, Breed et al. 2009). Individuals search for food either to feed themselves or to feed their offspring in species with parental care and that might also affect their movements (Welcker et al. 2009, Saraux et al. 2011). Furthermore, individuals adapt the straightness of their movement through the landscape in accordance to predation risk (Fischhoff et al. 2007, Martin et al. 2013). Second, the individual motion abilities comprise the individual biomechanical properties that allow movement. Species morphometric traits, especially body mass, determine the flight or swimming performance that strongly affects individual movements (Sato et al. 2003, Alerstam et al. 2007, Horvitz et al. 2014). Third, the navigation capacities that encompass the mechanisms guiding individuals to decide where and when to move. Individual age, which can be taken as a proxy for experience, has been described as a key element that shape movements. For example, adult birds are less drifted by crosswinds or spent less energy in flight than juveniles in migratory movements, allowing an earlier arrival with better body condition at the breeding grounds with the consequent benefits for the reproduction (Thorup et al. 2003, Sergio et al. 2014, Rotics et al. 2016). Finally, the external biotic and abiotic factors that influence individual movements. Wind speed and direction are some of the most important external factors affecting movement (Brattström et al. 2008, Kemp et al. 2010, Weimerskirch et al. 2012), but temperature and rainfall are also important (van Beest et al. 2013, Bohrer et al. 2014). Among the biotic external factors, it is worth highlighting the role of intraspecific competition in influencing the movement of colonial species (Grémillet et al. 2004, Breed et al. 2013) or the effect of anthropogenic activities on individual movements (Camacho et al. 2014, Marchand et al. 2015, Sommerfeld et al. 2016).

Therefore, the rise of the Movement Ecology appears as a new opportunity to improve species conservation efforts. Now we have better tools, so it is high time to use them to elaborate suitable conservation plans in order to preserve the worldwide threaten biodiversity.

The study model

The lesser kestrel (*Falco naumanni*, Fleischer 1818) is one of the smallest raptor of the Palearctic (wingspan 58-72 cm, body mass 120-140 g) (Cramp & Simmons 1980). This falcon species show a noticeable chromatic sexual dimorphism: lesser kestrel males show blue-gray plumage in head and tail, whereas lesser kestrel females show a uniform rusty plumage with black strikes (Figure 1). Moreover, the lesser kestrel is also a reversed sexual size dimorphic species with females being heavier than males (~15%), which is a common trait among the raptor group (Andersson & Norberg 1981). The lesser kestrel is a migratory species that winters in Africa, from the Sahel region to South Africa (Ferguson-Lees & Christie 2001, Rodríguez et al. 2009). The breeding grounds extend from the Mediterranean Basin of Western Europe to Central Asia. Nevertheless, it has been observed resident populations in the Iberian Peninsula and Northern Morocco (Negro et al. 1991).

The prenuptial migration takes place in early spring, whereas the postnuptial migration is performed in autumn, a couple of months after the end of the breeding season. That is explained because the lesser kestrel shows a premigratory dispersal towards northern latitudes and higher altitudes where prey phenology is delayed, presumably in order to improve its body condition before migrating (Olea et al. 2004, Sarà et al. 2014) (Figure 2).

Figure 1. Lesser kestrel breeding pair at the EBD colony, female on the left and male on the right.

The lesser kestrel is a hole-nesting species that shows colonial habits. The breeding colonies are usually located in buildings, such as churches, farm houses or castles, or in natural cliffs. These colonies are highly associated to steppe-like habitats, pastures and non-irrigated crops (Bustamante 1997). The diet of the lesser kestrels is mainly composed of insects but small vertebrates are eventually present (Rodríguez et al. 2010). This falcon shows diurnal habits, although nocturnal activity has been described during the migratory movements and also in urban breeding colonies under artificial light conditions (Negro et al. 2000, Limiñana et al. 2012).

The lesser kestrel world population suffered a dramatic decline during the second half of the 20th century, especially the Western Europe population that lessened its effectives in c. 95%. Indeed, this species was declared extinct in some European countries, like Austria, Czech Republic or Slovenia (IUCN 2013). About half of the lesser kestrel world population breeds in the Iberian Peninsula, where the Spanish population was estimated at 100,000 breeding pairs in the 1960s (Bijleveld 1974) but it decreased towards 4,000-5,000 breeding pairs in the late 1980s (González & Merino 1990). The shortage of nest-sites, interspecific competition for nest-sites and bioaccumulation of heavy metals in eggs were rejected as causes of the population decrease in Spain (Negro et al. 1993, Forero et al. 1996). However, Hiraldo et al. (1996) pointed out that nestling mortality due to starvation might be an important reason of lesser kestrel population decline in southern Spain. The reason seems to be the reduction in kestrel prey availability because of the intensive use of pesticides and the loss of suitable foraging habitats, such as field margins, grasslands or fallows, derived from the application of European agricultural policies (Donázar et al. 1993, Tella et al. 1998, Liven-schulman et al. 2004, Franco & Sutherland 2004, Rodríguez et al. 2006). Indeed, the lesser kestrel is not an isolated case and numerous farmland bird species have experienced similar negative population trends as a consequence of agricultural intensification (Donald et al. 2001). In spite of that, the lesser kestrel population seems to have established in the last years and consequently this species has moved from the "Vulnerable" to the "Least Concern" category according to UICN criteria (IUCN 2013). At the time this PhD is being defended, the Spanish Ornithological Society (SEO Birdlife) is carrying out a national census of the lesser kestrel population that will support (or not) the current status of the species.

The lesser kestrel is a good model to focus this PhD thesis on foraging movement ecology because of several reasons. First, the colonial habits of the lesser kestrel allow to study high number of individuals that experience the same environmental conditions, in this way increasing the replicates for every analysis. Second, the lesser kestrel is a well-studied species (more than 500 publications obtained when searching for "lesser kestrel" or "Falco naumanni" at the Web of Science platform,www.webofknowledge.com) that supposes an excellent background over which build a research project. Finally, the lesser kestrel acts as a central-place forager through the breeding season so it is possible to separate between the individual allocation to travel between the central place and the foraging area and that investment in searching for prey within the foraging areas. That provides with enormous possibilities when testing hypothesis under the framework of the optimal foraging theory.

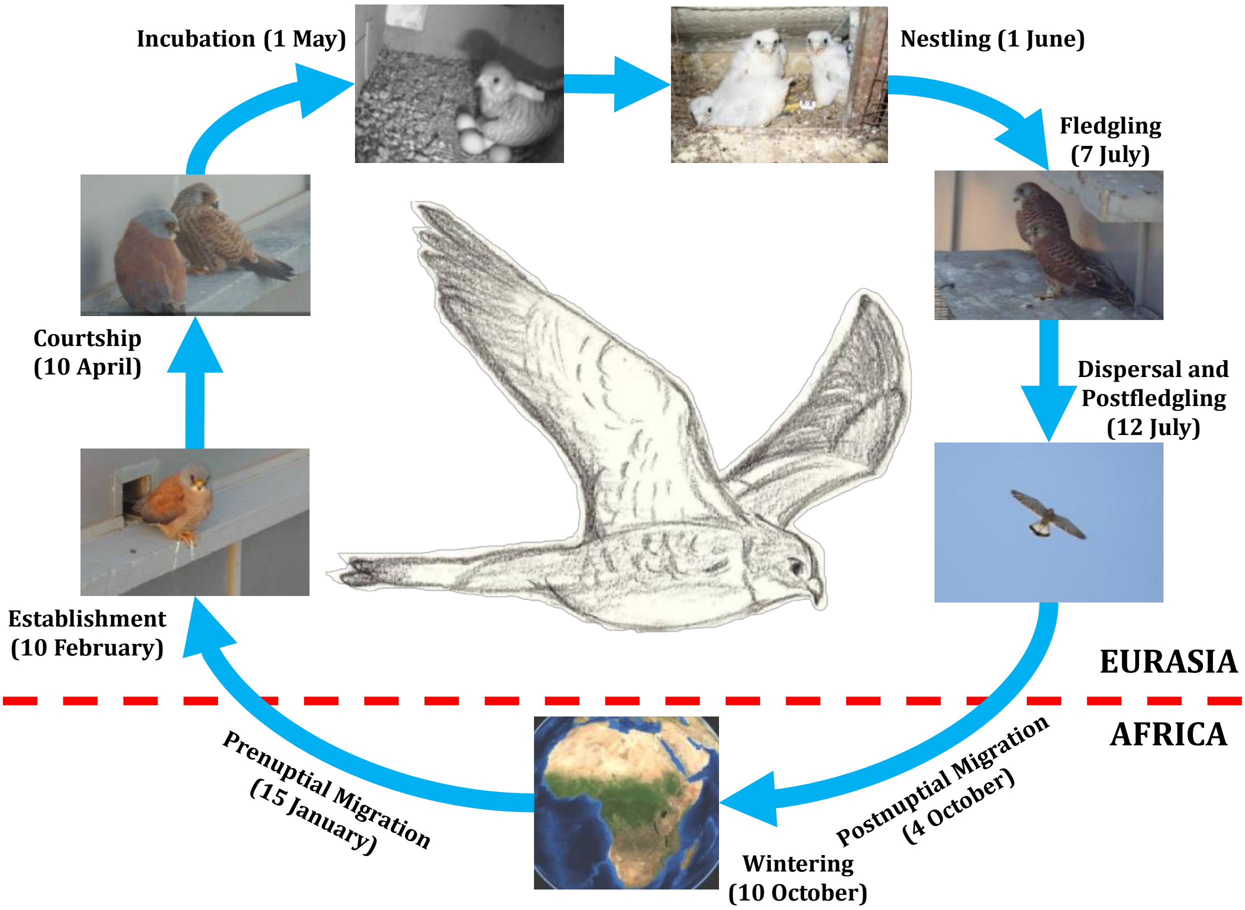

Figure 2. Lesser kestrel annual cycle. Starting date of phenological periods (shown in brackets) was obtained from literature (Negro et al. 1991, 1992, Bustamante & Negro 1994, Rodríguez et al. 2009, Limiñana et al. 2012).

The study area

The two lesser kestrel breeding colonies studied during the thesis are located within the Guadalquivir river basin (southern Spain) that has Mediterranean climate with mild and rainy winters and hot and dry summers. The study area is predominantly flat (elevation range 20-240 m above the sea level) but features some hills and escarpments and is dominated by arable crops (Fernandez et al. 1992). Primary crops are wheat and sunflowers, although cotton and legume crops, fruit tree plantations, olive groves and vineyards are also present in the area. The Silo colony is situated at a building with a grain elevator located within an agricultural landscape at La Palma del Condado (Huelva province). This colony has been monitored since 1994 and it has been occupied by 10-37 lesser kestrel breeding pairs. Meanwhile, the EBD colony is situated on the roof of the headquarters of the Doñana Biological Station (EBD-CSIC) in the city of Seville and mostly surrounded by urban ecosystem. This colony is the result of an experimental reintroduction in 2008-2010 by hacking (Rodríguez et al. 2013) and it has been occupied by 2-6 lesser kestrel breeding pairs. The two breeding colonies are 50 km apart (Figure 3). In both colonies, breeding pairs nest inside “smart nest-boxes” installed at the windowsills. These nest-boxes are equipped with several electronic devices that monitor the lesser kestrel pairs that use them to nest (see Larios et al. 2013). A RFID (Radio Frequency Identification) tag reader is located at the entrance of the nest-box. It identifies the individuals passing through the entrance by reading the code included in the PVC ring of kestrels. An electronic scale weights kestrels when they enter the nest-box. Temperature and humidity sensors register the atmospheric conditions inside the nest-boxes. A motion-sensing camera records videos and pictures in the nest-box, even during the night. HORUS nest-boxes act as untiring spies always watching what is happening inside during the breeding season of the lesser kestrel (Figure 4). All data collected by the smart nest-boxes are centralized and stored on computers to which is possible to get real-time access through the Internet from everywhere at anytime.

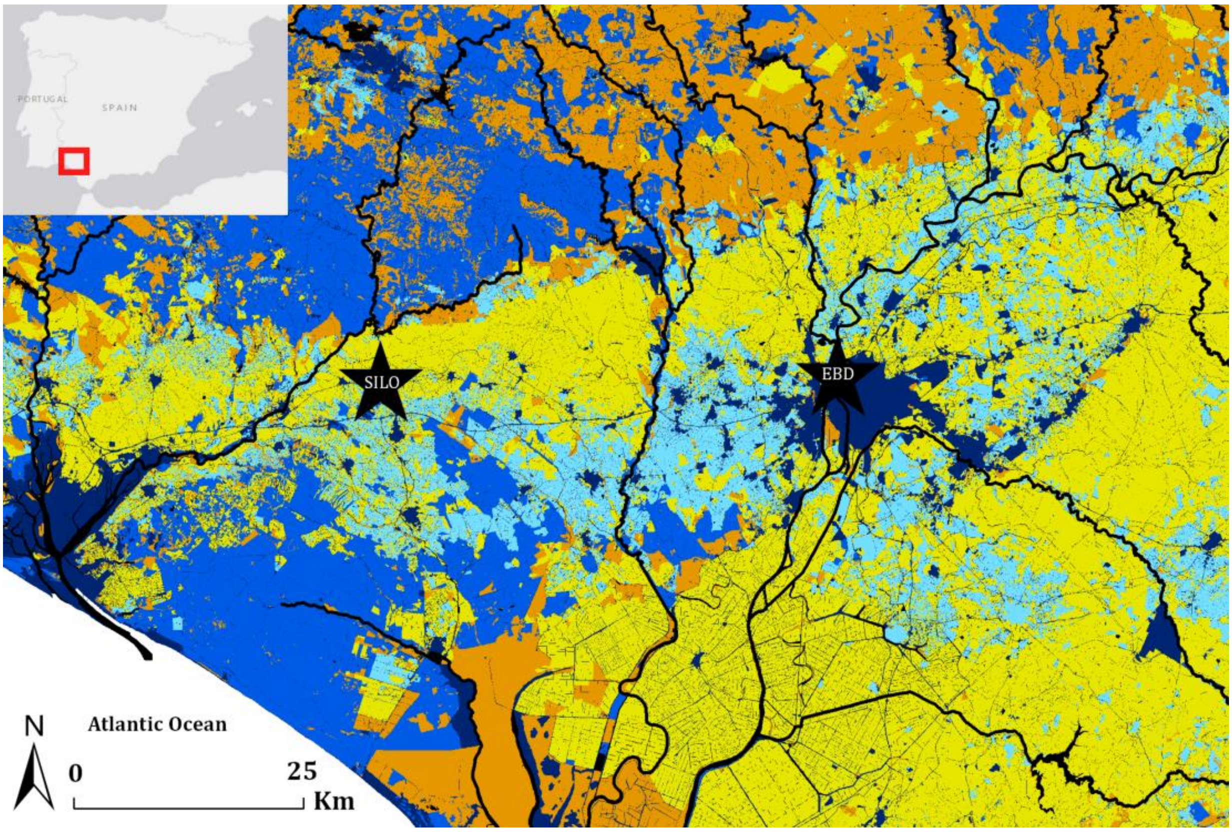

Figure 3. Map of the western Guadalquivir River Valley in southern Spain. Land-uses are shown in colors: herbaceous crops (yellow), pastures (orange), fruit tree, olive groves and vineyards (light blue), woodlands (dark blue), urban and human structures (purple) and water (black). The black stars indicate the two lesser kestrel breeding colonies included in the study. A small map of the Iberian Peninsula locates the study area at a greater scale (upper left corner).

Biologging procedure

We monitored lesser kestrel breeding pairs from the two colonies during four consecutive breeding seasons (years 2011-2014). We deployed a micro GPS-dataloggers (GiPSy models 2, 4, and 5; up to 1.8 g, 27 × 15 × 6 mm with whip antenna; Technosmart, Rome, Italy) and a tri-axial accelerometer-datalogger (model Axy-3; 0.7 g, 9.5 x 15 x 4 mm; Technosmart) with small batteries (90–100 mA) on lesser kestrels. GPS devices were fixed to the birds' backs using a micro back-pack harness supplied by Marshall Radio Telemetry (North Salt Lake, Utah, U.S.A.) or a similar hand-made harness formed by a carbon fiber plate and a 4mm wide Teflon ribbon (Bally Ribbon Mills, Pennsylvania, U.S.A.). The devices were covered with a thermoretractable case (Figure 5). The total mass of the equipment (harness + GPS + accelerometer) was about 6 g and never exceeded the 5% of the lesser kestrel's mean body mass, which is within the generally recommended limits for flying animals (Barron et al. 2010). At the beginning of the breeding season, we initiated the equipment fitting protocol. First, birds were captured and fitted a harness. One week later birds were recaptured and a dummy GPS-accelerometer-datalogger with the same weight of the real device was fixed on the harness. Another week later the bird was recaptured and the dummy was replaced by the real devices. This protocol was designed to get the birds used to the harness and the weight of the device before recording movement data. We removed the harnesses from the kestrels at the end of the breeding season.

Figure 4. An example of smart nest-box installed in a window of the Silo colony. An external view (left panel) and internal view (right panel).

Figure 5. GPS-datalogger with thermoretractable case. Detailed view of the device in comparison to a coin (left panel) and of its deployment on an individual lesser kestrel back (right panel).

General and particular objectives

The main objective of this PhD thesis is to study the foraging movements of the lesser kestrel throughout the breeding season under the Movement Ecology paradigm through using of high-frequency biologging devices (GPS and accelerometers). The specific objectives were:

1) In **Chapter One**, we evaluated the influence of wind conditions on lesser kestrel decisions about what direction to head when leaving the breeding colony to forage throughout the breeding season.
2) In **Chapter Two**, we analyzed the effect of the sexual role specialization of the lesser kestrel on its foraging movement patterns throughout the breeding season.
3) In **Chapter Three**, we studied the flight behavior of the lesser kestrel during foraging trips and the effect of solar radiation (as a proxy of thermal formation) on several foraging trip parameters during the breeding season.
4) In **Chapter Four**, we built a behavioral classification model based on tri-axial accelerometry and GPS data of the lesser kestrel. Then, we investigated the effect of internal (breeding phenology, role specialization) and external factors (prey availability, weather conditions) on the behavioral time and energy budget of the lesser kestrel through the day.

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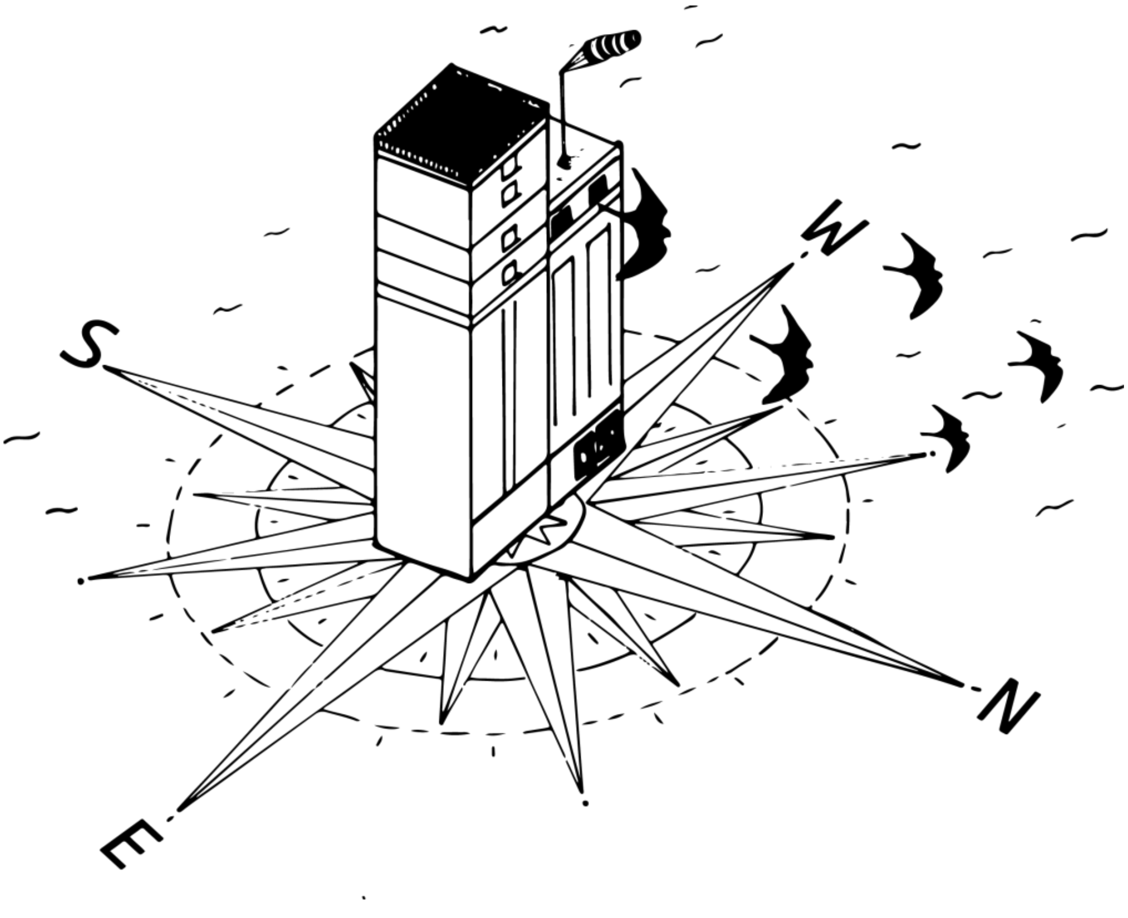
CHAPTER ONE

Gone with the wind:
Seasonal trends in foraging movement directions for a central-place forager



J. Hernández-Pliego, C. Rodríguez & J. Bustamante (2014)
Current Zoology 60 (5): 604-615

Abstract

Lesser kestrels (*Falco naumanni*) are migratory central-place foragers that breed in dynamic arable landscapes. After arriving from migration, kestrels have no knowledge of the distribution of crops, and consequently prey, around their colony. The energy demand of pairs increases as breeding season progresses, but at the same time prey abundance, and their knowledge on prey distribution, also increases. Wind can have a strong influence on flight cost and kestrels should try to reduce energy expenditure when possible. When prey abundance is low, kestrels have little knowledge of prey distribution, and pairs have no chicks, they could reduce foraging flight cost by leaving the colony with tailwinds. When prey is abundant, knowledge on prey distribution has increased, and chick demand is high, kestrels should fly to the most favorable foraging patches. We analyzed foraging trips directions in a lesser kestrel colony along the breeding season and in relation to wind speed and direction. We recorded 664 foraging trips from 19 individuals using GPS-dataloggers. We found that outward flights direction changed from uniform to a concentrated distribution along the season, as prey abundance and individual experience increased. We also found a temporal trend in the angular difference between outward flights and wind directions, with low values early in the season and then increasing as expected, but again low values at the end, contrary to expectation. Results suggest changes in kestrels foraging strategy along the season in relation to wind. Kestrels depart more with tailwinds in exploratory flights early in the season, while there is a spurious coincidence in direction to preferred foraging patches and dominant wind direction at the end.

Resumen

El cernícalo primilla (*Falco naumanni*) es una especie migratoria que cría en colonias frecuentemente asociadas a ambientes agrícolas, los cuales son muy dinámicos en el tiempo. Esta especie adopta la estrategia del lugar central de búsqueda durante la temporada de cría, es decir, los individuos reproductores están limitados a alimentarse en las cercanías de un lugar central, o colonia en este caso. Tras la migración primaveral, los cernícalos no conocen la distribución espacial de los cultivos, y por tanto de las presas, en los alrededores de la colonia. La demanda energética de las parejas reproductoras se incrementa a medida que la temporada de cría avanza al mismo tiempo que aumenta la abundancia de presas y el conocimiento de los individuos sobre la distribución de las mismas. El viento puede influir en gran medida en el coste de vuelo de los cernícalos por lo que los individuos deberían tratar de reducir el gasto energético siempre que fuera posible. Cuando la abundancia de presas es baja, los cernícalos tienen poco conocimiento de la distribución de las mismas y las parejas reproductoras aún no tienen pollos, los individuos podrían reducir el coste energético de los viajes de caza partiendo de la colonia con viento de cola. Cuando las presas son abundantes, los cernícalos conocen cómo éstas se distribuyen en el espacio y la demanda energética es alta debido a la crianza de los pollos, los individuos deberían volar hacia las áreas de caza más favorables. En este estudio, analizamos las direcciones de los viajes de caza en una colonia de cernícalo primilla a lo largo de la temporada de cría y en relación a la velocidad y dirección del viento. Se obtuvieron 664 viajes de caza de 19 individuos diferentes mediante el seguimiento con GPS-dataloggers. Encontramos que las direcciones de salida de la colonia en los viajes de caza cambiaron desde una distribución uniforme a una distribución concentrada a medida que la abundancia de presas y la experiencia de los individuos aumentaron a lo largo del período reproductor. También encontramos una tendencia temporal en la diferencia angular entre la dirección de salida de la colonia de los viajes de

caza y la dirección del viento, con valores pequeños al principio de la temporada de cría que se incrementaron a medida que esta avanzó, pero de nuevo obtuvimos valores pequeños al final de la temporada, al contrario de lo esperado. Los resultados sugieren la existencia de un cambio en las estrategias de caza de los cernícalos en relación a las condiciones de viento a lo largo de la temporada de cría. Los individuos partieron de la colonia con vientos de cola en viajes de caza más exploratorios al principio de la temporada de cría, mientras que ocurrió una coincidencia espuria entre la dirección dominante del viento y la dirección en la que se encontraban las áreas de caza preferidas de los cernícalos al final del período reproductor.

Introduction

Movement reflects an individual response to optimize its fitness within a heterogeneous environment. But movement transcends individual fitness and influences the dynamics of higher levels of organization, like populations or communities (Turchin 1998). It arises from the interplay of four components: the individual internal state, its motion capacity, orientation ability, and external factors (Nathan et al. 2008). Individuals constantly experience changes, endogenous and exogenous, along their life influencing their movements (Martin et al. 2013).

Wind is one of the most important external factors affecting the movement of animals that fly (Alerstam 1979, Liechti 2006). It can be the only way of displacement for some animals, as is the case in spiders dispersal by ballooning (Bell et al. 2005). For other animals, flying with or against wind may cause great differences in flight cost, for that reason different strategies have evolved in animals to increase the efficiency of movement when affected by wind (Chapman et al. 2011). Numerous studies have assessed the effect of wind on bird migratory movements. Birds actively choose to compensate or to be drifted by wind depending on endogenous and exogenous factors (Thorup et al. 2003, Klaassen et al. 2011) and that determines flight speed or altitude during migration (Kemp et al. 2010, Mateos-Rodriguez & Liechti 2012). However, there has been very little research on the effect of wind in dispersal or foraging movements of birds and most studies have been conducted in seabirds (Weimerskirch et al. 2000, Wakefield et al. 2009). For example, wandering albatrosses (*Diomedea exulans*) increase the flight speed and reduce the duration of their foraging movements by flying with wind support, and consequently they obtain lower hatching failure by increasing the incubating time (Weimerskirch et al. 2012).

The lesser kestrel is a small migratory falcon associated to agricultural landscapes. It breeds in colonies and behaves as central-place forager during the breeding season. The central-place foraging strategy predicts that the species would maximize the energy intake in their central place (Schoener 1971, Orians & Pearson 1979), so individuals should decide which prey to catch and the time or energy spent on it, balancing the trade-offs between costs and benefits to optimize the foraging behavior (MacArthur & Pianka 1966). Each individual decision emerges from a dynamic interaction between endogenous and exogenous factors that change with time. Lesser kestrel breeders experience an increasing energy demand for reproduction along the breeding season, in the same way as other species (Masman et al. 1988). Early in the season, when they arrive to a colony, they would not strictly behave as central-place foragers because they have no chicks to be fed and there are no important reasons to return to the colony frequently. As the breeding season progresses, energy demand increases and breeders should maximize the feeding rate of their chicks at the colony. Then they would behave as “true” central-place foragers. Such change could have a strong influence in individual foraging movements through the breeding season. Agricultural arable landscapes can be highly dynamic ecosystems and the spatial distribution of arable crops can change from year to year. In our study area the arable crops planted on a field alternates between sunflower and wheat in consecutive years with the occasional legume or fallow (see www.juntadeandalucia.es/agriculturaypesca). Lesser kestrels must update their knowledge on the spatial distribution of arable crops around the colony after they arrive from migration. Prey distribution and availability is determined by different factors ranging from crop type or degree of vegetation cover to agricultural activities (Rodríguez et al. 2013). High-quality foraging patches would be determined by prey size and abundance and both factors increase as the breeding season progresses (Rodríguez 2004, Rodríguez et al. 2010). At the same time as optimal prey become more available, kestrel knowledge of prey distribution refines, potentially influencing kestrels foraging movements.

In this paper, we study the influence of wind on foraging behavior of the lesser kestrel along the breeding season. The single paper we know (Limiñana et al. 2013), shows that lesser kestrels are strongly affected by crosswinds during their migratory movements. During the nestling period each member of a lesser kestrel pair feeds the chicks on average once per hour (Rodríguez et al. 2006) performing foraging trips 11 km long. As mean day length at this time is 15 hours, breeding kestrels may end up performing 165 km per day (Chapter Two). For this reason, the potential wind effect on foraging cost should not be underestimated. Wind is an exogenous factor that can influence bird movement decisions along the breeding season but there are also other endogenous factors likely influencing movement that also change along that period like energy demand and knowledge on prey distribution and availability. We expected that early in the breeding season, when prey abundance is low, kestrels have little knowledge about arable crop distribution and potential prey availability, and they have no temporal constraint for returning frequently to the colony, individuals would have no special preference for any area to forage and they could leave the colony flying more with tailwinds to reduce movement cost and in random directions to explore the wider area possible. If foraging flights are long and kestrels delay their return they could wait until wind direction and speed is more favorable. On the other hand, at the end of the breeding season when prey abundance is high, kestrels have chicks to be fed and they have accumulated knowledge on crop distribution and prey availability, we expected that kestrels would concentrate departure directions to the most favorable foraging patches. As they cannot wait for a favorable wind direction, foraging flights would leave independent of wind direction. Consequently, we hypothesized that: in a scenario of random wind directions (1) the departure direction of foraging flights would change from a random to a more concentrated distribution as the breeding season progresses. (2) The angular difference between foraging flight departure and wind directions would be small at the beginning of the breeding season but would increase towards the end. (3) Returning flights would show no temporal pattern in the angle between flight and wind direction because kestrels cannot choose the direction to return to the colony. And finally, (4) if wind is a limiting factor to kestrel foraging activity, individuals should reduce foraging activity, stay at the colony or perch somewhere when they are out of the colony, when strong winds are blowing.

Material and Methods

Study species and area

The lesser kestrel is one of the smallest raptor in the Palearctic (wingspan 58-72 cm, body mass 120-140 g). This insectivorous hole-nesting falcon breeds in colonies associated with urban areas and non-irrigated arable crops across the Mediterranean basin and Central Asia, and has its wintering quarters in Africa. Lesser kestrel populations in Europe suffered a strong decline during the second half of the twentieth century (Serrano & Delgado 2004) presumably due to changes in land-use derived from agricultural intensification (Tella et al. 1998, Franco & Sutherland 2004). However, the world population has apparently levelled in the last decades and the species has recently been cataloged as ‘Least Concern’ (IUCN 2013).

The study colony is situated at a building holding a grain elevator in La Palma del Condado (Huelva, Southwestern Spain). It is located in the Guadalquivir river basin, which is predominantly flat (elevation range 20-240 m above sea level) and dominated by arable crops (Fernandez et al. 1992). Primary crops are wheat and sunflowers, although cotton and legume crops, olive groves and vineyards are also present in the area. Kestrels nest in nest-boxes installed at the windowsills or directly on the windowsills.

Field Procedure

In 2012, we monitored all breeding pairs at the colony (18 breeding pairs, 10 of them nesting in nest-boxes) throughout the whole breeding season, from February to July. We attached GPS-dataloggers (GiPSy-2 model, 1.8 g, 27x15x6 mm with whip antenna, TechnoSmart, Rome, Italy) with small-sized batteries (100 mA, 2.4 g, 30x15x4 mm) to individual kestrels using the nest-boxes. The devices were fixed to their backs using a micro-size harness from Marshall Radio Telemetry (North Salt Lake, Utah, U.S.A.) or a hand-made harness formed by a carbon fiber plate and a 4 mm width teflon ribbon (Bally Ribbon Mills, Pennsylvania, U.S.A.). The teflon ribbon crossed just over the breastbone, passed under the wings and was fixed to the plate situated on the back following the attachment procedure recommended by Marshall Radio Telemetry. The GPS devices were covered by a thermoretractable case. The total mass of the equipment including harness was about 6 g, representing 4-5 % of mean body mass, the generally accepted recommended limits for birds (Barron et al. 2010).

At the beginning of the breeding season, we initiated the equipment fitting protocol. First, birds were captured and fitted a harness. One week later birds were recaptured and a dummy GPS-datalogger with the same weight was fixed on the harness. Another week later the bird was recaptured and the dummy was replaced by the GPS-datalogger. This protocol was designed to get the birds used to the harness and the weight of the device before recording movement data. The lesser kestrel body mass limits the battery weight we could use and so the battery life, which limits data collection frequency and duration. We configured the GPS devices to collect spatial locations at four different sampling frequencies: (1) one fix per second (mean battery life ± standard deviation = 2.57 hours ± 0.60, N = 14), or five consecutive fixes (one per second) (2) every minute (17.00 hours ± 6.31, N

= 11), (3) every three minutes (45.39 hours ± 10.76, N = 14) or (4) every five minutes (49.24 hours ± 24.13, N = 21). All the GPS, but those configured at five-minutes intervals, were programmed to start operating with a 24-hours delay to avoid monitoring abnormal behavior due to the capture stress. We recaptured kestrels to download the data stored in the logger and to recharge the GPS batteries to continue tracking the same individuals. Kestrels were recaptured when they entered the nest-boxes. They were recaptured a mean 7.28 ± 2.14 times during the study period (range 4 – 11, N = 19). Data collection ranged from 10th April to 8th July 2012. It is possible to view the tracking data in the study "Lesser Kestrels EBD" at Movebank (www.movebank.org).

Wind data

Wind data were obtained from a meteorological station located at ground level (192 m a.s.l.), less than 3 km away from the colony. It belongs to the agroclimatic stations network from the Agriculture Department of the Junta de Andalucía (IFAPA) (www.juntadeandalucia.es/agriculturaypesca/ifapa/ria). Wind speed and direction were registered by a windmill anemometer with a temporal resolution of 30 minutes. We use the term "wind direction" to indicate the direction the wind blows to and in the same way we use the term "track direction" as the direction the individual moves to.

Analytical Procedure

The foraging trips were split into three parts: (1) the "outward flight", i.e. the movement from the colony to the hunting area; (2) the "foraging event", i.e. the movements within the hunting area; and (3) the "inward flight", i.e. the return movement from the hunting area to the colony. Outward and inward flights are also called commuting flights. We were able to distinguish these parts of the trips according to the spatiotemporal distribution of the GPS locations (mostly straight between the colony and the hunting area during the commuting flights vs. winding and grouped within a discrete area during the foraging event) and the instantaneous speed and altitude measurements provided by the GPS (lower altitude and more variable speed during the foraging events). We only considered as foraging trips those that went further than 300 m from the colony and in which we were able to identify the foraging event (a 300 m radius from the colony mostly includes urban area). GPS locations were graphically explored using ArcGIS 10 (ESRI, Redlands, California, U.S.A.) to identify the foraging trip parts. To carry out the analysis, we discarded incomplete foraging trips, i.e. those foraging trips that had not recorded the departure or the return to the colony. Moreover, GPS locations collected by less than four satellites were removed to reduce spatial accuracy errors.

Visualizing the foraging trips recorded at one-second frequency, we observed that individuals started the commuting flights (outward and inward flights) with non-directional flights, soaring up using thermals to gain altitude. In addition, during the final part of the commuting flights individuals also made non-directional flights before reaching their goal. We calculated the distances from the departure site and to the arrival place at which the mean direction of commuting flights stabilized, i.e. oscillated <10º from the mean heading (N = 19). We used the values that corresponded with the 75 percentile of those distances to split the commuting flights into three sections: initial (< 600 m from departure site), middle, and final (< 775 m from arrival site) sections. We discarded those commuting flights in which the initial and final sections overlapped. To calculate the track direction of a commuting flight we discarded the GPS positions of the initial and final section of the flight (Figure 1).

Every commuting flight was assigned to one of the four phenology periods we divided the breeding season of each individual using the laying and hatching date at its nest: establishment (since the beginning of the study period until courtship), courtship (21 days from laying the first egg), incubation (between laying and hatching of the first egg), and nestling (from hatching of the first egg until the end of the study period). We calculated the mean track direction of every outward flight and analyzed their angular distribution throughout the breeding period.

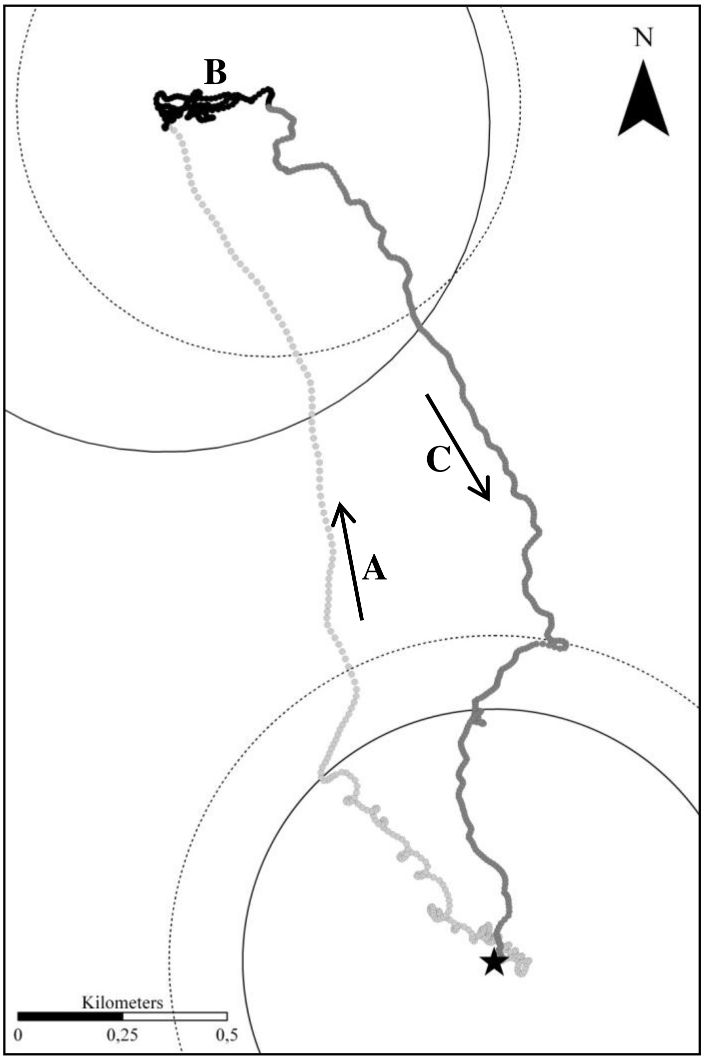


Figure 1. Example of foraging trip recorded at one-second frequency. Three parts are defined: (A) outward flight in pale grey, (B) foraging area in black and (C) inward flight in dark grey. Arrows indicate the direction of movement and the black star indicate the location of the colony. Continuous circles for the outward flights and dotted circles for the inward flights show the distance buffers from the colony and the foraging area applied to define the three sections of commuting flights (initial, middle, and final).

To explore the possible limitation to flight due to strong winds, for each half hour of tracking data, each individual was classified as “at the colony” or “out of the colony”. If more than half of the GPS locations of the individual were within a 50 m-radius from the colony the individual was considered “at the colony” and if not as “out of the colony”. Individuals “out of the colony” were classified as “perched” or “flying”, according to the altitude and speed registered by the GPS device. A bird was considered “perched” if more than half of the total GPS locations had flight speed below 1 km/h and altitudes below 150 m a.s.l.; on the contrary, the bird was considered “flying”. For each half hour we had a wind speed measurement registered by the weather station.

For every commuting flight we had a mean track direction and a mean wind direction, which was obtained rounding the track time-date to the nearest half hour. We also calculated the Track-Wind-Angle (hereafter TWA) as the angular difference between the track and the wind direction per commuting flight. The TWA ranges from 0º (purely tailwind) to 180º (purely headwind). A TWA of 90º for a single commuting flights indicates flying with crosswind, while a mean TWA of 90º could also indicate no influence of wind in mean track direction of the commuting flights as 0º and 180º TWA values of flights get averaged.

Statistical Analysis

We conducted circular statistics tests to analyze the track direction of outward flights and wind direction patterns (Jammalamadaka & SenGupta 2001). The Watson’s test assesses the homogeneity of two angular data samples and we used it to compare the outward flight direction distributions among phenological periods. The Rayleigh’s test evaluates the significance of the mean resultant length (ρ), i.e. the length of the mean of random direction vectors. It is a measure of angular dispersion that ranges between 0 (uniform distribution of directions) and 1 (maximum concentration of directions). The temporal correlation of daily mean wind direction along the study period was tested by a circular version of the Pearson’s correlation. Those tests were computed using the ‘circular’ package (Agostinelli & Lund 2011) for R-software 3.0.2 (R Core Team 2013). The temporal trend of the wind speed throughout the study period was tested with linear models and graphically explored for non-linearity using smoothing splines.

We fitted generalized linear mixed-effect models (GLMMs) to a binary response variable (0="at the colony" or 1="out of the colony") to model the probability of staying away of the colony and also to model the probability of being flying (0="perched" or 1="flying"), in relation to wind speed. We used a binomial distribution of errors and a logit link. The individual was included as a random factor to avoid pseudoreplication and the mean wind speed included as a continuous predictor. We also introduced the day-of-year as a continuous predictor to reduce the temporal autocorrelation of the response. We expected that the probability of staying out of the colony and the probability of being flying would decrease with the increasing wind speed if there was any limitation to flight due to strong winds. The significance of the wind speed was tested comparing models with and without wind speed using likelihood ratio tests.

We also fitted GLMMs using a Gaussian distribution of errors and identity link to model the variables that influenced the angle between wind and track directions: (1) the TWA of outward flights; (2) the TWA of inward flights; and (3) the TWA of outward flights performed with strong winds (when wind speed was higher than 9.98 km/h, 70 percentile of wind speeds associated with outward flights). In these models, the individual was included as a random factor. The day-of-year was included as a continuous predictor to test for the existence of a linear temporal trend of mean TWA. We expected a negative influence of wind speed and flight altitude on TWA, so these variables were included as predictors. We also introduced the gender of individual as a fixed factor and the GPS frequency at which the foraging trip was tracked as a correction factor, given that the different temporal resolution could influence the variables measured. We hypothesized that the mean TWA of outward flights would increase its value throughout the breeding season (from tailwinds to crosswinds) as the need to return frequently with prey to the colony increases and kestrels fly to the more favorable foraging patches. Meanwhile the mean TWA of inward flights is not expected to follow a particular pattern during the breeding season because kestrels cannot choose a direction when flying back to the colony. However, the true impact of wind on bird movements could be blurred by the relative weak winds observed in the area; for that reason we also analyzed mean TWA of outward flights considering only the strongest wind conditions (the upper 30% of wind speed distribution). The p-values for the fixed effects were calculated by Markov Chain Monte Carlo (MCMC) sampling (Baayen et al. 2008). Once the random effect was accounted for, non-significant variables were removed one by one using a backward stepwise procedure until all the variables remaining in the model were significant. Statistical assumptions of GLMMs (residual homocedasticity, collinearity of predictors, influential cases) were checked for all models. We also analyzed graphically the variation of TWA of outward flights, outward flights performed with strong winds, and inward flights by adjusting smoothing splines to the mean daily values per individual, as an alternative to the linear relationship fitted by the GLMMs. GLMMs and MCMC sampling were computed using the ‘lme4’ (Bates et al. 2013) and ‘languageR’ (Baayen 2011) packages, respectively, for R-software.

Results

We tracked 19 individuals (10 females and 9 males) throughout the study period. We recorded 664 foraging trips, most of them complete (N = 582). We discarded the trips of three individuals that did not breed, and remained 570 complete foraging trips. A mean 35.62 ± 31.07 foraging trips per individual (range 5 - 103 trips). The mean distance per foraging trip was 11.58 ± 9.24 km (range 1.09 – 57.50 km). Kestrels flew an average distance per day of 82.53 ± 35.22 km (range 34.25 – 238.99 km, N = 82) at a mean ground speed of 27.99 ± 11.39 km/h. After considering the buffers from the colony and from the foraging area to discard initial and final sections of the foraging trip, a total of 520 commuting flights, 240 outward and 280 inward flights, could be analyzed (Table 1).

Table 1. Distribution of complete foraging trips as function of phenological periods and sex. The values that appear within parentheses are the numbers of outward and inward flights, respectively, due to the different locations considered as first and last points of the foraging event to calculate the distance buffers.

Period\Sex	Females	Males	Total
Establishment	67 (27/32)	76 (21/26)	143 (48/58)
Courtship	15 (7/5)	112 (59/56)	127 (66/61)
Incubation	24 (12/12)	61 (24/20)	85 (36/32)
Nestling	119 (46/68)	96 (44/61)	215 (90/129)
Total	225 (92/117	345 (148/163)	570 (240/280)

Departure direction pattern of outward flights

We found significant differences in mean outward flight directions (Table 2). Individuals headed more to the East during the establishment period (mean direction: 125.85º, N = 48), to the West during courtship period (290.25º, N = 66), and to the North during incubation (349.08º, N = 36) and nestling periods (28.83º, N = 90). A Rayleigh's test indicated a variation in outward flights direction pattern going from a uniform angular distribution during the establishment period (Rayleigh's test $\rho = 0.20$, $p>0.1$) toward a more concentrated distributions in later periods (courtship: $\rho = 0.26$, $p = 0.01$; incubation: $\rho = 0.71$, $p = 0.001$; nestling: $\rho = 0.51$, $p = 0.001$), as expected (Figure 2).

Wind speed and direction

Wind speed and direction were recorded during the whole period the individuals were tracked (N = 4,317). The median wind speed was 5.93 km/h (percentile 25 = 3.85 km/h, percentile 75 = 8.69 km/h) ranged 0 to 23.68 km/h. Intraday mean variation of wind speed was 2.76 ± 0.74 km/h (N = 90). Wind had a prevalent direction, was non-uniformly distributed and blew dominantly to the East, both along the study period and in all phenological periods: overall: 105.02º, Rayleigh's test ρ = 0.55, p<0.001; establishment: 111.14º, ρ = 0.85, p<0.001, N = 816; courtship: 71.47º, ρ = 0.24, p<0.001, N = 1008; incubation: 113.27º, ρ = 0.61, p<0.001, N = 1488; and nestling: 96.11º, ρ = 0.58, p<0.001, N = 1005 (Figure 3). Intraday mean dispersion of wind direction was ρ = 0.73 ± 0.26 (N = 90).

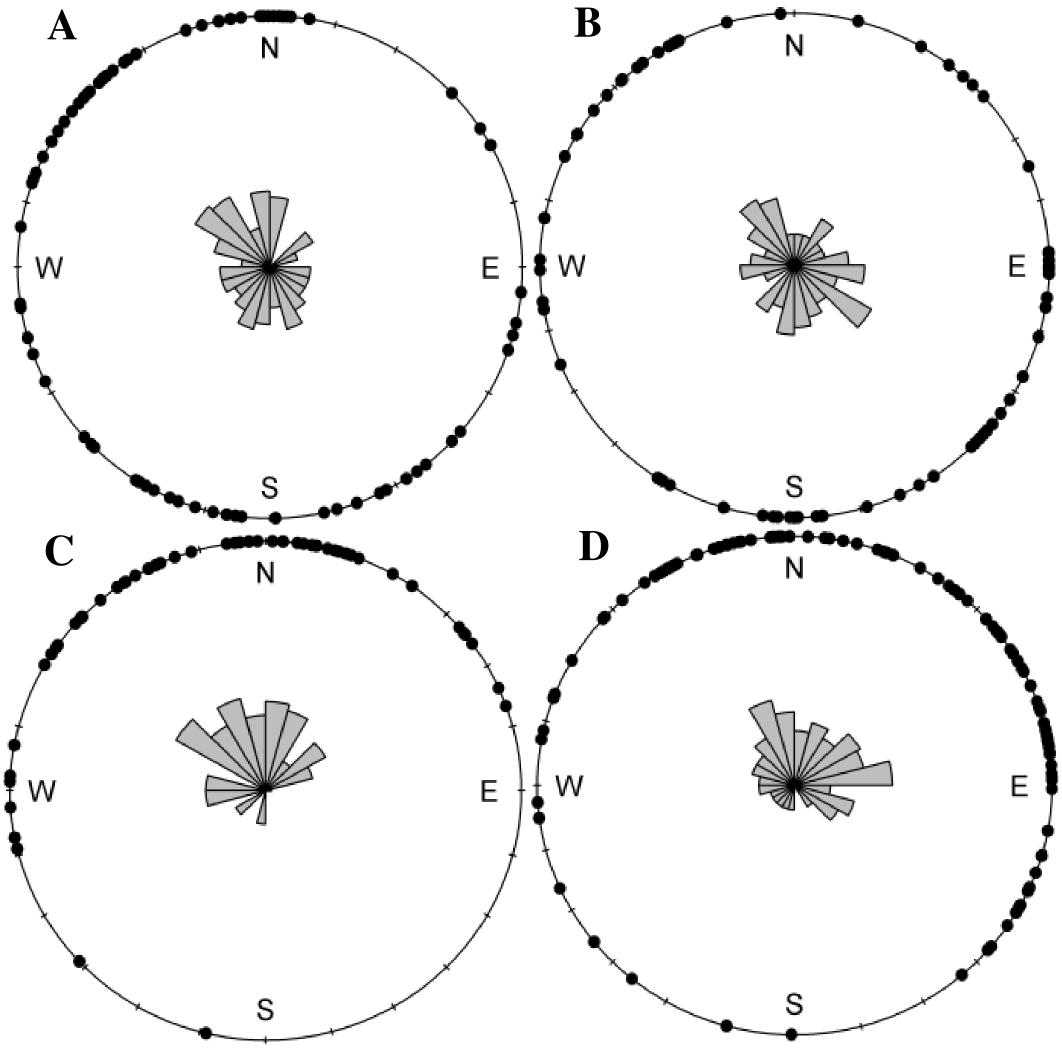


Figure 2. Angular distribution of mean directions of outward flights: (A) establishment, (B) courtship, (C) incubation and (D) nestling periods.

Table 2. Paired comparisons of mean outward flight directions at each phenological period (** p<0.01, *** p<0.001).

Phenological Period	Watson's Test			
	Establishment	Courtship	Incubation	Nestling
Establishment	-	0.29 **	0.75 ***	0.62 ***
Courtship		-	0.34 **	0.81 ***
Incubation			-	0.27 **
Nestling				-

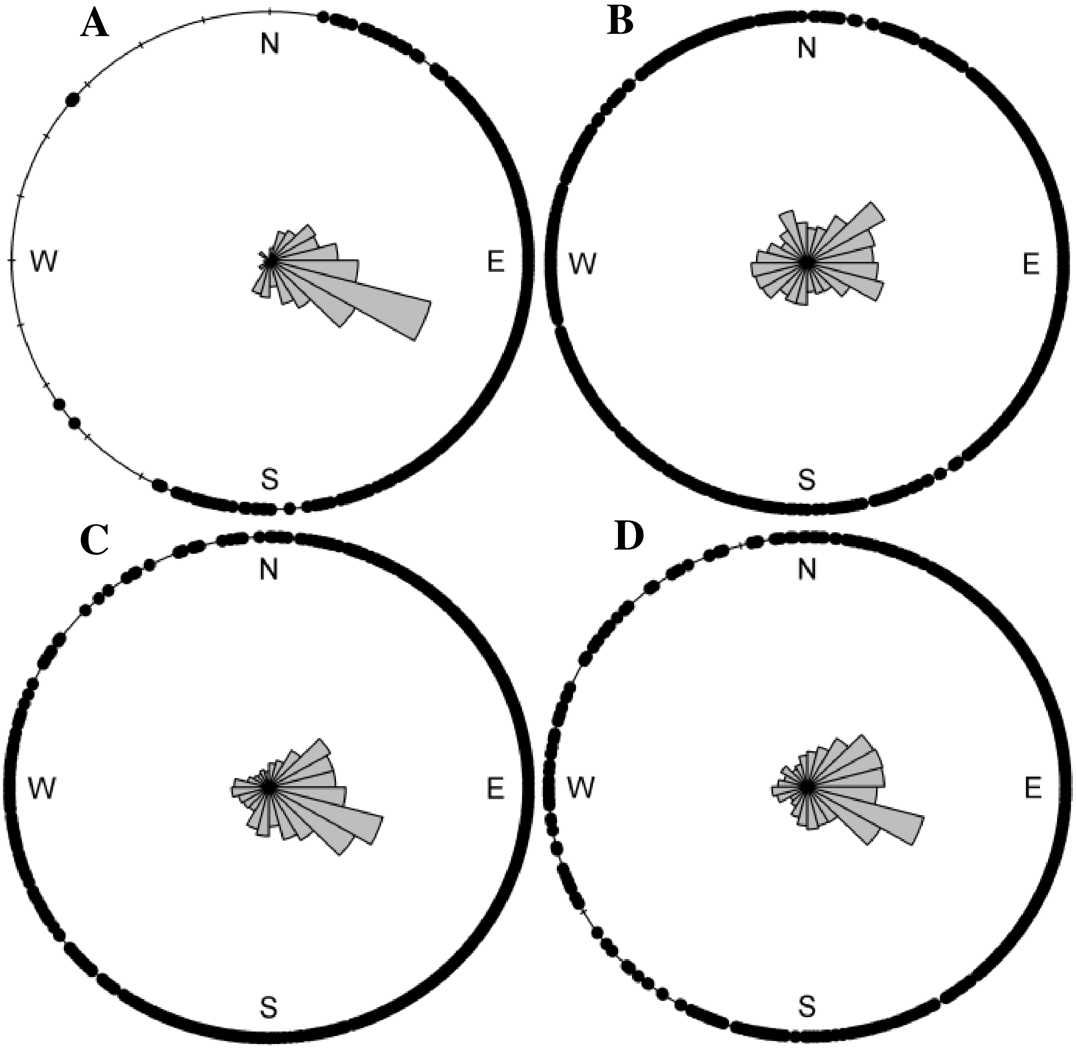


Figure 3. Angular distribution of wind directions: (A) establishment, (B) courtship, (C) incubation and (D) nestling periods.

A significant and negative seasonal trend appeared in the daily mean wind speed ($y = -0.03x + 10.12$, Pearson's $r = -0.33$, $p = 0.001$, $N = 90$), indicating that the wind blew stronger in the earlier periods of the breeding season than in the later ones (Figure 4). There was no evidence of any seasonal trend in daily mean wind direction (Pearson's $r = -0.04$, $p = 0.63$, $N = 90$).

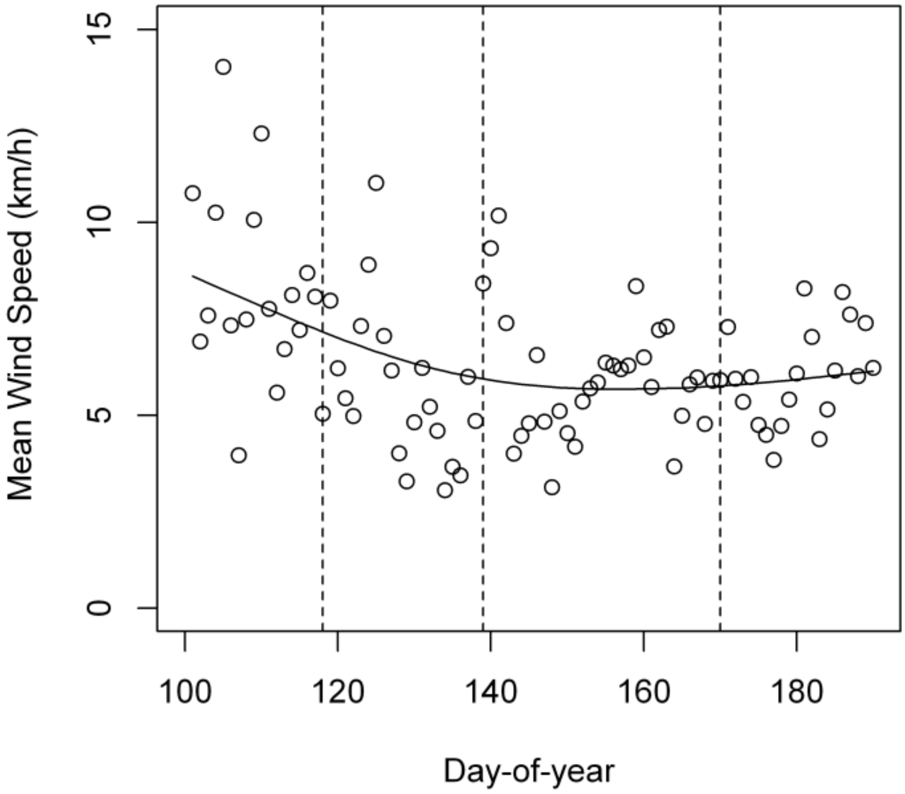


Figure 4. Temporal trend of daily mean wind speed. A smoothing spline of 3 degrees of freedom was adjusted to daily mean wind speed. The dashed lines show the mean starting days of courtship, incubation and nestling periods.

Wind Limitation Models

We had a sample of 3,355 half-hour x individual observations in which individual location was classified as 0 ("at the colony", N = 766) or 1 ("out of the colony", N = 2,589). The model showed a significant and positive effect of the wind speed on the probability of staying out of the colony ($\chi^2 = 58.61$, $p<0.001$). "Out of the colony" locations were classified as 0 ("perched", N =849) or 1 ("flying", N = 1,740). This model indicated that the wind speed did not affect the probability of being perched or flying ($\chi^2 = 2.58$, $p =0.12$). Both models suggested the absence of any limitation to flight for kestrels due to strong winds at our study site.

GLMM models for TWA

We fitted a model to the variable TWA based on the information of the 240 outward flights. Values of TWA close to 0º indicate kestrels flying with tailwinds while values close to 180º indicate kestrels flying with headwinds. Sex and GPS frequency had non-significant effects on the TWA. However, the model showed that the TWA decreased with increasing median flight altitude and mean wind speed, as expected, indicating that when flying higher and with stronger winds, kestrels flew more with tailwinds. There was a significant negative trend with the day-of-year indicating that TWA declined as the season progressed, contrary to our predictions. When only the data from outward flights performed with strong winds were analyzed (N = 71), the day-of-year showed a non-significant negative trend. We repeated the same model fitting procedure with the data from the 280 inward flights. The mean wind speed showed a significant positive effect on TWA, contrary to what could expect, as it indicates that kestrels prefer to fly with headwinds when winds are stronger. But, there was no significant trend in TWA with day-of-year, as predicted (Table 3).

We adjusted a smoothing spline with four degrees of freedom to TWA of outward flights, outward flights performed with strong winds and inward flights. The TWA of outward flights partially satisfied our hypothesis with values below 90º at the beginning of the season and then values above 90º during the intermediate periods (courtship and incubation) as we expected, but again values below 90º at the end, contrary to our expectation. The TWA of outward flights performed with strong winds showed a similar temporal trend but it was always below 90º. The TWA of inward flights first decreased with day-of-year and then increased toward the end of the breeding season (Figure 5).

Table 3. Estimates of GLMMs parameters.

A) On the mean TWA of outward flights (explained deviance = 0.69%).

Predictors	β	Standard Error	p-value
Intercept	131.07	14.19	< 0.001
Altitude	- 0.05	0.02	< 0.01
Wind Speed	- 1.26	0.64	0.05
Day-of-year	- 0.18	0.07	0.01

B) On the mean TWA of outward flights performed with strong winds (explained deviance = 0.47%).

Predictors	β	Standard Error	p-value
Intercept	104.91	17.37	< 0.001
Day-of-year	- 0.22	0.12	0.08

C) On the mean TWA of inward flights (explained deviance = 0.18%).

Predictors	β	Standard Error	p-value
Intercept	77.20	6.71	< 0.001
Wind Speed	1.48	0.65	0.03

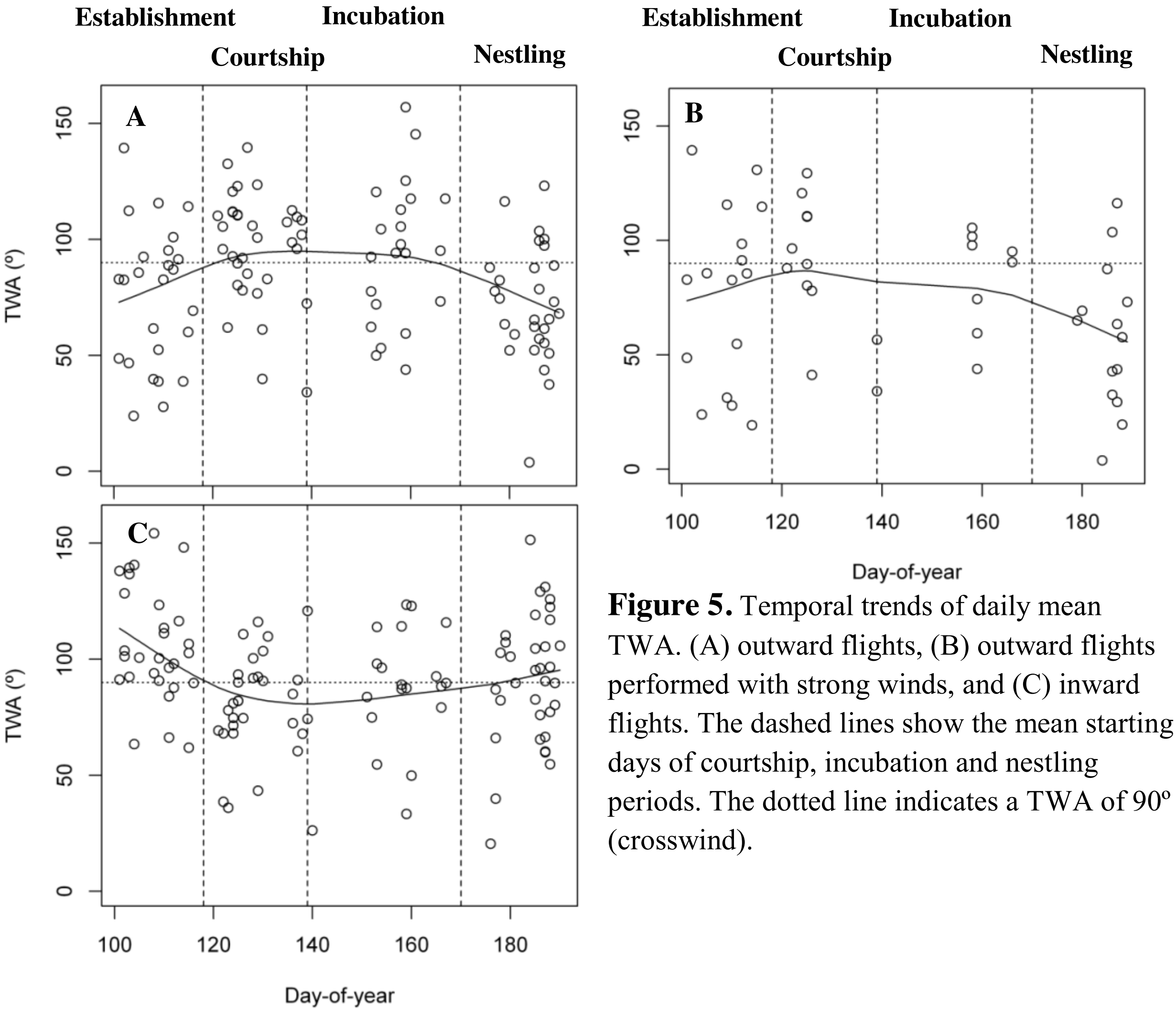


Figure 5. Temporal trends of daily mean TWA. (A) outward flights, (B) outward flights performed with strong winds, and (C) inward flights. The dashed lines show the mean starting days of courtship, incubation and nestling periods. The dotted line indicates a TWA of 90º (crosswind).

Discussion

Lesser kestrels showed a temporal pattern in the distribution of foraging trips departure direction from a uniform to a concentrated distribution along the breeding season in agreement with the hypothesis that during establishment they devote more time exploring the surroundings of the colony and during the nestling period they concentrate exploiting the areas with higher prey availability. Wind speed did not cause any limitation to kestrel flight. With stronger winds kestrels did not stay at the colony nor remained perched when they were away, indicating they could fly with all winds speeds we registered during our study period. We found some small influence of wind direction in foraging trips departure directions, especially at the beginning of the breeding season when individuals tended to leave the colony with tailwinds, in agreement with the hypothesis that during the initial exploratory phase kestrels could take advantage of tailwinds to leave the colony.

This is first study, up to our knowledge, that evaluates the effect of wind speed and direction on foraging movements on a terrestrial bird, and also the first one to study foraging trip departure direction patterns along the whole breeding season. Wind influence in foraging movements has only been assessed in colonial seabirds, and almost exclusively during the nestling period. Due to the absence of studies in terrestrial birds we can only compare our results to those published for seabirds even though the ecological conditions experience by kestrels can be very different.

Departure directions of lesser kestrels foraging trips changed from a uniform angular distribution in the establishment period to a concentrated distribution in later periods, as we predicted. The uniform angular distribution of departure directions resulted from leaving the colony in random directions at the beginning of the season. We consider that kestrels have little knowledge on the distribution of arable crops surrounding the colony when they arrive from migration and so they have no preference for any direction to move. Kestrels would leave the colony in random directions to explore the possible largest area around the colony at that time when they are not forced to return to the colony frequently. Individuals could locate the potential most favorable foraging patches at the beginning of the breeding season. In the process of learning and remembering the spatial distribution of prey in relation to crop type and phenological period, individual memory has a paramount role, which is acquired through individual experience as the breeding season progresses (Fagan et al. 2013). Thus, later in the season when they are feeding their chicks individuals would already know where the most favorable patches are and they would concentrate the departure direction of their foraging trips towards them, as suggested by our results. Kestrels would satisfy more efficiently the higher energy demand of the nestling period by following this strategy.

Our results concerning departure direction patterns are consistent with the findings of previous studies on seabirds. Several seabirds species (Northern gannets *Morus bassanus* and Peruvian boobies *Sula variegate*) concentrate the departures from the colony in the same directions repeatedly during the nestling period to exploit the same foraging areas (Hamer et al. 2001, Weimerskirch et al. 2010). Pettex et al. (2010) suggest that it could be the consequence of bird spatial knowledge about profitable foraging areas distribution that individuals acquired during previous breeding seasons and/or refined during the earlier periods of the same season. However, those studies did not cover the complete breeding period to confirm the hypothesis that knowledge was acquired or refined in a previous exploratory phase.

At the beginning of the breeding season, kestrels forage on a wide range of small prey, whereas at the end of the season when optimal prey (bush-crickets, Tettigoniidae) are abundant, individuals feed almost exclusively on them (Rodríguez 2004; Rodríguez et al. 2010). This change in diet is presumably caused by a synchronization of the lesser kestrel breeding phenology so that the maximum of energy demand, i.e. nestling period, is coincident with optimal prey availability (Masman et al. 1988). Thus, the more generalist and varied diet of the kestrels early in the season (Rodríguez et al. 2010) could be partially a consequence of the random distribution of the departure directions of foraging trips at the beginning of the season when kestrels do not know how prey are distributed and are exploring the territory. On the other hand, the more specialized diet of kestrel at the end of the season (Rodríguez et al. 2010) could be caused by the greater availability of optimal prey, and this would cause a concentration of departure directions towards the patches where individuals would already know that optimal prey are more available. However, it may be difficult to distinguish between causes and consequences in this relationship between lesser kestrel diet and departure direction of foraging trips.

Lesser kestrels concentrated their foraging trip departure directions towards the North at the end of the breeding season. The Northern and Eastern parts of the study area are mostly dominated by wheat crops which are usually harvested during June, coincident with the incubation and nestling periods. Thus, individuals would be heading to forage towards wheat crops, at a time they are started to be harvested, consistent with the described foraging habitat selection in the lesser kestrel (Donázar et al. 1993, Tella et al. 1998, Rodríguez et al. 2013).

Wind had some effect on the direction of outward foraging flights. The model fitted to TWA of outward flights suggests that stronger winds and flying at higher altitudes made kestrels fly more with tailwinds. It could be that kestrels choose to fly higher when wind direction is in the direction they want to depart, or that they are drifted as a consequence of flying higher with stronger winds. This model also showed a decreasing linear trend along the breeding season, indicating that kestrels leave the colony flying more with tailwinds as the season progresses, contrary to our expectation. The low values of TWA of outward flights at the end of the season seemed to result from the non-random distribution of wind directions and a spurious coincidence between wind direction and the location of the most favorable foraging patches in our study area. Kestrels headed towards the most favorable foraging patches independent of wind direction, but wind blows dominantly to the East and wheat crops are located predominantly to the North and East of the study colony. The graphical exploration of TWA of outward flights also shows an initial increase at the beginning of the breeding season and then a decreasing trend towards the end. This suggests the existence of some wind effect and that individuals would also be leaving the colony flying more with tailwinds early in the season as we predicted, but it was blurred in linear models by the stronger coincidence of foraging trip departure and wind direction at the end of the season. When we limited our analyses to outward flights performed with strong winds, the fitted model did not show any linear temporal trend of TWA; but the graphical exploration showed a similar result that obtained with all outward flights. However, in this case the temporal trend was shifted to values below 90º, suggesting that weak winds did not blur the true wind effect on kestrel foraging trips, although individuals tended to depart more with tailwinds when winds were strong. The model fitted to TWA of inward flights did not show any temporal trend, as predicted. But its graphical exploration showed a decreasing trend at the beginning of the breeding season and then increasing towards the end in a mirror image to TWA of outward flights. This pattern probably arises as consequence of leaving the colony in a certain direction and returning following usually the opposite one within a scenario of winds relatively constant in direction through the day, as occurred in our study area during the year of our study. That would also explain the positive relationship of TWA of inward flights and mean wind speed showed by the model, contrary to that showed by the model fitted to TWA of outward flights.

Wind effect has been evaluated in foraging movements of colonial seabirds. However, there are no common patterns across the studies and seabirds can leave the colony flying both with tailwinds or headwinds towards the foraging areas. Cory's shearwaters (*Calonectris diomedea*) and common murres (*Uria algae*) leave the colony flying with tailwinds in their foraging trips (Paiva et al. 2010, Evans et al. 2013). Wandering albatrosses leave the colony flying with headwinds and return flying with tailwinds, or they perform a loop to take advantage of tailwinds both in outward and inward flights with strong winds blowing in the area (Weimerskirch et al. 2000, Wakefield et al. 2009). Wind is usually variable in speed and direction through the day and seabirds could adjust their long lasting foraging movements to wind conditions to reduce flight cost daily. Grémillet et al. (2004) demonstrated that Cape gannets (*Morus capensis*) leave the colony flying with light headwinds in the morning and return flying with strong tailwinds in the evening. Wind was weak and constant in direction through day in our study site, so leaving the colony flying with tailwinds would not reduce flight cost because individuals would have to return to the colony most probably with headwinds, and vice versa.

We found that the probability of lesser kestrels being away from the colony was positive affected by the wind speed, probably because winds tend to be stronger at midday when kestrels are foraging far from the colony, but the probability of being flying or perched when individuals were outside the colony was independent of wind speed. Both results suggested an absence of a limitation to flight caused by wind speed, probably explained by the relative weak winds blowing during the study period, with the upper 25 percentile in approximately 9 km/h (light breeze according to Beaufort scale, and around 30% of recorded mean ground speed of lesser kestrel). While some studies have evaluated the limitation caused by wind on migratory flights, showing that birds tend to depart only under favorable wind conditions (Liechti 2006), this has been overlooked in relation to foraging movements. Åkesson & Hedenström (2000) found several passerines species departed in days with stronger tailwinds component in their migratory route direction. Bar-tailed godwits (*Limosa lapponica baueri*) even start migration as soon as favorable winds blow in the area, although birds have not reached the optimal fuel load to cope with the journey (Conklin & Battley 2011).

Future studies should focus on the effect of wind conditions on foraging movement of terrestrial birds. This aspect has received very little attention and wind effects could have important consequences at population level, especially for species foraging over large areas and for populations inhabiting areas with strong winds.

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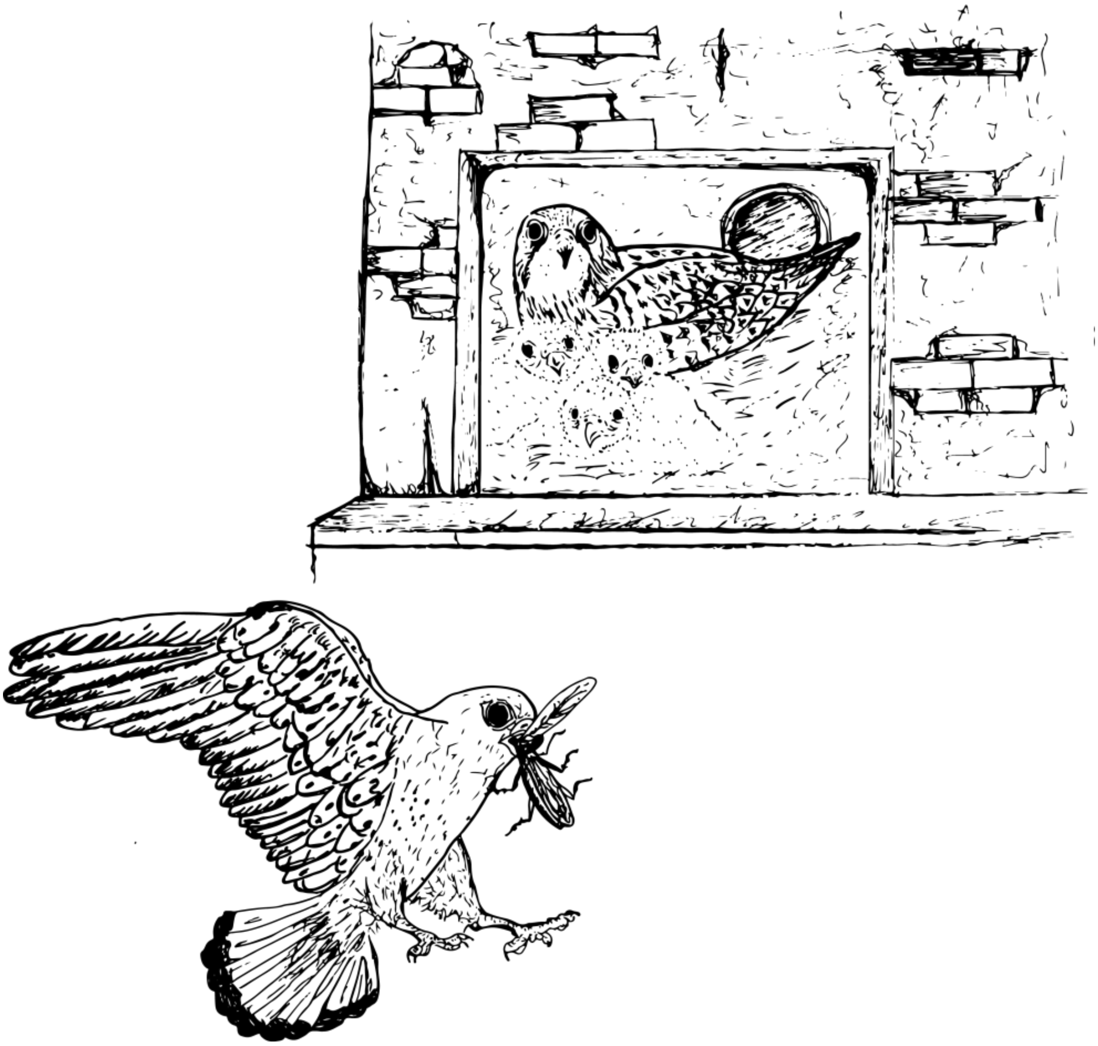
CHAPTER TWO

Who rules the roost? Sexual differences in foraging movements of the lesser kestrel throughout the breeding season



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(*In prep.*)

Abstract

In species with biparental care both members of the breeding pair cooperate to raise the offspring and they may do it either by assisting each other in every reproductive task or by specializing in different ones. The latter case is known as reproductive role specialization. Avian role specialization has been traditionally studied with direct observations at the nest because of the difficulties of tracking free-ranging animals through the landscape until the recent application of biologgers. Raptors are considered one of the most role-specialized groups with males being the main responsible for prey provisioning tasks and females entrusting with nest defense, egg incubation and chick brooding. However, little is known about off-nest parental behavior. In this paper, we analyze how the role specialization of the lesser kestrel (*Falco naumanni*) influences foraging movement patterns throughout the breeding season. We tracked 30 lesser kestrel breeders from two breeding colonies using high-frequency GPS-dataloggers over four consecutive breeding seasons. We found an absence of any sexual difference in foraging movement patterns early in the breeding season when lesser kestrel breeding pairs were not formed yet. However, we observed sexually distinct foraging movement patterns when breeding pairs were already formed in accordance with the role specialization of raptors. Lesser kestrel males traveled larger daily distances and performed a higher daily number of shorter foraging trips than females to maximize food provisioning rate at the nest. Meanwhile, lesser kestrel females spent more time at the colony than males to defend the nest and brood the chicks, but both sexes equally shared the incubation of eggs during the day. Moreover, females also increased foraging effort to help their mate to feed chicks when they were grown and required less protection and more food. Furthermore, the lesser kestrel showed a sexual spatial segregation of foraging areas with males foraging closer to the colony than females presumably as the result from an adaptive foraging strategy based on role specialization to reduce prey depletion close to the colony and intersexual competition in order to breed successfully.

Resumen

En especies con cuidado biparental, los dos miembros que componen la pareja reproductora cooperan para sacar adelante a la prole ya sea asistiéndose mutuamente en cada tarea reproductiva o especializándose en tareas diferentes. Este último caso es conocido como especialización de roles. La especialización de roles en aves ha sido estudiada tradicionalmente a través de observaciones directas en el nido debido a las dificultades que ha conllevado el seguimiento de animales silvestres campo a través hasta la reciente aplicación de los dispositivos de *biologging*. Las aves rapaces están consideradas como uno de los grupos con mayor especialización de roles: los machos son los principales encargados de las tareas de aprovisionamiento de alimento mientras que las hembras son responsables de la defensa del nido, la incubación de los huevos y el cuidado de los pollos. Sin embargo, aún se conoce poco sobre el comportamiento parental fuera del nido. En este artículo se analiza cómo la especialización de roles en el cernícalo primilla (*Falco naumanni*) afecta a los patrones de viajes de caza a lo largo de la temporada de cría. Se marcaron 30 cernícalos primilla reproductores procedentes de dos colonias de cría mediante GPS-dataloggers de alta frecuencia durante cuatro temporadas de cría consecutivas. Encontramos una ausencia de diferencias sexuales en los patrones de viajes de caza al principio de la temporada de cría cuando las parejas reproductoras no estaban formadas todavía. Sin embargo, observamos patrones de viajes de caza diferentes entre los sexos cuando las parejas reproductoras ya estaban formadas, de acuerdo con la tendencia general de especialización de roles en rapaces. Los cernícalos primilla machos volaron distancias diarias más largas a lo largo de un mayor número diario de viajes de caza, que además fueron más cortos, que las hembras para maximizar la tasa de

aprovisionamiento de alimento en el nido. Por su parte, los cernícalos primilla hembras pasaron más tiempo en la colonia que los machos para defender el nido y cuidar a los pollos, pero ambos sexos compartieron de forma equitativa la incubación de los huevos durante las horas de luz. Además, las hembras incrementaron su esfuerzo en tareas de aprovisionamiento de alimento para ayudar a los machos a alimentar a los pollos a medida que estos crecieron y requirieron menos protección pero más comida. Adicionalmente, el cernícalo primilla mostró una segregación espacial de las áreas de caza entre los sexos, con los machos alimentándose más cerca de la colonia que las hembras, probablemente como resultado de una estrategia adaptativa de alimentación basada en la especialización de roles para reducir la sobreexplotación de presas cerca de la colonia y la competencia intersexual con el objetivo de tener más exito en la reproducción.

Introduction

Parental care includes any behavior of adult breeders that results in increasing offspring survival at the cost of compromising their own survival and future reproductions because of the energy and time invested (Trivers 1972, Clutton-Brock & Vincent 1991). Different modalities of parental care have evolved from no parental care at all to that provided by non-breeders to help rearing the offspring of conspecifics. Biparental care is one of these modalities and entails that both members of the breeding pair are involved in raising the offspring (Maynard Smith 1977). Indeed, cooperation between parents is essential to breed successfully taking care of several reproductive tasks, such as construction and defense of burrows, incubation of eggs or provisioning the offspring, although breeders can manage them in different ways (see Kendeigh 1952). In some species each member of the breeding pair cooperates by assisting its partner in every reproductive task, whereas in other species each parent specializes in different tasks. The latter case is known as reproductive role specialization (Wesolowski 1994). Thus, the females of a role-specialized species are entrusted with certain reproductive tasks while the males are responsible for other tasks, in this way balancing parental investment throughout the breeding season. Role specialization has predominantly been studied in birds probably due to the elevated percentage (>80%) of biparental species among them (Cockburn 2006, Webb et al. 2010), although it has also been described in insects, fishes and mammals (Itzkowitz 1984, Mendoza & Mason 1986, Trumbo 2012). Literature on avian role specialization has been traditionally based on direct observation of task division between sexes at the nest, with no considerations about off-nest parental behavior because of the difficulty of tracking mobile individuals across the landscape (e.g. Wynne-Edwards 1995, Saraux et al. 2011, Snekser & Itzkowitz 2014). However, biologging technologies developed in the last years have provided us with new tools to study animal behavior by remote monitoring, which greatly enhances direct observation (Wilmers et al. 2015, Demšar et al. 2015).

The revolution of animal tracking systems has led to a rapid expansion of Movement Ecology as a new ecological discipline whose primary objective is to create a conceptual framework to unify the study of movement (Kays et al. 2015). Movement is a keystone process that determines individual life history by affecting its survival and reproduction, and subsequently it has a profound impact at higher levels of organization, from population dynamics to ecosystem functionality (Turchin 1998, Block et al. 2011, Weimerskirch et al. 2012, Jeltsch et al. 2013). Therefore, understanding the mechanisms underlying individual movements becomes a valuable as well as a daunting challenge in order to elaborate efficient species conservation programs. According to the movement ecology paradigm, individual movement results from the interaction of four elements: external agents, both biotic and abiotic, individual motion abilities, navigation capacities, and internal state or motivation (Nathan et al. 2008). Each member of a breeding pair performs specific reproductive tasks throughout the breeding season in role-specialized species, so it is expected that parental sex will strongly influence movement behavior in order to satisfy the temporally dynamic requirements during reproduction. However, because role specialization is often associated with sexual size dimorphism, the cause behind sexual differences in movements might be misleading (e.g., Phillips et al. 2004, Lewis et al. 2005). Despite of that, sexually distinct movement behaviors have clearly been attributed to role specialization of breeding pairs in several marine birds (e.g., Pinet et al. 2012, Ludynia et al. 2013, Rishworth et al. 2014). Nevertheless, the effect of role specialization on parental movements is almost unknown in raptor species, despite being this group among the most role-specialized birds (Andersson & Norberg 1981, Newton 2010). Role specialization is quite well known within the raptor group thanks to direct observation at the nest: males are responsible for provisioning tasks to feed their mate or chicks, whereas females are devoted to nest defense, egg incubation and chick brooding throughout the reproductive period (Ferrer 1990, Sergio & Bogliani 2001, Gaibani et al. 2005, Liébana et al. 2009). Furthermore, female raptors often help males provisioning chicks as the energy demand for raising them increases with age (Leckie et al. 2008). In this paper we investigate the influence of role specialization in foraging movement behavior of the lesser kestrel (*Falco naumanni*) throughout the breeding season.

The lesser kestrel is an insectivorous small-sized raptor that winters in Africa and breeds in colonies across the Palearctic (Cramp & Simmons 1980). Lesser kestrels are colonial breeders nesting in holes in buildings and cliffs in steppe-like habitats or non-irrigated arable crops in Western Europe (Bustamante 1997). This species shows reversed sexual size dimorphism with females being larger than males (~15% difference in weight), which is common among raptors (Newton 2010), and it also shows a strong sexual chromatic dimorphism in its plumage (males show blue-gray plumage in head and tail, whereas females show a uniform rusty plumage with black strikes) (Cramp & Simmons 1980). The role specialization of the lesser kestrel has been studied through direct observations at the nest and it agrees to the general trend of task division in raptors (Donázar et al. 1992, Negro et al. 1992, 2000, Plaza-Jurado 2012). Therefore, potential sexual differences in foraging movement patterns of the lesser kestrel might be caused either by sexual dimorphism or by role specialization between members of the breeding pair. If sexual differences in foraging movements would be mainly caused by the sexual dimorphism of the lesser kestrel, we expected differences between sexes that would be maintained throughout the whole breeding season. However, if sexual differences in foraging movements would be mostly caused by the role specialization of the lesser kestrel, we expected differences between sexes that would vary throughout the breeding season in relation to their different reproductive tasks. We tracked individual lesser kestrels using high-frequency

GPS-dataloggers to study foraging movement patterns throughout the breeding season. Kestrel breeders were expected to respond to changing energy demand and prey availability along phenological periods with their movement strategy, but differentially regarding to sex. In accordance to the role specialization of this species, 1) we hypothesized that there would be no sexual differences in any foraging movement variables during the establishment period of the lesser kestrel. 2) Lesser kestrel males were expected to perform higher number of shorter foraging trips per day than females to maximize prey provisioning rate at the nest during the courtship, incubation and particularly the nestling period. 3) Lesser kestrel females were expected to stay longer at the colony than males on a daily basis in order to defend the nest, incubate eggs and brood chicks during the courtship, incubation and nestling periods, respectively. 4) Individual lesser kestrels were expected to increase the daily distance traveled and the number of foraging trips per day and also to decrease daily colony attendance as foraging effort rose from the establishment period when they exclusively feed for themselves to the nestling period when they also feed their offspring, and even also within the nestling period as the energy demand increases with chick age (see Rodríguez et al. 2006). 5) We also analyzed the temporal trend of lesser kestrel body mass as an indicator of individual condition that would be inversely related to parental effort throughout the breeding season. 6) In addition, we evaluated potential differences in habitat selection, hunting strategy or foraging areas between sexes in the lesser kestrel throughout the breeding season.

Material and Methods

Study area

We studied lesser kestrels from two breeding colonies located in the Guadalquivir river basin (southwestern Spain), which is dominated by arable crops (Fernandez et al. 1992). Wheat and sunflower are the primary crops within the study area, although olives and vineyards are also present. The Silo colony is situated at a building holding a grain elevator and it is surrounded by agricultural landscape in La Palma del Condado (Huelva, Andalusia), whereas the EBD colony is situated at the roof of our research institute surrounded by mainly urban landscape in the city of Seville (Andalusia). The two colonies are 50 km apart. Lesser kestrel pairs breed inside nest-boxes installed at both buildings.

Biologging procedure

Lesser kestrel breeding pairs were monitored during 4 consecutive breeding seasons (years 2011-2014). We tracked individual lesser kestrels using GPS-dataloggers (GiPSy models 2, 4, and 5; weighing up to 2 g; Technosmart, Rome, Italy) with small-sized batteries (90 - 100 mA, 2.2 g). GPS were fixed to the birds' backs using a micro back-pack harness from Marshall Radio Telemetry (North Salt Lake, Utah, U.S.A.) or a similar hand-made harness formed by a carbon fiber plate and a 4 mm width teflon ribbon (Bally Ribbon Mills, Pennsylvania, U.S.A.). GPS-dataloggers were covered with a protective thermoretractable case. The total mass of the equipment (harness + GPS + battery) was about 6 g and never exceeded the 5% of lesser kestrel mean body mass (130 g, e.g. (Cramp & Simmons 1980)), which is within the recommended limits for flying animals (Barron et al. 2010) To get the birds used to the harness and the GPS device, we fixed a dummy GPS-datalogger with the same weight to the harness at least a week before fixing the real device and starting to record the birds' movement (see details of the procedure in Chapter One).

We obtained a total of 825,365 fixes from 35 individuals (a mean of 23,581.86 ± 16,113.46 fixes per individual, range 3,275 – 55,273). Some of them were tracked during two (8 individuals) or three (1 individual) breeding seasons. Nevertheless, 5 kestrels finally did not breed at the study colonies. As these individuals could be non-breeders we did not include their data in the analyses. Statistical analyses were performed using tracking data from 30 lesser kestrel breeders (16 males and 14 females). We configured GPS devices at different sampling frequencies: one fix per second, one fix per minute or one fix every 3, 5, and 10 minutes. We recaptured tracked kestrels to recover the data as they were stored in the logger. A new full-powered GPS device was then deployed before releasing the individual and resume tracking. Kestrels were captured when they entered nest-boxes using remote-controlled sliding doors. Individuals were captured a mean of 7.63 ± 2.46 times per year, range 2-11 (n = 30), and they were never captured more than once per week. Every time an individual kestrel was captured, we measured the body mass. GPS data were collected during daylight hours (5 to 20 h UTC) during the breeding season (March – July). We removed the harnesses from the kestrels at the end of each breeding season. The tracking data can be consulted on Movebank (www.movebank.org) (Hernández-Pliego et al. 2015).

Foraging movement variables

GPS locations were graphically explored using GIS (ArcGIS 10, ESRI, Redlands, California, U.S.A.) to identify individual foraging trips. We use the term foraging trip to refer to a set of consecutive locations of an individual kestrel that start from the breeding colony and extend beyond 300 m and in which we are able to identify a foraging event (mostly clumped locations at low altitude above the ground with highly variable instantaneous speed). Incomplete foraging trips, i.e. trips in which departure from or arrival at the colony or roost was not recorded by the GPS were removed from statistical analyses. GPS devices provided the flight altitude and instantaneous speed for each location.

For every lesser kestrel foraging trip we calculated: (1) duration, as the temporal difference between leaving and returning to the colony or roost; (2) distance, as the accumulated distance traveled between consecutive spatial locations along the trip; and (3) the maximum distance from the colony reached along the trip. For every complete day of tracking, which are those dates and individuals in which we obtained tracking data from sunrise to sunset, we calculated: (1) daily distance, as the accumulated distance traveled between consecutive spatial locations recorded through day; (2) the number of foraging trips performed along the day; and (3) daily colony attendance, as the percentage of daytime that individual spent at the colony. We considered that individuals were at the colony when spatial locations were registered within a 50 m-buffer distance from the colony. We calculated day length as the temporal difference between sunrise and sunset times provided by Ministerio de Fomento of Spain (http://www.fomento.es).

We studied differences between sexes in foraging habitat use by the lesser kestrel. To do that, we randomly selected one GPS location per foraging event in order to visit it in the field and register the predominant habitat type within a 50-m buffer. When different foraging events from an individual kestrel coincided in space and within the same GPS deployment (a time window of one week as individuals were never recaptured more than weekly), we considered them as a single location in the analyses. We used hand-held GPS (model GPSmap 60, Garmin) to find the selected locations and register habitat information. Habitat was categorized into nine different types: Cereal (mainly non-irrigated wheat), Stubble (harvested cereal), Sunflower, Seedlings (sunflower and cotton crops when vegetation height was lower than 50 cm), Vineyards, Tree Groves (fruit tree and olive groves), Pastures (non-arable lands), Ploughed (ploughed and sowed fields), and Others (habitats of minor use: alfalfa, beetroot, chickpea, cotton, garlic, maize, potatoes, and rice). Both sunflower and cotton plants may grow up to more than 1 m throughout the lesser kestrel breeding season, which might provide substantial differences at microhabitat level to consider a Seedlings category separated from the adult plants (see Rodríguez et al. 2013). Field visits were carried out with a minimum time delay of one week since kestrels were foraging in the selected locations because of the weekly recaptures. Fieldwork was carried out during three out of the four lesser kestrel breeding seasons included in the study (years 2012-2014).

We also studied sexual differences in hunting strategy of the lesser kestrel. Along foraging trips, lesser kestrels can capture prey either by hovering flights (an active hunting strategy in which kestrels remain suspended in the air flapping their wings) or from a perch (a passive sit-and-wait hunting strategy from an elevated position) (Village 1990). Using tri-axial accelerometry, we obtained that 99% of hovering flights lasted less than 30 seconds (N = 4933 hovering bouts, *authors unpub. data*, see Chapter Four), so they could be only identified from 1-second GPS data. In contrast, perching bouts can be also identified at lower GPS sampling frequencies since tri-axial accelerometry revealed that above 40% lasted more than 1 minute (N = 2798 perching bouts, *authors unpub. data*, see Chapter Four). Therefore, we focused the study of the lesser kestrel foraging strategy on the relative use of perch-hunting during foraging trips throughout the breeding season. We considered a perching bout as a sequence of GPS locations in which the distance between consecutive locations was up to 1 m (1-second GPS sampling frequency), 5 m (1-min frequency), 15 m (3-min frequency), 25 m (5-min frequency) or 50 m (10-min frequency). We increased the distance buffer to consider a perching bout because GPS spatial accuracy decreases as sampling frequency increases (Swain et al. 2008). Then, we calculated the total perching time per foraging trip as the sum of the duration of all perching bouts identified per foraging trip. Being conservative, we discarded from the statistical analyses those perching bouts that lasted less than 30 seconds as they might be hovering bouts.

Every foraging movement and complete day of tracking was classified into one of the four phenology periods we divided the breeding season of each individual lesser kestrel using the laying and hatching date at its nest: establishment (from the arriving at the breeding colony after spring migration until courtship), courtship (21 days before laying the first egg), incubation (between laying and hatching of the first egg), and nestling (from hatching of the first egg until chick fledging). Nest-boxes installed in both colonies are equipped with analogue video cameras (Videcon, model KPC-EX500B) that record 10-seconds video samples activated by movement inside the nest-boxes. Individual laying and hatching date were determined using these video samples collected in the corresponding nest-box. In addition, media samples also provided us with the brood size of every tracked kestrel and also chick age at any time during the nestling period.

Statistical Analysis

We fitted Generalized Linear Mixed Models (GLMMs) to lesser kestrel foraging movement variables at the daily and at the foraging trip levels of analyses so as to evaluate the effect of role specialization on foraging movement patterns throughout the breeding season. Furthermore, we also fitted GLMMs to total perching time per foraging trip and to a binary response variable (0 = “no perching bouts”, 1 = “at least one perching bout”) to model the probability of performing a perching bout during foraging trips in order to assess temporal changes in the use of perch-hunting by the lesser kestrel throughout the breeding season. We included the interaction between sex (categorical predictor with 2 levels: female and male) and phenological period (categorical predictor with 4 levels: establishment, courtship, incubation, and nestling) to test our hypotheses, except in the model fitted to the probability of performing a perching bout in which we included the interaction between sex and day-of-year (continuous predictor). We also included the breeding colony as a categorical predictor in the models with 2 levels (EBD and Silo) because the habitat-matrix in the surroundings of the colonies was different (urban versus arable landscape) and it affects kestrel foraging strategies (see Chapter Three). We previously explored the potential non-linear response of day-of-year to the probability of performing a perching bout during foraging trips by fitting Generalized Additive Mixed Models (GAMMs) with the same predictors and random factors, but the best model included the linear response of day-of-year so we fitted GLMM to this response variable (see model selection later in this section). Additionally, we fitted GAMMs to kestrel foraging variables at the daily level (distance, number of foraging trips and colony attendance) within the nestling period to check whether parental effort varies throughout the period in a non-linear way. We included the interaction between sex and eldest chick age (continuous predictor) in order to test our hypotheses. We also included brood size at the date each variable was registered as a continuous predictor in all models. We incorporated GPS sampling frequency as a correction factor with 5 levels (1-second, 1-minute, 3-minute, 5-minute and 10-minute frequency) in all models, except in those fitted at the daily level that only had 3 levels (1-minute, 3-minute and 5-minute frequency), because it could influence the estimation of movement variables. Furthermore, we fitted GAMMs to kestrel body mass in order to study its temporal trend throughout the breeding season. We incorporated the interaction between sex and day-of-year as predictors of the models. We included individual identity and year as random factors in all GLMMs and GAMMs.

Daily colony attendance, which is a percentage, was arcsine-square-root transformed to get a proper fitting of the models. Total perching time per foraging trip and foraging trip duration, distance and maximum distance from the colony were logarithmically transformed with the same purpose. We used a Gaussian distribution of errors and the identity link function for daily distance, daily colony attendance, kestrel body mass, total perching time per foraging trip, foraging trip duration, distance and maximum distance from the colony as response variables of the models. We used a Poisson distribution of errors and the logarithmic link function to daily number of foraging trips as response variable of the models. We used a binomial distribution of errors and the logit link function to model the probability of performing a perching bout during foraging trips. We applied penalized smoothing splines to eldest chick age in the GAMMs. The degrees of freedom of the smoothing function were automatically selected using restricted maximum likelihood (REML) (Ruppert et al. 2003). We followed the Akaike's Information Criterion (AIC) for model selection. As the best GAMMs fitted to all three daily foraging parameters were those including a linear effect of eldest chick age, we simplified the models fitting a GLMM to all three variables with the same distribution of errors and link function used to fit the GAMMs. They included the same fixed and random factors used in the GAMMs. We fitted the GLMMs following a backward-stepwise procedure, removing the non-significant predictors until only significant ones remained. The significance of the predictors was tested using likelihood ratio tests comparing the model with and without the predictor. We evaluated statistical significance between levels of the categorical predictors of the models by applying Holm's correction for multiple comparisons (Holland & Copenhaver 1988).

Statistical analyses were performed using the R-software 3.1.1 ("R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/." 2014) fitting GAMMs and GLMMs using "mgcv" (Wood 2011) and "lme4" (Bates et al. 2014) packages, respectively. Post-hoc comparisons between categorical predictor levels were assessed using "phia" package (De Rosario-Martínez 2015).

Results

Daily level

We obtained 244 complete days of tracking from 14 females (2 from the EBD colony and 12 from the Silo colony) and 16 males (3 from the EBD colony and 13 from the Silo colony), a mean of 8.41 ± 6.39 per individual kestrel (Table 1). We summarize descriptive statistics of foraging movement variables at the daily level in Table 2. We found a statistically significant effect of the interaction between sex and phenological period on the three kestrel foraging movement variables measured at the daily level (distance traveled, number of foraging trips, and colony attendance) (Table 3). Individual lesser kestrels flew on average daily distances of 97.82 ± 46.22 km (mean ± standard error) with a mean of 6.67 ± 6.14 foraging trips per day during the breeding season. We did not find overall statistically significant differences between sexes in daily distance, although males flew larger distances through the day than females in the nestling period. We found overall statistically significant differences between sexes in the daily number of foraging trips, with females performing fewer foraging trips per day than males, but both sexes performed similar daily number of foraging trips during the establishment period. Individuals stayed at the colony on average 19.41 ± 12.94 % of daylight hours during the breeding season, with no overall statistically significant differences between sexes, although females stayed longer than males at the colony during the nestling period. Regarding the breeding colony, individuals from the EBD colony flew larger distances per day than their counterparts from the Silo colony. However, individuals from both colonies performed the same daily number of foraging trips and stayed at the colony a similar percentage of daytime (Table 3).

We found intra-sexual differences in lesser kestrel daily foraging variables throughout the breeding season (Figure 1). Males flew similar daily distances than females during the establishment and courtship periods but they flew shorter distances during the incubation period and larger daily distances during the nestling period. Furthermore, they increased the daily number of foraging trips from the establishment to the courtship period, then decreased it during the incubation period and increased again towards the nestling period. As a consequence of this foraging behavior of kestrel males, they stayed at the colony similar percentages of daylight hours during the establishment and courtship periods but stayed longer during the incubation period and shorter during the nestling period. Meanwhile, lesser kestrel females traveled similar daily distances and did not vary daily colony attendance across all phenological periods of the breeding season. In addition, females completed similar number of foraging trips per day except during the nestling period when they increased the number. Within the nestling period, we found statistically significant effect of the interaction between parental sex and eldest chick age on the distance traveled, number of foraging trips and nest attendance at the daily level (Figure 2, Table 4). Kestrel males maintained daily distances traveled and performed similar number of foraging trips per day as chick grew older, whereas females deeply increased both daily distance traveled and number of foraging trips. At the same time, males and females reduced daily colony attendance as the nestling period progressed, although the trend was steeper in females. We did not find any significant effect of brood size on these foraging variables. The breeding colony only showed statistically significant effect on daily colony attendance: Individuals from the EBD colony stayed longer at the colony through day than those from the Silo colony during the nestling period (Table 4).

Table 1: Number of lesser kestrel foraging trips and complete days of tracking used in the statistical analyses separated by breeding colony individual sex and phenological period.

Level of Analyses	Breeding Colony	Establishment		Courtship		Incubation		Nestling	
		Female	Male	Female	Male	Female	Male	Female	Male
# Complete Days	EBD	0	2	0	6	1	8	9	14
# Complete Days	Silo	23	24	28	28	20	20	19	42
# Foraging Trips	EBD	0	2	0	47	5	52	115	261
# Foraging Trips	Silo	82	106	78	238	64	118	217	786

Table 2: Summary of lesser kestrel foraging variables at the daily and foraging trip levels of analyses. Mean ± standard deviation and range (in brackets) are shown per phenological period and sex. Sample size = 244 complete days and 2171 foraging trips.

Foraging Variable	**Establishment**		**Courtship**		**Incubation**		**Nestling**	
	Female	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
Daily distance traveled (km)	78.83 ± 27.92 (52.97–181.10)	81.51 ± 36.37 (47.96–239.00)	85.84 ± 40.89 (45.08–212.00)	108.40 ± 39.59 (42.76–209.40)	70.72 ± 12.56 (55.03–104.00)	70.79 ± 44.36 (22.56–203.90)	105.30 ± 65.22 (9.20–220.80)	132.70 ± 36.24 (66.05–226.90)
Daily # foraging trips	3.04 ± 1.49 (1.00–6.00)	3.15 ± 1.62 (1.00–7-00)	2.43 ± 1.42 (0.00–7.00)	6.00 ± 3.88 (1.00–17.00)	2.29 ± 0.64 (1.00–4.00)	4.17 ± 2.24 (1.00–9.00)	7.68 ± 5.94 (1.00–31.00)	14.79 ± 5.99 (4.00–31.00)
Daily colony attendance (%)	22.32 ± 7.29 (3.94–36.76)	18.31 ± 7.26 (8.26–36.65)	22.32 ± 8.20 (11.52–38.78)	15.54 ± 7.89 (1.35–36.92)	26.95 ± 7.95 (8.31–37.60)	30.29 ± 14.68 (1.73–58.26)	25.44 ± 20.64 (0.01–68.63)	8.32 ± 6.56 (1.06–28.45)
Foraging trip duration (h)	2.01 ± 1.93 (0.25–9.01)	1.59 ± 1.67 (0.13–7.67)	2.51 ± 2.21 (0.25–9.17)	1.24 ± 1.21 (0.12–7.92)	3.39 ± 1.70 (0.20–6.94)	1.57 ± 1.41 (0.15–8.06)	0.92 ± 0.92 (0.06–6.99)	0.79 ± 0.75 (0.05–7.01)
Foraging trip distance (km)	15.10 ± 13.69 (1.04–57.50)	12.77 ± 13.78 (1.01–84.39)	20.26 ± 20.25 (1.15–85.30)	11.56 ± 11.15 (0.99–85.85)	22.81 ± 12.37 (1.27–49.47)	12.64 ± 11.17 (1.09–50.29)	11.87 ± 12.39 (0.69–126.10)	8.29 ± 7.71 (0.90–70.37)
Foraging trip maximum distance (km)	3.91 ± 2.90 (0.47–13.13)	3.63 ± 3.22 (0.42–23.69)	5.35 ± 5.55 (0.47–32.23)	3.75 ± 3.87 (0.45–24.94)	5.98 ± 3.02 (0.50–14.63)	4.02 ± 3.24 (0.50–15.13)	4.30 ± 3.90 (0.34–19.09)	3.13 ± 2.79 (0.45–19.06)

Table 3. Parameters (estimate ± standard error) of the GLMMs fitted to kestrel foraging variables at the daily level. Statistically significant variables are shown in bold: * $p < 0.5$, ** $p < 0.01$, *** $p < 0.001$, indicated in the first level of each predictor. Sample size = 244 complete days.

Predictor	**Level**	**Response Variable**		
		Distance (km)	**# Foraging Trips**	**Colony Attendance (%)**
Intercept	(ϕ)	118.78 ± 16.24	3.33 ± 1.19	15.11 ± 0.16
Sex * Phenological Period	Male - Establishment	**-6.25 ± 13.95*** **	**-0.17 ± 1.24** **	**0.86 ± 0.24*** **
	Female – Courtship	**-5.82 ± 9.32**	**-0.77 ± 1.20**	**0.19 ± 0.11**
	Male – Courtship	**2.85 ± 12.97**	**2.37 ± 1.26**	**-0.60 ± 0.21**
	Female – Incubation	**-25.17 ± 11.10**	**-1.08 ± 1.24**	**7.23 ± 0.16**
	Male – Incubation	**-34.97 ± 14.50**	**0.57 ± 1.30**	**11.99 ± 0.26**
	Female – Nestling	**-17.41 ± 11.71**	**3.66 ± 1.20**	**2.93 ± 0.17**
	Male – Nestling	**31.60 ± 14.31**	**10.78 ± 1.25**	**-8.73 ± 0.26**
Sex	Male	14.95 ± 8.15	**1.78 ± 1.13*** **	-4.76 ± 0.10
Phenological Period	Courtship	**2.63 ± 7.03*** **	**0.76 ± 1.11*** **	**-0.54 ± 0.06*** **
	Incubation	**-25.69 ± 7.50**	**0.001 ± 1.13**	**9.37 ± 0.07**
	Nestling	**18.44 ± 7.30**	**5.53 ± 1.11**	**-6.76 ± 0.07**
Breeding Colony	Silo	**-37.94 ± 13.19***	0.21 ± 1.18	1.33 ± 0.21
Sampling Frequency	1-minute	**78.57 ± 10.96*** **	0.06 ± 1.13	5.01 ± 0.15
	3-minutes	**22.02 ± 5.49**	0.45 ± 1.08	0.01 ± 0.04

(ϕ) The intercept includes the effect of female sex, establishment period, EBD colony and 5-minute GPS sampling frequency.

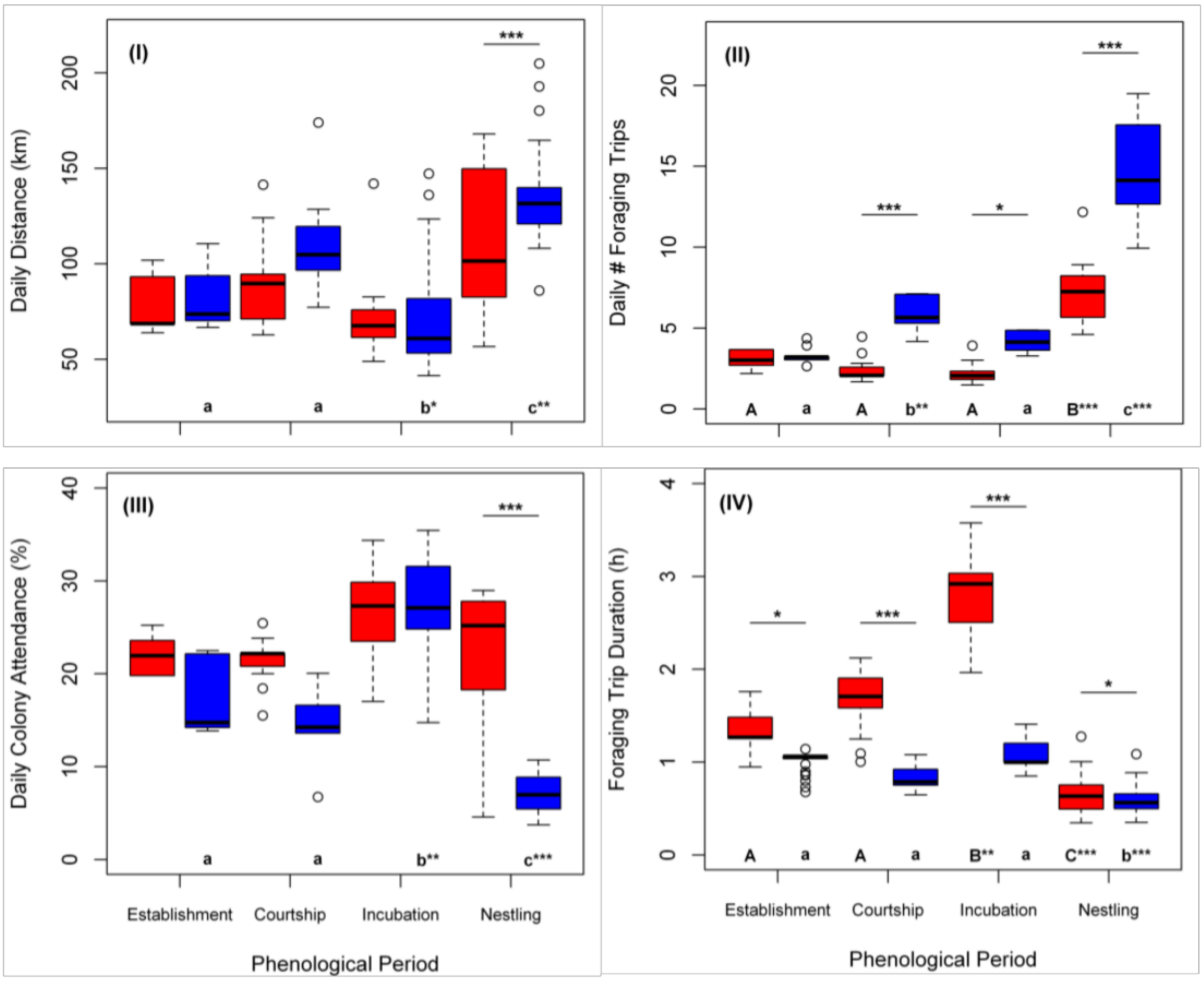


Figure 1. Effect of the interaction between sex and phenological period on lesser kestrel daily distance traveled (I), daily number of foraging trips (II), daily colony attendance (III), and foraging trip duration (IV) predicted by GLMMs. Colors indicate kestrel sex: female in red and male in blue. Significance of post-hoc comparison between sexes within phenological periods is indicated above the bar pairs. Significance of post-hoc comparison between phenological periods within sexes is indicated under the bars: values not sharing a common letter are significantly different, either capital letters for females or lowercase letters for males. P-values are indicated: <0.5 (*), < 0.01 (**) and < 0.001 (***).

Foraging trip level

We identified 2171 complete foraging trips from 14 females (2 from the EBD colony and 12 from the Silo colony) and 16 males (3 from the EBD colony and 13 from the Silo colony), a mean of 72.37 ± 69.88 per individual kestrel (Table 1). We summarize descriptive statistics of foraging movement variables at the foraging trip level in Table 2. The interaction between sex and phenological period was statistically significant for foraging trip duration, indicating a different foraging movement strategy between sexes during the breeding season (Table 5). Lesser kestrels performed foraging trips of a mean duration of 1.16 ± 1.28 hours throughout the breeding season. We found overall statistical differences between sexes, with females performing longer foraging trips than males. Foraging trip duration of males was maintained constant across all phenological periods except in the nestling period when trips were shorter. By contrast, foraging trip duration of females was similar during the establishment and courtship periods, but they became longer during the incubation period and became shorter during the nestling period (Figure 1). We did not find any significant interaction between sex and phenological period on foraging trip distance nor on foraging trip maximum distance from the colony, but we observed statistically significant effects of sex and phenological period on both variables (Figure 3, Table 5). Lesser kestrels flew on average 10.98 ± 11.22 km on each foraging trip and reached a mean of 3.68 ± 3.40 km from the colony throughout the breeding season. Females flew larger distances and also reached farther distances from the colony during their foraging trips in comparison to males. Moreover, lesser kestrels of both sexes flew similar distances and reached similar maximum distances from the colony during the establishment and courtship periods, but both variables increased in the incubation period and decreased during the nestling period. We did not find any statistically significant effect of the breeding colony on foraging trip duration, distance or maximum distance from the colony (Table 5).

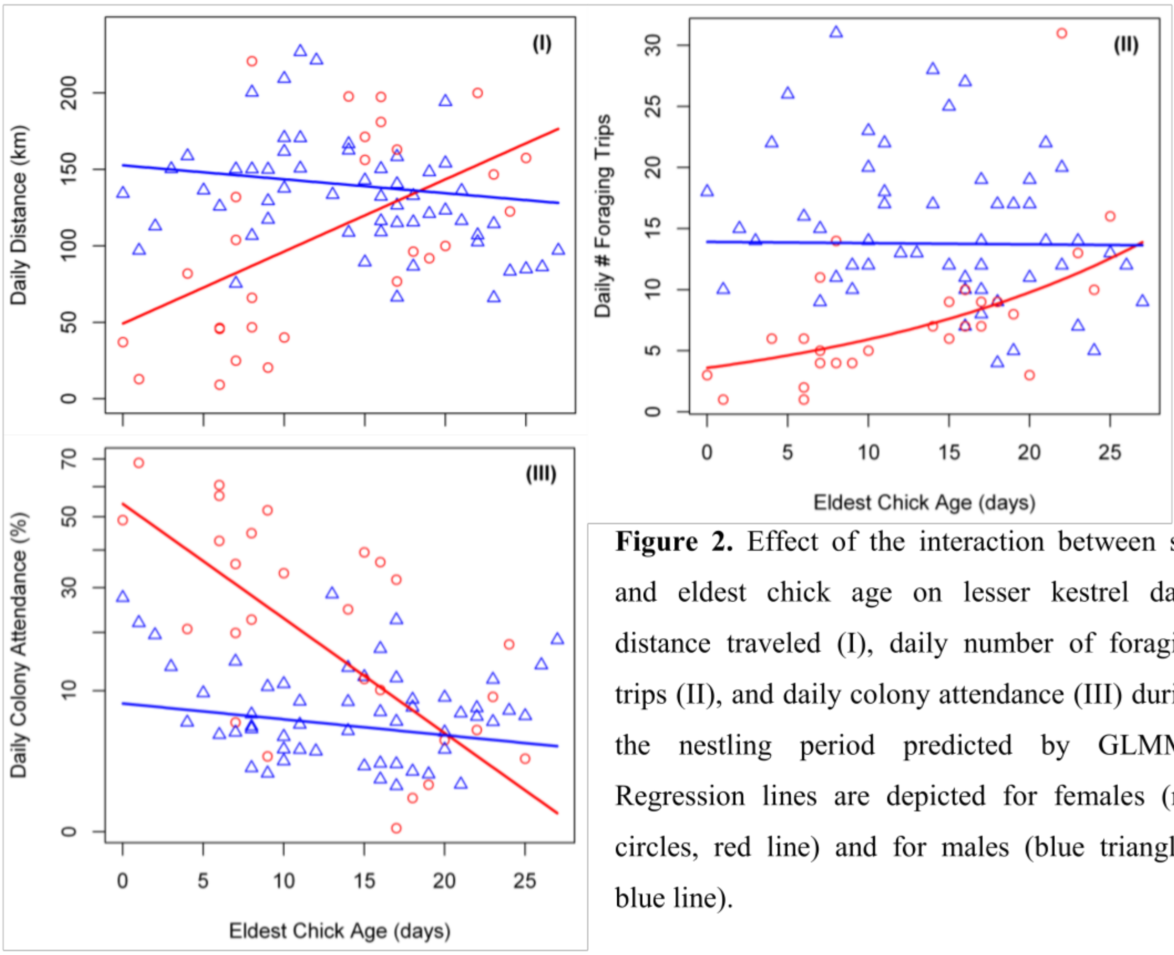


Figure 2. Effect of the interaction between sex and eldest chick age on lesser kestrel daily distance traveled (I), daily number of foraging trips (II), and daily colony attendance (III) during the nestling period predicted by GLMMs. Regression lines are depicted for females (red circles, red line) and for males (blue triangles, blue line).

Table 4. Parameters (estimate ± standard error) on the GLMMs fitted to kestrel foraging variables at the daily level during the nestling period. Statistically significant variables are shown in bold: * $p < 0.5$, ** $p < 0.01$, *** $p < 0.001$, indicated in the first level of each predictor. Sample size = 84 complete days.

Predictor	**Level**	**Response Variable**		
		Distance (km)	**# Foraging Trips**	**Colony Attendance (%)**
Intercept	(ϕ)	49.21 ± 19.21	3.60 ± 1.25	54.20 ± 0.50
Sex * Eldest Chick Age	Female	**4.71 ± 1.11*** **	**0.18 ± 1.01*** **	**-3.72 ± 0.001*** **
	Male	**-0.91 ± 1.31**	**0.003 ± 1.01**	**-0.52 ± 0.002**
Sex	Male	34.69 ± 20.63	**6.14 ± 1.22** **	**-45.91 ± 0.31***
Eldest Chick Age	-	0.70 ± 0.65	0.05 ± 1.01	**-1.51 ± 0.001*** **
Brood Size	-	3.75 ± 6.85	1.09 ± 1.07	-2.95 ± 0.03
Breeding Colony	Silo	-21.27 ± 19.41	0.35 ± 1.20	**-14.04 ± 0.19***
Sampling Frequency	1-minute	35.35 ± 15.52	-0.46 ± 1.17	**-5.01 ± 0.25** **
	3-minutes	4.54 ± 11.07	0.43 ± 1.13	**25.90 ± 0.18**

(ϕ) The intercept includes the effect of female sex, EBD colony and 5-minute GPS sampling frequency.

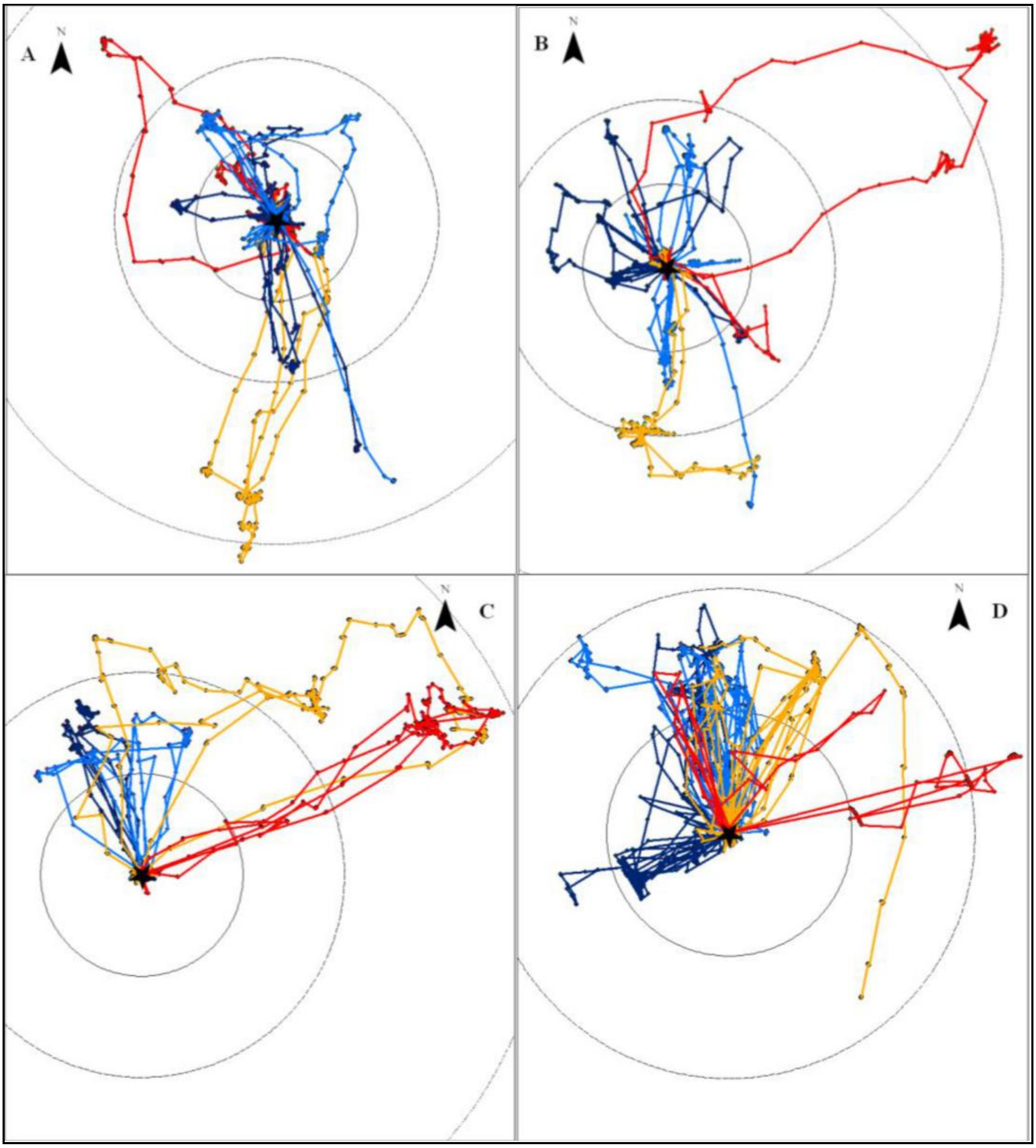


Figure 3. GPS data sampled at 3-min frequency obtained throughout a complete day of tracking from 4 random individual lesser kestrels in each phenological period of the breeding season: Establishment (A), courtship (B), incubation (C), and nestling (D). Colors indicate kestrel females (red and orange) and kestrel males (light and dark blue). Circles show distance buffers from the colony of 2 km (continuous), 5 km (dashed) and 10 km (dotted).

Table 5. Parameters (estimate ± standard error) of the GLMMs fitted to kestrel foraging variables at the foraging trip level. Statistically significant variables are shown in bold: * p < 0.5, ** p < 0.01, *** p < 0.001, indicated in the first level of each predictor. Sample size = 2171 foraging trips.

Predictor	Level	Response Variable		
		Duration (h)	Distance (km)	Maximum Distance (km)
Intercept	(ϕ)	1.03 ± 0.02	16.77 ± 1.16	3.64 ± 1.13
Sex * Phenological Period	Male-Establishment	**-0.30 ± 0.02*** **	-5.28 ± 1.18	-0.63 ± 1.17
	Female-Courtship	**0.27 ± 0.02**	0.77 ± 1.14	-0.19 ± 1.13
	Male-Courtship	**-0.38 ± 0.02**	-4.85 ± 1.41	-0.41 ± 1.16
	Female-Incubation	**1.01 ± 0.02**	9.38 ± 1.16	1.63 ± 1.14
	Male-Incubation	**-0.19 ± 0.02**	-2.95 ± 1.17	-0.04 ± 1.18
	Female-Nestling	**-0.52 ± 0.02**	-5.90 ± 1.19	-0.42 ± 1.13
	Male-Nestling	**-0.61 ± 0.02**	-8.59 ± 1.17	-1.15 ± 1.16
Sex	Male	**-0.35 ± 0.02*** **	**-5.06 ± 1.11** **	**-0.82 ± 1.11* **
Phenological Period	Courtship	**-0.001 ± 0.02*** **	**0.74 ± 1.08*** **	**0.22 ± 1.07*** **
	Incubation	**0.42 ± 0.02**	**4.92 ± 1.09**	**1.01 ± 1.08**
	Nestling	**-0.43 ± 0.02**	**-4.82 ± 1.08**	**-0.62 ± 1.07**
Breeding Colony	Silo	-0.01 ± 0.02	-0.28 ± 1.16	-0.15 ± 1.16
Sampling Frequency	1-minute	**0.24 ± 0.02*** **	**-2.10 ± 1.13*** **	-0.37 ± 1.11
	3-minutes	**0.44 ± 0.02**	**-4.18 ± 1.11**	0.16 ± 1.10
	5-minutes	**0.58 ± 0.02**	**-5.73 ± 1.12**	-0.05 ± 1.11
	10-minutes	**1.02 ± 0.02**	**-1.16 ± 1.35**	1.71 ± 1.32

(ϕ) The intercept includes the effect of female sex, establishment period, EBD colony and 1-second GPS sampling frequency.

Foraging habitat use

We gathered information about habitat use by lesser kestrels of 322 spatial locations, a mean of 10.73 ± 9.88 locations per individual lesser kestrel, range 0 – 34 (n = 30). We did not find any difference in foraging habitat use between lesser kestrel sexes during the breeding season (chi-squared test: $\chi^2 = 9.49$, $p = 0.30$) (Figure 4). Individuals predominantly used non-irrigated cereals as foraging habitat either when harvested (stubble = 25.05%) or non-harvested (cereal = 18.26%), followed by seedlings (12.42%), pastures (11.18%), ploughed (9.01%), sunflower (7.76%), others (7.14%), vineyards (5.90%) and tree groves (3.10%).

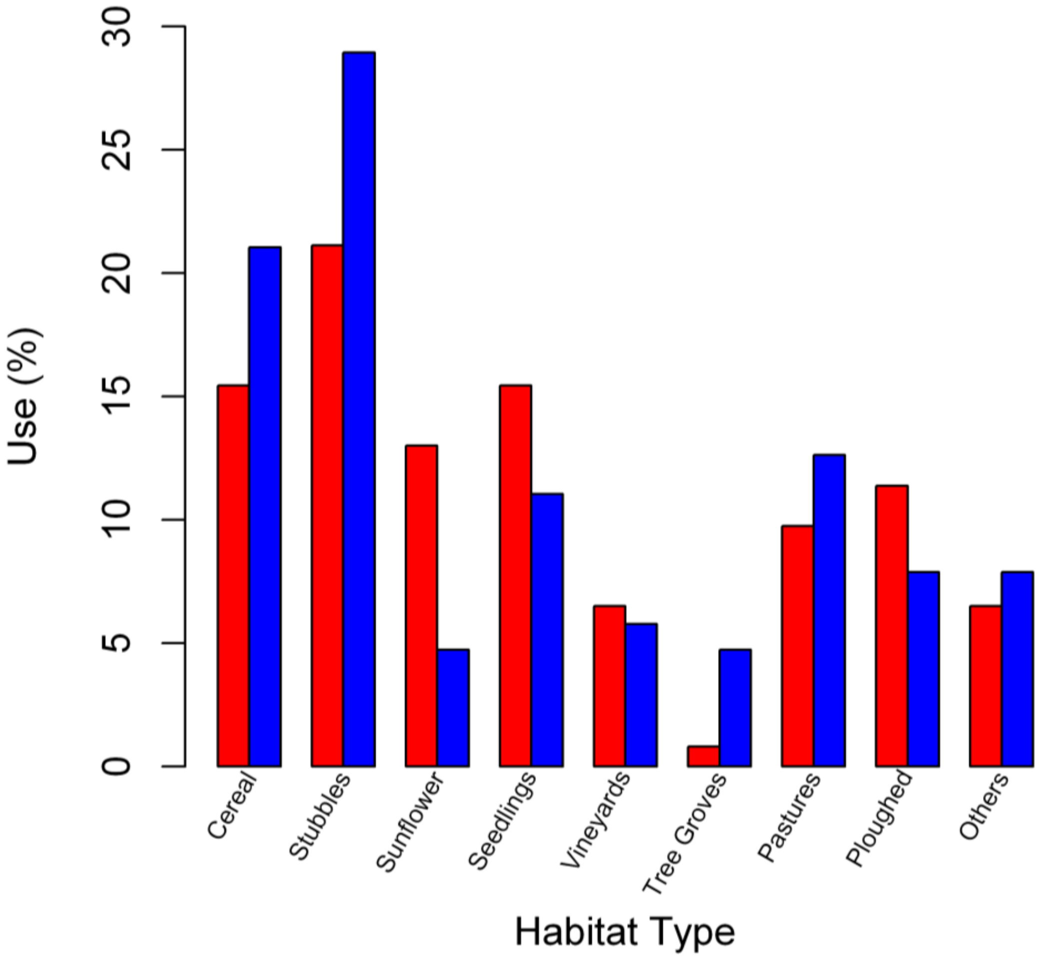


Figure 4. Lesser kestrel percentages of habitat type use separated by sex: female in red and male in blue. Sample size = 322 locations (123 from kestrel females and 199 from kestrel males).

Perch-hunting strategy

We identified 3271 perching bouts during foraging trips, a mean of 1.51 ± 3.07 bout per foraging trip, range 0 – 27 (n = 2171). We had a sample of 2171 foraging trips that were classified as 0 ("without perching bouts", n = 1263) or as 1 ("with perching bouts", n = 908). In those foraging trips with perching bouts, the total perching time was on average 21.79 ± 28.76 min, range 0.52 – 215.00 min per foraging trip. The best model fitted to the probability of performing a perching bout during foraging trips included the interaction between day-of-year and sex as predictors (Table 6). On average, lesser kestrel females showed higher probability of performing a perching bout during foraging trips than males throughout the breeding season. The probability of performing a perching bout during foraging trips decreased as the breeding season advanced, but the trend was steeper for females, both sexes showing similar probabilities in the nestling period (Figure 5).

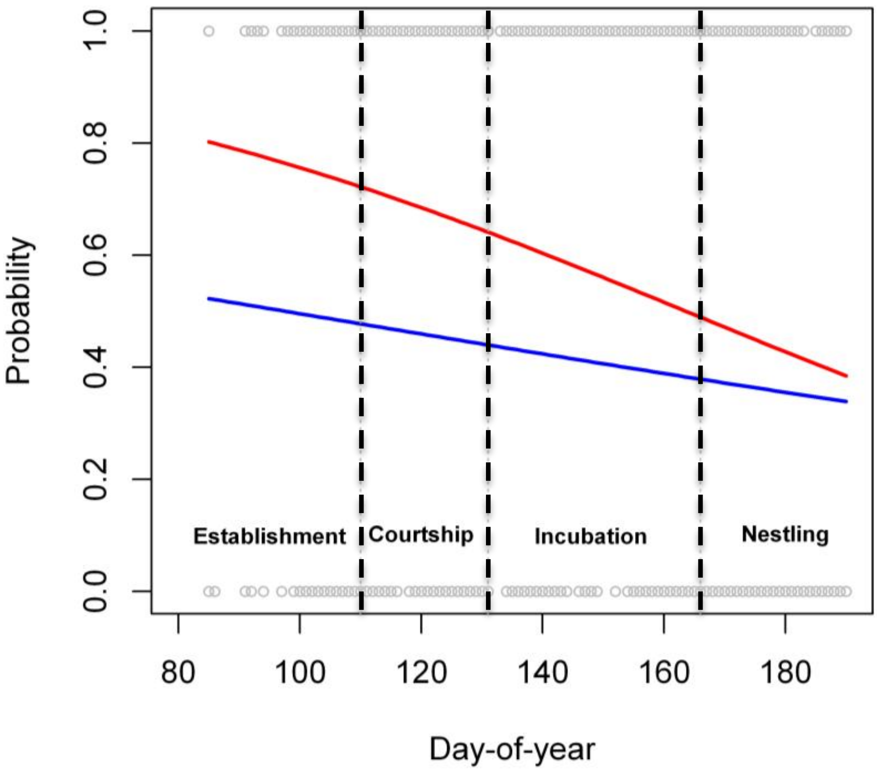


Figure 5. Effect of the interaction between sex and day-of-year on the probability of performing a perching bout during lesser kestrel foraging trips predicted by the GLMM. Regression lines are depicted for females (red line) and for males (blue line). Vertical dashed lines show the mean starting days of courtship, incubation and nestling periods. Circles represent binomial observations. Sample size = 2171 foraging trips.

The best model fitted to total perching time per foraging trip included the interaction between phenological period and sex and GPS sampling frequency as predictors (Table 7). Overall, lesser kestrel females perched longer during foraging trips than males throughout the breeding season, although that difference was more marked in the courtship and incubation periods because females spent more time perched during these periods in comparison to the establishment and nestling ones (Figure 6).

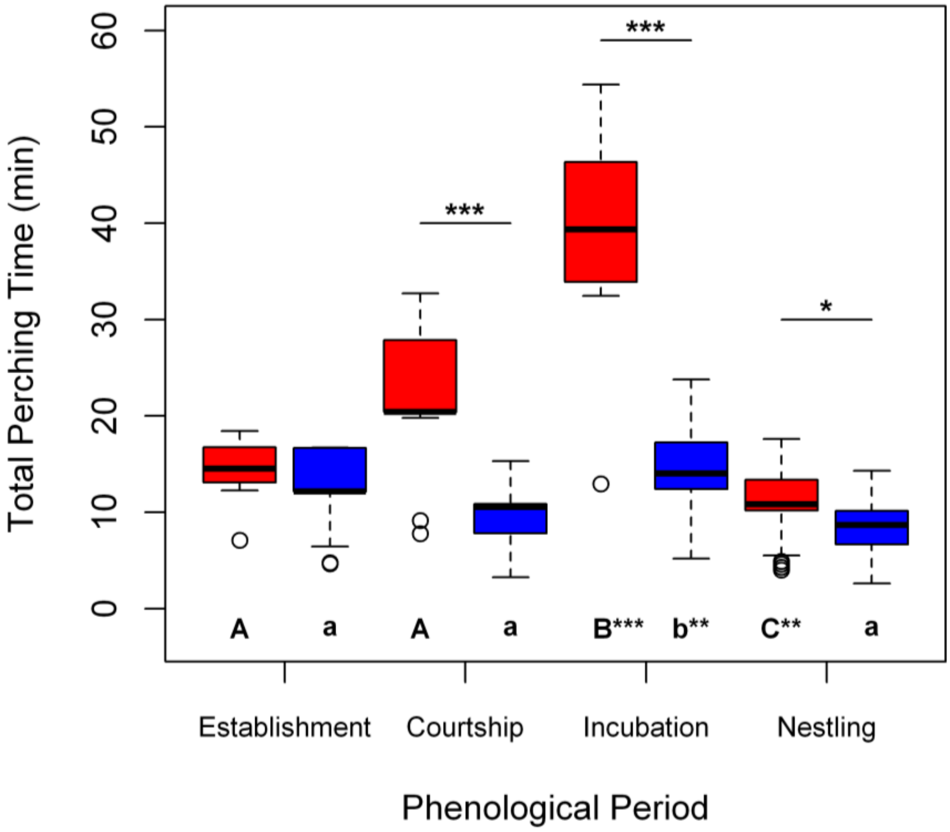


Figure 6. Effect of the interaction between sex and phenological period on total perching time during lesser kestrel foraging trips predicted by the GLMM. Colors indicate kestrel sex: female in red and male in blue. Significance of post-hoc comparison between sexes within phenological periods is indicated above the bar pairs. Significance of post-hoc comparison between phenological periods within sexes is indicated under the bars: values not sharing a common letter are significantly different, either capital letters for females or lowercase letters for males. P-values are indicated: <0.5 (*), < 0.01 (**) and < 0.001 (***).

Table 6. Estimates (β), standard error (S.E.) and statistical significance of predictors included in the GLMM fitted to the probability of performing at least a perching bout during lesser kestrel foraging trips**.** Statistically significant variables are shown in bold: * $p < 0.5$, ** $p < 0.01$, *** $p < 0.001$. Sample size = 2171 foraging trips.

Predictors	**Level**	**β ± S.E. (%)**
Intercept	(ϕ)	94.85 ± 66.39
Sex*Day-of-year*	Female	-0.09 ± 50.11
	Male	-0.03 ± 50.12
Sex**	Male	-9.46 ± 50.05
Day-of-year***	-	-0.13 ± 55.73
Breeding Colony	Silo	0.81 ± 57.28
Sampling Frequency	1-min	-1.14 ± 57.57
	3-min	-1.87 ± 56.65
	5-min	-1.24 ± 57.11
	10-min	-2.63 ± 70.79

(ϕ) The intercept includes the effect of female sex, EBD colony and 1-second GPS sampling frequency.

Table 7. Estimates (β), standard error (S.E.) and statistical significance of predictors included in the GLMM fitted to the total perching time of lesser kestrel foraging trips. Statistically significant predictors are shown in bold: * $p < 0.5$, ** $p < 0.01$, *** $p < 0.001$. Sample size = 908 foraging trips with perching bouts.

Predictors	Level	β ± S.E. (min)
Intercept	(ϕ)	6.96 ± 1.29
Sex*Phenological Period**	Male - Establishment	-0.91 ± 1.25
	Female - Courtship	4.62 ± 1.22
	Male - Courtship	-1.55 ± 1.29
	Female - Incubation	12.29 ± 1.23
	Male - Incubation	1.63 ± 1.31
	Female - Nestling	-0.54 ± 1.22
	Male - Nestling	-2.33 ± 1.28
Sex***	Male	-3.27 ± 1.11
Phenological Period***	Courtship	1.38 ± 1.14
	Incubation	7.74 ± 1.14
	Nestling	-0.95 ± 1.13
Breeding Colony	Silo	0.84 ± 1.14
Sampling Frequency***	1-min	-1.92 ± 1.24
	3-min	5.85 ± 1.21
	5-min	11.09 ± 1.23
	10-min	6.69 ± 2.11

(ϕ) The intercept includes the effect of female sex, establishment period, EBD colony and 1-second GPS sampling frequency.

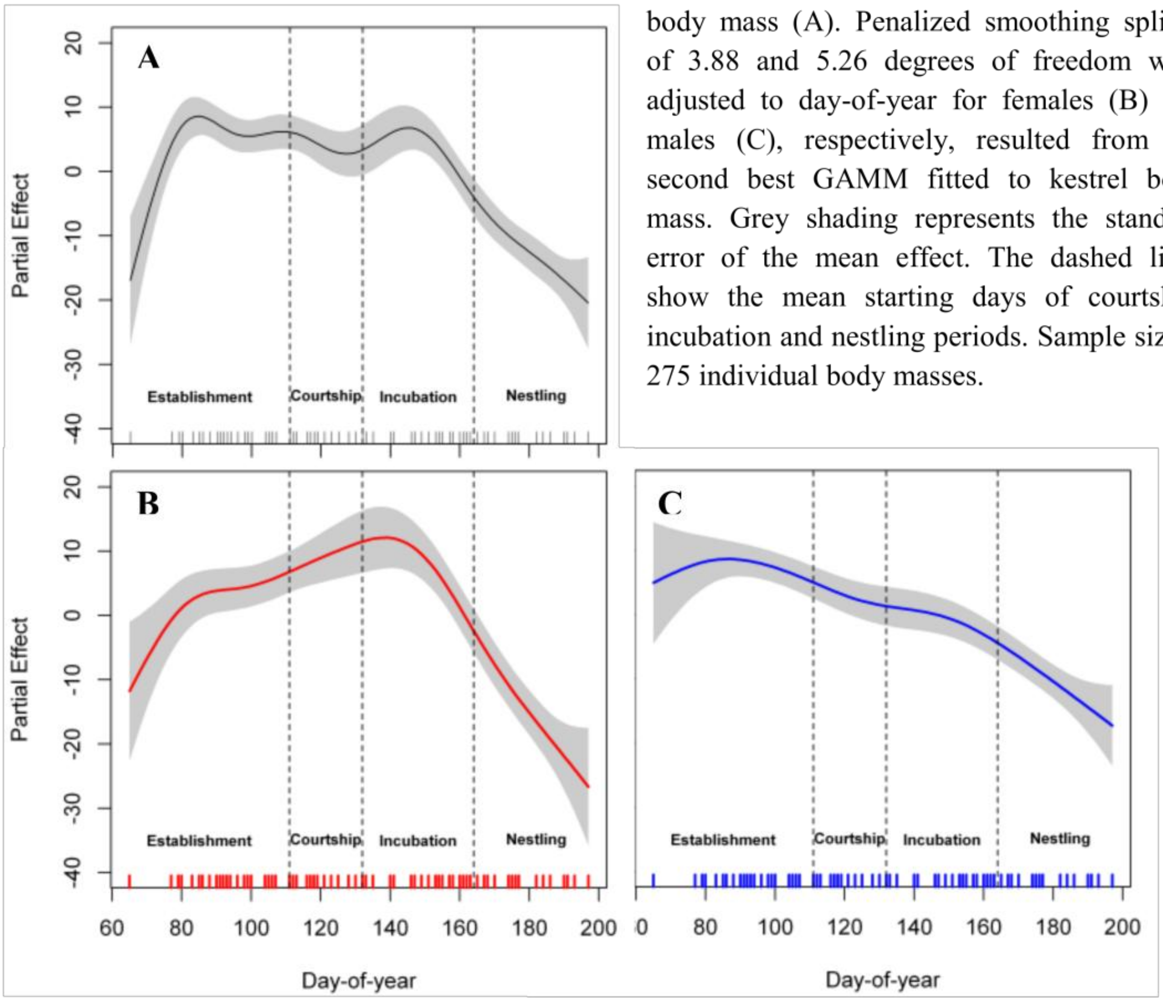
Body condition

We obtained 275 measures of body mass, a mean of 7.08 ± 2.87 measures per year and individual kestrel, range 0 - 11 (n = 30). The best model fitted to kestrel body mass included day-of-year and sex as predictors (Table 8). Lesser kestrel males weighted less than females (Model estimate ± standard error = -18.28 ± 3.49 g), as expected because of the reversed sexual size dimorphism of this species. Kestrel body mass showed a more or less steady trend from the beginning of the breeding season until the incubation period when it rapidly decreased towards the end of the nestling period (Figure 7). Although the best model fitted to kestrel body mass did not include the interaction between day-of-year and sex, we depicted the sexually different temporal trend of individual body mass throughout the breeding season for a better understanding of the process, since we already know that it is slightly different between sexes (Larios et al. 2013). Kestrel male body mass gradually decreased as the breeding season progressed, whereas female body mass increased from the establishment period to the incubation period and then rapidly decreased towards the end of the breeding season (Figure 7).

Table 8. AIC values of GAMMs fitted to lesser kestrel body mass.

Predictors	ΔAIC
Smoothed (Day-of-year)*Sex	11.21
Smoothed (Day-of-year)+Sex	**Best Model**
Day-of-year*Sex	61.28
Day-of-year+Sex	55.29
Smoothed (Day-of-year)	21.65
Day-of-year	76.70
Sex	125.25

Figure 7. Partial effects of the day-of-year (best GAMM) and the interaction between parental sex and day-of-year (second best GAMM) on lesser kestrel body mass. Penalized smoothing spline of 7.52 degrees of freedom was adjusted to day-of-year resulted from the best GAMM fitted to kestrel body mass (A). Penalized smoothing splines of 3.88 and 5.26 degrees of freedom were adjusted to day-of-year for females (B) and males (C), respectively, resulted from the second best GAMM fitted to kestrel body mass. Grey shading represents the standard error of the mean effect. The dashed lines show the mean starting days of courtship, incubation and nestling periods. Sample size = 275 individual body masses.



Discussion

The application of tracking technologies has provided researchers with valuable spatiotemporal information of parental behavior beyond the nest that has broadened the knowledge about avian breeding ecology (e.g., Salamolard & Weimerskirch 1993, Werner et al. 2014). This paper presents evidence on how role specialization by lesser kestrels during the breeding season is reflected in foraging movement patterns, as we hypothesized in accordance with the general trend of raptor role specialization. Studies on this field have been mostly conducted on marine birds as models, so we recurrently turn to them in order to compare our results across the discussion section although the ecological conditions experienced by kestrels can be completely different.

After the spring migration, lesser kestrel arrive at the colony in mid-February where they become established and start to search for the hole that will serve as the nest (Negro et al. 1991). However, it is not until mid-April when breeding pairs are formed and start reproduction (see Rodríguez & Bustamante 2003). How lesser kestrels spend their time and energy in this establishment period is not completely clear yet. Kestrels appear to allocate effort to explore the surroundings of the colony during this period presumably to create a cognitive map of prey availability to be used later in the breeding season when they are more energy and time constrained because of the effort of feeding the nestlings (Chapter One). Nevertheless, the spring migration is an energy-demanding period that deeply diminish fuel reserves, which may have serious carry-over effects on individual fitness (Baker et al. 2004, Strandberg et al. 2009). Thus, kestrels probably dedicate most of their effort in self-maintenance during the establishment period in order to recover fuel store to cope with the incoming breeding season. The absence of any sexual divergence in the daily foraging movement variables during this period indicates that sexual dimorphism of the lesser kestrel is not the main driver for the differences found in the phenological periods that follow (Figure 1), but role specialization is probably involved. Our findings also suggest that lesser kestrels of both sexes act as individual units before breeding pairs are formed early in the breeding season. In agreement with our results, killdeers *Charadrius vociferous* of both sexes dedicate most of their time to somatic effort (mainly foraging) before egg laying, after that individuals spend the major part of the day in parental effort (Brunton 1988). Thus, the establishment period might serve as a preparatory stage during which both kestrel males and females gather strength individually to start reproduction.

When breeding pairs are already formed (the courtship, incubation and nestling periods), the lesser kestrel shows different foraging movement patterns between sexes that suggests that role specialization strongly affects parental movements (Figure 1). In the courtship and incubation periods of many avian species, males continually deliver food to their mates so as to increase female body condition to help them coping with the energy demand associated with the production and incubation of eggs (Lily-Arison 2000, Bader & Bednarz 2011, Galvan & Sanz 2011). This mate-feeding behavior has been described in the lesser kestrel with direct observations at the nest (Donázar et al. 1992). In this study, the lesser kestrel mate-feeding behavior is indicated by the numerous short foraging trips performed by males through the day during the courtship and incubation periods. This constitutes an enormous breeding effort for males that has an effect in the gradual decrease in body mass at a time when kestrel females increase their weight, especially during the courtship period (Figure 7). However, at the same time they are being fed by males, kestrel females also perform a few long foraging trips through day, and as a result both sexes make similar breeding effort in terms of distance traveled per day. This was unexpected for kestrel females as they were supposed to save energy to deal with the cost of incubation. Perhaps the food delivered by kestrel males is not enough and females need to forage by themselves to accelerate the gaining in body mass. Kestrel females adopt the perch-hunting strategy more often and also dedicate longer to be perched during foraging trips than males, causing the observed difference in trip duration between sexes (Figures 5 and 6). The perch-hunting strategy is less energy-consuming than the active hover-hunting strategy, although it is also less time-efficient in finding prey (Anderson & Karasov 1981, Aparicio 1990), so kestrel females seem to prioritize saving energy than time when searching for prey at the foraging patch especially during the courtship and incubation periods. Furthermore, lesser kestrels recurrently replace energy-costly flapping flights with energy-saving soaring-gliding flights as soon as thermals are available along commuting flights, in this way reducing the energy cost of foraging trips (Chapters Three and Four). Therefore, kestrel females could reduce the energy expenditure of their long foraging trips to a great extent by adopting low-cost flight and hunting strategies. In addition, the chromatic dimorphism of the lesser kestrel might confer sex-specific foraging efficiency regarding environmental conditions, as it has been reported in two color morphs of black sparrowhawk *Accipiter melanoleucus* in relation to light levels (Tate et al. 2016). The brown plumage with black stripes of kestrel females may act as disruptive camouflage over the landscape background when using the perch-hunting strategy but in turn it may also makes females more easily detectable against the clear sky by prey when adopting the hover-hunting strategy. Meanwhile, the pallid belly of kestrel males might reduce the contrast over the sky as background and consequently make them more difficult to detect by prey when adopting the hover-hunting strategy but easier to be distinguished when using the perch-hunting strategy. This could partially explain the observed sexual preference for hunting strategies.

Lesser kestrel females tend to stay longer at the colony than males during the courtship period, as expected under the energy-saving hypothesis, although differences are non-significant. In reversed sexual size dimorphic species, such as raptors, females typically entrust with defensive tasks because its larger size should be advantageous when protecting nest or offspring (Andersson & Norberg 1981). This would also explain why females devote longer periods of time at the colony during the courtship period when repelling conspecifics from the chosen nest can be underpinning in colonial species (Wittenberg & Hunt 1985). Additionally, in raptors, it is frequent that females are the main responsible for egg incubation because the larger body mass provides them with higher incubatory efficiency in comparison to males and also allow them to endure better the incubation bouts without eating (Snyder & Wiley 1976, Hirons 1985). Lesser kestrel females are the main incubatory sex as they exclusively incubate eggs during the nighttime, but they equally share this task with males during the daytime (Donázar et al. 1992, Plaza-Jurado 2012). For this reason, we observe an unexpected similar daily colony attendance of both sexes in the incubation period since we only tracked individual lesser kestrel during the daytime, in this way underestimating the daily colony attendance of females because we did not take into account the nocturnal incubating bouts. The time limitation imposed by the incubatory task causes a reduction in the daily number of foraging trips and distance traveled from the courtship to the incubation period, especially in kestrel males. Furthermore, as a consequence of sharing the incubatory task, lesser kestrel females can perform even longer foraging trips in comparison to those of previous phenological period, as we observed, since they have no need of returning quickly to the colony because their mate would be incubating the eggs, similarly to what it has been described in some marine birds (González-Solís et al. 2000, Kato et al. 2008).

Rearing the offspring involves an enormous increase in parental effort for both members of the breeding pair in order to fulfill the high energy demand of the chicks (Masman et al. 1986, Dehnhard et al. 2011), as supported by the observed steepest negative trends of body mass of the whole breeding season (Figure 7). In agreement to the general trend of raptors, lesser kestrel males are the main responsible for provisioning chicks, as indicated by the highest daily number of foraging trips, the largest daily distance and the shortest daily colony attendance observed during the nestling period. However, lesser kestrel females also show higher daily number of foraging trips than in previous phenological periods, as they collaborate with males in feeding chicks (Cáceres 2014), as described in other species (Gaibani et al. 2005, Eldegard & Sonerud 2012, Rishworth et al. 2014). The highest daily number of foraging trips of both sexes observed in this period partially results from the shortening of foraging trip duration probably to maximize energy intake rate to the chicks, which is essential for their growth and survival (Rodríguez et al. 2006). Lesser kestrels can shorten foraging trip duration by reducing the exploratory component of the trips since they would already know about prey availability distribution in the surroundings of the colony so they can concentrate their movements towards high-quality foraging areas at the end of the breeding season (Chapter One). Furthermore, lesser kestrels could also reduce foraging trip duration by adopting the time-efficient hover-hunting strategy when searching for prey at the foraging patch. Prey availability determines lesser kestrel decision about which hunting strategy to use: kestrels preferentially adopt the perch-hunting strategy when preferred prey (large grasshoppers) are less available, whereas they mainly use hovering flights to capture them when prey availability is higher (Chapter Four). A peak in preferred prey availability takes place during lesser kestrel nestling period (Rodríguez et al. 2010), so individuals are expected to mostly use hovering flights to capture prey, as supported by the less-frequent use of perch-hunting and the shorter time invest in it during this period (Figures 5 and 6).

We do not find any evidence of lesser kestrels adjusting parental effort as a function of the energy demand associated to clutch size, contrary to what reported in other raptor species (Arroyo et al. 2002), but they appear to adjust it to the energy demand associated to chick growth. While kestrel males maintained constant parental effort throughout the nestling period, females increase it as the nestling period progresses. As chicks grow older and require more energy intake, the provisioning activity of males would not be enough and females would be forced to help them to deliver food to the nest. That would explain why kestrel females increase the daily number of foraging trips and the daily distance traveled as chick age increases, as described in some marine birds (Paredes et al. 2006). In addition, lesser kestrel males drastically decrease colony attendance from the incubation to the nestling period and maintain it through the nestling period, as expected because of the elevated energy demand, but females stay at the colony similar amount of time during the incubation period and early in the nestling period. Afterwards, females attended the colony less as chicks grow older. This agrees with that described in the Spanish imperial eagle *Aquila adalberti* (Margalida et al. 2007), but it disagrees with that reported in bearded vultures *Gypaetus barbatus* where both sexes gradually decrease nest attendance as chick age increases probably because this species is not role-specialized and shows little sexual dimorphism (Margalida & Bertran 2000). Our findings do not support the "energy constraint hypothesis" that expects females to increase the foraging effort to feed themselves at the beginning of the nestling period in order to restore the energy invested during incubation so they can successfully complete the breeding season (e.g., Welcker et al. 2009). Nevertheless, it has been stated that females of some bird species stay longer at the nest to brood the offspring during the first days after hatching as chicks are little capable to thermoregulate (Weimerskirch et al. 2009). Additionally, it has been proposed that raptor females stay longer at the nest during the nestling period because they feed the offspring by partitioning large prey delivered by males, especially when chicks have recently hatched, in this way maximizing the time males are foraging (Slagsvold & A. Sonerud 2007, Sonerud et al. 2013). Therefore, both options could explain the initial elevated colony attendance of lesser kestrel females before decreasing as the nestling period progresses.

Our results also indicate a sexual spatial segregation of the lesser kestrel throughout the breeding season: females consistently fly farther from the colony than males during their foraging trips. This would be the cause of the intersexual differences in home ranges previously described in this species with females covering larger areas than males during the breeding season (Negro et al. 1993). In contrast, Gustin et al. (2014) found the opposite pattern with kestrel females foraging closer to the colony than males, although they tracked individuals only during the nestling period when we found smaller differences in foraging trip parameters between sexes. Spatial segregation between sexes, and between age classes, has been attributed to foraging strategies that aims to reduce intraspecific competition, and the mechanisms that create it can be either competitive or non-competitive (Phillips et al. 2004, Breed et al. 2013). It has been pointed out that sexually different nutritional requirements may lead to a niche division in prey consumption and/or in foraging habitat selection between sexes that results in the spatial segregation (Breed et al. 2006, Ludynia et al. 2013, Camphuysen et al. 2015). There is no evidence of a different diet between sexes in the lesser kestrel, except during the courtship period when females consume higher proportion of mole-crickets (*Grillotalpa grillotalpa*) than males (Catry et al. 2016). However, we observe a maintained sexual spatial segregation throughout the whole breeding season, not only during the courtship period, so a different diet does not seem to be the cause. We do not observe any sexual difference in the habitat use of the lesser kestrel (Figure 4), so we also reject it as the driver for the sexual spatial segregation. Both sexes preferentially forage in cereal crops, either harvested or not, which is in the line of the foraging habitat selection previously described in the lesser kestrel (Tella et al. 1998, Franco & Sutherland 2004, Rodríguez et al. 2013, Catry et al. 2014). Sexual spatial segregation has been also related to sex-biased competition abilities (Catry et al. 2006). In sexual size dimorphic species, the larger sex normally outcompetes the smaller one and forces it to displace to suboptimal foraging areas (González-Solís et al. 2000, Hennicke et al. 2015). The American kestrel *Falco sparverius*, a closely related species, shows a sexual spatial segregation in its wintering grounds that reflects a despotic distribution presumably resulting from larger females selecting open areas with lower predation risk and displacing smaller males to forested areas with higher predation risk (Ardia & Bildstein 1997). From an individual perspective, it would be more advantageous for both lesser kestrel sexes to forage in areas located closer to the colony because of the lower energy and time invested in commuting flights than to forage in those located farther (Wilson et al. 2012). In an scenario of competitive exclusion, the larger lesser kestrel females would forage closer to the colony and would displace the smaller males to foraging areas located farther. Nevertheless, we observe the opposite pattern with the smaller lesser kestrel males foraging closer to the colony than the larger females. The fact that the spatial segregation between sexes is reduced during the establishment period than in the following phenological periods leads us to think that it may be not caused by a competitive exclusion, but role specialization might be involved. Lesser kestrel males, which are the main responsible for provisioning tasks, could forage closer to the colony in order to reduce foraging trip duration and consequently maximize prey delivering rate at the nest. Meanwhile, lesser kestrel females, which seem to prioritize saving energy when foraging, could fly with low flight cost by soaring on thermals towards foraging areas located farther from the colony in order to reduce competition for food with males since prey depletion in the surroundings of the colony has been reported as a common negative density-effect in colonial species, including the lesser kestrel (Ashmole 1963, Bonal & M. Aparicio 2008, Chapter Three). Indeed, in the nestling period when preferred prey availability is highest (Rodríguez et al. 2010) and both sexes contribute to feed the chicks, we observe that individuals forage closer to the colony than in previous phenological periods. Our findings suggest that the sexual spatial segregation could be caused by lesser kestrel breeders aiming to increase offspring survival at the cost of compromising their own (i.e., parental care) through reducing prey depletion close to the colony and intersexual competition between breeding pair members. Therefore, the sexual spatial segregation of the lesser kestrel might well be a result from an adaptive foraging strategy based on role specialization in order to be successful in reproduction.

To conclude, lesser kestrels changed their foraging movement strategy throughout the breeding cycle differently regarding individual sex. Both sexes show similar foraging movement patterns early in the breeding season when no role specialization has been established yet. However, as soon as the breeding pairs are formed, sexes show distinct foraging movement patterns in accordance with the role specialization of this species. Overall, males perform higher daily number of foraging trips and fly larger daily distances than females as they are entrusted with food provisioning tasks. In contrast, females tend to stay longer at the colony on a daily basis because of being primarily devoted to defensive tasks, although they also help males in feeding chicks when these get older. The lesser kestrel shows a sexual spatial segregation that may result from an adaptive foraging behavior based on role specialization to reduce intersexual competition in the surroundings of the breeding colony where prey depletion is a negative consequence of colonial breeding. This research complements traditional studies on breeding ecology by providing new perspectives of raptor parental behavior away from the nest using the newest tracking technologies. This study also highlights the plasticity of movements shown by a small raptor species in response to temporal dynamic requirements throughout the breeding season.

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CHAPTER THREE

Why do kestrels soar?

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Abstract

Individuals allocate considerable amounts of energy to movement, which ultimately affects their ability to survive and reproduce. Birds fly by flapping their wings, which is dependent on the chemical energy produced by muscle work, or use soaring-gliding flight, in which chemical energy is replaced with energy harvested from moving air masses, such as thermals. Flapping flight requires more energy than soaring-gliding flight, and this difference in the use of energy increases with body mass. However, soaring-gliding results in lower speeds than flapping, especially for small species. Birds therefore face a trade-off between energy and time costs when deciding which flight strategy to use. Raptors are a group of large birds that typically soar. As relatively light weight raptors, falcons can either soar on weak thermals or fly by flapping with low energy costs. In this paper, we study the flight behavior of the insectivorous lesser kestrel (*Falco naumanni*) during foraging trips and the influence of solar radiation, which we have adopted as a proxy for thermal formation, on kestrel flight variables. We tracked 35 individuals from two colonies using high frequency GPS-dataloggers over four consecutive breeding seasons. Contrary to expectations, kestrels relied heavily on thermal soaring when foraging, especially during periods of high solar radiation. This produced a circadian pattern in the kestrel flight strategy that led to a spatial segregation of foraging areas. Kestrels flapped towards foraging areas close to the colony when thermals were not available. However, as soon as thermals were formed, they soared on them towards foraging areas far from the colony, especially when they were surrounded by poor foraging habitats. This reduced the chick provisioning rate at the colony. Given that lesser kestrels have a preference for feeding on large insects, and considering the average distance they cover to capture them during foraging trips, to commute using flapping flight would result in a negative energy balance for the family group. Our results show that lesser kestrels

prioritize saving energy when foraging, suggesting that kestrels are more energy than time-constrained during the breeding season.

Resumen

Los individuos invierten considerables cantidades de energía para moverse, lo que en última instancia afecta sus capacidades de supervivencia y reproducción. Las aves pueden volar mediante el batido de sus alas, lo cual depende de la energía química producida por el trabajo de los músculos del vuelo, o mediante el planeo, en cuyo caso la energía química es reemplazada por energía extraída de masas de aire en movimiento, como las corrientes térmicas ascendentes. El vuelo batido requiere más energía que el vuelo planeado y esta diferencia se incrementa a medida que la masa corporal de las aves aumenta. Sin embargo, el vuelo planeado es más lento que el vuelo batido, especialmente en especies pequeñas. Por tanto, las aves se enfrentan a un balance entre costes de energía y tiempo a la hora de decidir qué estrategia de vuelo usar. Las rapaces son un grupo compuesto por grandes aves típicamente planeadoras. Como excepción, los halcones son pequeñas rapaces que pueden planear en débiles corrientes térmicas o pueden volar batiendo sus alas con bajo coste energético asociado. En este artículo, estudiamos el comportamiento de vuelo del cernícalo primilla (*Falco naumanni*), un pequeño halcón insectívoro, durante los viajes de caza y la influencia de la radiación solar (tomada como proxy de la formación de térmicas) en las variables de vuelo de los cernícalos. Se usaron GPS-dataloggers de alta frecuencia para el seguimiento de 35 individuos procedentes de dos colonias de cría durante cuatro temporadas de cría consecutivas. De forma contraria a lo esperado, los cernícalos dependieron fuertemente del planeo en térmicas durante los viajes de caza, especialmente en los períodos de alta irradiación solar. Esto produjo un patrón circadiano de las estrategias de vuelo de los cernícalos que conllevaron una segregación espacial de las áreas de caza. Los cernícalos usaron el vuelo batido para dirigirse a áreas de caza cercanas a la colonia

cuando no había corrientes térmicas disponibles. Sin embargo, tan pronto como éstas se formaron, los individuos planearon en ellas para dirigirse a áreas de caza más alejadas de la colonia, especialmente en aquella rodeada por áreas de caza de baja calidad. Esto produjo una reducción de la tasa de ceba de los pollos en el nido. Teniendo en cuenta que los cernícalos tienen preferencia por alimentarse de grandes insectos y considerando la distancia media recorrida para capturarlos durante los viajes de caza, volar batiendo las alas resultaría en un balance energético negativo para el grupo familiar. Nuestros resultados muestran que los cernícalos primilla priorizan el ahorro energético a la hora de buscar alimento, sugiriendo que los individuos están más limitados energéticamente que en términos de tiempo durante la época reproductora.

Introduction

Movement, as a crucial process that determines individual life history, affects survival and reproduction. Animals allocate energy to support physiological and behavioral traits, but especially to move within a landscape (e.g. (Gittleman & Thompson 1988, Gleiss et al. 2011)). Most avian species move by flying, either through flapping or soaring-gliding. The majority of birds fly by flapping their wings which requires their muscles to convert chemical energy into work (Pennycuick 2008), although they have also evolved morphological and behavioral adaptations to take advantage of the energy available in moving air masses and to fly by soaring-gliding with little muscle work (Hedenström 2008, Duerr et al. 2014). Some sea birds depend on strong winds to soar when flying large distances over ocean waters using dynamic soaring (Sachs et al. 2012). By contrast, terrestrial birds can exploit upward winds deflected by cliffs and ridges to fly without flapping their wings using slope soaring, or they can exploit rising air columns, also known as thermals, using thermal soaring (Lanzone et al. 2012). Thermals are created by the differential heating by solar radiation of the soil surface and the air in contact with it. Birds circle up on thermals , increase their flight altitude and then glide down to the next thermal in a similar way to man-made gliders (Ákos et al. 2010). Birds are therefore able to substitute muscle power with kinetic or potential energy extracted from the environment when soaring-gliding.

Flight theory predicts that the power needed for a soaring-gliding flight is about 1.5 times the basal metabolic rate, whereas flapping flight requires several times more energy (Pennycuick 1972, Norberg 1996). This statement has been verified in empirical studies on diverse flying species (Baudinette & Schmidt-Nielsen 1974, Duriez et al. 2014). Additionally, the power needed for flapping flight increases steeply with body mass (Pennycuick 1972, Ellington 1991), at the same time as the mass-specific basal metabolic rate decreases (Lasiewski & Dawson 1967). Therefore, the difference in energy expenditure between the two flight strategies increases with body mass (Hedenström 1993). As a consequence, the heavier a bird is, the more energy efficient it is to adopt soaring-gliding over the flapping flight strategy (Duerr et al. 2012). The question then arises of why not all birds use the soaring-gliding flight strategy if it is so advantageous.

There are other morphological traits apart from body mass, such as wing shape or wingspan that affect bird flight performance and consequently can be critical in deciding which flight strategy to adopt (Viscor & Fuster 1987, Norberg 1996). But, in the case of thermal soaring, the answer may also lie in the spatial and temporal constraints imposed by this flight strategy that potentially offsets its energy advantage. Thermals are the result of convective processes between the earth's surface and the air in contact with it, and do not develop uniformly over an heterogeneous landscape (Young 1988). The spatial scale of thermal formation is of the order of hundreds or thousands of meters, which usually exceeds the home range of smaller bird species and consequently prevents them from using thermal soaring when searching for resources (Schoener 1968). In addition, as thermals are weak over the sea, birds are forced to make detours over land when using soaring-gliding flights during migration, which in turn extends traveling time (Alerstam 2001). Furthermore, thermals are not permanently available because their formation depends on adequate weather conditions, which limits the time available to fly (Bohrer et al. 2011). Thermal formation follows a daily pattern: it begins shortly after sunrise, increases in depth and intensity throughout the morning, peaks around noon, and then decreases towards sunset (Young 1988). Soaring birds usually adapt their daily movements to this predictable pattern in order to exploit the thermals available in an efficient way and thus fly with reduced costs (Mellone et al. 2012). In addition, given the spatial and temporal pattern in thermal formation that soaring birds have to cope with, they fly at lower cross-country speeds when using thermal soaring than when flapping (Hedenström 1993, Spaar 1997, Pennycuick 2008). Birds therefore face a trade-off between energy and time costs when deciding which strategy to adopt when flying. As a general trend, large terrestrial birds use thermal soaring in order to reduce flight costs, whereas small birds use flapping flights as the energy benefits linked to soaring on thermals does not compensate for the time costs experienced (Hedenström 1993).

Raptors are a representative group of large soaring birds. Within this group, falcons are relatively light with a low body mass and low wing loading (Mendelsohn et al. 1988). These morphological characteristics allow them to soar on a wide range of thermal intensities (Pennycuick 1971) but also to fly by flapping with relatively low energy costs (Duerr et al. 2012). Falcons do not seem as constrained by thermal formation as larger raptors do, and they can fly throughout the entire day and even at night when thermals do not form (Strandberg et al. 2009, López-López et al. 2010, Limiñana et al. 2012). Moreover, falcons are able to cross large bodies of water where thermals are weak or absent (Kumar 2014, Agostini, Panuccio, et al. 2015). Accordingly, falcons have traditionally been considered flapping raptors with a preference for powered flight, without any need for thermals to fly (Viscor & Fuster 1987, Spaar & Bruderer 1997, Strandberg et al. 2009, Mateos-Rodriguez & Liechti 2012, Limiñana et al. 2013, Vansteelant et al. 2014, Agostini, Scuderi, et al. 2015). Nevertheless, preliminary data on the foraging movement of the lesser kestrel, *Falco naumanni* (one of the smallest falcons in the world), showed higher than expected frequencies of soaring when individuals were commuting between the breeding colony and the foraging areas. We therefore designed a study to evaluate to what extent this species relies on thermal soaring for foraging.

Lesser kestrels are small insectivorous colonial falcons that breed in buildings and cliffs in steppe-like habitats, pastures and non-irrigated crops

(Bustamante 1997). Throughout the breeding season, lesser kestrels continuously prospect the surroundings of their colonies to locate the ephemeral, concentrated, and unpredictable abundances of insects across a heterogeneous environment [30]. Because kestrels do not store prey items they have to return to the colony to provision their mates or chicks once they capture a prey. The soaring-gliding flight strategy would allow kestrels to reduce flight costs when searching for food during an energy-intensive period such as the breeding season (Masman et al. 1988). In this study, we tracked individual lesser kestrels using high frequency GPS-dataloggers to investigate flight behavior along foraging trips during the breeding season. 1) We hypothesized that lesser kestrels would adopt the soaring-gliding flight strategy along foraging trips in suitable thermal conditions. 2) We expected individuals to increase flight altitude as thermals increase in depth and intensity throughout the day in order to obtain higher potential energy values during foraging trips. 3) We also expected individuals to use this potential energy gain to fly larger distances with reduced costs and to reach foraging patches located far from the colony, especially if prey availability is low close to the colony. Additionally, 4) we calculated power requirements for lesser kestrels to complete a foraging trip and the daily energy expenditure when adopting a pure flapping or a pure soaring-gliding flight strategy in order to evaluate the trade-off between the two flight strategies.

Material and Methods

Ethics Statements

The environmental authority (Dirección General de Gestión del Medio Natural y Espacios Protegidos, Junta de Andalucía) provided permits to access the study colonies and to attach GPS-dataloggers to this endangered species. The Doñana Biological Station Ethics Committee on Animal Experimentation (CEEA-EBD), the Bioethics Subcommittee of the Spanish National Research Council (CSIC) and the Consejería de Agricultura, Pesca y Desarrollo Rural (Junta de Andalucía) all reviewed the marking protocol and approved the research plan of the HORUS project.

Study area

We studied lesser kestrels at two breeding colonies in the Guadalquivir river basin (southwestern Spain). The terrain is predominantly flat (20 – 240 m) but features some hills and escarpments and is dominated by arable crops (Fernandez et al. 1992), predominantly wheat and sunflower, although olive groves, fruit trees and vineyards are also present. The Silo colony is situated at a building with a grain elevator located in agricultural land, while the EBD colony is situated 50 km away on the roof of our research institute in Seville and dominated by urban land uses (Figure 1). At both sites, the lesser kestrels nest inside nest-boxes installed at both buildings.

Field procedures

Lesser kestrel breeding pairs were monitored during the 2011-2014 breeding seasons. We attached GPS-dataloggers (GiPSy models 2, 4, and 5; Technosmart, Rome, Italy) with small batteries (90 - 100 mA) to the birds nesting in nest-boxes. GPS devices were fixed to the birds' backs using a micro back-pack harness supplied by Marshall Radio Telemetry (North Salt Lake, Utah, U.S.A.) or a similar hand-made harness formed by a carbon fiber plate and a 4 mm wide Teflon ribbon (Bally Ribbon Mills, Pennsylvania, U.S.A.). GPS-dataloggers were covered with a protective thermoretractable case. The total mass of the equipment (harness + GPS+ battery) was about 6 g and never exceeded the 5% of the lesser kestrel's mean body mass, which is within the recommended limits for flying animals (Barron et al. 2010). To get the birds used to the harness and the GPS device, we fixed a dummy GPS-datalogger with the same weight to the harness at least a week before fixing the real device and starting to record the birds' movement (see details of the procedure in Chapter One).

We attached GPS-dataloggers to 39 individual lesser kestrels during the study period, but were unable to recover tracking data from 4 of them. Finally, we obtained a total of 825,365 GPS-fixes from 35 individuals (17 females and 18 males). Some of them were tracked during two (8 individuals) or three (1 individual) breeding seasons. We configured the GPS-dataloggers at five different sampling frequencies: one fix per second, one fix per minute, or every 3, 5, and 10-minutes. Since the GPS stored the data in the logger, we had to recapture the individuals to recover the data. A new full-powered device was then deployed before releasing the individual to be able to continue tracking. The kestrels were captured when they entered the nest-boxes using remote-controlled sliding doors. Individuals were telemetered during a mean of 55.86 ± 30.72 days per breeding season, range 6 – 100 days; they were recaptured a mean of 5.16 ± 2.44 times per year, range 2 – 11 (n = 45). Data were collected during daylight hours (5 to 20 h UTC) during the breeding season (March – July). We removed the harnesses from the kestrels at the end of each breeding season. The tracking data can be consulted on Movebank (www.movebank.org) (DOI: 10.5441/001/1.sj8t3r11).

Weather data

Because solar radiation is the engine for thermal updraft, it can be considered a proxy for thermal formation (Garratt 1994, Ákos et al. 2010). We obtained solar radiation data from the agroclimatic station network of the Andalusian Agricultural Department (http://www.juntadeandalucia.es/medioambiente/ servtc5/WebClima/), collected at the meteorological station of La Palma del Condado by a Skye SP1110 pyranometer every 30 minutes. The station is situated 192 m above sea level, 3 km from the Silo colony and 48 km from the EBD colony. It is possible to estimate directly thermal and orographic uplift from meteorological models, but the models available provide these data at low temporal (6 hours) and spatial (0.75 degrees) resolutions. We obtained estimates of thermal and orographic uplift throughout the study period from the Movebank Environmental Data Automated Track Annotation

(Env-DATA) system (Dodge et al. 2013). Thermal and orographic uplift estimates were calculated by reanalyzing weather data from the European Centre for Medium-Range Weather Forecasts (ECMWF). We obtained two orographic uplift estimates that were calculated using data from different digital elevation models (DEM): the Shuttle Radar Topography Mission (SRTM) 90-m DEM, and the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) 30-m DEM. We did not expect slope soaring to be a frequent flight strategy for lesser kestrels in our study area which is mostly flat. Nonetheless, because of the existence of hills and escarpments that can deflect wind that can be exploited by individuals, we decided to evaluate the effect of orographic uplift on lesser kestrel flight behavior. Because of the temporal and spatial resolutions of the estimates, we had only 4 values per day of thermal and orographic uplift at the location of each colony.

Flight variables

GPS locations were explored graphically using GIS (ArcGIS 10, ESRI, Redlands, California, U.S.A.) to identify individual foraging trips. We use the term foraging trip to refer to a set of consecutive locations of an individual kestrel which, start from the breeding colony and extend beyond 300 m and in which we are able to identify a foraging event (mostly clumped locations at low altitude above the ground with highly variable instantaneous speed). The details of the foraging trip identification and segmentation procedure can be found in Chapter One. The movements from the colony to the area where the foraging event took place and the return movement to the colony are referred to as commuting flights (outward and inward flight, respectively). Incomplete foraging trips, i.e. trips in which departure from or arrival at the colony was not recorded by the GPS were removed from statistical analyses. We also removed those foraging trips that started or finished at roosting sites away from the colony. GPS devices provided the flight altitude and instantaneous speed for each location. We calculated the flight altitude above ground as the difference between the flight altitude recorded by the GPS and the topographic elevation obtained from a 10 m-resolution DEM obtained from the Andalusian Environmental Department (REDIAM, Junta de Andalucía, 2010-2011). We removed any position with low accuracy (less than 4 satellites, dilution of precision over 3, or positions with negative altitude values).

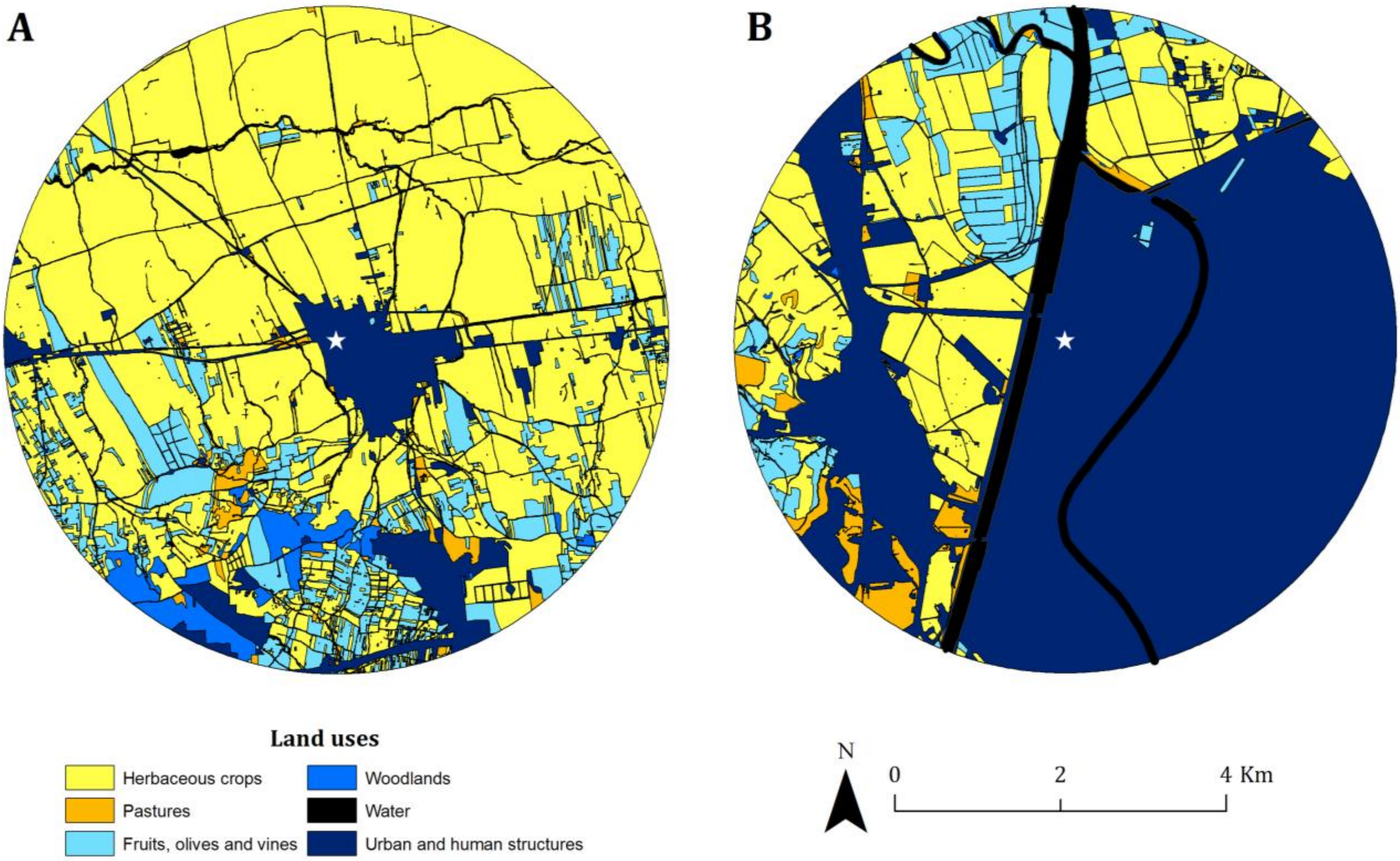

Figure 1. Land uses within a 4 km-buffer around the two study colonies: Silo colony (A) and EBD colony (B). The white star indicates the location of the colony in each panel. Good foraging habitats for the lesser kestrel are represented by shades of yellow and poor foraging habitats represented by shades of blue.

We analyzed commuting flights recorded at 1-second intervals in order to investigate the use of thermals by lesser kestrels. Thermal soaring events in these commuting flights recorded at 1-s are easily detectable through a circular flight path with an increase in flight altitude and positive climb speed (Figure 2) (Ákos et al. 2010, Duerr et al. 2012). Soaring events were considered to be any flight segment with a circular pattern lasting more than 5 s, with positive vertical speed and that resulted in an increase in altitude of at least 10 m. To err on the conservative side, we only considered the climbing phase of the thermal soaring events for our analyses since the gliding phase might include flapping flights. For commuting flights in which we identified thermal soaring events, we calculated the following parameters indicative of the intensity or efficiency in the use of thermals by kestrels: (1) number of thermal soaring events and (2) accumulated ascent per horizontal distance covered; and (3) total ascent and (4) mean climb speed per thermal soaring event. Furthermore, we analyzed all foraging trips regardless of the sampling frequency at which they were recorded, from 1-second to 10-minutes, in order to study changes in the daily pattern of lesser kestrel flights. For these foraging trips, we calculated the following flight variables: (1) mean cross-country speed and (2) maximum flight altitude recorded per commuting flight; and (3) maximum distance from the colony and (4) duration of the foraging trip. To reduce the influence of outliers we used the third quartile of flight altitude as the maximum flight altitude because a single maximum value might be highly influenced by GPS altitude errors. In order to study the influence of solar radiation in all those flight variables, we used the value of solar radiation measured at the time rounded to the nearest half-hour when each commuting flight started. In foraging trips in which the outward flight was not recorded because the sampling frequency was longer than its duration, we calculated the time rounded to the nearest half hour when the first location was obtained and the solar radiation measured at that time. Additionally, to estimate the importance of thermal or topographic uplift in determining lesser kestrel foraging flight strategies, we built models to evaluate its influence on flight variables. As thermal and orographic uplift are estimated at a rough temporal scale (6-h intervals), we calculated the mean values of every flight variable obtained from commuting flights or foraging trips (depending on the variable) included in each of these intervals, and separately for each colony. We pooled all individuals and flights tracked at each colony during each 6-h interval to estimate the mean values.

Energy expenditure

To calculate lesser kestrel flight power requirements we used Pennycuick's Flight software version 1.24 (http://www.bristol.ac.uk/biology/people/colin-j-pennycuick). We considered a body mass of 130 g (the mean value for the species (Cramp & Simmons 1980)) to carry out the calculations. We also assumed a mean wingspan of 0.68 ± 0.02 m (± standard deviation) and a mean wing area of 0.062 ± 0.0002 m^2, based on data obtained from field measurements (authors' unpub. data, n = 5) in line with Pennycuick's procedure (Pennycuick 2008). We estimated the energy needed for a lesser kestrel to perform a foraging trip when adopting a pure flapping or a pure soaring-gliding flight strategy. We calculated the mean time kestrels spent on foraging trips per day (both the time invested in commuting flights and in the foraging event) using complete days of tracking, using those dates and individuals in which we had continuous tracking data from sunrise to sunset. To estimate energy expenditure, we conservatively assumed that kestrels were resting when they were not on a foraging trip. Then, we estimated the individual daily energy expenditure from adopting a pure flapping or a pure soaring-gliding strategy in commuting flights during the breeding season. We considered 4.03 mLO_2/min as the resting oxygen consumption, a figure that has been determined empirically for the lesser kestrel by open-circuit respirometry (Rodríguez et al. 2014). To estimate energy expenditure we used the standard conversion coefficient of 20.1 KJ/LO_2 (Schmidt-Nielsen 1997), resulting in a resting metabolic rate for lesser kestrels of 1.35 W, which we adopted instead of the basal metabolic rate calculated using Pennycuick's software. Finally, we calculated the individual total daily energy requirement by adding the estimates of daily energy requirements for foraging and resting.

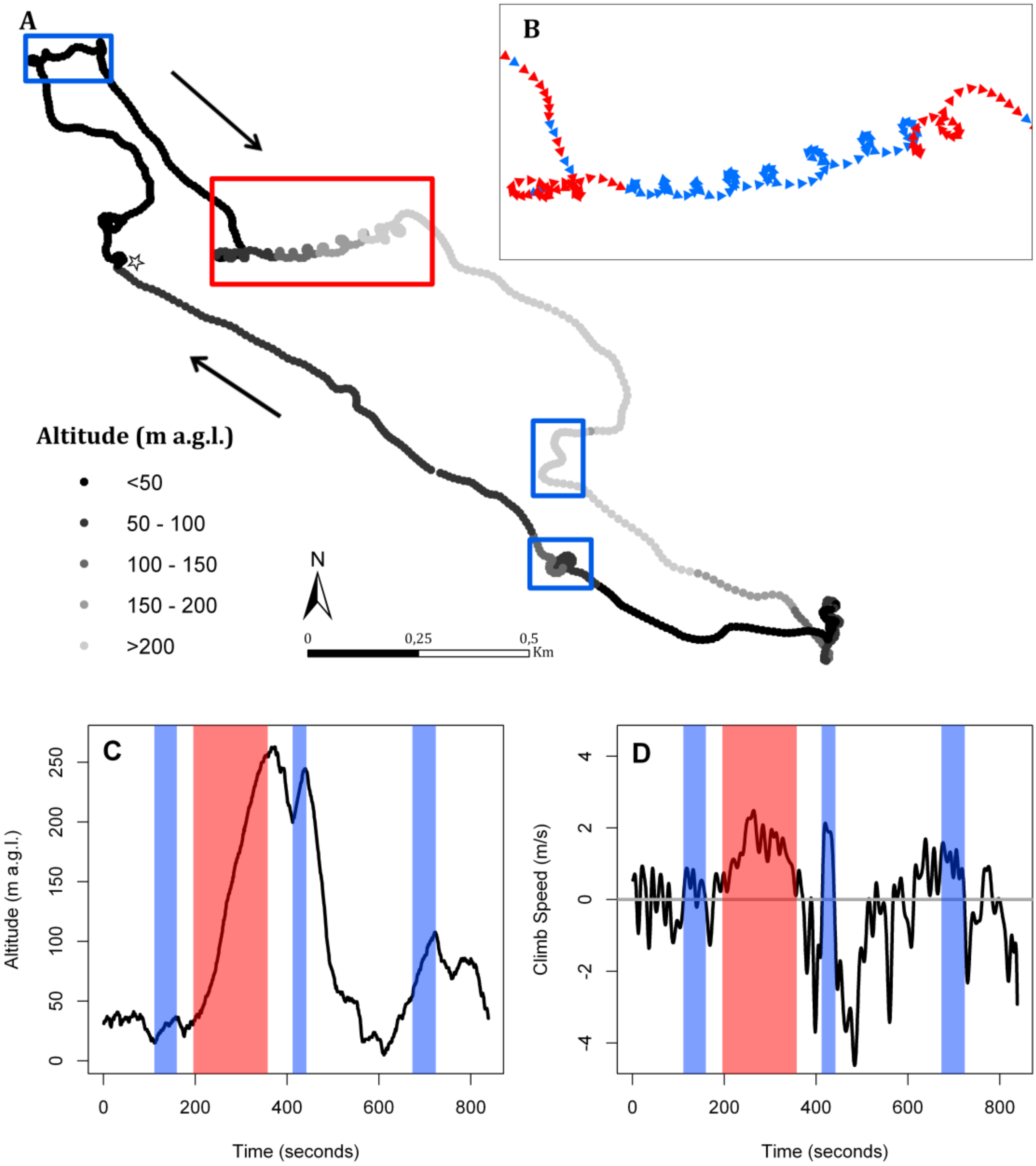

Figure 2. Track of a lesser kestrel foraging trip using thermal soaring along the commuting flights. (A) The white star represents the breeding colony. Each location of the path is colored according to flight altitude above ground level. Black arrows indicate movement direction. Red and blue boxes mark thermal soaring events. (B) Zoomed view of the thermal soaring event included in the red box. Locations are represented by triangles pointing to the direction of movement and its color indicates the circling direction either clockwise (red) or counterclockwise (blue). (C) Altitude and (D) climb speed profiles of the foraging trip. Red and blue shaded areas represent the thermal soaring events included in the boxes of panel A.

Statistical Analysis

We used Generalized Additive Mixed Models (GAMMs) to estimate the potential influence of solar radiation and thermal and orographic uplift in the flight variables of the lesser kestrel foraging trips. We analyzed two groups of models considering the two sets of meteorological predictors used: either solar radiation (in Wh/m^2) obtained at 30-minutes intervals, or thermal uplift (m/s) and orographic uplift (m/s) estimated at 6-h intervals (Table 1). Maximum foraging trip distance from the colony, duration, and its mean values per 6-h interval were logarithmically transformed.

In the first group of models, we fitted GAMMs to every variable indicative of intensity or efficiency in the use of thermals (i.e., number of thermal soaring events and accumulated ascent per horizontal distance, and total ascent and mean climb speed per thermal soaring event) to assess whether they were affected by solar radiation, which we were using as a proxy for thermal updraft intensity. We fitted GAMMs to maximum flight altitude in order to test our hypothesis of increasing flight altitude with increasing solar radiation based on the fact that thermal updraft increases in depth with solar radiation. We also fitted GAMMs to maximum distance from the colony to test the hypothesis that with higher values of solar radiation the kestrels have higher potential energy gain to fly larger distances at a lower cost. As soaring can have a negative influence on flight speed, we fitted GAMMs to study the effect of solar radiation on the cross-country speed of commuting flights and the duration of foraging trips. We used a Gaussian distribution of errors and the identity link function to fit models to all flight variables tested as a response variable excluding maximum flight altitude, cross-country speed, and total ascent and mean climb speed per thermal soaring event; for these variables we used a gamma distribution of errors and the logarithmic link function (which were more adequate after exploration of model residuals). We included solar radiation as a continuous predictor and individual identity as the random factor of all models. In models fitted to flight variables at commuting flight level (maximum flight altitude, cross-country speed and the 4 variables of efficiency of thermal use), we included the commuting flight type as a categorical predictor with 2 levels (outward and inward flight) so as to assess potential differences in the flight behavior of individuals when leaving or returning to the colony. In models fitted to flight variables at foraging trip level (maximum distance from the colony and trip duration) we included the breeding colony as a categorical predictor with 2 levels and also its interaction with solar radiation because the landscape mosaic of land uses in the surroundings of the two colonies was completely different (agricultural and urban) and had an impact on prey availability, and possibly strong effects on the kestrels' foraging strategy. Furthermore, we included the GPS sampling frequency as a correction factor with 5 levels because it could affect calculation of variables obtained from flights tracked at different frequencies (maximum flight altitude, cross-country speed, maximum distance from the colony and duration).

For a direct estimation of the influence of thermal and orographic uplift on lesser kestrel flight variables and to differentiate the influence of each factor on flight behavior, we built a second group of GAMMs using mean values of flight variables at 6-h intervals as response variables to match the temporal resolution of uplift estimations available from meteorological models. These models provide a more direct insight into the relationship between lesser kestrel flight variables and thermal and orographic uplift compared to previous models that used solar radiation as a proxy. However they are constrained by the lower temporal resolution of climatic models which is an important limitation considering diurnal fluctuations in uplift. We used a Gaussian distribution of errors and the identity link function to fit models to all mean flight variables used as response variables except in those fitted to mean maximum flight altitude where we used a gamma distribution of errors and a logarithmic link. Residual analysis indicated that this was the best error distribution. In these models we included thermal uplift as a continuous predictor and date (year and day-of-year combined) as the random factor because of the lack of independence between observations on the same day that usually belong to the same individual. We also tested orographic uplift as a continuous predictor in the model to evaluate if kestrels flew not only by thermal soaring but also using slope soaring, more dependent on wind conditions. Since Env-DATA provided us with two orographic uplift estimates, we built two models for every response variable, each of which included one of the predictors and which were subsequently compared to each other. The orographic uplift estimate included in the best model of these two was also included in the final model of every response variable (see model selection later in this section). We performed a Bonferroni correction to adjust the significance level when testing the effect of orographic uplift on all kestrel flight variables. As with the first group of models, we also included the breeding colony and its interaction with thermal uplift as predictors. We applied penalized smoothing splines to the solar radiation or thermal uplift estimate in all the GAMMs in order to take account of any nonlinear response to the predictor. The degrees of freedom of the smoothing function were automatically selected using restricted maximum likelihood (REML) (Ruppert et al. 2003). We followed the Akaike Information Criterion (AIC) for model selection since it indicates that the best model is that with the lowest AIC value. The best GAMMs for cross-country speed of commuting flights, maximum distance from the colony, and duration of foraging trips when using solar radiation as a predictor were those including the smoothed term of the predictor. For the remaining response variables, the best GAMMs were those including the linear effect of solar radiation or thermal uplift. We therefore fitted these variables to Generalized Linear Mixed Models (GLMMs) with the same distribution of errors and the same link function used to fit the GAMMs, and including the same predictors and random factors. We fitted the GLMMs following a backward-stepwise procedure, by removing non-significant predictors until only significant ones remained.

Table 1. Summary of statistical analyses of lesser kestrel flight variables divided in two categories: Use of thermals and daily patterns.

Analysis	Level	Sampling frequency	Response variables	Meteorological predictors	Other predictors
Use of thermals	Commuting flight	1-second	Number of thermals/distance, Accumulated ascent/distance, Total ascent/thermal event, Mean climb speed/thermal event	Solar radiation	Individual (Random), Commuting flight type
Use of thermals	6-hour intervals	1-second	Number of thermals/distance, Accumulated ascent/distance, Total ascent/thermal event, Mean climb speed/thermal event	Thermal uplift	Date (Random)
Daily pattern of foraging flights	Commuting flight	All	Maximum flight altitude, Cross-country speed	Solar radiation	Individual (Random), Commuting flight type, GPS sampling frequency
Daily pattern of foraging flights	Foraging trip	All	Maximum distance from the colony, Duration	Solar radiation	Individual (Random), GPS sampling frequency, Colony, Colony*Solar Radiation
Daily pattern of foraging flights	6-hour intervals	All	Maximum flight altitude, Cross-country speed, Maximum distance from the colony, Duration	Thermal uplift, Orographic uplift	Date (Random), Colony, Colony*Thermal uplift

We analyzed these categories at different levels (commuting flights, foraging trips, or 6-hour intervals) registered at 1-second or at all (1-second to 10-minutes) sampling frequencies, depending on the category. We list the flight variables modeled at every level of analysis and the predictors tested in those models. Response variables used at the 6-hour interval level are mean values per interval.

The significance of the predictors was tested using likelihood ratio tests comparing the model with and without the predictor.

Statistical analyses were performed using R-3.0.2 software (“R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.” 2014) fittingGAMMs and GLMMs using “mgcv” (Wood 2011) and “lme4” (Bates et al. 2014) packages, respectively.

Results

Use of thermals

We tracked 18 individual lesser kestrels (10 males and 8 females) with a GPS-datalogger programmed at 1 fix per second, and identified 303 thermal soaring events. Thermal soaring was present in 82.03 % of commuting flights tracked at a 1-second frequency (n = 128, 64 outward and 64 inward flights). When comparing commuting flights with and without thermal soaring events we found that individuals flew at higher altitudes with lower cross-country speeds when using thermal soaring along commuting flights. Foraging trips were farther away from the colony and lasted longer when thermal soaring was used in comparison to trips where thermal soaring did not occur (Table 2). The frequency of commuting flights in which thermal soaring events were identified increased from approximately 55 % at low solar radiation values to more than 90 % at the highest values (Figure 3). Kestrel efficiency during thermal soaring in commuting flights is shown in Table 3. The models showed statistically significant positive effects of solar radiation on accumulated ascent per horizontal distance covered ($\beta \pm$ standard error = 0.05 ± 0.01, $p<0.001$), total ascent per thermal soaring event ($1.34x10^{-3} \pm 3.24x10^{-4}$, $p<0.001$) and mean climb speed per thermal soaring event ($6.83x10^{-4} \pm 1.45x10^{-4}$, $p<0.001$). The number of thermals per distance covered did not vary with solar radiation intensity (1.36x10-5 ± 1.34x10-4, $p = 0.71$). We did not find any effect that could be attributed to commuting flight type (inward vs. outward) on the response variables ($p > 0.25$).

When considering 6-h intervals with flights recorded at 1 fix per second ($n = 28$), thermal uplift showed a statistically significant positive effect on mean values of all flight variables relating to thermal use efficiency (Table 4).

Table 2. Parameters of lesser kestrel commuting flights with and without thermal soaring events tracked at 1 fix per second.

Flight variables	With	Without	Statistic	p-value
Maximum altitude (m)	193.56 ± 179.21	40.88 ± 36.89	Z = - 6.18	< 0.001
Duration (min)	10.80 ± 8.73	3.10 ± 2.32	Z = - 5.61	< 0.001
Maximum distance (km)	3.51 ± 3.01	1.32 ± 0.82	Z = - 4.76	< 0.001
Cross-country speed (km/h)	21.13 ± 9.43	26.53 ± 8.53	t = 2.70	0.01

We used the Mann-Whitney U test or Student's t test to compare between commuting flights with and without thermal soaring events. Mean value ± standard deviation are shown. Sample size = 105 commuting flights thermal soaring events and 23 commuting flights without thermal soaring events.

Table 3. Parameters of lesser kestrel commuting flights with thermal soaring events tracked at 1 fix per second.

Flight variables	Mean ± SD	Min	Max	N
Number of thermals/distance (events/km)	0.64 ± 0.34	0.08	2.06	105
Accumulated ascent/distance (m/km)	59.44 ± 32.91	6.02	228.60	105
Total ascent/event (m)	123.07 ± 126.96	10	914	303
Mean climb speed/event (m/s)	1.37 ± 0.66	0.26	3.56	303

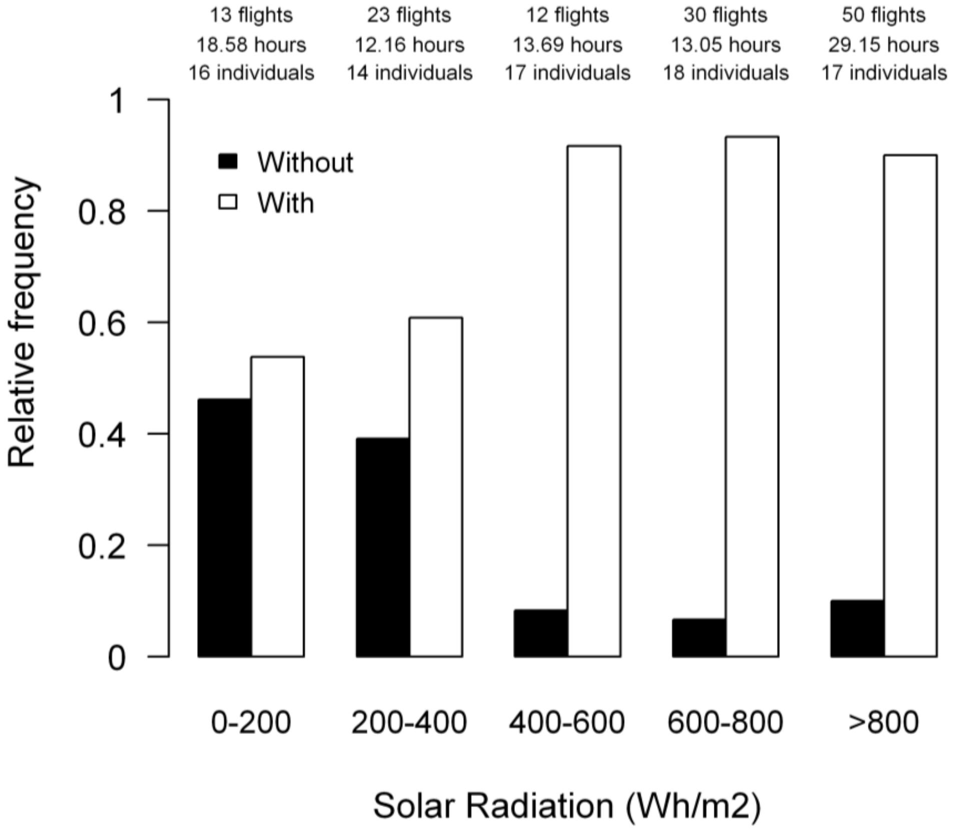

Figure 3. Relative frequency of commuting flights recorded at 1-second intervals with and without thermal soaring events in relation to solar radiation. Solar radiation is presented in categories of 200 Wh/m^2. Numbers of commuting flights, tracking hours and tracked lesser kestrels per category are indicated above the bars.

Table 4. Estimates (slope ± standard error) of the GLMMs fitted to 6-hour interval mean values of flight variables recorded in commuting flights with thermal soaring events tracked at 1 fix per second.

Predictors	Flight variables			
	Mean # thermal events/distance	Mean accumulated ascent/distance	Mean total ascent/event	Mean climb speed/event
Thermal Uplift	**0.08 ± 0.03 ***	**15.22 ± 6.01****	**22.94 ± 10.71***	**0.15 ± 0.06***

Mean values ± standard error are shown. Statistically significant variables are shown in bold, * p<0.05, ** p<0.01. Sample size = 28

Daily patterns

The flight parameters of lesser kestrel commuting flights and foraging trips recorded at all sampling frequencies are summarized in Table 5. On average individual kestrels flew at a maximum altitude of 149.70 ± 164.42 m (mean ± standard deviation) with a cross-country speed of 21.13 ± 9.43 km/h along commuting flights. GLMMs showed a statistically significant positive influence of solar radiation on maximum flight altitude (0.002 ± $5.08x10^{-5}$, $p < 0.001$; Figure 4), as we had hypothesized. Neither commuting flight type ($p = 0.15$) nor GPS sampling frequency ($p = 0.12$) showed statistically significant effects on maximum. flight altitude. The best GAMM fitted to cross-country speed included solar radiation and GPS sampling frequency (Table 6). Cross-country speed showed a negative curvilinear response to solar radiation, initially decreasing but then increasing as solar radiation values rose (Figure 5). Lesser kestrels reached a mean maximum distance from the colony of 3.63 ± 3.37 km during foraging trips that lasted on average 69.43 ± 79.20 min. We did not find any statistical differences between breeding colonies on maximum distances covered (Mann-Whitney U test, z = - 1.60, p = 0.10), nor in duration (z = - 1.04, p = 0.30) (Figure 6). The best GAMM fitted to maximum foraging trip distance from the colony included the interaction between solar radiation and the breeding colony (Table 6). The interaction indicated that although maximum distance from the colony increased with solar radiation in both colonies, the response was steeper in the urban colony (EBD) with poorer foraging habitats than in the Silo colony (Figure 7), as we hypothesized. We obtained two different GAMMs fitted to foraging trip duration, as their AIC values differed by less than 2. Both models included GPS sampling frequency, but the best one included the interaction between solar radiation and the breeding colony whereas the second best model included only solar radiation (Table 6). One model showed that foraging trip duration increased almost linearly with solar radiation, while the other showed a steeper trend in the urban colony (EBD) than in the Silo colony, where the relationship remained almost constant (Figure 8).

When considering 6-h intervals with all flights regardless of the sampling frequency at which they were recorded (n = 533), thermal uplift showed a statistically significant positive effect on mean maximum flight altitude and maximum distance from the colony, but it did not show any effect on mean cross-country speed and trip duration. The interaction between colony and thermal uplift presented a statistically significant influence on mean maximum distance from the colony, but it did not influence mean duration. Orographic uplift presented a statistically significant negative effect on mean maximum flight altitude and a positive effect on mean duration, but no effect on mean cross-country speed and maximum distance from the colony (Table 7).

Table 5. Parameters of lesser kestrel commuting flights and foraging trips tracked at all sampling frequencies.

Level of Analysis	Variable	Mean ± SD	Min	Max
Commuting flights	Flights per individual	82.60 ± 87.16	2	354
Commuting flights	Cross-country speed (km/h)	17.06 ± 8.24	1.08	81.21
Commuting flights	Maximum altitude (m)	149.70 ± 164.42	0.40	1330
Foraging trips	Trips per individual	61.20 ± 63.62	2	237
Foraging trips	Maximum distance (km)	3.63 ± 3.37	0.34	32.23
Foraging trips	Duration (min)	69.43 ± 79.20	3.28	624.30

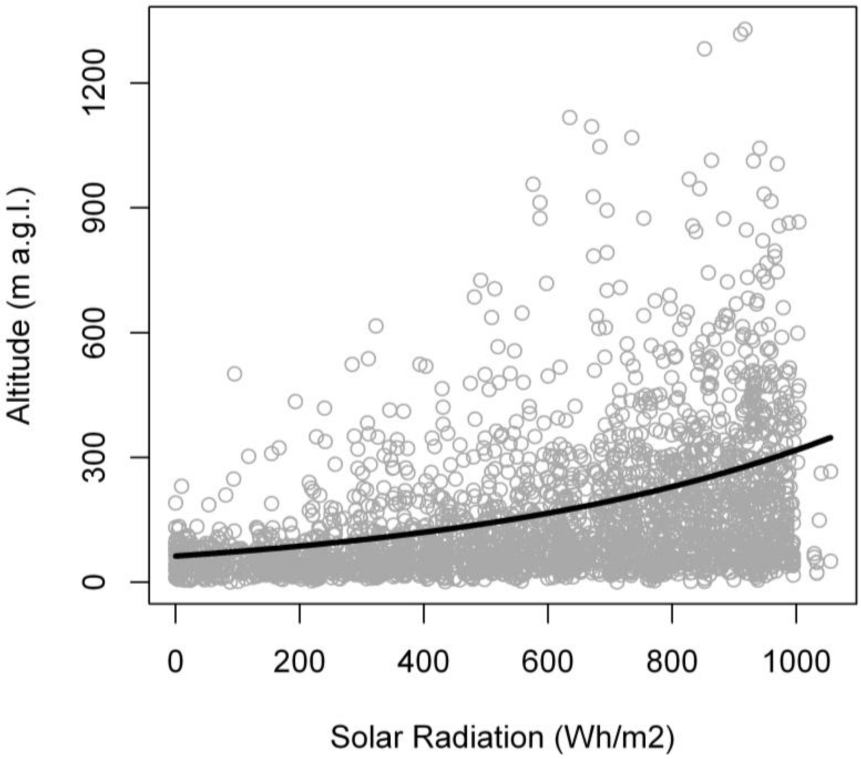

Figure 4. Effect of solar radiation on maximum flight altitude of lesser kestrels along commuting flights predicted by the GLMM. Circles represent the observed maximum altitude of commuting flights and the solid line represents the model prediction. Sample size = 2891 commuting flights.

Table 6. AIC values of GAMMs fitted to kestrel flight variables calculated from commuting flights or foraging trips tracked at all sampling frequencies.

Predictors	Cross-country speed ΔAIC	Maximum distance ΔAIC	Duration ΔAIC
Smooth(Solar) + Type + Frequency	13.03	-	-
Smooth(Solar) + Type	66.81	-	-
Smooth(Solar) + Frequency	**Best Model**	-	-
Solar+ Type + Frequency	59.42	-	-
Type + Frequency	103.99	-	-
Smooth(Solar)*Colony + Frequency	-	2.25	**Best Model**
Smooth(Solar) + Colony + Frequency	-	79.87	3.95
Smooth(Solar)*Colony	-	**Best Model**	31.66
Smooth(Solar) + Frequency	-	76.12	1.98 **(Second Best Model)**
Solar+ Colony + Frequency	-	23.43	20.99
Colony + Frequency	-	151.27	11.34

The predictors are classed as follows: Solar radiation as “Solar”, Commuting flight type (outward vs inward) as “Type”, GPS sampling frequency as “Frequency”, and Breeding colony as “Colony”. ΔAIC was calculated between the best model and each proposed model. The best model fitted for each kestrel flight variable is indicated in bold.

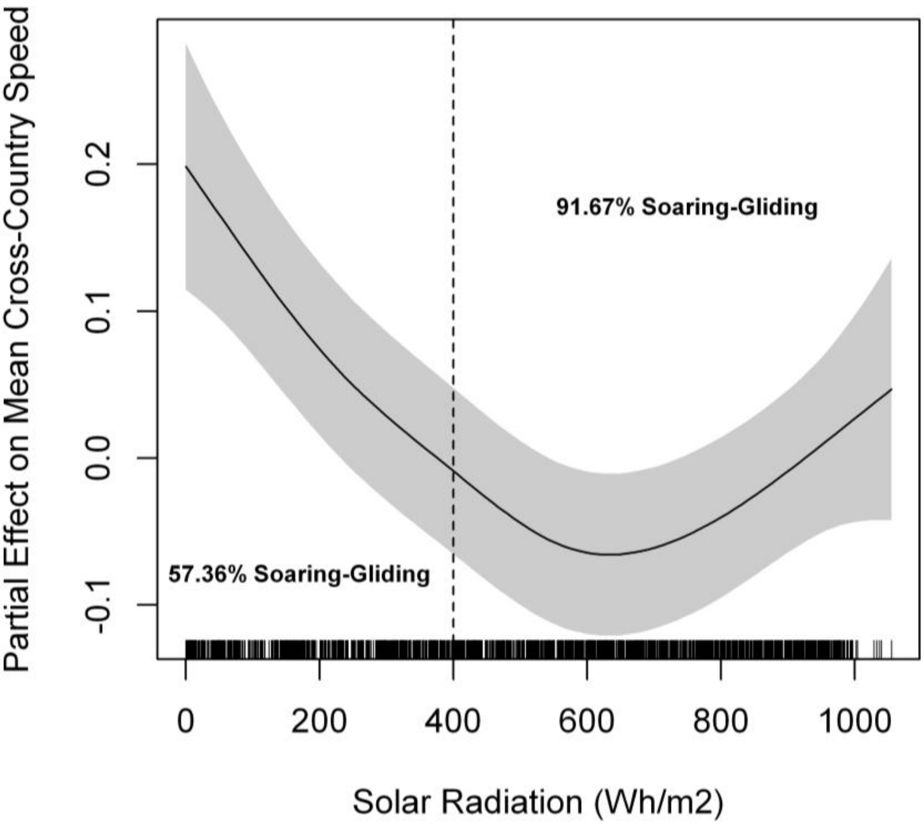

Figure 5. Partial effect of solar radiation in the model fitted to mean cross-country speed of lesser kestrel commuting flights. A penalized smoothing spline of 3.12 degrees of freedom was adjusted to solar radiation. Grey shading represents the standard error of the mean effect. Sample size = 2891 commuting flights.

Table 7. Estimates (slope ± standard error) of the GLMMs fitted to 6-hour interval mean values of flight variables recorded in commuting flights or foraging trips tracked at all sampling frequencies.

Predictors	Flight variables			
	Mean maximum altitude	Mean Cross-country speed	Mean Maximum distance	Mean Duration
Thermal Uplift	**0.34 ± 0.03 *****	-0.02 ± 0.08	**0.28 ± 0.04 *****	0.04 ± 0.02
Orographic Uplift	**-1.29 ± 0.21 (ASTER)*****	-0.48 ± 0.56 (ASTER)	0.68 ± 0.79 (SRTM)	**2.47 ± 0.97 (SRTM) ***
Colony (EBD)	-	-	**-0.11 ± 0.08 *****	-0.002 ± 0.08
Colony*Thermal Uplift	-	-	**-0.22 ± 0.05 *****	-0.10 ± 0.05

We indicate the orographic uplift model used to test its influence on each flight variable. Statistically significant variables are shown in bold, * p<0.25, *** p<0.001. Sample size = 533.

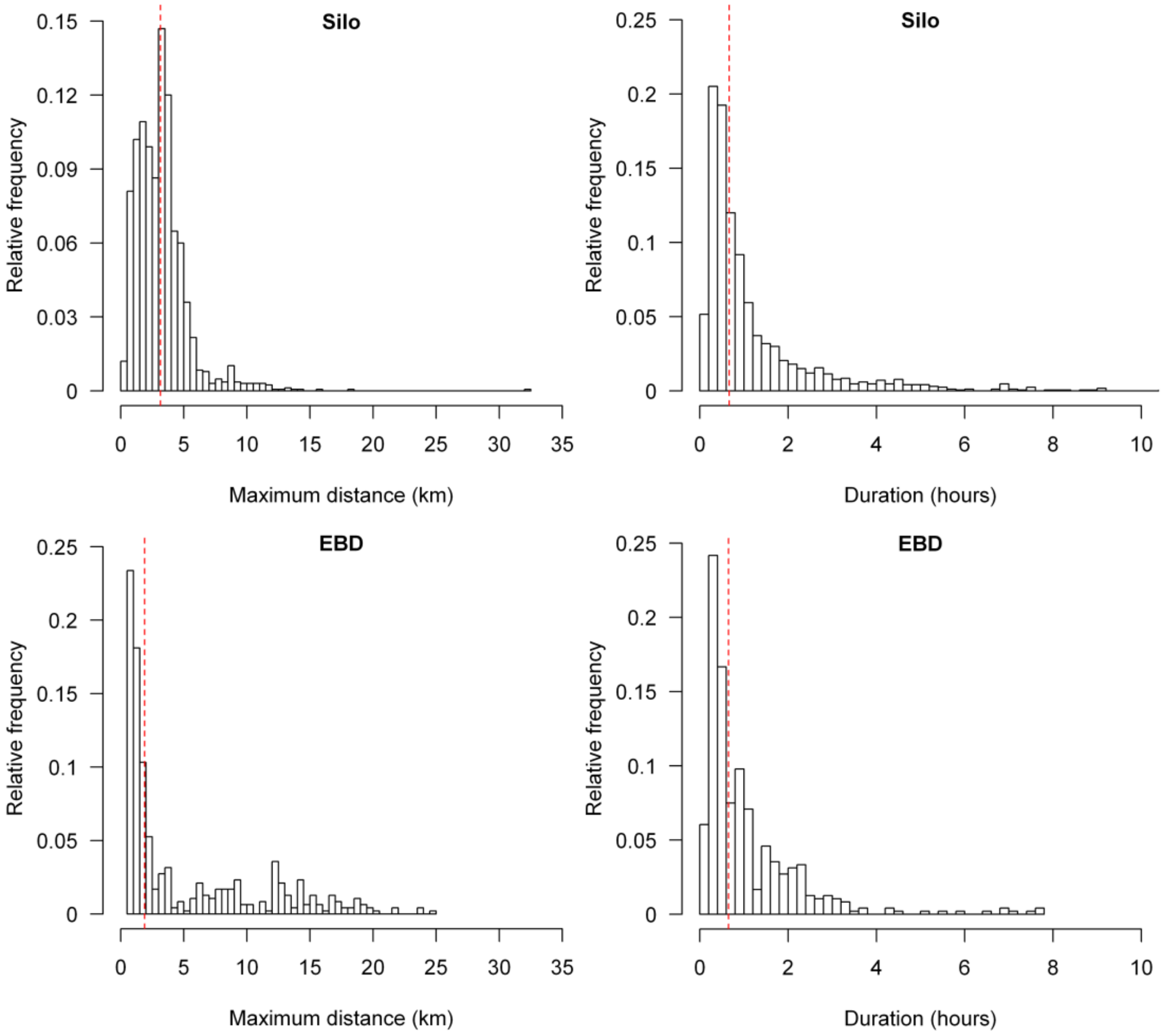

Figure 6. Frequency distributions of maximum distance (left panels) and duration (right panels) of lesser kestrel foraging trips from the Silo colony (upper panels) and the EBD colony (lower panels). The dashed lines represent the median value of flight variables. Sample size = 2142 foraging trips.

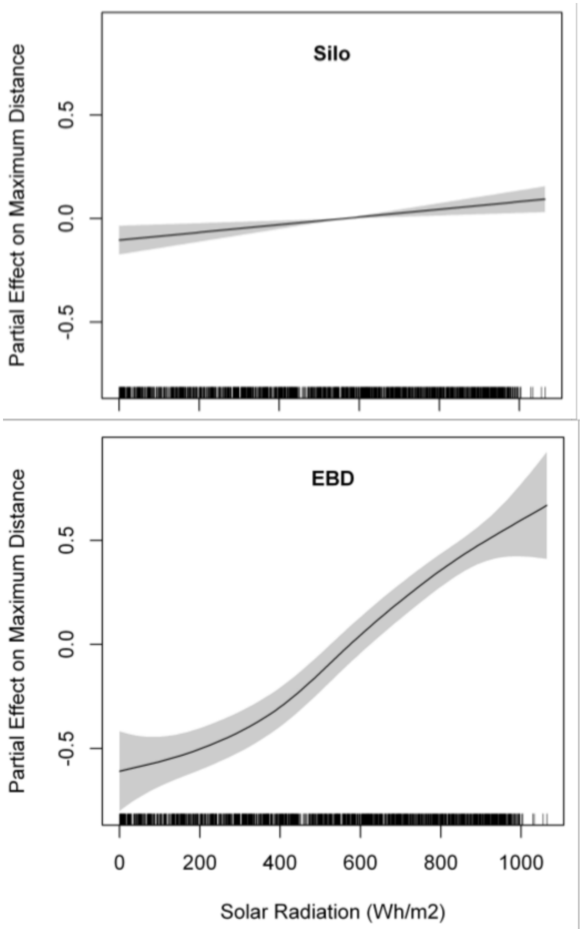

Figure 7. Partial effects of solar radiation on maximum distance from the colony of lesser kestrel foraging trips for individuals from the Silo colony (upper panel) and from the EBD colony (lower panel)**.** Penalized smoothing splines of 1 and 2.72 degrees of freedom were adjusted to solar radiation for the Silo and the EBD colonies, respectively. Grey shading represents the standard error of the mean effect. Sample size = 2142 foraging trips.

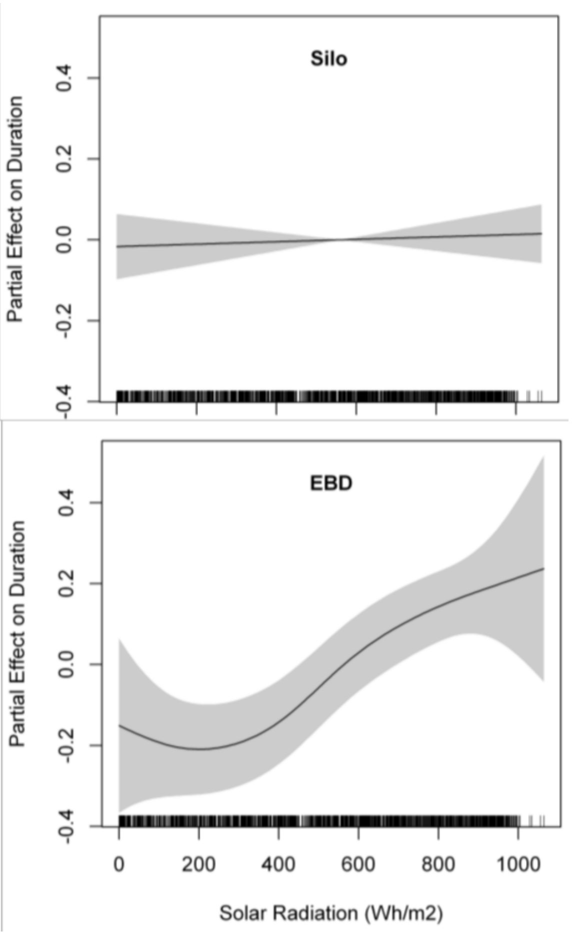

Figure 8. Partial effects of solar radiation on duration of lesser kestrel foraging trips for individuals from the Silo colony (upper panel) and from the EBD colony (lower panel). Penalized smoothing splines of 1 and 2.52 degrees of freedom were adjusted to solar radiation for the Silo and the EBD colonies, respectively. Grey shading represents the standard error of the mean effect. Sample size = 2142 foraging trips.

Energy expenditure

Using Pennycuick's Flight software we estimated 1.62 W of chemical power requirements for the lesser kestrel using a soaring-gliding flight strategy. Meanwhile, we estimated 5.02 W and 6.26 W of power required by the lesser kestrel using a flapping flight strategy at minimum power and maximum range speed, which were 31.36 and 54.72 km/h, respectively. Therefore, the power required for flapping flight ranged between 3.10 and 3.86 times the power required for soaring-gliding flight. Since the mean duration of the foraging trips was 69.43 min, the mean energy needed for kestrels to perform a foraging trip was 6.75 KJ when adopting a pure soaring-gliding strategy versus 20.91 KJ and 26.08 KJ for pure flapping at minimum power and maximum range speeds, respectively. The median time spent foraging per day was 7.48 hours; consequently the median time spent resting per day was 16.52 hours (n = 264 complete days). The median energy expenditure by the lesser kestrel during the breeding season would range from 124 KJ/day if using a pure soaring-gliding strategy in commuting flights to 249 KJ/day if commuting by flapping at maximum range speed. In Table 8 we provide our detailed estimates and calculation method.

Discussion

Lesser kestrels, like other falcons, have traditionally been considered flapping raptors [17,26,31–35]. They are frequently observed to be hovering when foraging (Rudolph 1982), they can fly at night when thermals are not available (Strandberg et al. 2009, López-López et al. 2010, Limiñana et al. 2012), they do not concentrate in big flocks over straits during migration as typical soaring raptors do (Vansteelant et al. 2014), and they cross large water bodies where thermals are weak or absent (Kumar 2014, Agostini, Panuccio, et al. 2015). However, our results show that lesser kestrels rely heavily on thermals and use them to soar in more than 80% of commuting flights between the colony and foraging areas during the breeding season. Unlike GPS tracking, direct observations are probably biased. While hovering kestrels are clearly visible in the field, a small kestrel gaining altitude on a thermal at more than 1000 m cannot be observed with the naked eye (Agostini, Scuderi, et al. 2015) (see S1 Video). Our research is a valuable example of new insights into bird flight strategies thanks to continuous tracking and the higher spatiotemporal resolution provided by recent bio-logging devices (Portugal et al. 2014, Bishop et al. 2015). According to current state of flight theory it was not expected that small-sized birds, such as falcons, would rely heavily on thermal soaring because of the low energy benefits obtained given the cost in flight speed (Duerr et al. 2012). Nevertheless, our results indicate that lesser kestrels fly at relatively high cross-country speeds when soaring on strong thermals, a factor that to a certain degree mitigates the trade-off between energy and time when deciding to use thermal soaring. This is not the first study to describe thermal soaring in small birds (Spaar 1997, Ákos et al. 2010, Sapir et al. 2010), but our study indicates that thermal soaring is used by lesser kestrels in a similar way to that characterizing large soaring raptors (Duriez et al. 2014). It could be argued that the extra load of the GPS-datalogger (6 g) forces the kestrels to use thermals more often than normal. If extra load was the cause of frequent thermal soaring we would expect a difference between inward and outward commuting flights. In inward flights kestrels usually return to the colony with a prey which is approximately an average 1-20 g of extra load. The results obtained from testing the commuting flight type as predictor (Table 1) indicated no significant differences between inward and outward flights (Tables 6 and 7).

During foraging trips in which thermal soaring is used, lesser kestrels fly towards foraging areas located farther from the colony (2.5 times) than during those without, but at the greater cost of time (3.5 times). Moreover, kestrels fly at higher altitudes (4.5 times) with lower cross-country speed (20% slower) when they use thermal soaring along commuting flights than when they do not (Table 2).

The use of thermals by kestrels increases with the availability and strength of thermal updrafts as observed by its increased use with solar radiation (Figure 3). Individual efficiency of thermal soaring (mean climb speed, total ascent per thermal and accumulated ascent per distance covered) increases with solar radiation (Table 3). Analyses, with a larger sample size, using all foraging trips throughout the breeding season also indicate that maximum flight altitude (Figure 4), maximum distance from the colony (Figure 7), and duration (Figure 8) increase with solar radiation. Cross-country speed in commuting flights initially decreases with solar radiation, but then increases again when the highest solar radiation values are reached (Figure 5). Our analyses show a consistent positive effect of solar radiation and thermal uplift on lesser kestrel flight variables that suggests that atmospheric kinetic energy is highly significant in kestrel foraging strategies. In contrast, we do not find any evidence of kestrels using slope soaring when commuting between the colony and the foraging areas. This is not surprising due to the low relief of our study area and the absence of strong constant winds, but lesser kestrels could take advantage of slope soaring to fly in more abrupt areas, as other raptor species do (Duerr et al. 2012, Chapter One). As the availability, strength and depth of thermals are promoted by solar radiation, individual lesser kestrels use them more frequently and can improve their thermal soaring efficiency when solar radiation increases, as previously reported in large soaring raptors (Spaar 1997). Our findings suggest a segregation of flight strategy of the lesser kestrel regarding solar radiation conditions. Kestrels seem to fly by flapping mostly at lower solar radiation intensities when thermals are weak or not available, but they prefer thermal soaring at higher values of solar radiation when thermals are stronger, in line with the flight strategy of European bee-eaters *Merops apiaster* (Sapir et al. 2011).

Flight-cost models for lesser kestrels indicate that the soaring-gliding flight strategy is much cheaper (3-4 times) than continuous flapping. The difference is not negligible. This would explain why lesser kestrels mostly use thermal soaring when thermals are available. The increase in flight altitude with solar radiation (Figure 4) suggests an adjustment of kestrel flight strategy to thermal conditions in order to harvest the greatest possible amount of potential energy to reduce flight costs, as many studies have previously described in a variety of large soaring birds (Shannon et al. 2002, Shamoun-Baranes et al. 2003, Mellone et al. 2012). Considering that kestrels carry back one prey at a time and that optimal prey are 2-3 g grasshoppers (Rodríguez et al. 2010), we estimate that long distance foraging flights for lesser kestrels would incur an energy deficit if flapping flights were used for commuting. A 2 g migratory locust *Locusta migratoria* (a typical prey species; see [57]) would provide14.98 KJ (van Huis et al. 2013). In our study area the average foraging trip performed with flapping flight would cost kestrels 20.91 KJ at minimum power but 6.75 KJ with soaring-gliding. Consequently, kestrels would need to feed on three prey every two foraging trips in order to maintain a positive energy balance if individuals fly by flapping during the foraging trips, whereas they would need a single prey every two foraging trips when thermal soaring. Thus, thermal soaring becomes a cost-effective flight strategy for foraging kestrels, especially when individuals also have to feed their mate or offspring. However, using a soaring-gliding strategy increases flight duration because of the lower cross-country speed (Table 2). Accordingly, when using this strategy, kestrels are optimizing the energy balance at the cost of a lower chick provisioning rate at the colony. The cross-country speed at which lesser kestrels fly in commuting flights when not using thermals (26.53 km/h) is closer to minimum power speed (31.36 km/h), a figure that is far from maximum range speed (54.72 km/h) indicated by flight models. Thus, even when using the powered flapping flight strategy kestrels try to reduce costs by flying at the speed of minimum energy cost along commuting flights.

Table 8. Estimates of daily energy expenditure (DEE) of a lesser kestrel for foraging, resting and total (foraging + resting) when using a pure soaring-gliding flight strategy or a flapping flight strategy at minimum power (Vmp) and maximum range (Vmr) speeds.

	Power Resting	DEE Resting	Power Foraging	DEE Foraging	Total DEE
Daytime		16.52 hours/day 14.26–18.11 9.29–24		7.48 hours/day 5.89–9.74 0.00-14.71	24 hours/day
Soaring-Gliding	1.35 W	80.29 KJ/day 69.30–88.01 45.15–116.64	1.62 W	43.62 KJ/day 34.35–56.80 0.00-85.79	123.91 KJ/day 122.36–126.10 116.64–130.94
Flapping at Vmp	1.35 W	80.29 KJ/day 69.30–88.01 45.15–116.64	5.02 W	135.18 KJ/day 106.44–176.02 0.00–265.84	215.47 KJ/day 194.45–245.32 116.64–310.99
Flapping at Vmr	1.35 W	80.29 KJ/day 69.30–88.01 45.15–116.64	6.26 W	168.57 KJ/day 132.74–219.50 0.00–331.50	248.86 KJ/day 220.75–288.80 116.64–376.65

We show median values of energy expenditure, the first and third quartiles, and the range, from top to bottom within each cell. Sample size = 264 complete days.

Thermal soaring is therefore an essential strategy for lesser kestrels to reduce flight cost when searching for food during the breeding season. Kestrels would develop a cognitive map of how prey are spatially distributed in the surroundings of the colony through direct experience or “public information” (Valone & Templeton 2002, Fagan et al. 2013). Individuals would overlay this cognitive map with thermal availability in order to decide where to go to forage and finally adopt the optimal flight strategy to be used after weighing up the trade-off between energy and time costs of the trip. This leads to the concept of energy landscape to describe the spatial distribution of movement costs regarding individual location (Wall et al. 2006). The energy landscape of a central-place forager, such as the breeding lesser kestrel, is strongly affected by the distance required to commute between the colony, or central place, and the foraging area: the greater the distance, the higher the flight cost (Wilson et al. 2012). However, the energy landscape is not static and may change in space and time because of individual endogenous or exogenous factors (Shepard et al. 2013). Intraday variations in solar radiation mean that the energy available in the atmosphere in thermal updrafts is continuously changing in a predictable pattern. Therefore, there is a spatiotemporal energy landscape that kestrels can exploit on a daily basis. As solar radiation increases, prey that are farther from the colony have a lower energy cost . Thus, when thermal updrafts are low in the first hours after sunrise or before sunset, lesser kestrels adopt the costly flapping flight strategy to fly towards foraging areas close to the colony, resulting in short commuting flights. Meanwhile, as thermal updraft increases throughout the day, kestrels adopt the slower soaring-gliding flight strategy to fly towards foraging areas farther from the colony at reduced cost, but at the expense of a longer flight (Figs 3-5, 7).

However, commuting to a foraging area far from the colony is only advantageous if prey are of higher quality in those areas, they are available in higher densities, or easier to catch. So, if kestrels increase foraging distance with solar radiation (Figure 7) or thermal uplift (Table 6) this is because foraging farther afield provides them with some advantage. Negative density-dependent effects, such as low prey availability or high intraspecific competition, are commonly experienced by colonial species in the surroundings of the colony (Ashmole 1963, Bonal & M. Aparicio 2008) and might provide kestrels with enough motivation to fly towards foraging areas located far from the colony as soon as thermals form. As kestrels could easily reach these areas with flapping flight in the absence of thermals at a higher cross-country speed, this also supports the idea that there is an energy rather than a time constraint in increasing commuting flight distance. This is clearer when we compare the two kestrel colonies. The Silo colony surrounded by herbaceous crops, an optimal habitat for the lesser kestrel (Rodríguez et al. 2013), shows a slight increase in foraging distance with solar radiation (Figure 7), while foraging trip duration remains almost constant (Figure 8). Lesser kestrels increase foraging distance with the help of thermals thereby reducing competition and prey depletion close to the colony only when they can maintain the same chick provisioning rate. The EBD colony, surrounded by poorer habitats is likely to suffer from greater competition or prey depletion. As soon as thermals are available lesser kestrels fly towards herbaceous crops far from the colony, causing a decrease in the chick provisioning rate. This explains the bimodal distribution in the maximum foraging trip distance from the colony (Figure 6), and the dramatic increase in that distance (Figure 7) and in foraging trip duration (Figure 8) with solar radiation. Therefore, thermal soaring is a crucial strategy for the lesser kestrel to prospect larger areas in the surroundings of the colony when searching for the unpredictable explosions of insects, especially when the colony is situated within a poor-quality habitat matrix.

Our estimates of daily energy expenditure for individual lesser kestrels during the breeding season (Table 8) overlap in range with those previously obtained for this species using doubly-labelled water (~ 300 KJ/day) by Tella

(Tella 1996). The difference in average values could be due to the study period, since Tella (Tella 1996) estimated mean daily energy expenditure of kestrels during the nestling period whereas our estimates relate to the whole breeding season. Indeed, our values were similar to the daily energy expenditure of common kestrels (*Falco tinnunculus)* for the entire breeding season (200 – 400 KJ/day) (Masman et al. 1986). However, when we examine the estimates of daily energy expenditure in relation to the flight strategy in foraging, we observe that those adopting a pure soaring-gliding flight strategy are much lower. The reason for this may be because lesser kestrels are unlikely to complete foraging trips by adopting only a pure soaring-gliding flight strategy, as they usually hunt by hovering, while they can use a pure flapping strategy when thermals are not available. Consequently, daily estimations of energy expenditure when foraging with a pure soaring-gliding flight strategy would underestimate the real values. Accordingly, our estimations of the lesser kestrel's daily energy expenditure when adopting one pure flight strategy or another establish the extreme values of the energy expenditure gradient, within which the real values would be located.

To conclude, lesser kestrels rely heavily on thermals for foraging flights during the breeding season. Our findings indicate that lesser kestrels show a temporal segregation of flight strategy that leads to a spatial segregation of foraging areas on a daily basis. Kestrels fly by flapping towards foraging areas close to the colony when thermals are absent, resulting in short foraging trips. But, as soon as thermals are available, kestrels use them to soar towards foraging areas far from the colony, presumably in order to avoid high competition, prey depletion or low-quality habitats in areas surrounding the colony, resulting in long foraging trips and consequently a reduced chick provisioning rate. This spatiotemporal segregation was more marked in the urban EBD colony, which is located in a poor-quality habitat. Our results indicate that during the breeding season lesser kestrels are more energy than time-constrained. The small size of the insect prey on which they forage and the limitation of providing a single prey at a time (kestrels transport a single prey to the colony in their beak or talons) mean that they can only forage far from the colony by harvesting energy from the environment, and at the expense of a reduced chick provisioning rate.

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Supporting information

S1 Video. Simulation of lesser kestrel flight during a real foraging trip tracked at 1-second frequency**.** Simulation has been produced using Doarama, an on-line 3D visualization engine that allows GPS tracks to be uploaded and uses aerial imagery from the Bing repository (https://www.doarama.com). In the upper left corner, Doarama offers some statistics of the foraging trip, from top to bottom: the flight speed, the accumulated distance out of the total distance traveled along the trip, flight altitude above sea level, climb rate between consecutive locations, and date-time information for the foraging trip. The bottom side of the frame shows the flight altitude profile throughout the trip.

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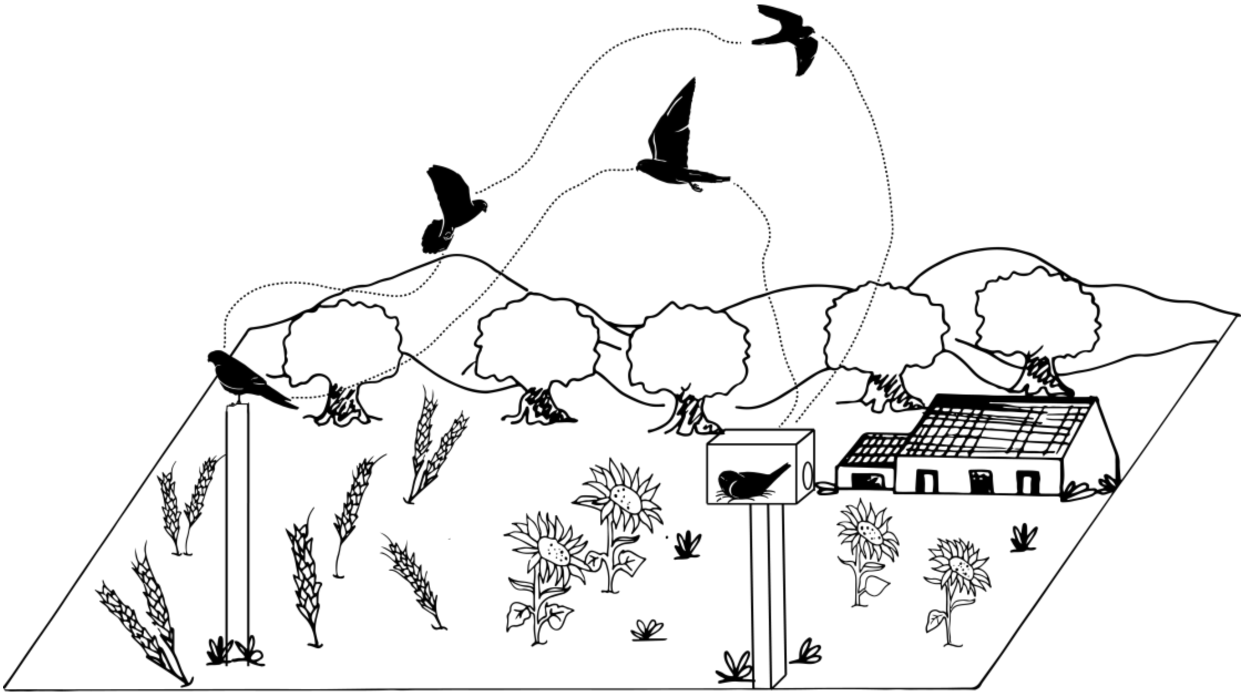
CHAPTER FOUR

Plasticity of lesser kestrel foraging strategy in relation to weather conditions



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(*In prep*.)

Abstract

Tri-axial accelerometry has been proved to be a useful technique to infer animal behavior with no need of direct observation and also an effective methodology to measure animal energy expenditure, which has allowed a refreshing revisit to the optimal foraging theory. This theory predicts that animals should gain the most energy for the lowest cost in terms of time and energy when foraging in order to maximize fitness. However, central-place foragers may face different cost-benefits trade-offs when commuting between the central-place and the foraging areas than when searching for food at the foraging patch that could determine behavioral decisions along the foraging trips. The lesser kestrel (*Falco naumanni*) is a small insectivorous falcon that behaves as a central-place forager during the breeding season. Kestrels can fly either by adopting the time-saving flapping flights or the energy-saving soaring-gliding flights along commuting flights. Furthermore, kestrels can capture prey either by using the time-saving hovering flights or the energy-saving perch-hunting at the foraging patch. In this study, we investigated the influence of internal and external factors on behavioral decisions of the lesser kestrel. We tracked 35 individual lesser kestrels (*Falco naumanni*) using dataloggers with GPS coupled with tri-axial accelerometers during a breeding season. We used a high-performance classification model that automatically classified lesser kestrel behaviors from accelerometry data. Our results indicated that lesser kestrel males dedicated a higher daily time and energy expenditure to flight behaviors in comparison to females because of being the main responsible for provisioning tasks according to the role specialization of the lesser kestrel. Our findings also pointed out that lesser kestrel replaced flapping flights with soaring-gliding flights as solar radiation increased, that is, as thermal updrafts got stronger. They also replaced perch-hunting with hovering flights as wind speed increased, that is, as they experience stronger lift forces. Nevertheless, individuals appeared to ultimately choose the hunt strategy regarding the activity level of the preferred prey that was influenced by air temperature, increasing the use of hovering flights as air temperature, and prey activity level, increased. Interestingly, the energy expenditure per foraging trip maintained constant although flight and hunting strategies dramatically changed with weather conditions, suggesting a fixed energy budget per foraging trip to which kestrels adjust their foraging strategies in response to environmental factors.

Resumen

La acelerometría triaxial ha resultado ser una metodología útil para inferir el comportamiento animal sin necesidad de realizar observaciones directas y también una alternativa útil a las técnicas tradicionales para medir el gasto energético, lo que ha permitido revisitar la teoría del aprovisionamiento óptimo. Esta teoría predice que los animales deberían obtener la mayor cantidad energía para el menor gasto de energía y tiempo posible cuando buscan alimento con el objetivo de maximizar su fitness. Sin embargo, aquellos individuos que adoptan la estrategia del lugar central de búsqueda pueden enfrentarse a diferentes balances costes-beneficios mientras se desplazan entre ese lugar central y las áreas de alimentación y mientras encuentran el alimento en el área de caza, lo que podría determinar las decisiones comportamentales a lo largo de los viajes de alimentación. El cernícalo primilla (*Falco naumanni*) es un pequeño halcón insectívoro que adopta la estrategia del lugar central de búsqueda durante la época reproductiva. Los cernícalos primilla pueden usar el vuelo aleteado, de alto coste energético pero de mayor velocidad, o el vuelo planeado, de bajo coste energético pero de menor velocidad, a lo largo de los desplazamientos entre el lugar el central y las áreas de caza. Además, los cernícalos primilla pueden capturar presas usando el vuelo cernido, más efectivo en términos de tiempo pero más caro en términos energéticos, o la caza desde posadero, menos eficiente en tiempo pero más económico en términos de energía, en el área de caza. En este estudio, se investigó la influencia de factores internos y externos en la toma de decisiones comportamentales del cernícalo primilla. Se marcaron 35 individuos con GPS y

acelerómetros triaxiales dataloggers durante una temporada de cría. Obtuvimos un modelo de clasificación de alto rendimiento que clasificó de forma automática los comportamientos de los cernícalos primilla a través de los datos recogidos por los acelerómetros. Nuestros resultados indicaron que los cernícalos primilla machos dedicaron una mayor parte del tiempo y gasto energético diario a comportamientos de vuelos en comparación con las hembras al ser los principales responsables de las tareas de aprovisionamiento de alimento al nido, de acuerdo con la especialización de roles de esta especie. Encontramos que los cernícalos reemplazaron los vuelos aleteados por vuelos planeados a medida que la radiación solar se incrementó, es decir, a medida que las corrientes térmicas ascendentes se hicieron más intensas. Los individuos también reemplazaron la caza desde posadero por los vuelos cernidos a medida que la velocidad del viento se incrementó, es decir, a medida que experimentaron mayores fuerzas para sostenerse en el aire. Sin embargo, parece que en última instancia los individuos eligieron la estrategia de caza según el nivel de actividad de las presas preferidas, que está influenciado por la temperatura del aire. Así, los cernícalos acrecentaron el uso de vuelos cernidos a medida que la temperatura y el nivel de actividad de las presas también aumentaron. Interesantemente, observamos que el gasto energético por viaje de caza se mantuvo constante aunque las estrategias de vuelo y caza cambiaron drásticamente con las condiciones climáticas, lo que sugiere que los individuos fijan un presupuesto energético por viaje al cual ajustan sus estrategias de alimentación en respuesta a factores ambientales.

Introduction

The application of the latest technological advances has expanded the frontiers of knowledge and has also opened new perspectives in ecological studies on free-ranging animals. The ongoing miniaturization and sophistication of tracking devices have allowed broadening the range of species to be studied with unprecedented spatial and temporal resolution (Rodríguez et al. 2012, Wilmers et al. 2015). In the light of the recent technological revolution, the number of studies on animal movement has risen and, with it, the need to create a framework to encompass all of them. That has been the breeding ground for the enhancement of the Movement Ecology paradigm (Nathan et al. 2008). This discipline advocates that individual movement results from the interaction between individual internal state, motion and navigation capacities and external factors. Apart from tracking devices, a series of animal-borne biological sensors or biologgers has been developed to help fully understand the movement path, perhaps being accelerometers one of the most widely used devices nowadays.

Accelerometers measure body acceleration across one, two or three spatial axes at high temporal resolutions (typically 10 Hz or more). These devices inform about animal body position via the static component of acceleration that indicates device orientation with respect to the Earth's gravitational field (Watanabe et al. 2005, Graf et al. 2015). Furthermore, accelerometers also allow researchers to deduce animal behavior through the dynamic component of acceleration that results from the inertia created when animal body moves (Shepard et al. 2008, Chimienti et al. 2016). Therefore, accelerometers help to disentangle how free-ranging animals adjust behaviors in time (and also in space when coupled with tracking devices) with no need of direct observation in the field and consequently reducing observer bias and also saving working time and effort (Cooke et al. 2004, Brown et al. 2013). In addition, accelerometry has been proved to be a useful technique to measure animal energy expenditure and an effective alternative to traditional methods such as doubly labeled water or heart rate telemetry (Halsey et al. 2008, Elliott et al. 2013). Animals require energy to perform their behaviors, which result in three-dimensional body movement. So it has been hypothesized that animal body movement would be proportional to the energy invested in producing it. Wilson et al. (Wilson et al. 2006) demonstrated that body acceleration correlates well with oxygen consumption in great cormorants *Phalacrocorax carbo* when walking at different speeds on a treadmill. Since then, several studies have come to the same conclusion using a variety of study species when moving freely across land, air or water (Green et al. 2008, Halsey et al. 2009, Gleiss et al. 2010). Thus, accelerometry also provides useful insights into energy expenditure of behaviors that can be associated to movement in wild animals. Accelerometers were deployed at first on marine mammals and seabirds in order to elucidate at-sea foraging behaviors that had remained almost unknown (Davis et al. 1999, Yoda et al. 1999). Although the accelerometry technique has been applied with different purposes such as identification of hidden or anomalous behaviors and analyses of daily activity budget, the study on foraging behavior has continued being dominant (Ropert-Coudert et al. 2004, Whitney et al. 2008, Tanida et al. 2011, Brown et al. 2014, Wilson et al. 2015, Wang et al. 2015). The reason might be the advantage of measuring the animal energy and time budget at the same time when using accelerometers, which is of paramount important under the framework of the optimal foraging (MacArthur & Pianka 1966), allowing a refreshing revisit to this theory.

The optimal foraging theory predicts that an individual should gain the most energy for the lowest cost in terms of energy and time during foraging to maximize its fitness (MacArthur & Pianka 1966). So, individuals should modulate their foraging strategies to adapt them to changing environmental conditions when these influence the cost-benefit ratio. However, individual requirements may vary with dynamic endogenous (e.g. age, body condition, breeding status) and exogenous factors (e.g. prey availability, intraspecific competition, wind conditions) experienced by individuals that shape their foraging strategies in space and time (Saraux et al. 2011, Fossette et al. 2012, Le Vaillant et al. 2012, Weimerskirch et al. 2012, Chivers et al. 2012, Wakefield et al. 2013). Central-place foragers are considered good models to test predictions derived from the optimal foraging theory since it is possible to separate the costs of travel between the central-place and the foraging patches from those of resource acquisition at the foraging patch during foraging trips (Orians & Pearson 1979). Central-place foragers usually experience different conditions when commuting versus when searching for food that leads them to behave differently in order to deal with those challenges along the foraging trip. For example, northern gannets *Morus bassanus* leave the breeding colony flying with the wind in order to reduce flight cost when commuting to foraging patches, whereas they fly against the wind presumably to increase prey detection by reducing flight ground speed (Amélineau et al. 2014). Therefore, central-place foragers may face different cost-benefit trade-offs when commuting than when searching for food that could influence their behavioral decisions along the path, which would ultimately determine the overall cost of foraging trips.

In this paper, we study the foraging behavior of the lesser kestrel (*Falco naumanni*) during the breeding season that behaves as a central-place foragers returning to the nest to provision its offspring. The lesser kestrel is a small insectivorous falcon that breeds in colonies across the Palearctic. During foraging trips, breeding individuals fly from the colony to foraging patches where they capture prey and return to the colony carrying a single prey item in their beak or talons. On the one hand, kestrels can fly between the colony and the foraging areas by using either flapping soaring-gliding flights (Spaar 1997). Birds using flapping flights require mechanical energy produced by muscle work to beat their wings. Meanwhile, birds using soaring-gliding flights replace that mechanical energy by kinetic energy harvested from the atmosphere, mostly from uprising thermal air currents. Thus, flapping flights are more energy-consuming than soaring-gliding flights, but birds fly at higher cross-country speeds with flapping flights compared to those obtained with soaring-gliding flights (Hedenström 1993). On the other hand, kestrels can capture prey at the foraging patch either by hovering flights (an active hunting strategy in which kestrels remain suspended in the air flapping their wings) or from a perch (a passive sit-and-wait hunting strategy from an elevated position) (Village 1990). The active hunting strategy involves that kestrels fly continuously with eventual hoverings while searching for prey with the subsequently elevated energy expenditure. By contrast, in the sit-and-wait hunting strategy the kestrels wait from a perch until a prey enter its vision field and then fly and attempts a capture. Therefore, the active hunting strategy requires more energy per unit time than the sit-and-wait hunting strategy, but the former is more efficient in finding prey (Anderson & Karasov 1981, Jaksic & Carothers 1985, Aparicio 1990). In this study, we investigate how lesser kestrels allocate their daily time and energy to different behaviors both considering the whole day and during foraging. We also investigate the influence of internal (phenological period, role specialization) and external factors (prey availability, weather conditions) on lesser kestrel behavioral decisions. We tracked individual lesser kestrels from two colonies using dataloggers with GPS coupled with tri-axial accelerometers during the breeding season. We identify and classify lesser kestrel behaviors in order to study individual energy and time budget at three hierarchical levels of analyses: the day, the foraging trip, and the foraging trip segment (distinguishing commuting flight and hunting event). First, we analyze the effect of sex, phenological period and breeding colony on the lesser kestrel daily energy and time budget because these variables strongly affect kestrel movements (Chapters One, Two and Three). Second, we analyze the effect of time of day on foraging trip energy and time budget to unravel how lesser kestrels partition their foraging behaviors through the day. Finally, we analyze how lesser kestrels adapt their flight (flapping versus soaring-gliding) and hunting strategies (hovering versus perching) during commuting flights and hunting event of the foraging trips, respectively, to weather conditions (wind speed, air temperature, solar radiation and rainfall).

Material and Methods

Study species and area

The lesser kestrel is one of the smallest raptor in the Palearctic (wingspan 58–72 cm, body mass 120–140 g) and its diet is mostly based on large insects. This hole-nesting species breeds in colonies in buildings and cliffs associated with steppe-like habitats, pastures and non-irrigated crops across the Mediterranean basin and Central Asia, and it has its wintering grounds in Africa (Cramp & Simmons 1980, Bustamante 1997). European lesser kestrel populations suffered a severe decline during the second half of the twentieth century presumably due to changes in land-use derived from agricultural intensification (Tella et al. 1998, Franco & Sutherland 2004). However, the world population has apparently leveled in the last decades (IUCN 2013).

We studied individual lesser kestrels at two breeding colonies located in the Guadalquivir river basin (southwestern Spain), which is predominantly flat (20 – 240 m above sea level) and dominated by arable crops (Fernandez et al. 1992). Primary crops are wheat and sunflowers, although cotton and legume crops, olive groves and vineyards are also present in the area. The Silo colony is situated at a building with a grain elevator located in agricultural land, while the EBD colony is situated 50 km away on the roof of our research institute within the urban landscape of the city of Seville. Kestrel pairs breed inside nest-boxes installed at both buildings.

Field procedures

Lesser kestrel breeding adults were monitored during the 2014 breeding season. We deployed tracking devices that included a GPS-datalogger (GiPSy-5 model) and a tri-axial accelerometer-datalogger (Axy-3 model) with a small battery (100 mA) on lesser kestrels. Tracking devices were supplied by Technosmart (Rome, Italy). They were fixed to the birds' backs using a hand-made harness formed by a carbon fiber plate and a 4 mm wide Teflon ribbon (Bally Ribbon Mills, Pennsylvania, U.S.A.) (S1 Figure). The devices were covered with a thermoretractable case. The total mass of the equipment (harness + tracking device) was about 6 g and never exceeded the 5% of the lesser kestrel's mean body mass, which is within the generally recommended limits for flying animals (Barron et al. 2010). To get the birds used to the harness and the tracking device, we fixed a dummy tracking device with the same weight to the harness at least a week before fixing the real one and starting to record the birds' movement (see details of the procedure in Chapter One).

We deployed tracking devices on 6 lesser kestrel breeders, 4 males and 2 females (Table 1). We configured GPS devices at two different sampling frequencies: one fix per second (that gives a very detailed track) and one fix every three minutes (that maximizes battery duration). GPS provided spatial location and registered flight altitude and instantaneous speed. We configured accelerometer devices to record acceleration at 10 Hz on three axes: the kestrel's antero-posterior axis (surge, X), the lateral axis (sway, Y) and the dorso-ventral axis (heave, Z). Since the GPS and the tri-axial accelerometers stored the data in loggers, we had to recapture the individuals to recover the data. A new full-powered tracking device was then deployed before releasing the individual to resume tracking. Kestrels were captured when they entered the nest-boxes using remote-controlled sliding doors. Individuals were recaptured a mean of 2 times during the study period (range 1 - 3, n = 6). GPS data were collected during daylight hours (5 to 20 UTC), while accelerometer data were collected during the entire day. Data collection ranged from 3rd June to 24th June 2014. At some nests kestrels where incubating while at others eggs had started to hatch, so we collected data during the incubation and nestling periods. We removed the harnesses from the kestrels at the end of the breeding season. GPS data can be consulted on Movebank (www.movebank.org) (Hernández-Pliego et al. 2015).

Table 1. Details of individual lesser kestrels tracked during the study period.

Individual ID	Sex	Phenological Period	Breeding Colony	# Complete Days	# Foraging Trips	Date of First Deployment	Hatching Date	Clutch Size
B[6.U]	Male	Incubation	Silo	3	6	03/06/2014	11/06/2014	1
B[6.U]	Male	Nestling	Silo	2	25	03/06/2014	11/06/2014	1
B[D.A]	Female	Nestling	Silo	6	18	09/06/2014	04/06/2014	4
B[H.J]	Male	Incubation	Silo	0	5	03/06/2014	04/06/2014	4
B[H.J]	Male	Nestling	Silo	10	220	03/06/2014	04/06/2014	4
B[H.Y]	Male	Incubation	Silo	6	9	03/06/2014	10/06/2014	3
B[H.Y]	Male	Nestling	Silo	0	6	03/06/2014	10/06/2014	3
V[0A7]	Male	Nestling	EBD	5	118	11/06/2014	04/06/2014	3
V[0AF]	Female	Nestling	EBD	3	37	17/06/2014	04/06/2014	3

Weather data

We obtained wind speed, air temperature, solar radiation and rainfall data from the agroclimatic station network of the Andalusian Agricultural Department (http://www.juntadeandalucia.es/medioambiente/servtc5/WebClima/), collected at the meteorological station of La Palma del Condado by a RM Young 05103 windmill anemometer, a Vaisala HMP45C temperature sensor, a Skye SP1110 pyranometer and a Campbell ARG100 pluviometer, respectively. All weather variables were sampled every 30 minutes. The station is situated 192 m above sea level, 3 km from the Silo colony and 48 km from the EBD colony.

Analytical procedures

High-frequency GPS (1 fix per second) allowed us to distinguish unequivocally if a kestrel was flying or stationary by using instantaneous speed and relative spatial position of fixes. Additionally, accelerometer signature on the three axes permitted us to know which kind of flight was adopted by the kestrel when flying, and whether they were simply perching when stationary. We identified and labeled three different flight behaviors (flapping, soaring-gliding, and hovering) and two different stationary behaviors (perching and incubating/brooding) on 3 individuals (2 males and 1 female) tracked with the GPS at 1 fix per second (Figure 1). Individuals mostly used flapping and gliding flights along commuting flights of the foraging trip when moving between the colony and the foraging area. Hovering flights are the main hunting strategy for kestrels (active hunting), so this flight behavior appeared exclusively during the foraging event. Kestrels also hunt from a perch (sit-and-wait strategy). Thus, perching behavior recorded during the foraging events was considered to be perch-hunting, but when associated with the colony or roosts was considered resting behavior. Incubating behavior was only adopted at the colony while incubating eggs or brooding chicks. We used 1-s intervals of acceleration data, i.e. 10 acceleration measures, as the minimum sample unit to label behaviors. Flapping and hovering flights were characterized by regular oscillations in the surge (X) and heave (Z) axes due to wing beats, but the former was associated with GPS instantaneous speed higher than zero whereas the latter was associated with speeds close to zero (as kestrels remain suspended in the air while hovering). Gliding flight was differentiated from flapping flight because of the absence of a regular oscillation in any axis. Similarly, GPS instantaneous speed allowed us to distinguish between gliding flight with speeds higher than zero and stationary behaviors with speeds equal to zero. Within stationary behaviors, perching showed negative values in the surge (X) axis, whereas incubating showed values around zero in this axis because of the different angle of the body between the the two behaviors (Figure 1). A similar identification protocol for bird behavior has been followed in previous studies (Duriez et al. 2014, Williams et al. 2015). We labeled the acceleration data from time series of ~11.000 s of foraging trips of one of the females, and 4950 and 4750 seconds of two of the males. Then, we trained the classification model in order to classify behaviors automatically following the procedure described in Shamoun-Baranes *et al*. (Shamoun-Baranes et al. 2012). We used decision trees as the learning method of the model. We selected at random 70% of the labeled acceleration data to train the model leaving the remaining 30% to test it. We tested as predictors 18 variables derived from acceleration data: mean value and standard deviation of acceleration in each of the three axes, mean value and standard deviation of pitch and roll, pairwise correlation between the axes, fundamental frequency of acceleration cycles in the three axes, mean overall dynamic body acceleration (ODBA) and mean vectorial dynamic body acceleration (VeDBA) (see Shamoun-Baranes *et al*., 2012). Each variable was calculated for every 1-s interval of acceleration data. GPS instantaneous speed is widely used as a predictor of behavior in classification models (Shamoun-Baranes et al. 2012, Amélineau et al. 2014), but we did not include it in our model because we did not have instantaneous speed measures associated with every 1-second interval of acceleration data as most GPS had a fix every 3 min. Including instantaneous speed as a model predictor would have prevented us from applying that model to classify behaviors automatically using only the acceleration data. As a consequence, gliding flight and incubating behavior were misclassified since both showed similar acceleration signature on the three axes. In order to solve this problem, we carried out *a posteriori* classification to tag those time 1-s intervals labeled as gliding as incubating when: the GPS location closest in time situated the individual kestrel at the breeding colony (300-m radius), provided an instantaneous speed of zero and the acceleration time series revealed that the individual was still stationary. We used this final model to classify behaviors using only the accelerometer data from all 6 individual lesser kestrels tracked regardless of the GPS sampling frequency.

We evaluated the classification efficiency of the final model using a jack-knife procedure, building a model with the data of two of the kestrels and classifying the behaviors of the third, and repeating this procedure until all three kestrels had been used as test individuals. Furthermore, we carried out an extra validation of the final classification model using nighttime data between 21 p.m. to 4 a.m., when individuals are supposed to be resting in order to test the percentage of correct classification of stationary behaviors. Nest-boxes from the Silo colony are equipped with video cameras (analog camera KPC-EX500B with an IR illuminator and a Vivotek 8102 video server) that record 10-second video sequences activated by movement detection. In order to validate the decision rule to classify the incubating behavior using instantaneous speed and distance to the colony using the GPS position closest in time (1 fix every 3 min), we randomly sampled 25 intervals classified as incubating per day from individuals breeding at the Silo colony, then we cross-classified this information with what could be observed on the video samples from the corresponding nest-box.

Activity budget variables

GPS data were explored graphically using GIS (ArcGIS 10, ESRI, Redlands, California, U.S.A.) to identify the foraging trips. We use the term foraging trip to refer to a set of consecutive locations of a kestrel that, starting from the breeding colony, go farther than 300 m and in which we are able to identify a foraging event (mostly clumped locations at low altitude above the ground with highly variable instantaneous speed). We segmented every foraging trip in three parts: (1) the outward flight, i.e. the movement from the colony or roost to the foraging area; (2) the foraging event, i.e. the movement within the foraging area; and (3) the inward flight, i.e. the return movement from the foraging area to the colony or roost. We considered the foraging event as the segment of the foraging trip between the first and last hovering or perching bout identified along the trip. Therefore, the outward flight is the foraging trip segment before the first hovering or perching bout, whereas the inward flight is the foraging trip segment after the last hovering or perching bout. The outward and inward flights are the two types of commuting flights of the foraging trip. The foraging event is the foraging trip segment between the first and the last hovering or perching bout. We considered a hovering or perching bout as a sequence of at least five 1-s intervals of acceleration data labeled as hovering or perching, respectively. If two hovering bouts or two perching bouts were separated in time by less than 5 seconds of another behavior, we considered them as a single hovering or perching bout.

We estimated individual energy and time devoted to each behavior at the daily, foraging trip and foraging trip segment levels. We used ODBA to study individual energy activity budget at all levels of analyses since it can be taken as a proxy for energy expenditure (Wilson et al. 2006). We estimated ODBA per day, per foraging trip or per foraging trip segment adding the ODBA values obtained in each 1-s interval. ODBA per 1-s interval was calculated by summing the dynamic accelerations measured in the three orthogonal axes in each interval. Dynamic accelerations were obtained by subtracting the static component of the acceleration from the raw acceleration data, which was obtained by calculating the mean value of raw acceleration data in each 1-s interval. At the day level, we only included in the analyses complete days of tracking that are those in which we obtained 24 hours of continuous acceleration data. At the foraging trip level, we calculated the maximum distance from the colony and the duration of foraging trips. Incomplete foraging trips, i.e. trips in which departure from or arrival at the colony or roost was not recorded by the GPS were removed from the analyses. At the foraging trip segment level, we calculated the duration of the three foraging trip segments (outward and inward commuting flights, and the foraging event). Moreover, we calculated the proportion of time and energy invested in each flight strategies (flapping versus gliding) during the commuting flights and the proportion of time and energy invested in each hunting strategies (hovering versus perch-hunting) during the foraging event. We estimated a flapping ratio as the time devoted to flapping flight divided by the total time invested in flight behaviors during commuting flights. Similarly, we estimated a hovering ratio as the time devoted to hovering flight divided by total time invested in hunting behaviors during the foraging event. Additionally, we calculated the number of hovering and perching bouts per foraging event to estimate foraging efficiency. When provisioning the nest, kestrels return to the colony with a single prey after a foraging trip. We also calculated the number of hovering bouts that were followed by a perching bout (hereafter, hovering-perching bouts) per foraging event to estimate when kestrels were feeding themselves, since kestrels usually perch after capturing prey in order to eat it (Rudolph 1982).

Statistical analysis

We evaluated the influence of sex, phenological period and breeding colony on the energy and time activity budget of the lesser kestrel at the day level. Furthermore, we assessed the effect of time of day on the kestrel energy and time activity budget at the foraging trip and foraging trip segment levels. In addition, we analyzed the influence of weather variables (wind speed, air temperature and solar radiation) on the flight and hunting strategies of the lesser kestrel at the foraging trip segment level. The effect of rainfall on these variables was not finally tested because 98.20% of rainfall samples were 0 mm during the study period (n = 1056).

At the day level, we fitted Generalized Linear Mixed Models (GLMMs) to total ODBA (as a proxy for the energy investment) and to ODBA and time percentage devoted to each behavior (energy and time allocation to different behaviors) per day. We included the individual identity as the random factor in the models. We included individual sex as a categorical predictor in the models with two levels (male and female) because raptors are mostly role-specialized species (Andersson & Norberg 1981) and sex can have a strong influence on individual behavior. We also included phenological period as a categorical predictor in the models with two levels (incubation and nestling periods) because individuals have different energetic demands and behave differently when incubating eggs or raising chicks (Chapter Two). We included breeding colony as the third categorical predictor in the models with two levels (Silo and EBD colony) because the Silo colony has better foraging habitats and closer to the colony than the EBD colony where urban and irrigated agriculture dominate its surroundings and this has important effects on lesser kestrel foraging behavior (Chapter Three).

We fitted Generalized Additive Mixed Models (GAMMs) to total ODBA, percentage of ODBA and percentage of time devoted to each behavior, trip duration and trip maximum distance from the colony at the foraging trip level of analysis. We included hour-of-day when foraging trip started as a continuous predictor in these models in order to test the presence of a circadian pattern in lesser kestrel flight and hunting strategies since kestrels have already shown a marked circadian pattern in soaring behavior (Chapter Three). We included individual identity as the random factor of these GAMMs. Sex, phenological period and breeding colony were also included as correction factors in all models as they might have important influence on the variables analyzed at this level of analysis (see previous paragraph). At the foraging trip segment level, we fitted GAMMs to segment ODBA and duration, flapping ratio of commuting flights, hovering ratio of foraging events and to the number of hovering, perching and hovering-perching bouts per foraging event. We included hour-of-day when segment started as a continuous predictor in the models fitted at this level of analysis. We also included commuting flight type as a categorical predictor with 2 levels (outward and inward flight) in the models fitted to response variables calculated of commuting flight segments to assess potential differences in flight behavior of kestrels when leaving or returning to the colony or roost. In the models fitted to flapping and hovering ratio we also included wind speed and air temperature or solar radiation as continuous predictors, which were measured at the time rounded to the nearest half-hour when each foraging trip segment started. We did this in order to evaluate the influence of weather variables on kestrel flight and hunting behavioral decisions throughout the day (S2 Figure). We built two models for both flapping and hovering ratio, each of which included either air temperature or solar radiation and which were subsequently compared to each other on predictive ability. The weather predictor included in the best model of these two was also included in the final model of each response variable (AIC criteria, see model selection later in this section). The reason of this was because air temperature and solar radiation were moderately correlated (*air temperature* = 0.01 x *solar radiation* + 19.05, Pearson's $r = 0.71$, $t = 27.34$, $p < 0.001$, $n = 1{,}056$), so we could find a problem of collinearity if both variables were included as predictors in a single model. We included individual identity as the random factor in all models. Sex, phenological period and breeding colony were also included as correction factors in all GAMMs fitted at this level of analysis.

Percentage of energy and percentage of time devoted to each behavior were arcsine-square-root-transformed to meet the normality assumptions of generalized models. Foraging trip ODBA and duration were logarithmically transformed to improve fitting of the models. Flapping and hovering ratio were logit-transformed with the same aim. We used a Gaussian distribution of errors and the identity link function to fit models to all variables tested as a response variable excluding foraging trip maximum distance from the colony and foraging trip segment ODBA and duration; for these variables we used a gamma distribution of errors and the logarithmic link function (which were found more adequate after exploration of model residuals). We applied penalized smoothing splines to the hour-of-day, wind speed, air temperature or solar radiation in the GAMMs to account for the potential nonlinear response to the predictor. The degrees of freedom of the smoothing function were automatically selected using restricted maximum likelihood (REML) (Ruppert et al. 2003). We followed the Akaike Information Criterion (AIC) for model selection that indicates that the best model is the one with the lowest AIC value. The best GAMMs for foraging trip ODBA, foraging event ODBA and flapping ratio were those including the linear effect of the predictor, so we fitted a GLMM to those response variables using the same predictors and random factor. We fitted the GLMMs following a backward-stepwise procedure, by removing non-significant predictors until only significant ones remained. The significance of the predictors was tested using likelihood ratio tests comparing the model with and without the predictor.

Statistical analyses were performed using R-3.0.2 software (R Core Team 2013). We fitted GAMMs and GLMMs using “mgcv” (Wood 2011) and “lme4” packages (Bates et al. 2014), respectively.

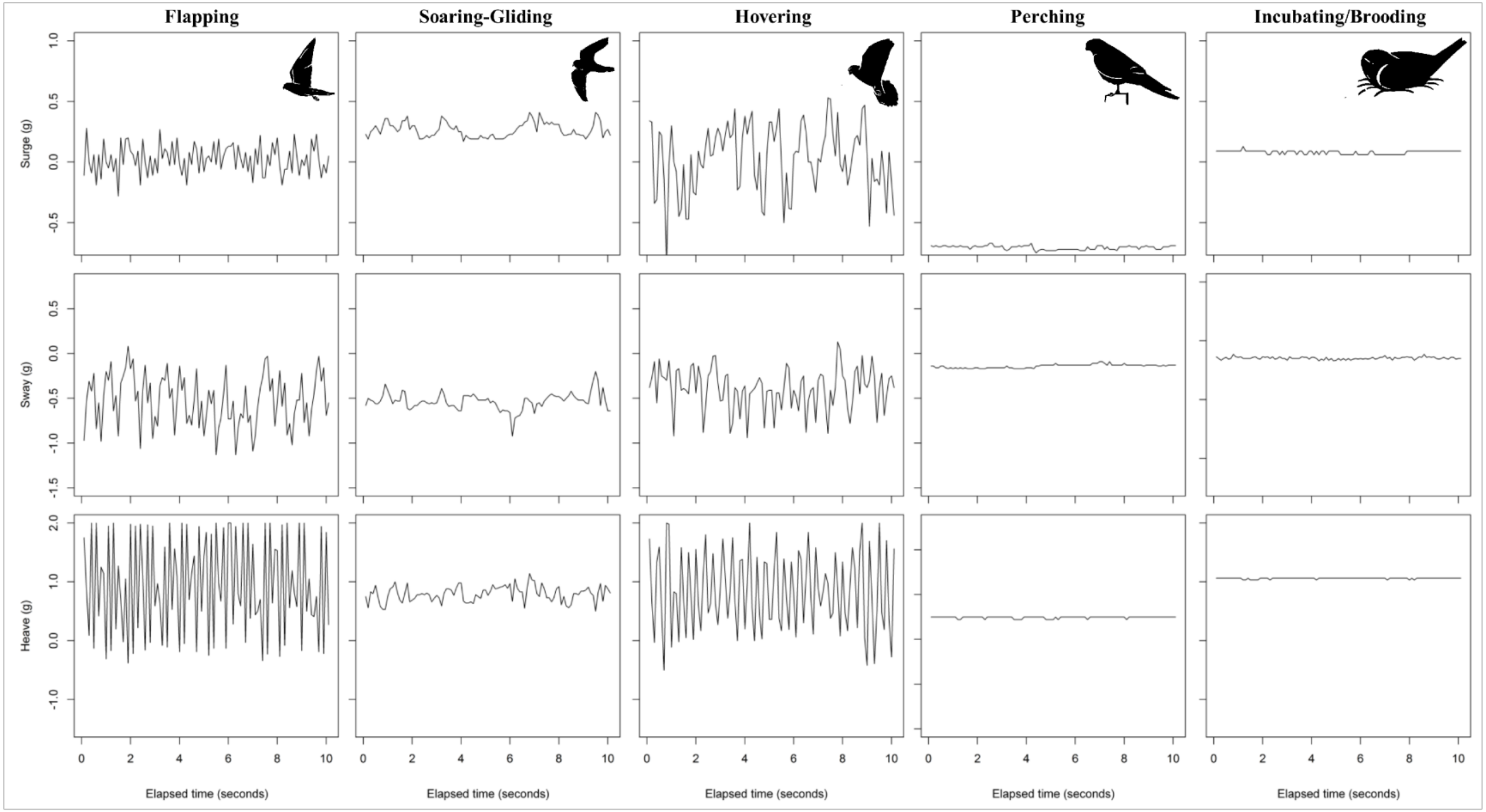

Figure 1 (Part 1). Acceleration signature of different lesser kestrel behaviors: Raw acceleration measured in the surge (X), sway (Y) and heave (Z) axes (rows) in flapping flight, soaring-gliding flight, hovering flight, perching and incubating/brooding behaviors (columns).

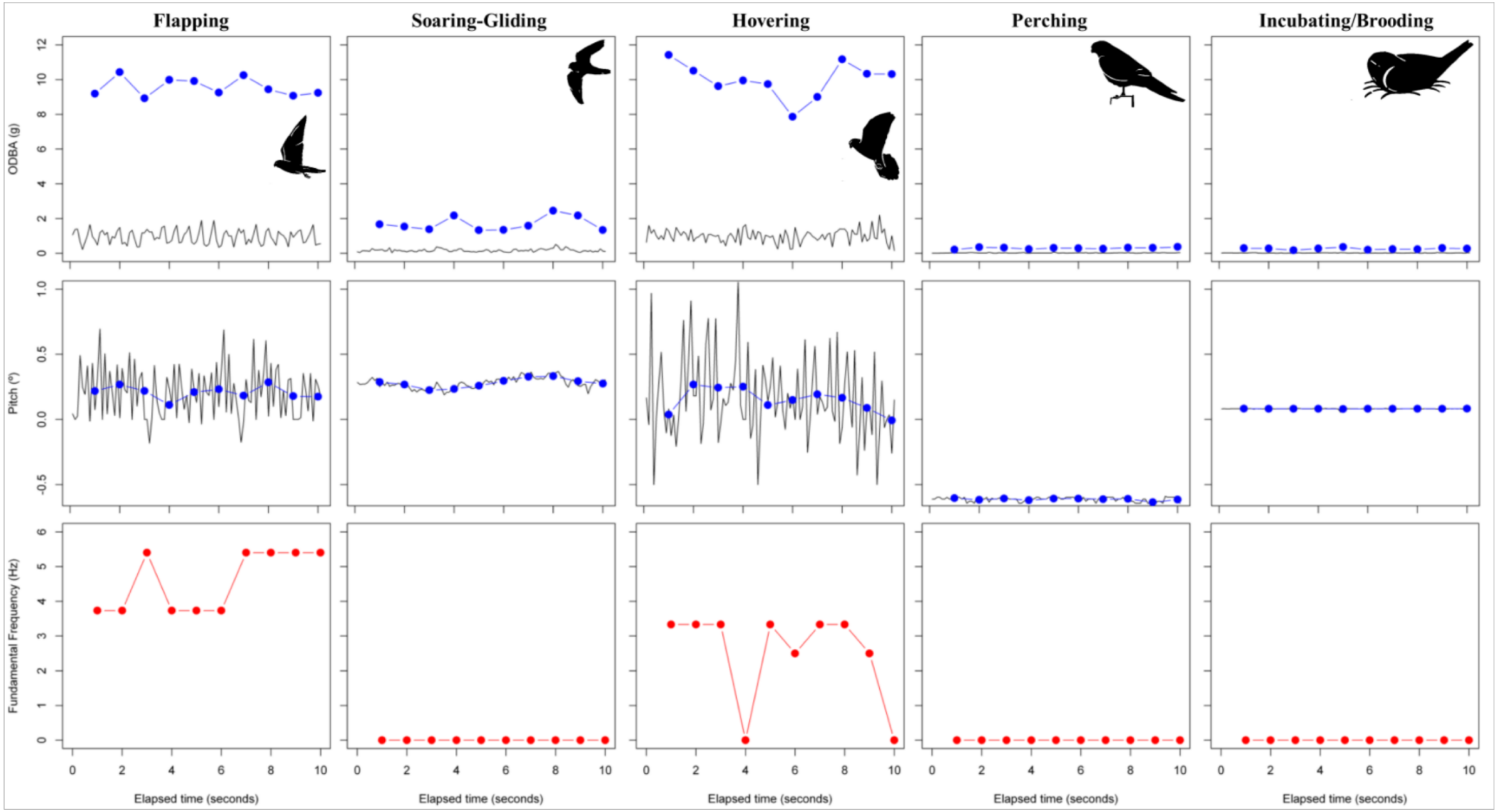

Figure 1 (Part 2). Acceleration signature of different lesser kestrel behaviors: ODBA, pitch and fundamental frequency of the heave axis (rows) in flapping flight, soaring-gliding flight, hovering flight, perching and incubating/brooding behaviors (columns). Blue dots indicate mean ODBA and pitch per 1-second interval. Red dots indicate fundamental frequency of the heave axis per 1-second interval.

Results

Energy investment models for the lesser kestrel were analogous to time investment ones in many cases. Therefore, we present here mainly the results of the time investment models, showing the results of the energy investment models as supplementary material.

Behavioral identification from tri-axial accelerometers

The final model to classify lesser kestrel behavior (flapping, soaring-gliding, hovering, perching and incubating) included as predictors the mean ODBA, the mean pitch and the fundamental frequency of the heave axis per 1-s interval of acceleration data (Figure 1), as well as the instantaneous speed and the distance from the colony provided by the GPS (Figure 2, Table 2). The model showed 95% accuracy and 93% kappa value, indicating a reliable classification of behavior with low classification error (Table 3). The jack-knife testing also indicated good model performance, although slightly worse than when using a random sample of all individuals to test it, indicating that is always better to train the classification model with samples from the same individual (S1 Table). This suggests that the model can be safely used for individuals with no training data. Validation of stationary behavior (perching and incubating) with nighttime video data resulted in, on average, 98.83 ± 2.76% of correct classification of motionless behaviors (n = 635,252 intervals). The validation of the classification rule to distinguish between incubating and gliding using video sequences showed a mean of 77.33 ± 20.03% of correct classification of incubating behavior (n = 675 intervals).

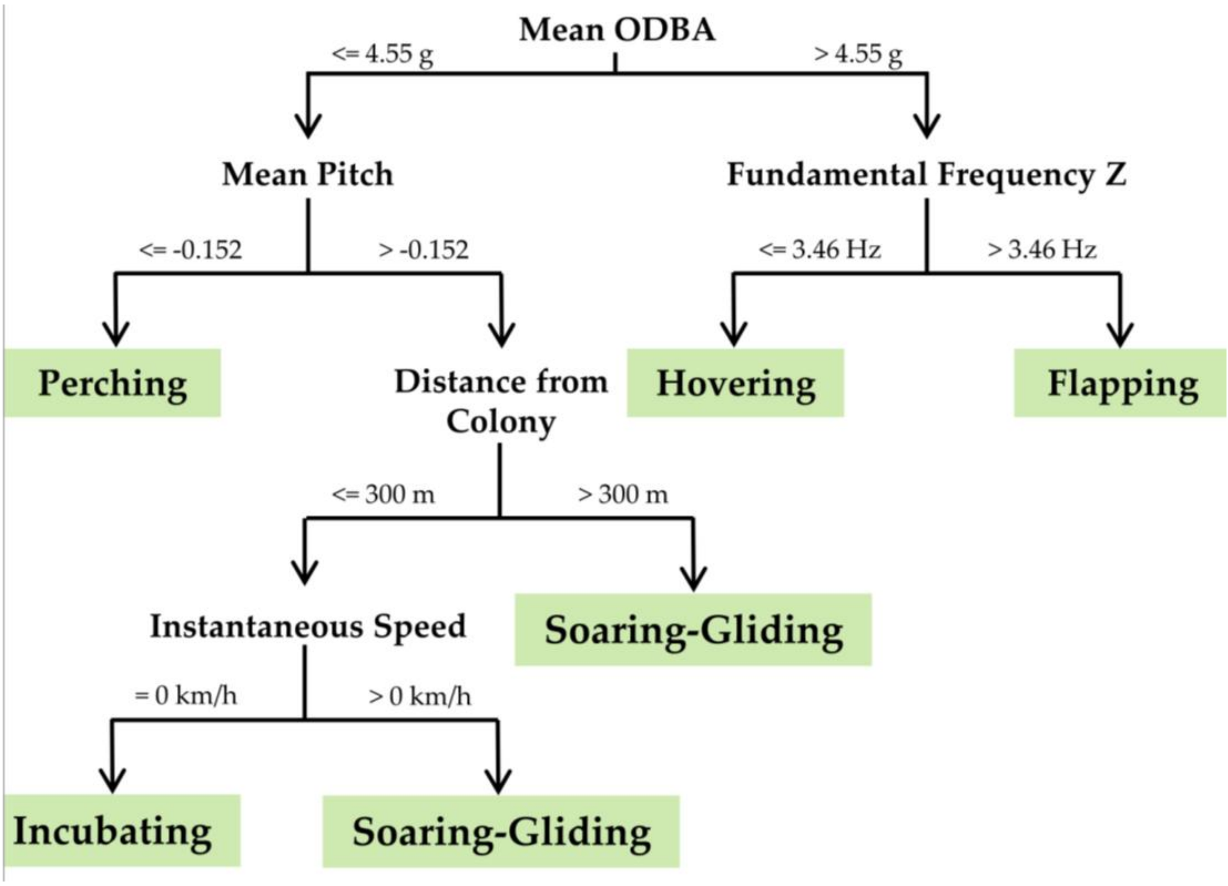

Figure 2. Decision tree for the final classification model.

Table 2. Mean and standard deviation of raw acceleration measured in the surge (X), sway (Y) and heave (Z) axes, ODBA, pitch and fundamental frequency of heave axis per lesser kestrel behavior. N = 3,024,000 intervals from 6 individual lesser kestrel (35 complete days of tracking).

Behavior	Surge (g)	Sway (g)	Heave (g)	ODBA (g)	Pitch (º)	Fundamental Frequency Heave (Hz)
Perching	-0.54 ± 0.16	-0.02 ± 0.16	0.75 ± 0.12	0.4 ± 0.06	-0.62 ± 0.21	0.004 ± 0.001
Incubating	0.004 ± 0.17	-0.07 ± 0.16	0.90 ± 0.12	1.1 ± 0.14	0.004 ± 0.19	0.003 ± 0.001
Soaring-Gliding	0.10 ± 0.12	-0.16 ± 0.14	0.98 ± 0.27	2.9 ± 0.25	0.10 ± 0.14	0.003 ± 0.001
Flapping	0.02 ± 0.21	-0.11 ± 0.22	1.00 ± 0.80	9.2 ± 0.47	0.02 ± 0.27	4.01 ± 0.94
Hovering	-0.04 ± 0.33	-0.08 ± 0.29	0.94 ± 0.79	9.5 ± 0.61	-0.04 ± 0.40	3.15 ± 0.63

Table 3. Confusion matrix for the final classification model of behaviors. We built this matrix using the 30% of the tagged acceleration data selected at random to test the model after training it with the remaining 70%. Observations correctly classified per behavior are shown in bold.

		Predicted Behaviors					
		Flapping	Gliding / Incubating	Hovering	Perching	Total	**Recall**
Actual Behaviors	Flapping	**934**	16	15	1	966	97 %
	Gliding / Incubating	7	**1,257**	2	12	1,278	98 %
	Hovering	46	12	**205**	1	264	78 %
	Perching	3	36	3	**751**	793	95 %
	Total	990	1,321	225	765	3,301	**Mean Recall** = 92%
	Precision	94 %	95 %	91 %	98 %	**Mean Precision** = 95%	**Accuracy** = 95% **Kappa** = 93%

Day level

We recorded 35 days with 24-hour accelerometer data, a mean of 5.83 ± 2.32 days per individual kestrel. Model for daily ODBA showed a statistically significant effect of phenological period and sex (Table 4). Male lesser kestrels showed higher daily ODBA than females, and they also showed higher daily ODBA during the nestling period compared to the incubation period. We also found statistically significant effects of phenological period and sex on time and energy investment per behavior during the daytime (Table 5, S2 Table). Kestrels dedicated on average 53.20 ± 22.55% of daytime to be stationary (perching and incubating). Perching behavior was recorded equally frequently at the colony (50.69 ± 29.02%) and out of the colony (49.31 ± 29.02%) regardless the sex and the phenological period. Nevertheless, individuals allocated a higher fraction of daytime to incubate eggs during the incubation period than to brood chicks during the nestling period, and this behavior was less frequent in males than in females. On the other hand, kestrels devoted on average 46.85 ± 22.55% of daytime to fly (flapping, gliding and hovering flight behaviors). The time investment in flapping and gliding flights during the daytime was smaller during the incubation period than during the nestling period and both time investments were higher in males than in females. However, the time spent in hovering flights during the daytime was affected neither by phenological period nor by individual sex. We only found statistically significant effect of the breeding colony on the time expenditure on gliding flights and incubating, although the latter might well be spurious since we did not record any data from the EBD colony during the incubating period. During the nighttime, kestrels allocated on average 98.12 ± 2.31% to perching behavior.

Foraging trip level

We recorded 444 foraging trips, a mean of 74 ± 83.15 foraging trips per individual kestrel. The best GAMM fitted to foraging trip duration included phenological period and hour-of-day as predictors (Table 6, S3 Table). Lesser kestrels reduced foraging trip duration as the day progressed (Figure 3). The best GAMM fitted to foraging trip maximum distance included phenological period, sex, breeding colony and hour-of-day as predictors (Table 6, S3 Table). Individuals went farther from the colony during foraging trips departing at noon, and made shorter flights in the morning and in the evening (Figure 4). In contrast, foraging trip ODBA was not affected by hour-of-day, indicating that kestrels spent a similar amount of energy per foraging trip throughout the day (S4 Table). Lesser kestrels allocated on average more than 82% of foraging trip time and more than 96% of foraging trip ODBA to flight behaviors (Table 7). The best GAMM fitted to all variables of time and energy investment per behavior at the foraging trip level included the hour-of-day as predictor (Table 6, S5 Table, S3 Figure). Time investment in flapping and hovering flights per foraging trip tended to remain constant as the day progressed, both increasing in the afternoon (Figure 5). Time devoted to gliding flights per foraging trip showed a positive curvilinear response to hour-of-day, reaching the maximum at noon (Figure 5). Time allocated to perching behavior per foraging trip decreased as the day progressed, showing a minimum at noon and increased again in the afternoon (Figure 5).

Table 4. Estimates (β), standard error (S.E.) and statistical significance of predictors included in the GLMM fitted to daily ODBA of the lesser kestrel. Statistically significant variables are shown in bold: * $p < 0.5$, ** $p < 0.01$, *** $p < 0.001$. N = 35 complete days of tracking.

Predictors	**β**	**S.E.**	**χ^2**	**p-value**
Intercept	203,237	18,269	-	-
Sex (Female)	- 64,922	25,914	3.96	**0.05**
Phenological Period (Incubation)	- 100,396	23,495	13.18	**< 0.001**
Breeding Colony (EBD)	4,904	26,068	0.03	0.85

Table 5. Estimates (β) and standard error (S.E) of predictors included in the GLMM fitted to daily time investment in different behaviors by the lesser kestrel. Statistically significant variables are shown in bold: * p < 0.5, ** p < 0.01, *** p < 0.001. N = 35 complete days of tracking.

Predictors	**Intercept**	**Sex (Female)**	**Phenological Period (Incubation)**	**Breeding Colony (EBD)**
Behaviors	β ± S.E. (%)	β ± S.E. (%)	β ± S.E. (%)	β ± S.E. (%)
Flapping	22.13 ± 0.10	**- 14.68 ± 0.20** *	**- 21.95 ± 0.15** ***	0.70 ± 0.21
Gliding	28.10 ± 0.04	**- 14.78 ± 0.10** **	**- 24.61 ± 0.11** ***	**20.91 ± 0.11** ***
Hovering	5.49 ± 0.04	- 2.37 ± 0.08	- 2.92 ± 0.05	- 1.37 ± 0.08
Perching	30.97 ± 0.09	13.69 ± 0.18	5.41 ± 0.19	- 3.36 ± 0.19
Incubating	6.20 ± 0.07	**13.36 ± 0.16** **	**33.25 ± 0.18** ***	**- 8.16 ± 0.17** *

Table 6. Evaluation of the relative importance of each predictor in the GAMMs fitted to variables analyzed at the foraging trip level. ΔAIC indicates the difference between the best model and the same model adding (negative values) or removing (positive values) the target predictor (depending on the predictors included in the best model). The higher the ΔAIC, the higher the relative importance of the predictor in the model. The predictors are coded as follows: Phenological period = "PP", individual sex = "S", breeding colony = "BC" and smoothed hour-of-day = "H". # indicates second and third best model when ΔAIC < 2. N = 444 foraging trips.

Response Variables		**Best Model** ΔAIC = 0	**PP** ΔAIC	**S** ΔAIC	**BC** ΔAIC	**H** ΔAIC
Duration		H+PP / H+PP+S(ΔAIC=1.54)$^{\#}$ / H+PP+BC(ΔAIC=1.99)$^{\#}$	18.95	1.54	1.99	26.38
Maximum Distance		H + PP + S + BC	6.04	7.83	10.98	30.12
Time Investment	Flapping	H	- 4.39	- 14.37	- 13.07	93.22
	Soaring-Gliding	H	- 12.92	- 12.85	- 13.54	378.20
	Hovering	H	- 16.02	- 14.65	- 11.65	47.68
	Perching	H	- 3.11	- 12.78	- 13.23	174.87

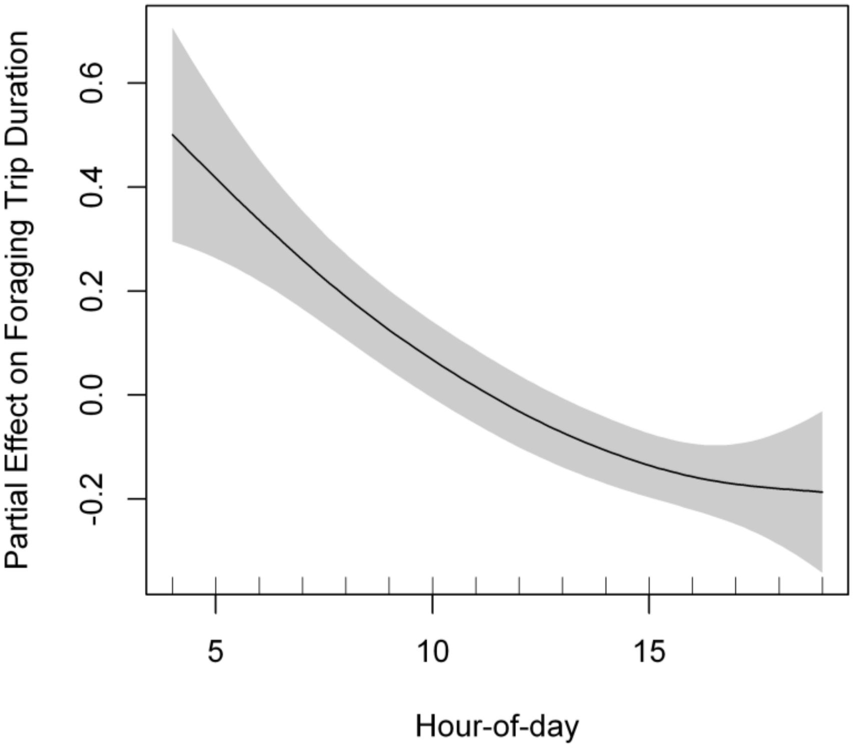

Figure 3. Partial effect of hour-of-day in the model fitted to lesser kestrel foraging trip duration. Penalized smoothing spline of 2.15 degrees of freedom was adjusted to hour-of-day. Grey shading represents the standard error of the mean effect. N = 444 foraging trips.

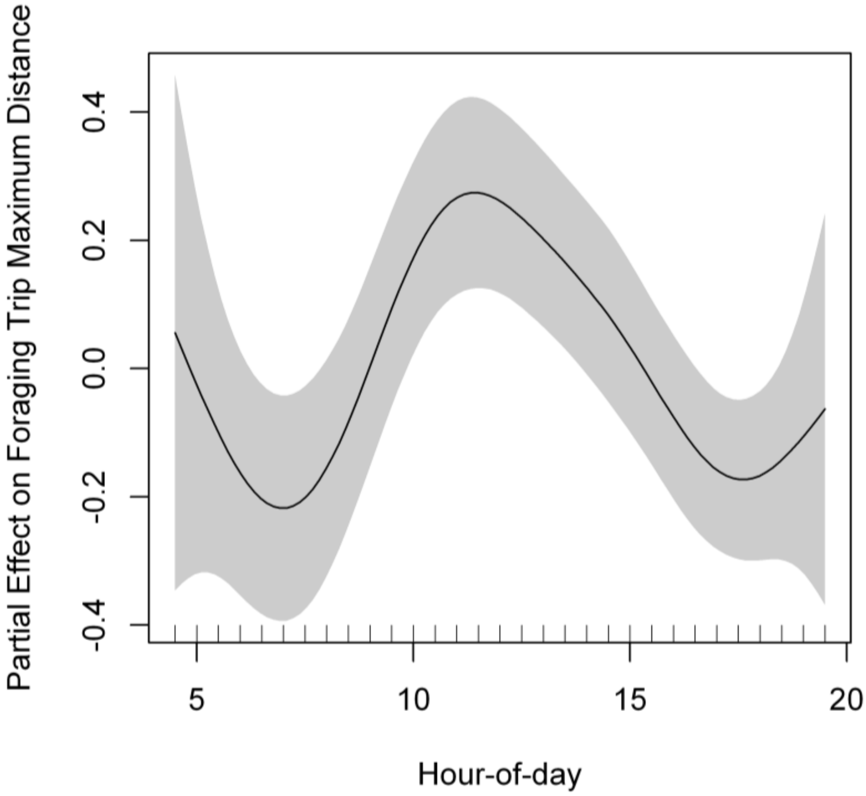

Figure 4. Partial effect of hour-of-day in the model fitted to lesser kestrel foraging trip maximum distance from the colony. Penalized smoothing spline of 4.70 degrees of freedom was adjusted to hour-of-day. Grey shading represents the standard error of the mean effect. N = 444 foraging trips.

Table 7. Time and ODBA investments (mean value ± standard deviation) devoted to different behaviors during the entire foraging trip, commuting flights and foraging event of the lesser kestrel. N = 444 foraging trips (888 commuting flights and 444 foraging events).

Segment	Behavior	Time Investment (%)	ODBA Investment (%)
Foraging Trip	-	100	100
Foraging Trip	Flapping	31.84 ± 15.58	55.85 ± 14.19
Foraging Trip	Gliding	43.01 ± 22.33	27.98 ± 16.22
Foraging Trip	Hovering	7.33 ± 5.39	12.39 ± 6.26
Foraging Trip	Perching	17.82 ± 24.82	3.78 ± 6.47
Commuting Flights	-	33.00 ± 29.94	33.64 ± 28.74
Commuting Flights	Flapping	40.78 ± 24.99	68.53 ± 22.76
Commuting Flights	Gliding	53.56 ± 25.39	30.44 ± 18.44
Foraging Event	-	67.00 ± 29.94	66.36 ± 28.74
Foraging Event	Hovering	15.87 ± 17.18	26.82 ± 19.95
Foraging Event	Perching	26.22 ± 33.47	5.56 ± 8.72

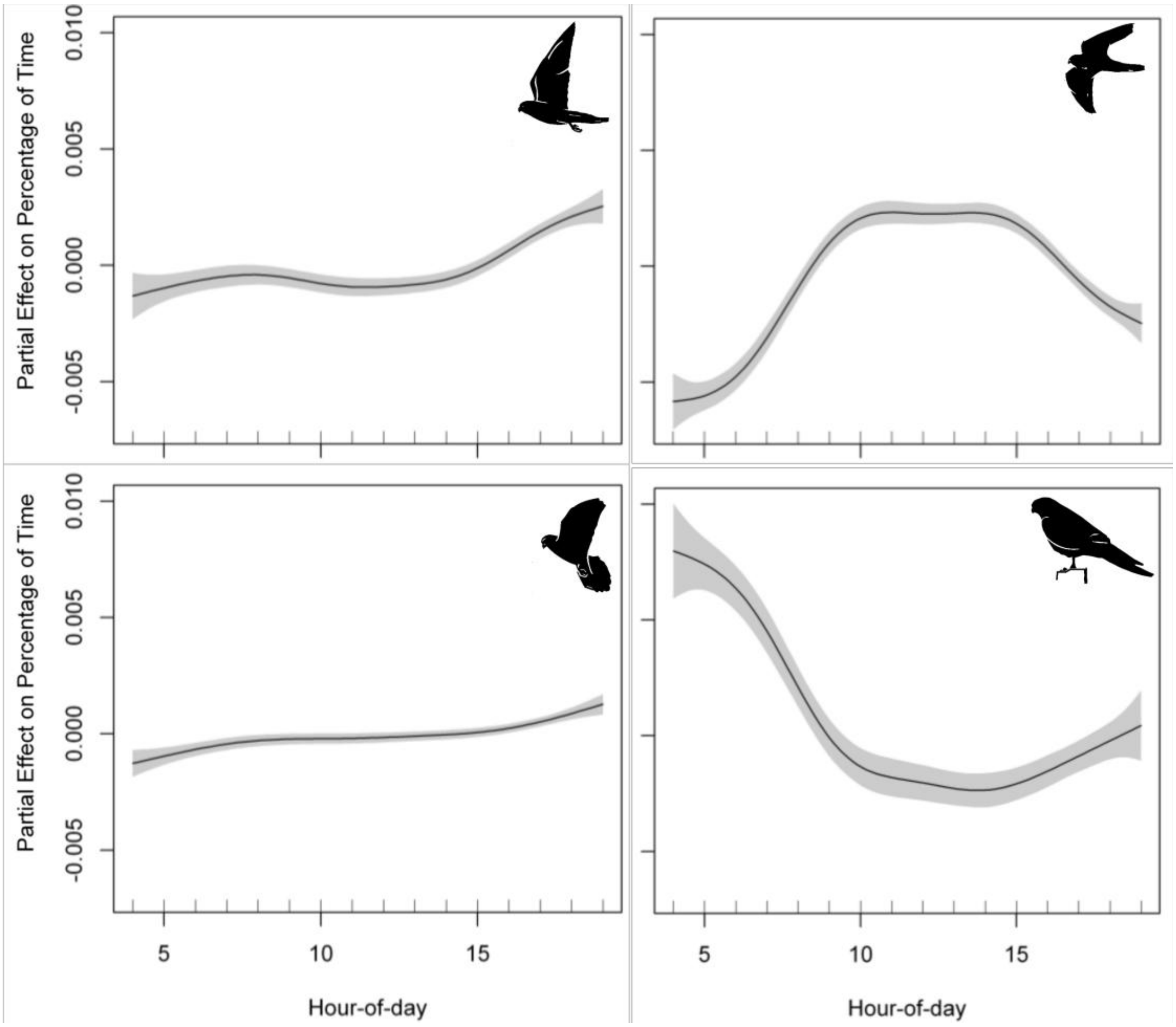

Figure 5. Partial effect of hour-of-day in the model fitted to percentage of time in each behavior along foraging trips. Flapping flight (upper left panel), soaring-gliding flight (upper right panel), hovering flight (bottom left panel) and perching (bottom right panel). Penalized smoothing splines of 4.78, 7.00, 3.82 and 5.55 degrees of freedom were adjusted to hour-of-day for flapping flight, gliding flight, hovering flight and perching, respectively. Grey shading represents the standard error of the mean effect. N = 444 foraging trips.

Foraging Trip Segment Level

We recorded 888 commuting flights (outwards and inwards) and 444 foraging events in foraging trips. The best GAMM fitted to commuting flight duration included breeding colony, commuting flight type and hour-of-day as predictors (Table 8). Outward flights were shorter and had lower ODBA than inward flights (S3 Table). Lesser kestrels increased commuting flight duration and ODBA as the day progressed, reaching a maximum at noon and decreasing again towards the sunset (Figure 6, S3 Table, S4 Figure). Outward flight ODBA was lower than inward flight ODBA (S3 Table). We obtained on average a flapping ratio of 0.43 ± 0.26 that indicated a slight dominance of soaring-gliding flights over flapping flights during commuting flights (Figure 7). Flapping ratio showed a negative linear response to solar radiation (Figure 8). Kestrels tended to use lower proportion of flapping flights during outward flights than during inward flights (Table 9). The best GAMM fitted to foraging event duration included phenological period and hour-of-day as predictors (Table 8, S3 Table). Foraging event duration decreased as the day progressed reaching a minimum at noon and increased slightly towards the sunset (Figure 6). We did not find any statistically significant effect of hour-of-day on foraging event ODBA (S6 Table). We obtained on average a hovering ratio of 0.58 ± 0.41 that indicated a relative dominance of hovering flights over perching behavior during the foraging events (Figure 7b). The best GAMM fitted to hovering ratio included phenological period, breeding colony, wind speed and air temperature as predictors (Table 8, S3 Table). Hovering ratio linearly increased with increasing wind speed and it also increased with increasing air temperature until a threshold at 25 ºC of above which hovering ratio showed a stable or slightly decreasing trend with higher temperatures (Figure 9).

Table 8. Evaluation of the relative importance of each predictor in the GAMMs fitted to variables analyzed at foraging trip segment level. ΔAIC indicates the difference between the best model and the same model adding (negative values) or removing (positive values) the target predictor (depending on the predictors included in the best model). The higher the ΔAIC, the higher the relative importance of the predictor in the model. The predictors are coded as follows: Phenological period = "PP", individual sex = "S", breeding colony = "BC", smoothed hour-of-day = "H", commuting flight type = "CF", smoothed air temperature = "T" and smoothed wind speed = "W". # indicates second best model when ΔAIC < 2. N = 888 commuting flights and 444 foraging events.

Response Variables		**Best Model** ΔAIC = 0	**PP** ΔAIC	**S** ΔAIC	**BC** ΔAIC	**H** ΔAIC	**CF** ΔAIC	**T** ΔAIC	**W** ΔAIC
Commuting Flights	Duration	H+BC+CF / H+BC+CF+S(ΔAIC=1.28)$^{\#}$	- 8.52	1.28	4.02	123.42	30.26	-	-
	ODBA	H + BC + S + CF	- 5.34	11.95	2.75	14.20	79.33	-	-
Foraging Events	Duration	H + PP / H+PP+S(ΔAIC=1.71)$^{\#}$	31.94	1.71	- 2.73	118.91	-	-	-
	Hovering Ratio	T + PP + BC + W / T+PP+BC+W+S(ΔAIC=0.43)$^{\#}$	7.83	0.43	2.55	-	-	5.23	27.43

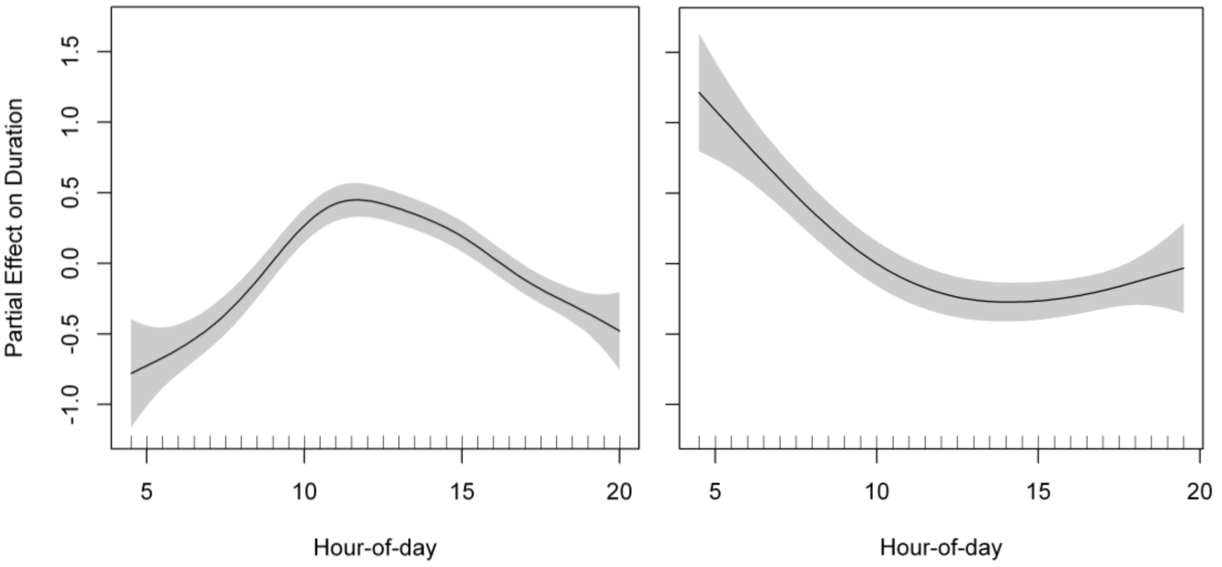

Figure 6. Partial effect of hour-of-day in the models fitted to duration of commuting flights (left panel) and foraging events (right panel) of the lesser kestrel. Penalized smoothing splines of 4.89 and 2.84 degrees of freedom were adjusted to hour-of-day for commuting flight and foraging event duration, respectively. Grey shading represents the standard error of the mean effect. N = 888 commuting flights and 444 foraging events.

Table 9. Estimates (β), standard error (S.E.) and statistical significance of predictors included in the GLMM fitted to flapping ratio of lesser kestrel commuting flights. Statistically significant predictors are shown in bold. N = 888 commuting flights.

Predictors	β	S.E.	χ^2	p-value
Intercept	0.83	0.57	-	-
Solar Radiation	- 0.0004	0.50	369.32	< 0.001
Wind Speed	- 0.001	0.51	0.02	0.89
Commuting Flight Type (Inwards)	0.07	0.52	20.43	< 0.001
Sex (Female)	0.02	0.59	0.39	0.53
Phenological Period (Incubation)	0.11	0.56	5.06	0.02
Breeding Colony (EBD)	0.03	0.59	0.51	0.47

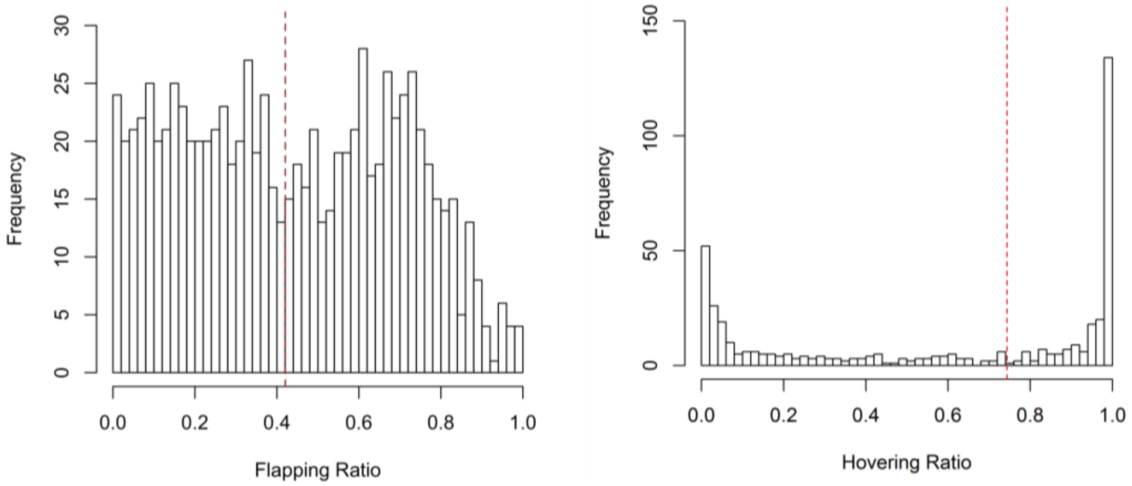

Figure 7. Frequency histogram of flapping (left panel) and hovering ratio (right panel) during commuting flights and foraging events, respectively, of lesser kestrel foraging trips. The dashed line indicates the median value of ratios. N = 888 commuting flights and 444 foraging events.

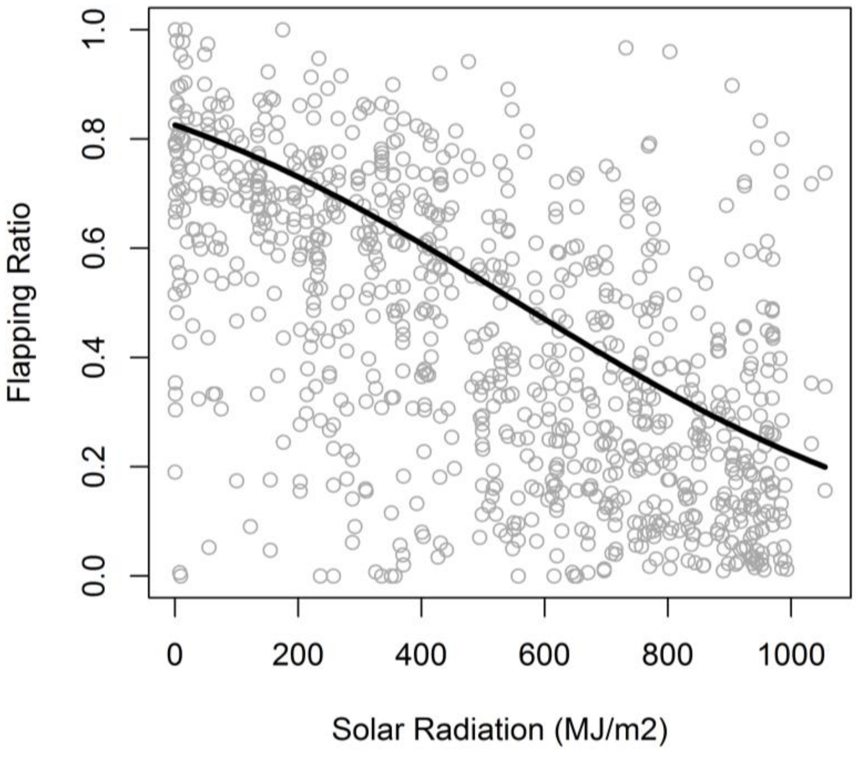

Figure 8. Effect of solar radiation on flapping ratio of lesser kestrel commuting flights predicted by the GLMM. Circles represent the observed flapping ratio of commuting flights and the solid line represents the model prediction. N = 888 commuting flights.

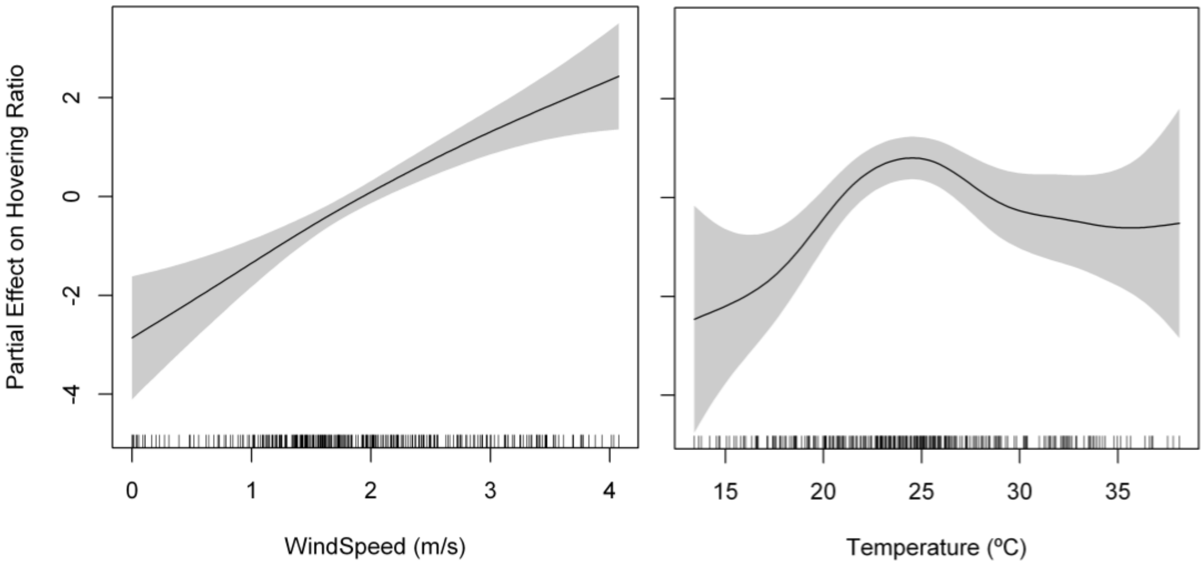

Figure 9. Partial effect of wind speed (left panel) and air temperature (right panel) in the model fitted to hovering ratio of lesser kestrel foraging events. Penalized smoothing splines of 1.54 and 4.15 degrees of freedom were adjusted to wind speed and air temperature, respectively. Grey shading represents the standard error of the mean effect. N = 444 foraging events.

Hovering and perching bouts

We identified 4,933 hovering bouts (a mean of 8.91 ± 11.60 bouts/foraging event) and 2,798 perching bouts (a mean of 4.65 ± 10.04 bouts/foraging event). Both the best GAMM fitted to the number of hovering bouts and perching bouts per foraging event included phenological period and hour-of-day (Table 10, S3 Table). The number of hovering bouts per foraging event remained constant along the day but it showed an increase towards the sunset, whereas the number of perching bouts per foraging event decreased as the day progressed reaching a minimum at noon and then increased again towards the sunset (Figure 10). Furthermore, we identified 476 hovering-perching bouts (hovering followed by perching, a mean of 1.07 ± 2.10 bouts/foraging event). The best GAMM fitted to the number of hovering-perching bouts per foraging event also included phenological period and hour-of-day as predictors (Table 10, S3 Table). The number of hovering-perching bouts per foraging event decreased as the day progressed reaching a minimum at noon and then increased again towards the sunset (Figure 10). The number of hovering-perching bouts per foraging event was higher in those foraging trips that end at a roost site (4.81 ± 4.17 hovering-perching bouts/event; Mann-Whitney U test, $z = 6.91$, $p < 0.001$, $n = 16$) compared to those that end at the colony (0.93 ± 1.86 hovering-perching bouts/event, $n = 428$).

Discussion

The use of accelerometers in ecological studies was originally promoted by the difficulty of observing directly the behavior of marine mammals and seabirds at-sea mostly due to the enormous foraging ranges of these species but also because many behaviors take place underwater (Davis et al. 1999, Yoda et al. 1999, Arai et al. 2000). The fact that accelerometers provide an unbiased record of animal behavior with no need of observation in the field has strengthened their use as a powerful tool in behavioral research, and as a result the number of studies based on this technique has vastly increased in last years (Brown et al. 2013). Accelerometers have proved to be highly efficient identifying behaviors on a wide range of animal taxa across marine, aerial o terrestrial ecosystems (Tsuda et al. 2006, Shamoun-Baranes et al. 2012, Graf et al. 2015). In this study, we were able to identify five different behaviors (flapping, soaring-gliding and hovering flights, perching and incubating/brooding) of free-ranging lesser kestrels during the breeding season through the combination of tri-axial accelerometry and GPS tracking. Overall, we obtained a high performance of the behavior classification model indicating a good ability to predict kestrel behaviors from accelerometer data (Table 3). The use of tri-axial accelerometers combined with a behavior classification model allows us to estimate the lesser kestrel behavior-specific energy expenditure in terms of ODBA (Table 2). Flight behaviors (flapping, soaring-gliding and hovering flights) require more energy to be performed than stationary behaviors (perching and incubating/brooding). Within the flight behaviors, flapping and hovering are more energy-consuming than soaring-gliding, as predicted by flight theory (Pennycuick 2008) and in agreement with empirical studies on bird flight dynamics (Sakamoto et al. 2009, Duriez et al. 2014). Therefore, accelerometers provide us with an efficient tool to study how lesser kestrels partition their time and energy into different behaviors throughout the day.

We observed sexual differences in the daily energy and time activity budget of the lesser kestrel (Table 4). Males invest more time and energy in flight behaviors and less energy and time in stationary behaviors than females on a daily basis (Table 5, S2 Table). This different daily level of activity between sexes is consistent with the role specialization in raptors. Raptors tend to show reversed size sexual dimorphism and are considered to be one of the most role-specialized group among birds: Each member of the breeding pair entrust with separately tasks involved in reproduction (Andersson & Norberg 1981). Male raptors usually provision their mate and/or offspring whereas females are typically devoted to egg incubation, chick brooding and nest defense. The higher investment of male kestrels in flight behaviors is in accordance with the elevated prey provisioning rate previously reported in this species, in a similar way that the higher investment of female kestrels in stationary behaviors agrees with the elevated daily nest attendance described (Donázar et al. 1992). Contrary to the general trend in raptors, both sexes of the lesser kestrel share the incubation of eggs (Donázar et al. 1992), explaining the lower dedication in energy and time to flight behaviors and the higher devotion to incubating/brooding behavior during the incubation period in comparison to the nestling period. Kestrels show similar daily energy expenditure regardless of the colony they were breeding, although individuals from the EBD colony allocated more energy and time to soaring-gliding flights than their counterparts from the Silo colony. This discrepancy seems to be guided by the different foraging quality of the habitat matrix in the surroundings of the colonies. Kestrels from the EBD colony, mostly surrounded by low-quality urban landscape, fly farther to reach suitable foraging patches and they do it by soaring on thermals, whereas kestrels from the Silo colony do not need to do so since the colony is immersed within *a priori* optimal non-irrigated arable landscape (Chapter Three).

This is supported by the overall larger foraging trip maximum distance and longer commuting flight duration observed in the individuals from the EBD colony (S3 Table). Therefore, the behavior-specific costs and the role specialization of the lesser kestrel determine the individual daily energy expenditure.

The lesser kestrel shows a daily distribution of behaviors that is far from uniformity. Individual kestrels spend the nighttime resting with stationary behaviors in accordance with the diurnal habits of this species. Individuals from the EBD colony are inactive despite nocturnal activity in lesser kestrels has been described at other urban colonies (Negro et al. 2000). Kestrels dedicate the daytime mostly to flight behaviors, that is, individuals allocate almost the complete daylight period to foraging activities, especially during the nestling period. Our results indicate a dramatic impact of hour-of-day on the percentage of energy and time devoted to different behaviors during foraging trips, suggesting that kestrels show a flexible foraging strategy throughout the diurnal cycle (S5 Figure). During the commuting flights of the foraging trips, lesser kestrels can either decide to fly by using a flapping or a soaring-gliding flight strategy and such decision seems to follow circadian patterns influenced by the time of day. Kestrels mainly use flapping flights to commute between the colony and the foraging areas early in the morning. As the day progresses, soaring-gliding becomes the predominant strategy reaching the maximum around midday, and then the use of flapping flights increases again towards the sunset (Figure 5). When the flapping ratio is analyzed, the solar radiation arises as the most important weather variable in determining the behavioral decision about which flight strategy to use during commuting flights (Table 9). Solar radiation is the causal agent of thermal formation since thermal currents result from the differential heating of the ground and the low level of the atmosphere by the sun (Cushman-Roisin 2014), so it can be taken as a proxy for thermal development. Thus, as solar radiation increases the flapping ratio linearly decreases meaning that kestrels progressively replace the flapping with the soaring-gliding flights as thermals get stronger through the day. This quantitative result supports the qualitative ones obtained in Chapter Three where foraging trips in which thermal soaring events were identified along the flight track were compared with foraging trips without thermal soaring events. This allows us to reaffirm that as solar radiation increases, kestrels harvest more kinetic energy from the atmosphere, transform it into potential energy by circling up in stronger thermals and fly with lower energy cost (as estimated by ODBA). Individual kestrels take advantage of this reduction in flight cost to fly farther from the colony during foraging trips around midday when solar radiation is higher and consequently using a higher percentage of soaring-gliding flights, instead of flapping flights (Figure 4). This, together with the lower cross-country speed provided by thermal soaring, results in longer and more energy expensive commuting flights in the central hours of the day (Figure 6, S4 Figure). We also found that kestrels used higher proportion of flapping flights during the inward flights in comparison to the outward flights (Table 9). Kestrels carrying a single prey item to the colony during inward flights carries an extra-load that implies an increase in the sinking rate of the individual, that is, an increase in its downward speed in relation to the forward speed when gliding (Pennycuick 2008). Consequently, kestrels probably use more flapping flights when returning to the colony in order to compensate the faster loss of altitude when gliding between thermals. As a result the energy expenditure of inward flight increases, as we observed (S3 Table). Wind speed did not influence the flapping ratio of commuting flights, in agreement with the absence of a strong effect of wind on lesser kestrel flights previously reported in Chapter One.

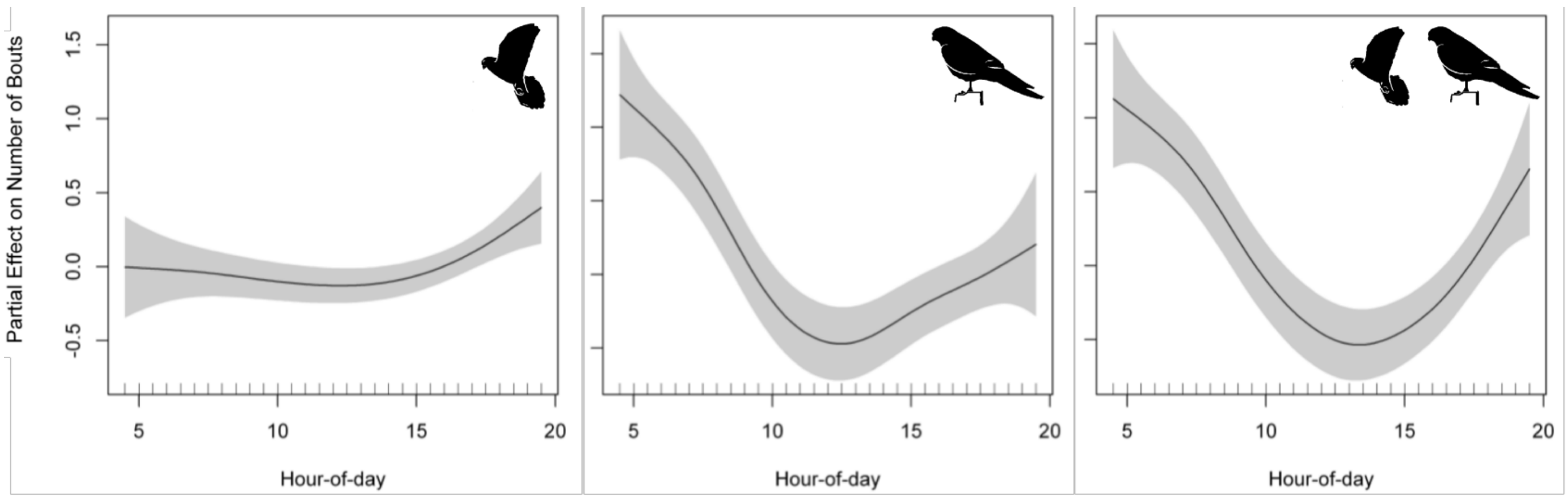

Figure 10. Partial effect of hour-of-day in the models fitted to the number of hovering bouts (left panel), to the number of perching bouts (middle panel) and to the number of hovering-perching bouts (right panel) per lesser kestrel foraging event. Penalized smoothing splines of 2.35, 3.56 and 3.47 degrees of freedom were adjusted to hour-of-day for the number of hovering bouts, perching bouts, and hovering-perching bouts per foraging event, respectively. Grey shading represents the standard error of the mean effect. N = 444 foraging events.

Table 10. Evaluation of the relative importance of each predictor in the GAMMs fitted to the number of hovering bouts, perching bouts and hovering-perching bouts per lesser kestrel foraging event. ΔAIC indicates the difference between the best model and the same model adding (negative values) or removing (positive values) the target predictor (depending on the predictors included in the best model). The higher the ΔAIC, the higher the importance of the predictor in the model. The predictors are coded as follows: Phenological period = "PP", individual sex = "S", breeding colony = "BC" and smoothed hour-of-day = "H". # indicates second best model when ΔAIC < 2. N = 444 foraging events.

Response Variables	**Best Model** ΔAIC = 0	**PP** ΔAIC	**S** ΔAIC	**BC** ΔAIC	**H** ΔAIC
# Hovering Bouts	H + PP / H+PP+BC(ΔAIC=1.48)$^{\#}$	8.10	- 2.05	1.48	8.78
# Perching Bouts	H + PP	52.18	- 3.51	- 2.10	98.90
# Hovering-Perching Bouts	H + PP / H+PP+BC(ΔAIC=0.33)$^{\#}$	18.87	- 3.00	0.33	96.97

On the other hand, during the foraging events of the foraging trips kestrels can either decide to hunt by using hovering flights (i.e. active hunting) or perch-hunting (i.e. sit-and-wait strategy) and such decision also seems to be influenced by the time of day. Kestrels mostly hunt from perches early in the morning, but as the day progresses they switch to hovering flights that remain dominant until close to sunset when perch-hunting increases again (Figure 5). When the hovering ratio is analyzed, wind speed and air temperature arise as important weather variables in determining the behavioral decision of which hunting strategy to use during foraging events (Table 8). As wind speed increases the hovering ratio linearly increases that indicates that kestrels gradually replace the perch-hunting with the hovering flights as wind blows stronger through the day (Figure 9). Hovering flights are an energetically costly behavior (Table 2). However, kestrels could take advantage of the lift force originated by winds that would help them to remain aloft with less reliance on wing beats during hovering flights (Withers 1979). So as wind speed increases through day, kestrels would experience stronger lifts and consequently would reduce energy expenditure of hovering flights to a greater extent. Nevertheless, the bimodal frequency distribution of the hovering ratio seems to not be completely explained by the gradual switch from perch-hunting to hovering flight mediated by wind speed. Here, the effect of air temperature on the hovering ratio would play an important role. As air temperature increases the hovering ratio also increases, that is, kestrels change from the sit-and-wait hunting strategy to the active hunting strategy as the day gets warmer until certain values of temperature above which the hovering ratio stabilizes (Figure 9). We hypothesize that this change in hunting strategy of the lesser kestrel may be mediated by the activity pattern of its preferred prey. The diet of the lesser kestrel changes through the breeding season, but it is predominantly composed by bush crickets (family Tettigoniidae, mostly genus *Ephippiger* and *Decticus*) during the incubation and nestling periods in our study area (Rodríguez et al. 2010). Bush crickets show marked stridulatory and locomotory activities that are highly determined by air temperature (Walker 1975, Berggren 2005). *Ephippiger ephippiger* males sing to attract mate and, in response, females synchronically increase their mobility as soon as air temperature increases above 17 ºC through the day (Stiedl & Bickmeyer 1991). Therefore, early in the morning when air temperature is low, preferred prey would be less active and subsequently more difficult to be found by kestrels, so individuals adopt the sit-and-wait hunting strategy to save energy costs, although it takes longer to detect and capture prey. As the day progresses and gets warmer, preferred prey would become more active and consequently make them easier to find by kestrels, triggering a change of individual strategy to active hunting, which is more energy-consuming but requires less time to encounter prey (as can be seen in our data of foraging event duration). However, hovering-specific energy expenditure is reduced as wind speed increases through the day, in this way relaxing the trade-off between the two hunting strategies. Our results agree with those found in the American kestrel (*Falco sparverius*), a closely related species, that increases the percentage of hunting time devoted to hovering flights as wind speed and air temperature increase until a threshold of both variables above which that percentage decreases again (Rudolph 1982). Vlachos *et al*. (2003) found a negative linear relationship between wind speed and hovering hunting rate in the lesser kestrel. In the study area, maximum wind speed is probably too low (~ 4 m/s, see Chapter One) during kestrel breeding season to detect any negative response of the hovering ratio to wind speed. It is not surprising, however, that kestrels modify their foraging strategy in response to prey availability since food abundance and density have been identified as key factors affecting foraging behavior in numerous species (Salamolard & Weimerskirch 1993, Wilson et al. 2002, 2013, Chivers et al. 2012, Spiegel et al. 2013, Penteriani et al. 2013). Furthermore, the fact that hovering ratio is lower in individuals from the EBD colony than in those from the Silo colony also suggests that hunting strategy choice may be influenced by prey availability. Kestrels from the EBD colony seem to adopt more often the sit-and-wait hunting strategy when foraging at poor-quality areas in the surroundings of the colony where prey availability is expected to be low, whereas kestrels from the Silo colony usually adopt the active hunting strategy as prey availability would be high within their suitable foraging areas. Our findings are also in accordance with the decreasing probability of performing perching bouts during foraging trips as breeding season advances, and consequently preferred prey abundance also increases (as previously reported in Chapter Two). The combination of wind conditions, prey availability and hunting strategy efficiency results in the observed daily pattern of foraging event duration: foraging events are longer early in the morning but its duration decreases as the day progresses, with a slight increase towards the sunset (Figure 6). Nevertheless, energy expenditure associated to foraging events did not change on a daily basis, which in turn explained why the overall energy expenditure of foraging trips neither change through day since foraging event supposed on average the major part of the foraging trip (Table 7, S4 Table).

Hovering flights constitute the main hunting strategy of kestrels (Village 1990), but it is also a recurring strategy when searching for food among insects, bats or hummingbirds (Norberg 1976, Ellington 1984, Warrick et al. 2005), so its identification should be key when studying foraging ecology. Tri-axial acceleration signature of both flapping and soaring-gliding flights has been described on numerous bird species (Ropert-Coudert et al. 2004, Weimerskirch et al. 2005, Duriez et al. 2014, Williams et al. 2015), but this is, up to our knowledge, the first time that the acceleration signature of hovering flights is detailed. However, a limitation of our study is that we were not able to distinguish whether kestrels were successful or not in capturing prey after performing a hovering or perching bout. Nevertheless, we can infer the number of prey captured per foraging trip because foraging behavior of the lesser kestrel has been widely studied in the field. The number of hovering bouts necessary to make a strike has been estimated at 4.3-5.5 that are successful on average 39-73% of the times in the lesser kestrel (Zank & Kemp 1996, Tella et al. 1998, Vlachos et al. 2003, Rodríguez et al. 2013). Zank and Kemp (Zank & Kemp 1996) situated at 59% the success rate of the lesser kestrel when hunting from perches, which is similar to the 54% described in the

American kestrel (Mills 1979). We obtained a mean of 8.91 hovering bouts and a mean of 4.65 perching bouts per foraging event. Therefore, being conservative, individual kestrels would be capturing on average a single prey per foraging event, which is what would be expected as they have to return to the colony to feed their offspring and they only carry one item at a time. Another limitation of our study is the difficulty of identifying when kestrels capture prey to be self-consumed. Observations in the field support that kestrels usually fly towards a perch to eat the prey after capture (Rudolph 1982), so we could consider the number of hovering-perching bouts as an indicator of kestrel self-feeding activity. The higher number of hovering-perching bouts observed in those foraging trips that end in overnight roost sites instead of returning to the colony supports this assumption. The number of hovering-perching bouts shows a marked daily pattern: it is high early in the morning, decreases as the day progresses and slightly increases towards the sunset. Therefore, breeding kestrels could feed themselves especially during the first hours after sunrise but also close to sunset. In addition, early in the morning, when preferred prey are supposed to be less active, kestrels might capture by perch hunting any prey they could find, including beetles or crickets that also appears in the lesser kestrel diet but are smaller and probably less energetically rewarding than bush crickets (Rodríguez et al. 2010). At this time of the daylight period there are no thermals so the cost of returning to the colony by using flapping flights would outweigh the benefits provided by the prey captured, so it is more economical to sue them for self-feeding instead of provisioning the offspring. This is in accordance to what has been reported in other species of genus *Falco* that small prey are destined to be self-consumed by individual foragers at the foraging patches, while bigger prey are delivered to the nest to feed the offspring (Rudolph 1982, Palatitz et al. 2015). Close to sunset, lesser kestrels would find a similar scenario in relation to thermals, but then hovering flights are more often than during the morning. The reason may be because wind speed is highest during the evening so kestrels can hover with the lowest energy expense. Furthermore, as the day progresses towards the sunset, the difference between air and ground temperatures reduces and consequently thermal intensity weakens, although air temperature is still elevated and bush crickets could remain active (Jin & Mullens 2014). This would allow lesser kestrel breeders to continue capturing their preferred prey by using hovering flights with a similar success rates to those obtained around midday, but in this case to feed themselves. It is common that the last foraging trip of the day ends at an overnight roost sites, especially for kestrel males. By staying in these roost sites, individuals save the flight costs of returning to the colony using flapping flights at the end of the daylight period. Moreover, individuals also save the flight cost associated with the first foraging trip outward commuting flight the next morning, since they are already within suitable foraging patches located far from the colony. This is supported by the large foraging trip maximum distance from the colony found early in the morning and late in the evening (Figure 4). Therefore, kestrels seem to time their self-feeding activity to those periods of the day when commuting flight costs outweigh the potential benefits of prey transport to the nest.

To sum up, our classification model based on GPS and tri-axial accelerometer data performs well when classifying lesser kestrel behaviors, in this way supporting the efficiency of this methodology to study behaviors of free-ranging animals. Our results indicate that the role specialization of the lesser kestrel explains the differences between sexes in daily energy expenditure during the breeding season. Our findings also show that lesser kestrel behavioral decisions about which flight and hunting strategies to use during foraging trips are deeply affected by environmental conditions (solar radiation, wind speed and air temperature) that change throughout the day resulting in marked daily patterns of foraging strategy. Interestingly, the energy expended per foraging trip does not vary through the day, suggesting that kestrels have a fixed energy budget per foraging trip to which they adjust their flight and hunting strategies in response to the environmental conditions.

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Supporting information

S1 Table. Mean confusion matrix for the three classification model obtained from the jack-knife procedure. We built this matrix adding the results of the confusion matrix of each of the three models, which were built with the data of two of the three kestrels to classify behaviors of the third. Observations correctly classified per behavior are shown in bold.

		Predicted Behaviors					
		Flapping	Gliding / Incubating	Hovering	Perching	Total	**Recall**
Actual Behaviors	Flapping	**3,622**	48	163	18	3,851	94 %
	Gliding / Incubating	251	**3,842**	133	446	4,672	78 %
	Hovering	195	26	**704**	4	929	68 %
	Perching	12	152	10	**2,474**	2,648	93 %
	Total	4,080	4,068	1,010	2,942	12,100	**Mean Recall** = 83%
	Precision	87 %	94 %	56 %	81 %	**Mean Precision** = 80%	**Accuracy** = 88% **Kappa** = 83%

S2 Table. Estimates (β) and standard error (S.E.) of predictors included in the GLMM fitted to daily energy investment to different behaviors of the lesser kestrel. Statistically significant predictors are shown in bold.: * p < 0.5, ** p < 0.01, *** p < 0.001. Sample size = 35 complete days.

Predictors	**Intercept**	**Sex (Female)**	**Phenological Period (Incubation)**	**Breeding Colony (EBD)**
Behaviors	β ± S.E. (%)	β ± S.E. (%)	β ± S.E. (%)	β ± S.E. (%)
Flapping	53.33 ± 0.03	**- 17.83 ± 0.07** **	- 16.19 ± 0.07 ***	0.35 ± 0.07
Gliding	22.92 ± 0.02	**- 4.81 ± 0.06** *	- 6.80 ± 0.06 **	12.93 ± 0.06 ***
Hovering	15.20 ± 0.03	0.51 ± 0.06	2.90 ± 0.03	- 7.18 ± 0.09 *
Perching	5.02 ± 0.06	**7.29 ± 0.16** *	8.51 ± 0.15 **	- 1.06 ± 0.17
Incubating	0.99 ± 0.18	**7.41 ± 0.48** *	11.40 ± 0.24 ***	- 2.19 ± 0.39

S3 Table. Estimate (β) ± standard error (S.E.) predicted for sex, phenological stage and breeding colony included in the GAMMs fitted to variables analyzed at the foraging trip or segment levels. Predictors included in the best model fitted to each variable as response are shown in bold. Sample Size = 444 foraging trips (888 commuting flights and 444 foraging events).

Level of Analyses	Response Variable	Intercept	Sex (Female)	Phenological Period (Incubation)	Breeding Colony (EBD)	Commuting Flight (Inwards)
Foraging Trip	Duration (min)	36.28 ± 0.02	9.89 ± 0.03	**45.35 ± 0.02**	4.62 ± 0.02	-
Foraging Trip	Maximum Distance (km)	2.64 ± 1.14	**2.80 ± 1.24**	**1.03 ± 1.22**	**0.58 ± 2.62**	-
Commuting Flights	Duration (min)	5.78 ± 0.02	4.00 ± 0.02	0.23 ± 0.02	**2.55 ± 0.02**	**2.44 ± 0.02**
Commuting Flights	ODBA (g)	148.94 ± 1.07	**146.71 ± 1.11**	- 27.73 ± 1.15	**10.88 ± 1.10**	**92.15 ± 1.05**
Foraging Event	Duration (min)	22.66 ± 0.02	4.67 ± 0.02	**73.94 ± 0.02**	1.13 ± 0.02	-
Foraging Event	Hovering Ratio	0.85 ± 0.66	0.06 ± 0.79	**- 0.56 ± 0.71**	**- 0.38 ± 0.75**	-
Foraging Event	# Hovering Bouts	8.81 ± 1.25	5.09 ± 1.37	**7.86 ± 1.21**	- 6.25 ± 1.36	-
Foraging Event	# Perching Bouts	3.87 ± 1.16	0.75 ± 1.36	**11.84 ± 1.24**	-0.10 ± 1.32	-
Foraging Event	# Hovering-Perching Bouts	1.02 ± 1.19	0.92 ± 1.23	**1.91 ± 1.27**	- 0.32 ± 1.19	-

S4 Table. Estimates (β), standard error (S.E.) and statistical significance of predictors included in the GLMM fitted to foraging trip ODBA. Statistically significant predictors are shown in bold. Sample size = 444 foraging trips.

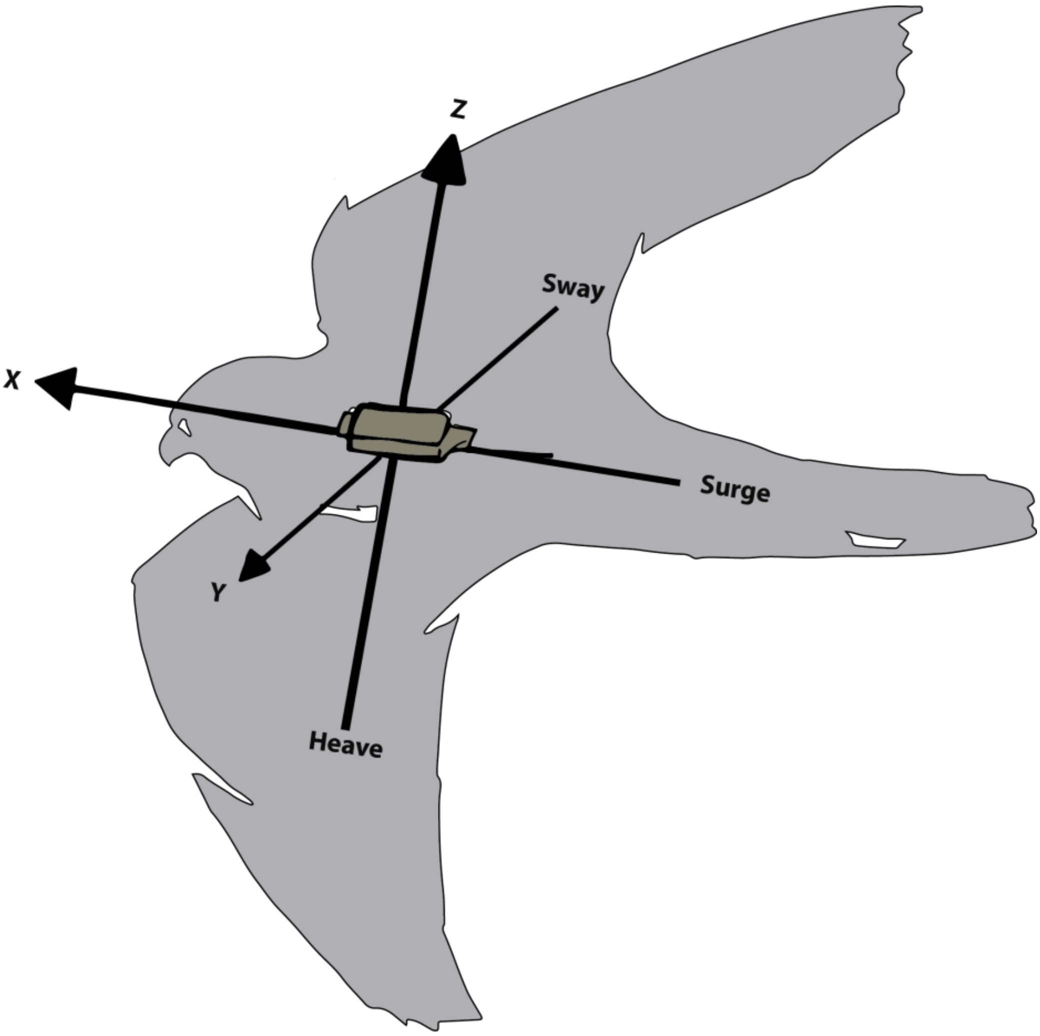
Predictors	**β**	**S.E.**	**χ^2**	**p-value**
Intercept	9,352.51	1.16	-	-
Hour-of-day	- 6.29	1.01	0.01	0.93
Sex (Female)	5,590.74	1.29	2.53	0.11
Phenological Period (Incubation)	9,445.38	1.19	17.52	< 0.001
Breeding Colony (EBD)	- 1,221.22	1.28	0.38	0.53

S5 Table. Evaluation of the importance of each predictor separately in the GAMMs fitted to variables of lesser kestrel foraging trips. ΔAIC indicated the difference between the best model and the same model adding or removing (depending on the predictors included in the best model) the target predictor. The higher the ΔAIC, the higher the importance of the predictor in the model fit. The predictors are classed as follows: Phenological period as “PP”, individual sex as “S”, breeding colony as “BC” and smoothed hour-of-day as “H”. Sample size = 444 foraging trips.

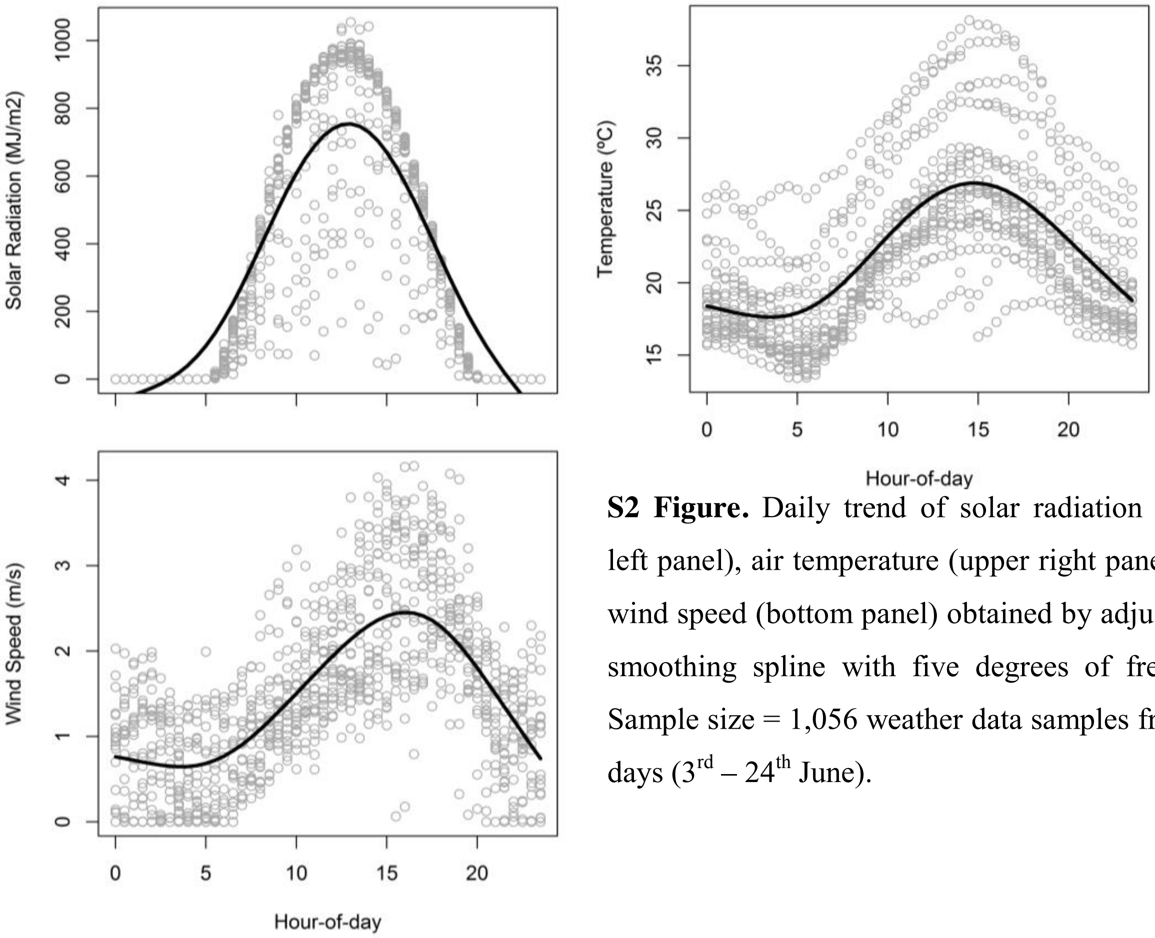
Response Variables		**Best Model** ΔAIC = 0	**PP** ΔAIC	**S** ΔAIC	**BC** ΔAIC	**H** ΔAIC
Energy Investment	Flapping	H	- 7.96	- 15.65	- 13.93	139.66
	Soaring-Gliding	H	- 15.50	- 14.30	- 12.13	336.63
	Hovering	H	- 11.80	- 14.49	- 8.93	2.91
	Perching	H + PP	4	- 14.86	- 12.97	138.46

S6 Table. Estimates (β), standard error (S.E.) and statistical significance of predictors included in the GLMM fitted to foraging event ODBA. Statistically significant predictors are shown in bold. Sample size = 444 foraging trips.

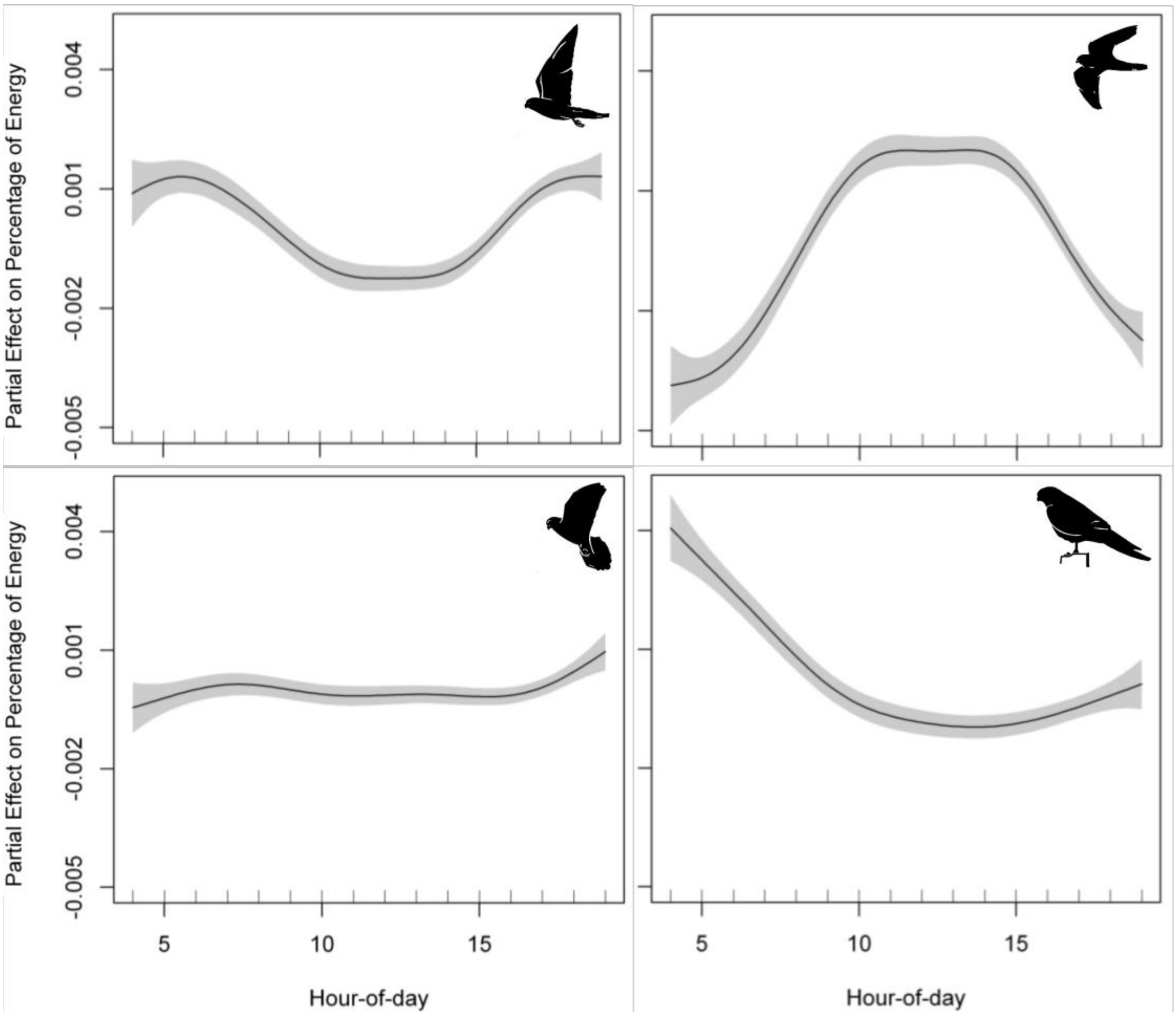
Predictors	**β**	**S.E.**	**χ^2**	**p-value**
Intercept	660.11	1.19	-	-
Hour-of-day	- 7.52	1.01	0.95	0.33
Sex (Female)	343.18	1.43	1.02	0.31
Phenological Period (Incubation)	1,269.65	1.36	19.24	< 0.001
Breeding Colony (EBD)	- 134.80	1.40	0.07	0.79



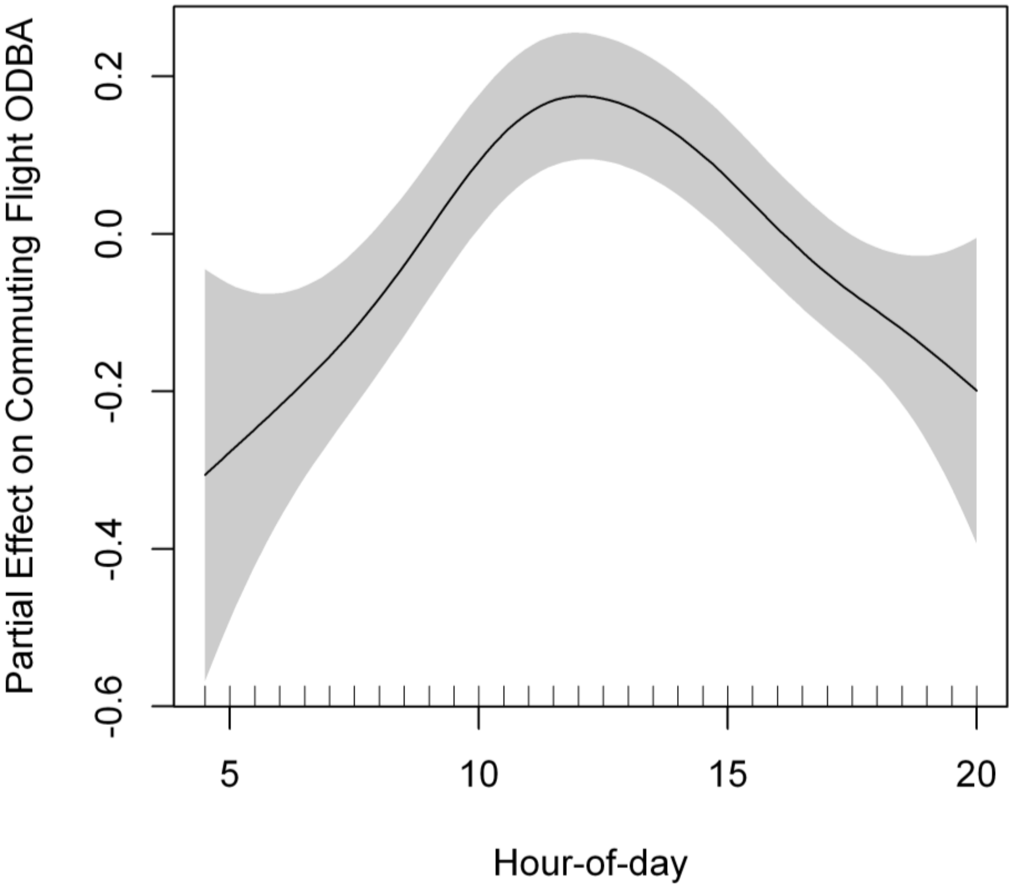
S1 Figure. Position of the tracking device on the lesser kestrel's back and direction of the three axes in which acceleration was measured.



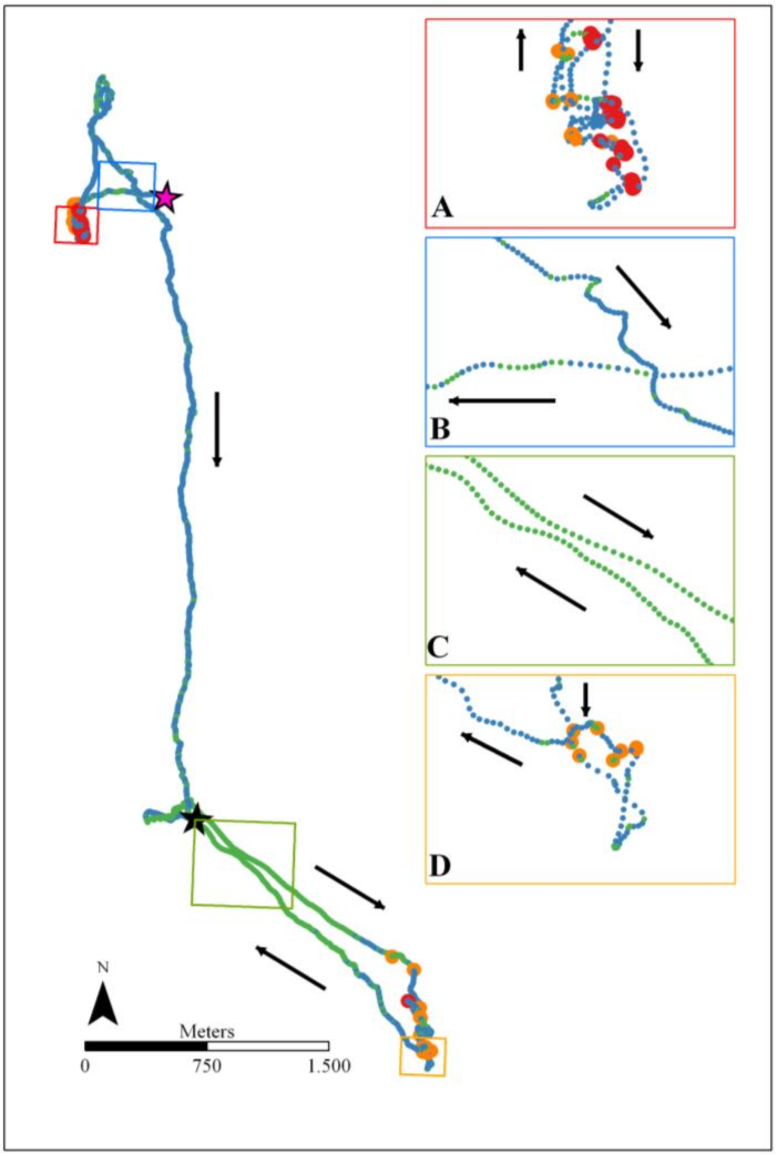
S2 Figure. Daily trend of solar radiation (upper left panel), air temperature (upper right panel) and wind speed (bottom panel) obtained by adjusting a smoothing spline with five degrees of freedom. Sample size = 1,056 weather data samples from 22 days (3rd – 24th June).



S3 Figure. Partial effect of hour-of-day in the model fitted to foraging trip energy investment per behavior. Flapping flight (upper left panel), gliding flight (upper right panel), hovering flight (bottom left panel) and perching (bottom right panel). Penalized smoothing splines of 6.29, 6.64, 4.67 and 4.20 degrees of freedom were adjusted to hour-of-day for flapping flight, gliding flight, hovering flight and perching, respectively. Grey shading represents the standard error of the mean effect. Sample size = 444 foraging trips.



S4 Figure. Partial effect of hour-of-day in the models fitted to lesser kestrel commuting flight ODBA. Penalized smoothing spline of 3.34 degrees of freedom was adjusted to hour-of-day. Grey shading represents the standard error of the mean effect. Sample size = 888 commuting flights.



S5 Figure. Example of time budget obtained using the final classification model during two lesser kestrel foraging trips recorded at 1-second frequency. The colors of the icons represent different behaviors: flapping (blue), soaring-gliding (green), hovering (orange), and perching (red). The black star indicates the breeding colony and the pink star indicates an overnight roost. Black arrows indicate movement direction. Boxes include a zoomed view of the foraging trip segment indicated with the same color in the main panel: A) foraging event (hovering ratio = 0.02); (B) commuting flights (mean flapping ratio = 0.71); (C) commuting flights (mean flapping ratio = 0.29); and (D) foraging event (hovering ratio = 0.77).

GENERAL DISCUSSION AND SYNTHESIS

All animals require energy to survive and reproduce and this energy is obtained by feeding. This statement has historically aroused the interest of researchers to study animal feeding behavior. Therefore, it is not surprising that foraging ecology is considered as one of the pillars of modern animal ecology. Numerous theoretical and empirical studies define the extensive literature on animal foraging ecology that can be consulted in the present day—19,290 articles found in ISI Web of Science (Thomson Reuters 2010) with keywords "foraging ecology" or "foraging behavior". However, foraging ecology experienced its major impulse at the end of the 1960s when Emlen (1966) and MacArthur and Pianka (1966) published their seminal works (Perry & Pianka 1997). These studies established the bases on which the optimality for feeding behavior was developed. The optimal foraging theory, as was later called, tries to understand animal decisions in relation to feeding behavior through the cost-benefit ratio in terms of time and energy allocated to resource acquisition (Schoener 1971). This theory predicts that an individual should gain the most energy for the lowest time and energy cost, in this way maximizing its fitness. Schoener (1971) differentiated between two alternative optimal foraging strategies: a time minimizing strategy, which maximizes fitness by reducing the time allocated to obtain food; and an energy maximizing strategy, which maximizes fitness by increasing the net energy intake when feeding. Optimal foraging strategy mostly comprised the optimality of diet and foraging patch that governs individual feeding behavior (Mittelbach 1981, Brown 1988). As an example, Elliot (1988) demonstrated that pine squirrels *Tamiasciurus hudsonicus fremontii* feed on cones of increasing quality as the distance from their nests to target pines increased. Squirrels might spend more time and energy to move towards pines located farther compared to closer ones but the energy obtained from feeding on the higher-quality cones of the former should positively balance the net energy intake. In spite of being reasonably well supported from empirical data, optimal foraging models faced some controversy at the beginning. They were considered too simple to represent natural scenarios and consequently it was proposed the inclusion of additional parameters, such as predation risk, reproductive events or territorial defense, in order to generate a more comprehensive theoretical framework of animal feeding behavior (Pyke et al. 1977, Pyke 1984, Mangel & Clark 1986). New optimal foraging models were later developed so as to surpass some of the assumptions imposed by the optimal foraging theory, such as individual perfect knowledge about food distribution in the landscape (Bartumeus et al. 2005). Thus, optimal foraging models have been refined since they were postulated in order to help understand the processes that determine animal feeding behavior. Furthermore, the technological revolution of biologging devices over the last decades, which promoted the rise of Movement Ecology, has provided researchers with new tools to study animal behavior and has kept alive the interest in optimal foraging theory (Portugal et al. 2014, Bishop et al. 2015).

Central-place foraging is a feeding strategy that entails animals traveling between a central-place, usually the nest or burrow, and discrete foraging areas, in this way constraining individual use of space to the surroundings of that central-place. Under the optimal foraging theory, central-place foragers are expected to maximize energy intake at the central-place, so accordingly individuals should balance the value of the food item to acquire and the time and energy needed to commute between the central-place and the foraging patch where they obtain it (Orians & Pearson 1979). Central-place foragers are considered good models to test the predictions derived from the optimal foraging theory as it is possible to separate the costs of traveling between the central-place and the foraging areas and those of searching and handling food at the foraging patch. In this sense, the application of satellite tracking systems and tri-axial accelerometry to ecological studies on free-ranging animals have expanded the frontiers of knowledge on foraging ecology since they permit to measure the time and energy allocation to movement behaviors (e.g., Shepard et al. 2009, Wilson et al. 2012, Amélineau et al. 2014). However, studies on foraging movements have been traditionally focused on seabird and marine mammals because of the great interest in revealing their at-sea behaviors that were difficult to observed directly before the deployment of biologgers (Stewart et al. 1989, Davis et al. 1999, Yoda et al. 1999, Phillips et al. 2008). Moreover, the first biologgers were too heavy to be used on a wide range of animal taxa, but marine species are generally large enough to carry them (Kays et al. 2015, Elliott 2016). In this context, this PhD thesis offers an innovative perspective as we have studied the foraging ecology of a small-sized terrestrial bird during the breeding season when it behaves as a central-place forager thanks to the application of small biologging devices.

The lesser kestrel is a well-studied raptor. Probably because of being a common species that suffered a world population decline due to the agricultural intensification since the second half of the 20th century (IUCN 2013), there have been numerous studies that have attempted to elaborate suitable conservation actions. Lesser kestrel foraging ecology has received considerable research attention mainly focusing on habitat selection and diet (e.g., Donázar et al. 1993, Bustamante 1997, Tella et al. 1998, Franco & Sutherland 2004, Catry et al. 2016). Indeed, this PhD thesis aims to contribute to the foraging ecology of the lesser kestrel through a change in scope. Here, we have studied lesser kestrel foraging movements under the Movement Ecology paradigm that is to reveal the internal (motivation, motion abilities and navigation capacities) and external factors shaping individual movement (Nathan et al. 2008). Therefore, we have addressed the effect of these elements on lesser kestrel foraging movements during the breeding season using the optimal foraging theory as a background scenario across all chapters included in this dissertation.

Why to move?

This PhD thesis focuses on the foraging movements of the lesser kestrel, so the individual initial motivation to move — to search for food resources — was clear from the very beginning. However, during reproduction, lesser kestrel breeders may capture prey either to feed themselves or to provision their mate and offspring.

Individual sex has relevance in this dichotomy because of the role specialization showed by the lesser kestrel, which is a common trait among the birds of prey (Andersson & Norberg 1981, Newton 2010). Overall, lesser kestrel males fly larger daily distances and perform higher number of shorter foraging trips per day than females as they are the main responsible for provisioning their mate/offspring. By contrast, lesser kestrel females dedicate more time during the day to stay at the colony than males because they are entrusted with defensive tasks, but when they move to forage they mostly do it to feed themselves. Thus, individual sex can be considered as an important motivational factor since largely determines foraging movement strategy in the lesser kestrel breeding pair. However, the motivation to move of both sexes varies with time as the energy demand changes throughout the reproductive period. Early in the breeding season, when breeding pairs are not formed yet, lesser kestrels of both sexes move in a similar way as they might allocate foraging effort to gather energy resources individually in order to face the incoming breeding season. Meanwhile, as soon as breeding pairs are formed, lesser kestrels show sex-specific foraging movement patterns to deal with the differential reproductive tasks. In the courtship and incubation periods, males mainly dedicate foraging effort to feed their mate (i.e., mate-feeding behavior), whereas females stay at the colony to defend the nest and incubate eggs (Donázar et al. 1992). At the end of the breeding season, lesser kestrels increase their foraging effort to fulfill the higher energy demand derived from rearing the chicks, although they have differential roles in relation to sex. Kestrel males maintain a constant foraging effort to feed chicks at the maximum level throughout the nestling period, not influenced by chick age or brood size, whereas females are initially entrusted with chick brooding and defense but then increase foraging effort as chicks get older and require more food and less protection. Therefore, role specialization strongly regulates foraging movements of the lesser kestrel and so seems to balance parental investment of both members of the breeding pair throughout the breeding season (Chapter Two).

How to move?

The lesser kestrel, like most avian species, moves by flying and can do it either through flapping, which requires muscle work, or through soaring-gliding harvesting energy from the environment (Pennycuick 2008, Hedenström 2008). Energy cost for flapping flights steeply increases with body mass (Pennycuick 1972, Ellington 1991), so the difference in energy expenditure between the two flight strategies also increases with body mass. Based on its small size, the lesser kestrel has been traditionally considered as a flapping raptor (Strandberg et al. 2009, Limiñana et al. 2013). However, we found that lesser kestrels gradually replace flapping with soaring-gliding during commuting flights as solar radiation increases, that is, as thermal updrafts get stronger. Therefore, the lesser kestrel decides which flight strategy to use as a function of the kinetic energy available in the atmosphere. The flight strategy adopted has in turn important effects on foraging movement patterns of the lesser kestrel. Individuals fly with slower cross-country speeds and reach farther distances from the colony during foraging trips with thermal soaring events than in those without them. As a consequence, the daily cycle of thermal formation creates a circadian pattern of lesser kestrel foraging movements. When thermals are weak or absent early in the morning and close to sunset, kestrels flap towards foraging areas located close to the colony. Meanwhile, as soon as thermals are formed, they soar on them and fly towards presumably high-quality foraging areas located far from the colony. In return, kestrels obtain lower prey provisioning rates to the chicks at the colony when using soaring-gliding flights. Hence, the lesser kestrel prioritizes saving energy instead of time by soaring on thermals when traveling between the colony and the foraging areas during the breeding season (Chapters Three and Four).

Where and when to move?

The lesser kestrel breeds in colonies associated to arable landscapes, especially in western Europe where natural steppes are scarce (Cramp & Simmons 1980). Arable landscapes are usually highly dynamic ecosystems and the spatial distributions of crops can change from year to year. For this reason, when lesser kestrels arrive to the breeding grounds after spring migration, they need to prospect the surroundings of the colony in order to acquire or update knowledge about habitat distribution and its relation with prey distribution. This exploratory behavior is reflected in the lesser kestrel movements and they show a uniform distribution in the departure direction of foraging trips early in the breeding season. So presumably, the lesser kestrel leaves the colony in random directions to explore the greatest possible area around the colony when the energy demand for reproduction is low. In this context, individual memory has a paramount role in the process of learning and remembering prey spatial distribution in order to create a cognitive map of suitable foraging areas, which is acquired through individual experience as the breeding season progresses (Fagan et al. 2013). Consequently, kestrels would learn how suitable foraging areas are spatially distributed and use this knowledge at the end of the breeding season. This fits with the concentrated distribution of foraging trip departure directions observed at this stage. Thus, the lesser kestrel probably concentrates foraging trip departure directions towards high-quality foraging areas when they are probably more time constrained because of rearing chicks (Chapter One). In this context, the change in the diet composition of the lesser kestrel from a generalist early in the breeding season to a specialist at the end of the breeding season as preferred prey abundance increases (Rodríguez et al. 2010) can be associated with the change in foraging trip departure direction distribution, either as a cause or as a consequence.

Who and what is out there?

There are a multitude of external factors affecting individual movements, and they can be classified as abiotic or biotic regarding their origin. Among those that are frequently considered in relation to animal movement are those derived from weather conditions. We have already shown the influence of solar radiation on lesser kestrel decision about which flight strategy to adopt (see *How to move?*). Within weather variables, wind speed and direction have been reported as an important factor affecting movement of flying animals, even with profound influence on population dynamics (Brattström et al. 2008, Wakefield et al. 2009, Weimerskirch et al. 2012). For this reason, we evaluated the influence of wind conditions in foraging trip departure directions of the lesser kestrel. However, we found little effect probably because of the prevailing winds of the study area that are weak and constant in direction. In spite of this, wind speed influences lesser kestrel decision about which hunting strategy to use at the foraging patch. Individuals replace perch-hunting with hover-hunting as wind speed increases, that is, as they experience stronger lift forces that reduce the energy cost of hovering flights. Nevertheless, the lesser kestrel appears to ultimately decide the hunt strategy to adopt depending on another weather variable: air temperature. The reason behind is because air temperature regulates the activity level of lesser kestrel preferred prey (bush crickets) (Walker 1975, Berggren 2005). Thus, when air temperature is low, and consequently preferred prey are inactive and in turn more difficult to be detected, lesser kestrels prioritize saving energy by using the perch-hunting strategy. However, as air temperature increases, lesser kestrels preferentially use the hover-hunting strategy that requires more energy but less time to capture prey, in this way reducing the total energy expenditure of hunting when preferred prey are more active and in turn easier to be detected. Therefore, results indicate that it is prey availability, mediated by air temperature, what largely conditions the relative use of different hunting strategies by the lesser kestrel (Chapters One and Four).

Prey availability has been identified as a paramount biotic external factors shaping movement behavior of numerous species (see e.g., Salamolard & Weimerskirch 1993, Chivers et al. 2012, Wilson et al. 2013), so it is not surprising that it also influences lesser kestrel foraging strategy. On the one hand, daily activity cycle of the preferred prey guides to a circadian pattern of lesser kestrel hunting strategy, with perch-hunting being predominantly used early in the morning when bush crickets are inactive but giving way to hover-hunting as the day progresses and gets warmer. On the other hand, preferred prey phenology also influences the relative use of hunting strategies by the lesser kestrel throughout the breeding season. Lesser kestrels show the lowest probability of using perch-hunting during foraging trips in the nestling period when the abundance of preferred prey reaches a peak (Rodríguez et al. 2010). Apart from the effect of temporal changes in prey availability on lesser kestrel movements, there is an additional effect associated with the spatial distribution of prey availability. Colonial species, including the lesser kestrel, usually experience prey depletion as a common negative-density effect due to the high intraspecific competition at the vicinity of the colony (Ashmole 1963, Bonal & M. Aparicio 2008). This negative consequence of coloniality may explain why kestrels fly towards foraging areas located farther from the colony by soaring on thermals as soon as these are available. Indeed, this phenomenon is more marked in individuals from an urban colony surrounded by a poor-habitat matrix where prey availability was expected to be lower than in the surroundings of a colony situated within an arable landscape. Moreover, the fact that kestrels from the urban colony adopt the perch-hunting strategy more frequently than kestrels from the rural colony also suggests the idea of lower preferred prey availability in its surroundings. Nevertheless, the lesser kestrel appears to reduce prey depletion close to the colony by displaying a sexual spatial segregation of foraging areas. This seems to be the result from an adaptive foraging strategy based on role specialization by members of the breeding pairs to reduce intersexual competition and breed successfully. Thus, the lesser kestrel male, which is the main responsible for food provisioning, reduces the energy cost associated to commuting flights by using intensively foraging areas located close to the colony and at the same time reducing the time spent in commuting flights and maximizing chick feeding rate at the nest. Meanwhile, the lesser kestrel female reduces the energy expenditure of their long self-feeding foraging trips by soaring on thermals to fly towards foraging areas located farther from the colony and adopting preferentially the perch-hunting strategy at the foraging patch (Chapters Two, Three and Four).

To sum up, the present PhD thesis provides insight into the lesser kestrel foraging ecology from a novel perspective thanks to the high spatiotemporal resolution of biologgers. We evaluated the internal and external factors influencing lesser kestrel foraging movements throughout the breeding season across the research works included in this PhD thesis. In order to achieve this, we deployed lightweight GPS and tri-axial accelerometer dataloggers on lesser kestrel breeders that provided us with detailed individual behavioral information at high spatiotemporal resolution. We pointed out that role specialization largely determines foraging movement patterns of the lesser kestrel throughout the breeding season. Lesser kestrels replace flapping with soaring-gliding along commuting flights as thermal updrafts get stronger, which results in a circadian spatial pattern of foraging areas. The lesser kestrels seem to allocate effort to explore the surroundings of the colony early in the breeding season to acquire knowledge about habitat and prey spatial distribution, and as a result they probably head towards high-quality foraging areas that they learn in that process at the end of the breeding season. Prey availability is a key element when deciding which hunting strategy to use by the lesser kestrel. Overall, our findings support predictions derived from the optimal foraging theory and indicate that the lesser kestrel prioritizes saving energy instead of time when foraging during the breeding season.

Future perspectives

This thesis is based on tracking individual lesser kestrels, but results have been analyzed and discussed from a population perspective considering individuals as random samples of the population. Further work should deal with individual personality traits and how they influence individual movement patterns and ultimately affect individual breeding success or survival rate (Biro & Stamps 2008, Dingemanse et al. 2010). Individuals from a population could all behave in similar ways or show individual specialization. Foraging habitat selection has been widely studied at the population level, but the newest tracking devices can potentially reveal differences in individual preferences for particular foraging habitats. Similarly, individual movement repeatability should be explored in detail to ascertain: how often individuals use specific foraging patches or which are the triggers that condition kestrel to start and stop visiting particular habitat patches (marginal value theorem) (Charnov 1976). Public information has been considered not only as one of the major benefits of coloniality but also one of the possible causes of its evolution (Danchin & Wagner 1997, Valone & Templeton 2002). Therefore, the colonial habits of the lesser kestrel make it an excellent study model to shed light about the importance of movement as a driver for transferring information between individuals about resource location. Furthermore, it has been recently suggested the application of network analytical tools to animal movement research in order to reveal individual social interactions (Jacoby & Freeman 2016), which might be useful to disentangle the mechanisms underlying foraging movement patterns of a colonial species, such as the lesser kestrel.

Conservation implications

This PhD thesis was not conceived initially only for conservation purposes, but some of its results should be further considered by managers. Foraging habitat selection of the lesser kestrel has been traditionally studied through direct observations or radiotracking. These studies might be biased because both methodologies experience a limitation: the detection probability decreases with distance. In fact, the majority of these studies concentrate sampling effort within a 3-km buffer around the colony (e.g., Tella et al. 1998, Franco et al. 2004, Rodríguez et al. 2006, Catry et al. 2012), but our results show that the median maximum distance from the colony reached by the kestrels during foraging trips is just 3.03 km (n = 2,171 foraging trips). Hence, the conclusions obtained could be not completely valid since they have ignored an important fraction of lesser kestrel foraging areas. Therefore, conservation recommendations derived from those studies may require an update. Additionally, our findings indicate that the lesser kestrel displays a highly flexible foraging movement strategy that changes throughout the breeding season, as well as the foraging habitat selection (Hernández-Pliego et al., *unpub. results*). In the study area, lesser kestrels mostly forage in olive groves and vineyards early in the breeding season, but they predominantly select ploughed and sowed fields as foraging habitats during intermediate stages of the season. Afterwards, they forage on wheat fields and stubbles at the end of the breeding season. Moreover, kestrels often use natural pastures and they occasionally select alfalfa or potatoes when being harvested as foraging habitats. Therefore, the lesser kestrel acts as an opportunistic species that takes advantage of agricultural activity (plowing, sowing, harvesting) that results in an increase in prey availability, by reducing vegetation cover or giving access to fossorial prey (Rodríguez et al. 2013). Also, studies on foraging habitat selection by the lesser kestrel may be also biased because the majority of them have not been carried out throughout the entire breeding season (e.g., Donázar et al. 1993, Tella et al. 1998); specifically none included the establishment period. Furthermore, human agricultural activities usually take place in short time lapses what require an enormous field-work effort to gather information about kestrel behavior regarding those events when using traditional tracking methodologies (Catry et al. 2014). However, the application of GPS system that provides high spatiotemporal resolution can shed light about the opportunistic behavior of the lesser kestrel when foraging. Our findings indicate that lesser kestrels can benefit from a heterogeneous habitat matrix in the surroundings of the colony where they can cover the temporally dynamic energy and nutrient demand throughout the breeding season. In addition, GPS devices have revealed that lesser kestrels, especially males, recurrently use overnight roosts and that they repeatedly use the same roosts throughout the breeding season (Hernández-Pliego et al., *unpub. results*). We have suggested that individuals use them to reduce the energy cost of foraging trips because they would need to flap their wings to return to the colony (Chapter Four). However, some of these overnight roosts are shared by numerous individuals (e.g., up to 80 kestrels were repeatedly observed at a telephone antenna close to the Silo colony during three consecutive years), which suggest that this behavior may be associated with something more than just saving energy. Communal roosts have been proposed to be centers where individuals reunite and benefit from sharing information (Ward & Zahavi 1973, Dall & Wright 2009), so lesser kestrels could also use them with similar purposes. Therefore, the identification and protection of those intensively used overnight roosts could be paramount in order to protect the lesser kestrel.

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CONCLUSIONS

1) The lesser kestrel foraging movements are influenced both by internal and external factors that change throughout the breeding season.
2) Role specialization of the lesser kestrel largely determines the differences in foraging movement patterns by sexes throughout the breeding season.
3) Lesser kestrels seem to reduce the exploratory component of their foraging movements as the breeding season advances once they have acquired information about how different habitats are spatially distributed.
4) Lesser kestrels choose the flight strategy to use (flapping versus soaring-gliding) regarding thermal updraft availability.
5) Lesser kestrels decide the hunting strategy to use (hovering versus perch-hunting) regarding prey availability, although wind speed also influences this choice.
6) Lesser kestrels soar on thermals to fly towards foraging areas far from the colony in order to avoid prey depletion and intraspecific competition in its surroundings.
7) Lesser kestrels show a sexual spatial segregation of foraging areas that seem to be an adaptive strategy to reduce prey depletion and intersexual competition between members of the breeding pair.
8) Lesser kestrels show circadian patterns of foraging movements as a result from adjusting its flight and hunting strategies to weather conditions and prey availability that change on a daily basis.
9) Tri-axial accelerometers coupled with GPS have proved to be efficient tools to study free-ranging lesser kestrel movement behavior.
10) Overall, lesser kestrels prioritize saving energy when foraging, suggesting that kestrels are more energy than time-constrained during the breeding season.

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The **lesser kestrel** *(Falco naumanni)* is a small insectivorous falcon that suffered a world population decline during the second half of the 20th century due to the agricultural intensification. This PhD thesis aims to study the foraging behavior of the lesser kestrel throughout the breeding season under the **Movement Ecology** perspective. According to this ecological discipline, individual movement results from the interaction between four elements: individual motivation, motion abilities, navigation capacities, and external factors. Therefore, it has been addressed the effect of these elements on the lesser kestrel foraging movements through using the latest **biologging technology.**

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