Special issue: Trending Topics in Current Ornithology

INDIVIDUAL-BASED TRACKING SYSTEMS IN ORNITHOLOGY: WELCOME TO THE ERA OF BIG DATA

SISTEMAS DE SEGUIMIENTO INDIVIDUAL EN ORNITOLOGÍA: BIENVENIDOS A LA ERA DE LOS DATOS MASIVOS

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Word count: 5918 words (including summary, main text and acknowledgements; excluding references, tables and figures).

Short running title: Ornithology in the era of big data

SUMMARY.- Technological innovations have led to exciting fast-moving developments in science. Today, we are living in a technology-driven era of biological discovery. Consequently, tracking technologies have facilitated dramatic advances in the fundamental understanding of ecology and animal behaviour. Major technological improvements, such as the development of GPS dataloggers, geolocators and other bio-logging technologies, provide a volume of data that were hitherto unconceivable. As a consequence, we can claim that ornithology has entered in the era of big data. In this paper, which is particularly addressed to undergraduate students and starting researchers in the emerging field of movement ecology, I summarise the current state of the art of individual-based tracking methods for birds as well as the most important challenges that, as a personal user, I consider we should address in the future. To this end, I first provide a brief overview of individual tracking systems for birds. Then, I discuss current challenges for tracking birds with remote telemetry, including technological challenges (i.e., tag miniaturization, incorporation of more bio-logging sensors, better efficiency in data archiving and data processing), as well as scientific challenges (i.e., development of new computational tools, investigation of spatial and temporal autocorrelation of data, improvement in environmental data annotation processes, the need for novel behavioural segmentation algorithms, the change from two to three, and even four, dimensions in the scale of analysis, and the inclusion of animal interactions). I also highlight future prospects of this research field including a set of scientific questions that have been answered by means of telemetry technologies or are expected to do so in the future. Finally, I discuss some ethical aspects of bird tracking, putting special emphases on getting the most out of data, and enhancing a culture of multidisciplinary collaboration among research groups.

Key words: animal tracking, Argos, bio-logging, computational science, conservation, datalogger, geolocator, GPS, movement ecology, PTT, ringing, satellite transmitter, telemetry.

RESUMEN.- Las innovaciones tecnológicas han dado lugar a grandes progresos en ciencia. Estamos viviendo actualmente en una era en la que los descubrimientos científicos vienen mediados por la tecnología. Consecuentemente, la tecnología de seguimiento a distancia ha permitido avances extraordinarios en nuestra comprensión fundamental de la ecología y el comportamiento animal. Las grandes mejoras tecnológicas, como por ejemplo el desarrollo de dispositivos GPS dataloggers, geolocalizadores y otras tecnologías de seguimiento animal, proporcionan un volumen de datos que era hasta hace poco inconcebible. Por todo ello, podemos afirmar sin ambages que la ornitología ha entrado en la era de los datos masivos. En este artículo, que está especialmente dirigido a estudiantes universitarios y a investigadores que se inicien en el campo emergente de la ecología del movimiento, resumo el estado actual de los sistemas de seguimiento individual para aves, así como los retos más importantes que, como usuario personal, considero que deberíamos afrontar en el futuro. Para ello, en primer lugar muestro un pequeño resumen sobre los sistemas de seguimiento individual que existen para aves. A continuación, discuto los retos actuales que debemos afrontar gracias al seguimiento de aves mediante telemetría remota, entre los que se incluyen retos tecnológicos (i.e., miniaturización de los transmisores, incorporación de más sensores biológicos, mejor eficiencia en el archivo y procesamiento de datos), así como retos científicos (i.e., desarrollo de nuevas herramientas de análisis, investigar la autocorrelación espacial y temporal de los datos, mejora del proceso de toma de datos ambientales, la necesidad de nuevos algoritmos de segmentación del comportamiento, el paso de dos a tres, e incluso cuatro, dimensiones en la escala de análisis, y la inclusión de las interacciones entre animales). También destaco las perspectivas de futuro de este campo de investigación incluyendo una serie de preguntas científicas que han sido respondidas mediante telemetría o que se espera que así sea en el futuro. Por último, discuto algunos aspectos éticos del seguimiento de aves haciendo especial hincapié en la necesidad de obtener el máximo rendimiento de los datos y de promover una cultura de colaboración multidisciplinar entre grupos de investigación.

Palabras clave: anillamiento, Argos, biologging, ciencia computacional, conservación, datalogger, ecología del movimiento, geolocalizador, GPS, PTT, seguimiento animal, telemetría, transmisor satelital.

INTRODUCTION

From early observation of planets through telescopes by Galileo and Kepler, the development of time measurement methods which allowed navigation, the discovery of the elemental parts of cell through microscopes, the use of x-ray diffraction to discover the DNA structure, chromatography, spectroscopy or DNA sequencing, to modern use of fast computational tools in the Internet era, technological innovations have led to exciting fast-moving developments in science. Many philosophers and science historians have long debated whether scientific advances are driven mostly by novel ideas or by new tools and, although there is no clear response to this question, no-one doubts that technology has played a fundamental role in scientific progress (Dyson, 2012).

Today, we are living in a technology-driven era of biological discovery where extremely large datasets are routinely used in biology (Ropert-Coudert and Wilson, 2005; Shade and Teal, 2015). In this sense, the fields of ecology, ethology, zoology and ultimately, ornithology, have not been unaware of these technological innovations, thus allowing the generation of large amounts of data owing to the increasingly extensive use of remote tracking technologies. As happened some decades ago with genomics, proteomics, metabolomics and other "–omics", ecology has entered in the so called era of "big data" (Hampton et al., 2013). Therefore, the study of animal movement, as an important part of ecology, does not constitute an exception.

Animal movement, and particularly bird movement, has long called the attention of naturalists and scientists since the times of Aristotle. As a consequence, there is a vast amount of information gathered across different taxa and geographic regions which has been the subject of analysis of many different scientific disciplines. In order to provide a conceptual framework to integrate all this information, some scientist proposed the foundation of a new scientific discipline called "movement ecology" eight years ago (Nathan et al., 2008). As their proposers claim, the aim of the movement ecology concept is "proposing a new scientific paradigm that places movement itself as the focal theme, and promoting the development of an integrative theory of organism movement for better understanding the causes, mechanisms, patterns, and consequences of all movement phenomena" (Nathan, 2008). Accordingly, individual tracking technologies are the link between the emerging field of movement ecology and the vast body of knowledge gathered in traditional scientific disciplines.

This paper is particularly addressed to undergraduate students in their final years, recent graduates in the field of biology or environmental sciences and is especially addressed to young scientists wishing to start their careers in the emerging field of movement ecology. It reflects my personal point of view of the current state of the art of individual-based tracking methods for birds and the most important challenges that, as a personal user, I consider we should address in the future. First, I provide a brief overview of individual tracking systems for birds. Then, I discuss current challenges for tracking birds with remote telemetry, including technological and scientific challenges. I also highlight future prospects of this research field including a set of scientific questions that have been answered by means of remote telemetry data or are expected to do so in the future. Finally, I discuss some ethical aspects in animal tracking with particular focus on bird trapping, attachment methods, tag mass to body mass ratio and behaviour of the species subject to individual tracking.

INDIVIDUAL TRACKING IN ORNITHOLOGY: A BRIEF OVERVIEW

Individual tracking, or simply tracking *sensu lato* (see Box 1), is the collection of methodological techniques aimed at following and determining where an animal is located spatially on earth. Individual tracking has a long tradition in ornithology, principally due to bird ringing (Newton, 2014). Since the first metal rings were attached to birds by Hans Christian Cornelius Mortensen in 1899, the individual identification of birds by means of metal rings and wing tags has provided many of the most significant advances in many fields of animal ecology, which reach far beyond the field of ornithology. Basically, ringing has facilitated dramatic advances in the fundamental understanding of ecology, animal behaviour, bird conservation and even evolution. Primarily focused on the fascinating study of bird migration, individual tracking of birds by using metal rings has provided valuable insight into other aspects of bird biology, such as population monitoring, population dynamics, dispersal, biometrics, breeding and moult phenology, orientation and navigation mechanisms, mating systems, genetics, territoriality, feeding behaviour, physiology, disease transmission and, more recently, the study of global climate change (Spina, 1999; Baillie, 2001; Newton, 2014; EURING, 2015), to cite a few examples. A comprehensive description of major achievements in animal ecology attributable to bird ringing is beyond the scope of this paper. I would kindly ask the reader to excuse me for this omission.

For the aims of this paper, hereafter I will refer to remote telemetry methods (Box 1) to refer to the study of individual tracking. After ringing, one of the most significant advances in the study of bird movements was the development of the first radio transmitters in the late 1950s (Lemunyan et al., 1959; Cochran and Lord, 1963; White and Garrott, 1990). Due to the low cost of equipment and its basic technology, very high frequency (VHF) radio tracking has been the conventional tracking system used for decades (Kenward, 2001). Like bird ringing, conventional ground-tracking is still a very useful (and in some cases the only) system available to track small organisms including the majority of bird species (Figure 1). Later, one of the major advances in individual tracking was the development of the first satellite transmitters in the 1980s (Fuller et al., 1984; Jouventin and Weimerskirch, 1990; Nowak et al., 1990). Satellite transmitters allowed tracking animals remotely across the globe without the need to locate the signal by the researcher (Börger, 2016). Hence, questions that so far had remained unsolved, such as where long-distance migrants spent their winters, and important aspects of migratory connectivity began to be answered. With the incorporation of GPS receivers, data transmission through the Argos system and the increase of data storage and battery capacity (firstly in on-board batteries and afterward by using solar-powered rechargeable panels), satellite transmitters have definitely revolutionized the study of animal movement. Furthermore, new technological innovations such as the development of light-level geolocators, which allowed estimating geographical position by calculating the time of sunrise and sunset, were made available in the 1990s (Wilson, 1992), helping to address major research and conservation questions in avian ecology (Bridge et al., 2013). Their main advantage is that they provide a relatively lightweight, low-cost alternative to traditional tracking technologies and, consequently, have allowed significant advances in the study of small bird species (Stutchbury et al., 2009). Unfortunately, the main disadvantage is that geolocators must be retrieved to download data (i.e., only useful for species exhibiting high site-fidelity and easy recapture) and that location accuracy, ranging from 50 km up to 200 km, is low (particularly close to the Poles, the equator, and during equinoxes). Finally, archival data loggers (or dataloggers, see Box 1) were firstly available in late 1990s and have become more popular in recent years mainly due to their capability to incorporate new sensors along with GPS location, including accelerometers, temperature, heart rate, conductivity or even video recording sensors (Cooke et al., 2004; Ropert-Coudert and Wilson 2005; Tomkiewicz et al., 2010; Brown et al., 2013; Hays, 2015). This fact, combined with improved remote data download capabilities through the mobile communications GSM network and the possibility of duty cycle reconfiguration based on users' request, has made near-real-time monitoring of animals possible. Commercial dataloggers currently available allow the collection of up to several thousand locations per day due to their high frequency of data acquisition (i.e., 1 Hz = 1 location/second) and bigger internal memory storage capacity. In addition, the current dataloggers also have increased accuracy of location estimation. As a consequence of these major technological improvements, many researchers claim that animal movement ecology has entered in a “golden age” in which the current generation of scientists will be witness to unprecedented exciting discoveries in upcoming years (Wilcove and Wikelski, 2008; Kays et al., 2015).

BIRD TRACKING IN THE CONTEXT OF SCIENTIFIC PUBLISHING

Movement has long held great interest for ornithologists. Consequently, the number of published papers using individual-based tracking technologies for birds has increased considerably in the last decades (Holyoak et al., 2008). For example, according to a literature survey for the period 1950 – 2015, the first papers about satellite tracking, dataloggers, geolocators and accelerometry were published in 1990, 1991, 2002 and 2002, and have increased by an average of 42.7%, 27.7%, 79.5%, 51.5% per year in the last 25 years, respectively (Figure 2). In parallel, scientific publishing has experienced an exponential increase in the last decades (Bornmann and Mutz, 2015). However, whereas the percentage of papers regarding ecology has increased on average by 7.0% per year, the number of papers regarding individual-based tracking technologies for birds has increased on average by 17.6% per year (i.e., 2.52 times in the same period) (Figure 2). This clearly indicates that tracking technologies have played a fundamental role in our understanding of birds' ecology. Modern individual-based tracking technologies have made significant contributions on many important topics in ornithology, or are expected to do so in the future (Table 1), building on our knowledge gained through other methodological techniques (e.g., ringing and conventional radio-tracking).

CURRENT CHALLENGES OF BIRD TRACKING

Technological challenges

Since Gordon E. Moore, co-founder of Intel company, stated in 1965 his famous law based on the observation that the number of transistors in a dense integrated circuit doubles approximately every two years (also known as Moore's law) (Moore, 1965), electronic devices have undergone a dramatic miniaturization process in the last five decades. Like mobile phones and computers, animal tracking technologies have downsized three or four orders of magnitude, from the first radio-transmitters weighing as much as one or two kilograms to small geolocators lighter than 0.5 g (Figure 1; Appendix 1). Obviously, there is a trade-off between operational life of tracking devices, maximum number locations recorded per day, temporal and spatial resolution, battery size, and weight. As a consequence, engineers are struggling to get the most from current technologies, developing new smaller components and installing more energy efficient microprocessors in tracking devices. For example, just a decade ago, Platform Transmitters Terminals (PTTs) attached to resident and migratory birds provided one or two locations per day based on Argos Doppler shift (e.g. Cadahía et al., 2005; Thorup et al., 2006), whereas the best Argos/GPS transmitters were able to get one fix every 2-3 hours in the most demanding duty cycle configuration (e.g. Soutullo et al., 2007, 2008; Cadahía et al., 2008). In contrast, modern dataloggers are able to provide up to 1 location per second (Figure 3), including also additional information from other activity sensors, and are able to send data packages through the GSM network (e.g., Lanzone et al., 2012) or by means of automatic downloading to a base station (e.g., Holland et al., 2009; Kays et al., 2011; Bouten et al., 2013; Pfeiffer and Meyburg 2015).

More sensors in smaller tags

The current technological challenge is to continue shrinking transmitters' size together with increasing the number of incorporated bio-logging sensors (Cooke et al., 2004; Rutz and Hays, 2009).

Unlike traditional tracking methods such as metal rings or conventional radio-tracking, cutting-edge tracking devices are very expensive (from several hundred to several thousand euros) and thus there is an enormous commercial market behind tracking technologies. As a consequence, companies are immersed in an all-out war attempting to manufacture increasingly smaller transmitters with higher capacities at competitive prices (see some examples in Appendix 1). Future transmitters will have higher internal storage capacity and longer battery lifetime expectancy (i.e., more charge/discharge cycles). In addition, it is expected that remotely downloadable dataloggers (i.e., transmitters using radio link for wireless communication) will have shorter processing times for data retrieval from multiple tags. Interesting enterprises such as the promising ICARUS project (see Box 1), which is aimed at observing global migratory movements of small animals through a satellite system installed in the International Space Station, are under development (Wikelski et al., 2007). This initiative aims to revolutionize current tracking systems, mimicking conventional radio-tracking by pointing antennas toward earth from near-earth orbit in the International Space Station (ISS). This will allow locating radio transmitters attached to small animals, from birds to insects, in any place on earth. The scientific community has great interest on this initiative and, although several questions still remain unanswered (e.g., how much will transmitters weigh, how much will they cost, or who will be the final users), if it becomes successful, this could facilitate a quantum leap in our knowledge of animal movement.

Data archiving and data processing

As a result of improved characteristics of modern dataloggers, we have jumped from recording very few locations per animal to hundreds and thousands of locations per animal and per day. Until recently, raw data were accessed and downloaded directly by users with a relatively low frequency (e.g. usually every week or every ten days from the Argos system) and could be easily stored in conventional desktop computers. However, current dataloggers, especially those transmitting information through the GSM mobile network, transmit large amounts of raw data every day (Fig. 2). Hence, storage and management of extremely large datasets can be overwhelming, especially for beginners. To improve this situation, several data repositories freely available on the Internet allow long-term data archiving in an offsite location. In addition, these repositories provide useful services such as automatic data download from transmitters, data parsing, data managing, data analysis and environmental annotation (see Box 1). Although data repositories are freely accessible on the Internet, it is important to emphasize that researchers retain ownership of their data and can choose between different levels of data accessibility to the public (e.g., data manager, project's collaborators, public at large). One of the most popular data repositories is Movebank (Wikelski and Kays, 2015), although others such as Satellite Tracking and Analysis Tool (Coyne and Godley, 2005) were pioneers in the field and have been used since early 2000s. Therefore, I recommend using external data repositories not only for data backup but also for data sharing with other members of the scientific community and citizens at large, which is probably the most important application (e.g., seaturtle.org, seabirdtracking.org). This facilitates the participation in collaborative work to help scientists to address bigger scientific questions, and also allows attraction from the public. Finally, the information available in public repositories is a great tool for raising public awareness of conservation problems (e.g., for migratory species) and as a teaching tool for all academic levels.

Scientific challenges

New computational tools

In addition to technological challenges, individual tracking systems raise many different scientific challenges. Once data are collected, filtered, and adequately stored in external repositories, one of the most important challenges is data analysis. The analysis of extremely large datasets introduces computational and statistical challenges mainly due to massive sample size and high dimensionality of big data (Fan et al., 2014). To overcome this problem, the development of new sophisticated data-management tools to analyse movement data is needed (Shamoun-Baranes et al., 2011). This opens new possibilities for research not only for ornithologists but also for scientists in general. In particular, we need to train the next generation of scientists in computing, a field that has been largely overlooked in graduate programs in biology, as well as to create multidisciplinary teams in which ornithologists take part contributing to data interpretation (Hampton et al., 2013; Shade and Teal, 2015). Hence, we need to encourage a culture of data sharing and interdisciplinary collaborative work. New toolboxes specially developed for Geographic Information Systems such as Animal Movement Analysis software (Hooge and Eichenlaub, 1997), Home Range Tools (Rodgers et al., 2007), or Geospatial Environmental Modelling software (Beyer, 2012) have been developed. In addition, freely-available software packages that contain functions to access movement data as well as tools to visualize and statistically analyse animal movement datasets have become very popular. Some examples are “adehabitat” (Calenge 2006), “move” (Kranstauber et al., 2012; Kranstauber and Smolla, 2015), “GeoLight” (Lisovski and Hahn, 2012), and reproductible home range “rhr” (Signer and Balkenhol 2015) R-packages. Importantly, data reproducibility is an important issue that still remains a challenge (Peng, 2011). Further improvements in computational science will provide interesting tools that will open new avenues of research in the analysis of birds’ movement.

Spatial and temporal autocorrelation

Animals move over large spatial and temporal scales delineating extremely variable trajectories among individuals. For example, birds’ movements may vary from ballistic trajectories (i.e., movements nearly following a constant direction at high speed) recorded during migration, to crooked paths with continual turns and changes in direction at low speed during intensive foraging. Furthermore, the relocations from individuals show a spatiotemporal autocorrelation pattern (Otis and White, 1999), which is moreover stochastic and often subject to severe observation error (Patterson et al., 2008). Dealing with both uncertainty and spatiotemporal autocorrelation (i.e., the location at time t+1 is dependent on the bird’s location at time t) is one of our biggest challenges in the analysis of movement data (Cagnacci et al., 2010; Fieberg et al., 2010). Depending on duty cycle configuration, transmitters record this information at different sampling rates. Hence, the length of the gap between consecutive locations makes necessary the utilization of one set of analytical tools or others (Kie et al., 2010). This fact gave rise to the development of statistical methods such as state-space models (Jonsen et al., 2005; Patterson et al., 2008) and Brownian Bridges models (Horne et al., 2007), which were aimed at interpreting where an animal could be between consecutive relocations. Nowadays, the degree of uncertainty in animal movement has been dramatically reduced owing to high-resolution GPS telemetry, making analytical tools that have been very useful until now somewhat obsolete. For example, current dataloggers (at least those available for larger birds, see Fig. 1 and Appendix 1) record GPS locations with 1Hz frequency and thus is no longer necessary to interpolate where the bird has moved between consecutive relocations. We have shifted from the analysis of a schematic representation of bird's path, to the analysis of its true trajectory. Therefore, our current challenge is to develop analytical tools that take into consideration the intrinsically autocorrelated nature of animal movement and to investigate the underlying mechanisms that cause this spatiotemporal autocorrelation (e.g. cognitive processes and memory effects) (Boyce et al., 2010).

Environmental data annotation

No-one would study fish or cetaceans' movements without taking into account the movement of oceanic currents. Correspondingly, analysing bird movement data without considering environmental conditions would be meaningless too. For their locomotion birds must push against a fluid, either air (most species) or water (e.g., penguins, albatrosses, ducks, etc.), which is itself also moving. Hence, it is necessary to correlate the information of animal movement with the particular characteristics of the media in which they actually move. Linking animal tracks with environmental data and the underlying context, that is, the "environmental data annotation process", is thus necessary to understand birds' behaviour (Mandel et al., 2011). However, this represents an analytical challenge due to the different spatiotemporal resolution of tracking data and environmental information (e.g. weather conditions, topography, primary productivity, land use, vegetation, snow cover, etc.). The Env-DATA system (Dodge et al., 2013) implemented in the Movebank data repository provides an interesting free automated annotation service of movement trajectories that facilitates the study of bird movements in their environmental context (e.g., wind currents, temperature, thermal uplift, air pressure, and other measures recorded by remote sensing technologies). Notwithstanding, our current challenge is to continue creating new analytical tools (e.g., under R and MATLAB statistical software as well as specific extensions for Geographical Information Systems software), and developing new interpolation algorithms to facilitate data integration, resampling, and interpolation at the same rate at which movement data is recorded.

Behavioural segmentation

Inferring behaviour from animal movement data is an important topic in behavioural ecology. To this end, removing subjectivity in data interpretation and understanding behaviour at the appropriate scale in which it happens becomes crucial. To this end, researchers have developed several tools aimed at splitting behaviour into its elementary basic units or behavioural modes (i.e., displacement, foraging, resting, etc.). This process is thus known as behavioural segmentation. Traditional approaches include machine learning languages, fractal analysis, first passage time, state-space models, behavioural change point analysis, k-clustering, autocorrelation functions, and hierarchical Bayesian algorithms, but they need important input from the researcher and are thus subject of certain degree of subjectivity (Jonsen et al., 2003, 2005; Morales et al., 2004; Schick et al., 2008; Gurarie et al., 2009; Dean et al., 2012). Recent advances in this field are unsupervised and non-intensive computing algorithms such as the Expectation-Maximization Binary Clustering implemented in the “EMbC” R-package (Garriga et al., 2014). EMbC focuses only on the analysis of two movement variables (velocity and turn) obtained from the successive locations of a trajectory and has been proved to be well suited for big data recorded at high-frequency as well as large-scale analysis (e.g., Louzao et al., 2014). Other novel approaches take advantage of acceleration data to identify behavioural modes (Nathan et al., 2012; Williams et al., 2015). Therefore, our current challenge is to continue developing new reliable tools for behavioural segmentation that reflect complexity in behavioural modes, independent of *a priori* assumptions and with the highest explanatory potential (Gurarie et al., 2016). Understanding how different behavioural modes interact at different spatiotemporal scales and incorporating cognitive processes, behavioural plasticity (i.e., personality) (Patrick and Weimerskirch, 2014), and memory effects in the models also remain a challenge.

From 2D to 3D (and 4D)

Birds use space in three dimensions. However, despite computational advances, the analysis of animal movements has typically been reduced to the quantification of space use in two dimensions (latitude and longitude) and has failed to integrate vertical data into habitat use estimates (Belant et al., 2012), mainly due to the low precision of most altitudinal measurements. Therefore, it is necessary to incorporate the third dimension (i.e., altitude or depth) in the analysis of animal movement because this will lead to better understanding of habitat use and selection (Cooper et al., 2014). Although several algorithms to generate novel movement-based kernel density estimators have been developed such as “ks” (Duong, 2015) and “mkde” (Tracey et al., 2014) R-packages, there are very few examples of movement analysis that consider 3D in the analysis of space use and quantification of utilization distributions (Keating and Cherry, 2009; Cooper et al., 2014; Cleasby et al., 2015). Modelling birds’ movements in three dimensions (or even in fourth dimensions, thus also considering time) is in consequence a promising field of research, especially for the analysis of animal interactions both in space and time. In addition, we need better computer visualization tools for generating and exploring 3D as well as incorporating colour images and videos in traditional publishing (Shamoun-Baranes et al., 2011; Demšar et al., 2015).

Animal interactions

Complex behaviour exhibited by birds is the outcome of the sum of animal-environment interactions and animal-animal interactions, both at intraspecific and interspecific level. There is vast body of ecological literature on the study of the relationship between animals and their environment (e.g., habitat selection, resource use, environmental niche analysis, etc.). However, the role of intra- and interspecific interactions and how they affect birds’ movements and ultimately shape space use remains poorly understood. Traditionally, most studies on bird interactions have focused on spatial overlap in home ranges or static interactions (i.e., the joint occurrence in space of two or more individuals), but very few have addressed dynamic interactions (i.e., co-occurrence in both space and time) (Benhamou et al., 2014). A combination of the availability of high-resolution telemetry data and new analytical tools opens new avenues for future research in the field of movement ecology (Kays et al., 2015). A good tool is the “wildlifeDI” R-package (Long, 2014), which includes a suite of functions and indexes to quantify animal interaction (e.g., proximity analysis, coefficient of association, correlation index, dynamic interaction index) (Long et al., 2014). Importantly, these metrics take into account the intrinsically autocorrelated nature of movement data and are thus particularly suited for analysis of information recorded by individual-based tracking methods. Evaluating how intraspecific and interspecific interactions affect movement is extremely important in ornithology, especially to address interesting topics such as spread of invasive species, disease transmission, or for studying territorial and anti-predator behaviour (see some examples in Table 1). In addition, multi-individual GPS-tracking expands the scope of animal ecology to the study of collective behaviour and the roles of social networks and hierarchy in decision-making processes (e.g. leadership in flocking behaviour) (Couzin et al., 2005; Usherwood et al., 2011; Flack et al., 2015; Kays et al., 2015). Our current challenge is to shift from individual tracking to multi-individual tracking (e.g., tracking cohorts of individuals of the same guild, parents and young of the same family, or different members in social or colonial species), in order to link collective movement with environmental characteristics and ultimately with population dynamics (Morales et al., 2010). Inferring population-level spatial patterns from underlying individual movement and interaction processes, and developing mechanistic models of territorial interactions, also constitute a promising field of research (Potts et al., 2015).

ETHICAL ASPECTS

Studies using individual-based tracking systems are based on an underlying basic assumption: birds' behaviours are not altered (or are insignificantly altered) by the effect of transmitters. However, this basic assumption has been rarely tested and is arbitrary in some way (Caccamise and Hedin 1985; Barron et al., 2010; Constantini and Møller, 2013). There is a vast literature about the effects of transmitters on birds, yet results are not conclusive (Murray and Fuller, 2000). Whereas some authors report negative effects on birds, with an overall negative effect on fitness components (i.e., survival and breeding) (Constantini and Møller, 2013), other researchers have not found such effects (e.g. Igual et al., 2005) and argue that sample size in most papers reporting deleterious effects is low (Sergio et al., 2015). The correct selection of the type of transmitter (i.e., PTTs, dataloggers, geolocators, etc.) in combination with an appropriate method of attachment (i.e., backpack harness, collar, glue, tailmount, leg rings, leg-loop backpack harness, anchor, and even implantable transmitters that need surgery) is critical in order to reduce potentially harmful effect on bird behaviour (e.g., Vandenabeele et al., 2013; Blackburn et al., 2016).

There is a common widely accepted 3% - 5% “rule of thumb” for the ratio of tag mass to body mass, which limits the tracking devices suitable for a given species (Brander and Cochran, 1969; Kenward, 2001) (Figure 1). However, some review studies suggest that there is no empirical support for this rule (Barron et al., 2010) and it is up to the researcher’s arbitrary decision to follow the rule or not. Nowadays there is a big pressure to push technologies to the limit in order to get better chances of final publication of results, and consequently some researchers succumb to the temptation of exceeding the 3% - 5% tag mass/body mass ratio in some cases. Nevertheless, the precautionary principle should be respected (i.e., if the effects of the combination of a transmitter and method of attachment is unknown or is suspected of harmful effects in similar species (i.e., morphologically or taxonomically), the tracking project should not be permitted). Hence, further research is needed to assess which tracking methods are appropriate, including not only the effects of tag mass, but also tag impact on aerodynamics on different groups of species and the resulting possible drag effect (e.g., Pennycuick et al., 2012). Trial studies with common not endangered species could be a good chance to check transmitters’ effects on birds under controlled conditions (e.g., using irrecoverable species in rehabilitation centres).

Finally, it would be desirable to regulate the use of individual-based tracking technologies in some way, including (for example) more stringent licensing criteria and enforcing attendance at training courses (Sergio et al., 2015). Fitting transmitters implies trapping birds, in some cases of vulnerable, rare or endangered species, and therefore a cost/benefit analysis should be done before starting a tracking project (Latham et al., 2015; Pimm et al., 2015). Trapping, handling, and attaching tracking devices require a set of skills that must be taught and constantly re-evaluated. Hence, I recommend creating special working groups, as well as open symposia and specific workshops for interested researchers. Public administration and financial entities should ask for strong ethical commitments before starting a tracking project. In addition, scientist should clearly justify why tracking a given species is needed, which are the main goals of the project, and how these goals are achievable only using individual-based tracking technologies. Currently, the cost of transmitters is decreasing rapidly, making them more accessible for everyone. Consequently, some public administrations, NGOs, land managers, and amateur groups have found tracking bird an entertaining hobby that feeds numerous public profiles in social media (e.g., Facebook, project websites, etc.) without the intention of addressing clear questions supported by sound scientific projects. In my opinion, the simple curiosity of where animals move does not justify trapping and tracking birds in and of itself. Hence, collaboration among multidisciplinary groups and enhanced sharing of information should be promoted (Hampton et al., 2013; Pimm et al., 2015).

CONCLUDING REMARKS

We are possibly experiencing the most productive time for the study of birds' movements since the time of Aristotle. Fast-developing technologies are allowing cutting-edge studies with an unprecedented level of detail about animal movements. As a consequence, some have taken this opportunity to coin the term “movement ecology” as a scientific discipline in order to call attention to this emerging field. Although from my point of view movement in itself does not constitute a separate scientific discipline, no-one doubts the importance of movement and its essential role in ecology and behaviour. Individual tracking technologies are usually criticized for their elevated cost, which gives raise to small sample size and thus to limited capacity for ecological inference (Hebblewhite and Haydon, 2010). Notwithstanding, continual improvements in current tracking technologies and an increasingly number of companies commercializing remote-tracking devices assure a promising future for the study of animal movement. Current challenges are, on one hand, how to scale-up from individual fine-scale movements to coarse-scale resource selection and population-level dynamics (Hebblewhite and Haydon, 2010; Morales et al., 2010) and, on the other hand, to put the information derived from telemetry in the general framework of the theoretical body of knowledge of ecology.

Finally, we should not forget that individual-based tracking systems are just methods and do not constitute an end in themselves (Sokolov, 2011). Trapping, handling, and attaching transmitters entail a disturbance (tolerable in most cases) and, accordingly, a great responsibility. Prior to start a tracking project, researchers should carefully consider the main goals of the study, the convenience of tracking this or these species, and whether remote tracking is the best methodology for this end (Latham et al., 2015). The key challenges ahead are to get the most out of data and to enhance a culture of multidisciplinary collaboration among research groups (Pimm et al., 2015). We have definitely entered into the golden era of the study of animal movement and we should not miss this opportunity.

ACKNOWLEDGMENTS.- I would like to thank E. Barba for his kind invitation to write this paper. C. Dykstra, C. García-Ripollés, U. Mellone, V. Urios, V. García-Matarranz, J. González-Solís and an anonymous referee made helpful comments on some aspects of this paper. J. de la Puente and A. Bermejo, of the SEO/BIrdLife's MIGRA project, provided interesting information on tracking devices. P. López-López is supported by a "Juan de la Cierva-incorporación" postdoctoral grant of the Spanish Ministry of Economy and Competitiveness (reference IJCI-2014-19190). The author declares that no conflict of interest exists.

BIBLIOGRAPHY

ADAMÍK, P., EMMENEGGER, T., BRIEDIS, M., GUSTAFSSON, L., HENSHAW, I., KRIST, M., LAAKSONEN, T., LIECHTI, F., PROCHÁZKA, P., SALEWSKI, V. and HAHN, S. 2016. Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. *Scientific Reports*, 6: 21560.

ADELMAN, J. S., MOYERS, S. C., and HAWLEY, D. M. 2014. Using remote biomonitoring to understand heterogeneity in immune-responses and disease-dynamics in small, free-living animals. *Integrative and Comparative Biology*, 54: 377 – 386.

ÅKESSON, S., and HEDENSTRÖM, A. 2007. How migrants get there: migratory performance and orientation. *BioScience*, 57: 123 – 133.

ALERSTAM, T. 2006. Conflicting evidence about long-distance animal navigation. *Science*, 313: 791-794.

ALERSTAM, T., HAKE, M. and KJELLÉN, N. 2006. Temporal and spatial patterns of repeated migratory journeys by ospreys. *Animal Behaviour*, 71: 555-566.

ARGOS. 2015. Argos User's Manual, 2007-2015 CLS. http://www.argos-system.org/manual/

ARLT, D., LOW, M. and PÄRT, T. 2013. Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. *PLoS ONE*, 8: e82316.

BÄCHLER, E., HAHN, S., SCHAUB, M., ARLETTAZ, R., JENNI, L., FOX, J. W., AFANASYEV, V., and LIECHTI, F. 2010. Year-round tracking of small trans-Saharan migrants using light-level geolocators. *PLoS ONE*, 5: e9566.

BAILLIE S. R. 2001. The contribution of ringing to the conservation and management of bird populations: a review. *Ardea*, 89: 167-184.

BARRON, D. G., BRAWN, J. D. and WEATHERHEAD, P. J. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution*, 1: 180 - 187.

BELANT, J. L., MILLSPAUGH, J. J., MARTIN, J. A. and GITZEN, R. A. 2012. Multi-dimensional space use: the final frontier. *Frontiers in Ecology and the Environment*, 10: 11–12.

BENHAMOU, S., VALEIX, M., CHAMAILLÉ-JAMMES, S., MACDONALD, D. W. and LOVERIDGE, A. J. 2014. Movement-based analysis of interactions in African lions. *Animal Behaviour*, 90: 171-180.

BENTZEN, R. L., and POWELL, A. N. 2015. Dispersal, movements and site fidelity of post-fledging King Eiders *Somateria spectabilis* and their attendant females. *Ibis*, 157: 133 – 146.

BEYER, H.L. 2012. Geospatial Modelling Environment (Version 0.7.2.0). (software). URL: http://www.spatialecology.com/gme.

BIRO, D., SUMPTER, D. J., MEADE, J., and GUILFORD, T. 2006. From compromise to leadership in pigeon homing. *Current Biology*, 16: 2123 – 2128.

BLACKBURN, E., BURGESS, M., FREEMAN, B., RISELY, A., IZANG, A., IVANDE, S., HEWSON, C. and CRESSWELL, W. 2016. An experimental evaluation of the effects of geolocator design and attachment method on between-year survival on whinchats *Saxicola rubetra*. *Journal of Avian Biology*, doi: 10.1111/jav.00871

BONADONNA, F., BAJZAK, C., BENHAMOU, S., IGLOI, K., JOUVENTIN, P., LIPP, H. P., and DELL'OMO, G. 2005. Orientation in the wandering albatross: interfering with magnetic perception does not affect orientation performance. *Proceedings of the Royal Society B: Biological Sciences*, 272: 489 – 495.

BÖRGER, L. 2016. Stuck in motion? Reconnecting questions and tools in movement ecology. *Journal of Animal Ecology*, 85: 5 – 10.

BORNMANN, L. and MUTZ, R. 2015. Growth rates of modern science: A bibliometric analysis based on the number of publications and cited references. *Journal of the Association for Information Science and Technology*, arXiv: 1402.4578.

BOUTEN, W., BAAIJ, E. W., SHAMOUN-BARANES, J., and CAMPHUYSEN, K. C. 2013. A flexible GPS tracking system for studying bird behaviour at multiple scales. *Journal of Ornithology*, 154: 571-580.

BOYCE, M. S., PITT, J., NORTHRUP, J. M., MOREHOUSE, A. T., KNOPFF, K. H., CRISTESCU, B. and STENHOUSE, G. B. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365: 2213-2219.

BRAHAM, M., MILLER, T., DUERR, A. E., LANZONE, M., FESNOCK, A., LAPRE, L., DRISCOLL, D., and KATZNER, T. 2015. Home in the heat: dramatic seasonal variation in home range of desert golden eagles informs management for renewable energy development. *Biological Conservation*, 186: 225 – 232.

BRANDER, R. B. and COCHRAN, W. W. 1969. Radio location telemetry. In, R. H. Giles Jr. (ed): *Wildlife Management Techniques*, pp. 95–103. The Wildife Society, Washington DC, USA.

BRIDGE, E. S., THORUP, K., BOWLIN, M. S., CHILSON, P. B., DIEHL, R. H., FLÉRON, R. W., HARTL, P., KAYS, R., KELLY, J.F., ROBINSON, W.D., and WIKELSKI, M. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. *BioScience*, 61: 689-698.

BRIDGE, E. S., KELLY, J. F., CONTINA, A., GABRIELSON, R. M., MACCURDY, R. B., and WINKLER, D. W. 2013. Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal of Field Ornithology*, 84: 121-137.

BRIDGE, E. S., ROSS, J. D., CONTINA, A. J., KELLY, J. F. in press. Do molt-migrant songbirds optimize migration routes based on primary productivity? *Behavioral Ecology*, doi:10.1093/beheco/arv199

BROTHERS, N., GALES, R., HEDD, A., and ROBERTSON, G. 1998. Foraging movements of the Shy Albatross *Diomedea cauta* breeding in Australia; implications for interactions with longline fisheries. *Ibis*, 140: 446 – 457.

BROWN, D. D., KAYS, R., WIKELSKI, M., WILSON, R. P. and KLIMLEY, A. P. 2013. Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry*, 1:20

CACCAMISE, D. F., and HEDIN, R. S. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin*, 97: 306-318

CADAHÍA, L., URIOS, V., and NEGRO, J. J. 2005. Survival and movements of satellite-tracked Bonelli's Eagles *Hieraaetus fasciatus* during their first winter. *Ibis*, 147: 415-419.

CADAHÍA, L., LÓPEZ-LÓPEZ, P., NEGRO, J.J., and URIOS, V. 2008. Estimating the onset of dispersal in endangered Bonelli’s Eagle *Hieraaetus fasciatus* tracked by satellite telemetry: a comparison among methods. *Ibis*, 150: 416-420.

CADAHÍA, L., LÓPEZ-LÓPEZ, P., URIOS, V., SOUTULLO, Á., and NEGRO, J. J. 2009. Natal dispersal and recruitment of two Bonelli's Eagles *Aquila fasciata*: a four-year satellite tracking study. *Acta Ornithologica*, 44: 193-198.

CADAHÍA, L., LÓPEZ-LÓPEZ, P., URIOS, V., and NEGRO, J. J. 2010. Satellite telemetry reveals individual variation in juvenile Bonelli’s eagle dispersal areas. *European Journal of Wildlife Research*, 56: 923-930.

CAGNACCI, F., BOITANI, L., POWELL, R. A., and BOYCE, M. S. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365: 2157-2162.

CALENGE, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197: 516-519.

CAUDILL, D., MESSMER, T. A., BIBLES, B., and GUTTERY, M. R. 2014. Greater sage-grouse juvenile survival in Utah. *The Journal of Wildlife Management*, 78: 808-817.

CHEVALLIER, D., LE MAHO, Y., BROSSAULT, P., BAILLON, F. and MASSEMIN, S., 2011. The use of stopover sites by Black Storks (*Ciconia nigra*) migrating between West Europe and West Africa as revealed by satellite telemetry. *Journal of Ornithology*, 152: 1 – 13.

CLEASBY, I. R., WAKEFIELD, E. D., BEARHOP, S., BODEY, T. W., VOTIER, S. C. and HAMER, K. C. 2015. Three-dimensional tracking of a wide-ranging marine predator: flight heights and vulnerability to offshore wind farms. *Journal of Applied Ecology*, 52: 1474-1482.

COCHRAN, W. W., LORD, R. D., JR. 1963. A radio-tracking system for wild animals. *Journal of Wildlife Management*, 27: 9–24.

CONKLIN, J. R., BATTLEY, P. F., and POTTER, M. A. 2013. Absolute consistency: Individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLoS ONE*, 8: e54535.

COSTANTINI, D. and MØLLER, A. P. 2013. A meta-analysis of the effects of geolocator application on birds. *Current Zoology*, 59: 697–706.

COOKE, S. J., HINCH, S. G., WIKELSKI, M., ANDREWS, R. D., KUCHEL, L. J., WOLCOTT, T. G., and BUTLER, P. J. 2004. Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution*, 19: 334-343.

COOPER, N. W., SHERRY, T. W. and MARRA, P. P. 2014. Modeling three-dimensional space use and overlap in birds. *The Auk*, 131: 681-693.

COUZIN, I. D., KRAUSE, J., FRANKS, N. R., and LEVIN, S. A. 2005. Effective leadership and decision-making in animal groups on the move. *Nature*, 433: 513-516.

COYNE, M. S., and GODLEY, B. J. 2005. Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. *Marine Ecology Progress Series*, 301, 1-7.

CRESSWELL, W. 2014. Migratory connectivity of Palaearctic–African migratory birds and their responses to environmental change: the serial residency hypothesis. *Ibis*, 156: 493–510.

DAUNT, F., REED, T. E., NEWELL, M., BURTHE, S., PHILLIPS, R. A., LEWIS, S., and WANLESS, S. 2014. Longitudinal bio-logging reveals interplay between extrinsic and intrinsic carry-over effects in a long-lived vertebrate. *Ecology*, 95: 2077-2083.

DEAN, B., FREEMAN, R., KIRK, H., LEONARD, K., PHILLIPS, R. A., PERRINS, C. M. and GUILFORD, T. 2012. Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden

Markov model reveals the distribution of at-sea behaviour. *Journal of The Royal Society Interface*, 10: 20120570.

DELL'ARICCIA, G., DELL'OMO, G., WOLFER, D.P., and LIPP, H.P. 2008. Flock flying improves pigeons' homing: GPS track analysis of individual flyers versus small groups. *Animal Behaviour*, 76: 1165 – 1172.

DELUCA, W. V., WOODWORTH, B. K., RIMMER, C. C., MARRA, P. P., TAYLOR, P. D., MCFARLAND, K. P., MACKENZIE, S. A., and NORRIS, D. R. 2015. Transoceanic migration by a 12 g songbird. *Biology Letters*, 11: 20141045.

DEMŠAR, U., BUCHIN, K., CAGNACCI, F., SAFI, K., SPECKMANN, B., VAN DE WEGHE, N., WEISKOPF, D. and WEIBEL, R. 2015. Analysis and visualisation of movement: an interdisciplinary review. *Movement Ecology*, 3: 5.

DIAS, M. P., GRANADEIRO, J. P., and CATRY, P. 2013. Individual variability in the migratory path and stopovers of a long-distance pelagic migrant. *Animal Behaviour*, 86: 359–364.

DODGE, S., BOHRER, G., WEINZIERL, R., DAVIDSON, S. C., KAYS, R., DOUGLAS, D., CRUZ, S., HAN, J., BRANDES, D., and WIKELSKI, M. 2013. The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. *Movement Ecology*, 1: 1-14.

DOMENECH, R., BEDROSIAN, B. E., CRANDALL, R. H., SLABE, V. A. 2015. Space Use and Habitat Selection by Adult Migrant Golden Eagles Wintering in the Western United States. *Journal of Raptor Research*, 49: 429 – 440.

DOMINONI, D. M., CARMONA-WAGNER, E. O., HOFMANN, M., KRANSTAUBER, B., and PARTECKE, J. 2014. Individual-based measurements of light intensity provide new insights into the effects of artificial light at night on daily rhythms of urban-dwelling songbirds. *Journal of Animal Ecology*, 83: 681 – 692.

DUONG, T. 2015. ks: Kernel Smoothing. R package version 1.9.4. http://CRAN.R-project.org/package=ks

DUNNING, J. B. 2007. *CRC Handbook of Avian Body Masses*, Second Edition. CRC Press, Taylon and Francis. Updated on March 07, 2014. https://www.crcpress.com/CRC-Handbook-of-Avian-Body-Masses-Second-Edition/Dunning-Jr/9781420064445

DURIEZ, O., KATO, A., TROMP, C., DELL'OMO, G., VYSSOTSKI, A. L., SARRAZIN, F., and ROPERT-COUDERT, Y. 2014. How cheap is soaring flight in raptors? A preliminary investigation in freely-flying vultures. *PloS ONE*, 9: e84887.

DYSON, F. J. 2012. Is science mostly driven by ideas or by tools? *Science*, 338: 1426-1427.

EGEVANG, C., STENHOUSE, I. J., PHILLIPS, R. A., PETERSEN, A., FOX, J. W. and SILK, J. R. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences*, 107: 2078-2081.

EURING. 2015. Bird Ringing for Science and Conservation. EURING brochure. Available on http://www.euring.org/about-euring/euring-brochure

FAN, J., HAN, F. and LIU, H. 2014. Challenges of big data analysis. *National Science Review*, 1: 293-314.

FIEBERG, J., MATTHIOPOULOS, J., HEBBLEWHITE, M., BOYCE, M. S. and FRAIR, J. L. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365: 2233-2244.

FLACK, A., BIRO, D., GUILFORD, T., and FREEMAN, R. 2015. Modelling group navigation: transitive social structures improve navigational performance. *Journal of The Royal Society Interface*, 12: 20150213.

FLACK, A., FIEDLER, W., BLAS, J., POKROVSKI, I., MITROPOLSKY, B., KAATZ, M., AGHABABYAN, K., KHACHATRYAN, A., FAKRIADIS, Y., MAKRIGIANNI, E., JERZAK, L., SHAMIN, M., SHAMINA, C., AZAFZAF, H., FELTRUP-AZAFZAF, C., MOKOTJOMELA, T., and WIKELSKI, M. 2015. Data from: Migration costs of eight Eurasian white stork populations. *Movebank Data Repository*, doi:10.5441/001/1.78152p3q

FOCARDI, S., and CECERE, J. G. 2014. The Lévy flight foraging hypothesis in a pelagic seabird. *Journal of Animal Ecology*, 83: 353-364.

FULLER, M. R., LEVANON, N., STRIKWERDA, T. E., SEEGAR, W. S., WALL, J., BLACK, H. D., WARD, F. P., HOWEY, P. W., and PARTELOW, J. 1984. Feasibility of a bird-borne transmitter for tracking via satellite. In, H. P. Kimmich and H.-J. Klewe: *Biotelemetry VIII: Proceedings of the Eighth International Symposium on Biotelemetry*. International Society on Biotelemetry, Nijmegen, Netherlands.

GARCÍA-RIPOLLÉS, C., LÓPEZ-LÓPEZ, P., and URIOS, V. 2010. First description of migration and wintering of adult Egyptian vultures *Neophron percnopterus* tracked by GPS satellite telemetry. *Bird Study*, 57: 261–265.

GARRIGA, J., PALMER, J. R . B., OLTRA, A., and BARTUMEUS, F. 2014. EMbC: Expectation-Maximization binary Clustering. R package version 1.2. arXiv:1503.04059

GIL, J. A., BÁGUENA, G., SÁNCHEZ-CASTILLA, E., ANTOR, R. J., ALCÁNTARA, M., and LÓPEZ-LÓPEZ, P. 2014. Home ranges and movements of non-breeding Bearded vultures tracked by satellite telemetry in the Pyrenees. *Ardeola*, 61: 379 – 387.

GILL, R. E., TIBBITTS, T. L., DOUGLAS, D. C., HANDEL, C. M., MULCAHY, D. M., GOTTSCHALCK, J. C., WARNOCK, N., MCCAFFERY, B.J., BATTLEY, P.F, and PIERSMA, T. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proceedings of the Royal Society of London B: Biological Sciences*, 276: 447-457.

GONZÁLEZ-SOLÍS, J., CROXALL, J.P. and WOOD, A.G. 2000. Foraging partitioning between giant petrels *Macronectes spp*. and its relationship with breeding population changes at Bird Island, South Georgia. *Marine Ecology Progress Series*, 204: 279 – 288.

GONZÁLEZ-SOLÍS, J., CROXALL, J.P., ORO, D. and RUIZ, X. 2007. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment*, 5: 297 – 301.

GOOCH, S., ASHBROOK, K., TAYLOR, A. and SZÉKELY, T. 2015. Using dietary analysis and habitat selection to inform conservation management of reintroduced Great Bustards *Otis tarda* in an agricultural landscape. *Bird Study*, 62: 289 – 302.

GRECIAN, W. J., WITT, M. J., ATTRILL, M. J., BEARHOP, S., GODLEY, B. J., GRÉMILLET, D., HAMER, K. C. and VOTIER, S. C. 2012. A novel projection technique to identify important at-sea areas for seabird conservation: An example using Northern gannets breeding in the North East Atlantic. *Biological Conservation*, 156: 43-52.

GRÉMILLET, D., KUNTZ, G., WOAKES, A. J., GILBERT, C., ROBIN, J. P., LE MAHO, Y., and BUTLER, P. J. 2005. Year-round recordings of behavioural and physiological parameters reveal the survival strategy of a poorly insulated diving endotherm during the Arctic winter. *Journal of Experimental Biology*, 208: 4231 – 4241.

GSCHWENG, M., KALKO, E. K., QUERNER, U., FIEDLER, W., and BERTHOLD, P. 2008. All across Africa: highly individual migration routes of Eleonora's falcon. *Proceedings of the Royal Society of London B: Biological Sciences*, 275: 2887-2896.

GUILFORD, T., MEADE, J., WILLIS, J., PHILLIPS, R. A., BOYLE, D., ROBERTS, S., COLLETT, M., FREEMAN, R. and PERRINS, C. M. 2009. Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society of London B: Biological Sciences*, 276: 1215–1223.

GUILFORD, T., ÅKESSON, S., GAGLIARDO, A., HOLLAND, R. A., MOURITSEN, H., MUHEIM, R., WILTSCHKO, R., WILTSCHKO, W., and BINGMAN, V. P. 2011. Migratory navigation in birds: new opportunities in an era of fast-developing tracking technology. *The Journal of Experimental Biology*, 214: 3705 – 3712.

GURARIE, E., ANDREWS, R., and LAIDRE, K. 2009. A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, 12: 395-408.

GURARIE, E., BRACIS, C., DELGADO, M., MECKLEY, T. D., KOJOLA, I., and WAGNER, C. M. 2016. What is the animal doing? Tools for exploring behavioral structure in animal movements. *Journal of Animal Ecology*, 85: 69–84.

HAMPTON, S. E., STRASSER, C. A., TEWKSBURY, J. J., GRAM, W. K., BUDDEN, A. E., BATCHELLER, A. L., DUKE, C. S., and PORTER, J. H. 2013. Big data and the future of ecology. *Frontiers in Ecology and the Environment*, 11:156-162.

HARRISON, X. A., BLOUNT, J. D., INGER, R., NORRIS, D. R., and BEARHOP, S. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, 80: 4 – 18.

HAWKES, L. A., BALACHANDRAN, S., BATBAYAR, N., BUTLER, P. J., FRAPPELL, P. B., MILSOM, W. K., TSEVEENMYADAG, N., NEWMAN, S. H., SCOTT, G. R., SATHIYASELVAM, P. and TAKEKAWA, J. Y. 2011. The trans-Himalayan flights of bar-headed geese (*Anser indicus*). *Proceedings of the National Academy of Sciences*, 108: 9516 – 9519.

HAYS, G. C. 2015. New insights: animal-borne cameras and accelerometers reveal the secret lives of cryptic species. *Journal of Animal Ecology*, 84: 587-589.

HEBBLEWHITE, M., and HAYDON, D. T. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365: 2303-2312.

HERNÁNDEZ-PLIEGO, J., RODRÍGUEZ, C., and BUSTAMANTE, J. 2015. Why Do Kestrels Soar? *PLoS ONE*, 10: e0145402.

HOLLAND, R.A., WIKELSKI, M., KÜMMETH, F., and BOSQUE, C. 2009. The Secret Life of Oilbirds: New Insights into the Movement Ecology of a Unique Avian Frugivore. *PLoS ONE*, 4: e8264.

HOLYOAK, M., CASAGRANDI, R., NATHAN, R., REVILLA, E., and SPIEGEL, O. 2008. Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences*, 105: 19060-19065.

HOOGE, P.N., and EICHENLAUB, B. 1997. Animal movement extension to ArcView, Version 1.1.: Alaska Science Center—Biological Science Office, U.S. Geological Survey, Anchorage, AK, USA.

HORNE, J. S., GARTON, E. O., KRONE, S. M. and LEWIS, J. S. 2007. Analyzing animal movements using Brownian bridges. *Ecology*, 88: 2354-2363.

HORTON, T. W., BIERREGAARD, R. O., ZAWAR-REZA, P., HOLDAWAY, R. N., and SAGAR, P. 2014. Juvenile osprey navigation during trans-oceanic migration. *PloS ONE*, 9: e114557.

IGUAL, J.M., FORERO, M.G., TAVECCHIA, G., GONZÁLEZ-SOLÍS, J., MARTÍNEZ-ABRAÍN, A., HOBSON, K.A., RUIZ, X. and ORO, D. 2005. Short-term effects of data-loggers on Cory's shearwater (*Calonectris diomedea*). *Marine Biology*, 146: 619 – 624.

JONSEN, I., MYERS, R. and FLEMMING, J. M. 2003. Meta-analysis of animal movement using state-space models. *Ecology*, 84: 3055–3063.

JONSEN, I. D., FLEMMING, J. M. and MYERS, R. A. 2005. Robust state-space modeling of animal movement data. *Ecology*, 86: 2874-2880.

JOUVENTIN, P., and WEIMERSKIRCH, H. 1990. Satellite tracking of wandering albatrosses. *Nature*, 343: 746-48.

KAYS, R., JANSEN, P. A., KNECHT, E. M., VOHWINKEL, R., and WIKELSKI, M. 2011. The effect of feeding time on dispersal of Virola seeds by toucans determined from GPS tracking and accelerometers. *Acta Oecologica*, 37: 625-631.

KAYS, R., CROFOOT, M. C., JETZ, W., and WIKELSKI, M. 2015. Terrestrial animal tracking as an eye on life and planet. *Science*, 348: aaa2478.

KEATING, K. A., and CHERRY, S. 2009. Modeling utilization distributions in space and time. *Ecology*, 90: 1971–1980.

KENWARD, R. E. 2001. *A Manual for Wildlife Radio Tagging*. London: Academic Press. UK.

KESSLER, A. E., BATBAYAR, N., NATSAGDORJ, T., BATSUUR, D. and SMITH, A. T. 2013. Satellite telemetry reveals long-distance migration in the Asian great bustard *Otis tarda dybowskii*. *Journal of Avian Biology*, 44: 311 – 320.

KIE, J. G., MATTHIOPOULOS, J., FIEBERG, J., POWELL, R. A., CAGNACCI, F., MITCHELL, M. S., GAILLARD, J. M., and MOORCROFT, P. R. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365: 2221 – 2231.

KLAASSEN, R. H. G., STRANDBERG, R., HAKE, M., OLOFSSON, P., TØTTRUP, A. P., and ALERSTAM, T., 2010. Loop migration in adult marsh harriers *Circus aeruginosus*, as revealed by satellite telemetry. *Journal of Avian Biology*, 41: 200–207.

KLAASSEN, R. H., HAKE, M., STRANDBERG, R., and ALERSTAM, T. 2011. Geographical and temporal flexibility in the response to crosswinds by migrating raptors. *Proceedings of the Royal Society of London B: Biological Sciences*, 278: 1339–1346.

KLAASSEN, R. H., HAKE, M., STRANDBERG, R., KOKS, B. J., TRIERWEILER, C., EXO, K. M., BAIRLEIN, F., and ALERSTAM, T. 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, 83: 176 – 184.

KÖLZSCH, A., BAUER, S., BOER, R., GRIFFIN, L., CABOT, D., EXO, K. M., JEUGD, H. P., and NOLET, B. A. 2015. Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. *Journal of Animal Ecology*, 84: 272 – 283.

KRANSTAUBER, B., KAYS, R., LAPOINT, S. D., WIKELSKI, M. and SAFI, K. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, 81: 738 – 746.

KRANSTAUBER, B., and SMOLLA, M. 2015. "Move" R-Package. Visualizing and Analyzing Animal Track Data. http://computational-ecology.com/main-move.html

LANZONE, M. J., MILLER, T. A., TURK, P., BRANDES, D., HALVERSON, C., MAISONNEUVE, C., TREMBLAY, J., COOPER, J., O'MALLEY, K., BROOKS, R. P., and KATZNER, T. 2012. Flight responses by a migratory soaring raptor to changing meteorological conditions. *Biology Letters*, 8: 710-713.

LATHAM, A. D. M., LATHAM, M. C., ANDERSON, D. P., CRUZ, J., HERRIES, D., and HEBBLEWHITE, M. 2015. The GPS craze: Six questions to address before deciding to deploy GPS technology on wildlife. *New Zealand Journal of Ecology*, 39: 143-152.

LEMUNYAN, C. D., WHITE, W., NYBERG, E. and CHRISTIAN, J. J. 1959. Design of a miniature radio transmitter for use in animal studies. *Journal of Wildlife Management*, 23: 107–110.

LIECHTI, F., WITVLIET, W., WEBER, R., and BÄCHLER, E. 2013. First evidence of a 200-day non-stop flight in a bird. *Nature Communications*, 4: 2554

LISOVSKI, S. and HAHN, S. 2012. GeoLight‐processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution*, 3:1055-1059.

LONG, J. A. 2014. wildlifeDI: Calculate Indices of Dynamic Interaction for Wildlife Telemetry Data. R package version 0.2. http://CRAN.R-project.org/package=wildlifeDI

LONG, J. A., NELSON, T. A., WEBB, S. L., and GEE, K. 2014. A critical examination of indices of dynamic interaction for wildlife telemetry studies. *Journal of Animal Ecology*, 83: 1216-1233.

LÓPEZ-LÓPEZ, P., LIMIÑANA, R., and URIOS, V. 2009. Autumn migration of Eleonora's falcon *Falco eleonorae* tracked by satellite telemetry. *Zoological Studies*, 48: 485-491.

LÓPEZ-LÓPEZ, P., LIMIÑANA, L., MELLONE, U., and URIOS, V. 2010. From the Mediterranean Sea to Madagascar. Are there ecological barriers for the long-distance migrant Eleonora's falcon? *Landscape Ecology*, 25: 803–813.

LÓPEZ-LÓPEZ, P., BENAVENT-CORAI, J., GARCÍA-RIPOLLÉS, C., and URIOS, V. 2013a. Scavengers on the move: behavioural changes in foraging search patterns during the annual cycle. *PLoS ONE*, 8: e54352.

LÓPEZ-LÓPEZ, P., ZUBEROGOITIA, Í., ALCÁNTARA, M., and GIL, J.A. 2013b. Philopatry, natal dispersal, first settlement and age of first breeding of Bearded Vultures *Gypaetus barbatus* in central Pyrenees. *Bird Study*, 60: 555–560.

LÓPEZ-LÓPEZ, P., GARCÍA-RIPOLLÉS, C., and URIOS, V. 2014a. Individual repeatability in timing and spatial flexibility of migration routes of trans-Saharan migratory raptors. *Current Zoology*, 60: 642–652.

LÓPEZ-LÓPEZ, P., GIL, J. A., and ALCÁNTARA, M. 2014b. Post-fledging dependence period and onset of natal dispersal in Bearded Vultures (*Gypaetus barbatus*): new insights from GPS satellite telemetry. *Journal of Raptor Research*, 48: 173-181

LÓPEZ-LÓPEZ, P., GARCÍA-RIPOLLÉS, C., and URIOS, V. 2014c. Food predictability determines space use of endangered vultures: implications for management of supplementary feeding. *Ecological Applications*, 24: 939-949.

LOUZAO, M., WEIGAND, T., BARTUMEUS, F. and WEIMERSKIRCH, H. 2014. Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. *Movement Ecology*, 2: 8.

MAGALHÃES, M. C., SANTOS, R. S. and HAMER, K. C., 2008. Dual-foraging of Cory's shearwaters in the Azores: feeding locations, behaviour at sea and implications for food provisioning of chicks. *Marine Ecology Progress Series*, 359: 283 – 293.

MANDEL, J. T., BILDSTEIN, K. L., BOHRER, G., and WINKLER, D. W. 2008. Movement ecology of migration in turkey vultures. *Proceedings of the National Academy of Sciences*, 105: 19102 – 19107.

MANDEL, J. T., BOHRER, G., WINKLER, D. W., BARBER, D. R., HOUSTON, C. S. and BILDSTEIN, K. L. 2011. Migration path annotation: cross-continental study of migration-flight response to environmental conditions. *Ecological Applications*, 21: 2258-2268.

MARGALIDA, A., CARRETE, M., HEGGLIN, D., SERRANO, D., ARENAS, R., and DONÁZAR, J. A. 2013. Uneven large-scale movement patterns in wild and reintroduced pre-adult bearded vultures: conservation implications. *PLoS ONE*, 8: e65857.

MARTELL, M. S., HENNY, C. J., NYE, P. E., SOLENSKY, M. J. 2001. Fall migration routes, timing, and wintering sites of North American Ospreys as determined by satellite telemetry. *The Condor*, 103: 715-724.

MASELLO, J. F., MUNDRY, R., POISBLEAU, M., DEMONGIN, L., VOIGT, C. C., WIKELSKI, M., and QUILLFELDT, P. 2010. Diving seabirds share foraging space and time within and among species. *Ecosphere*, 1(6): art19. doi:10.1890/ES10-00103.1

MELLONE, U., LÓPEZ-LÓPEZ, P., LIMIÑANA, R., and URIOS, V. 2011.Weather conditions promote route flexibility during open ocean crossing in a long-distance migratory raptor. *International Journal of Biometeorology*, 55: 463-468

MELLONE, U., LÓPEZ-LÓPEZ, P., LIMIÑANA, R., and URIOS, V. 2012a. Wintering habitats of Eleonora's Falcons *Falco eleonorae* in Madagascar. *Bird Study*, 59: 29-36

MELLONE, U., KLAASSEN, R. H. G., GARCÍA-RIPOLLÉS, C., LIMIÑANA, R., LÓPEZ-LÓPEZ, P., PAVÓN, D., STRANDBERG, R., URIOS, V., VARDAKIS, M., ALERSTAM, T. 2012b. Interspecific comparison of the performance of soaring migrants in relation to morphology, meteorological conditions and migration strategies. *PLoS ONE*, 7: e39833.

MELLONE, U., LÓPEZ-LÓPEZ, P., LIMIÑANA, R., PIASEVOLI, G., and URIOS, V. 2013a. The trans-equatorial loop migration system of Eleonora's falcon: differences in migration patterns between age classes, regions and seasons. *Journal of Avian Biology*, 44: 417–426.

MELLONE, U., DE LA PUENTE, J., LÓPEZ-LÓPEZ, P., LIMIÑANA, L., BERMEJO, A., and URIOS, V. 2013b. Migration routes and wintering areas of Booted Eagles *Aquila pennata* breeding in Spain. *Bird Study*, 60: 409-413.

MELLONE, U., LÓPEZ-LÓPEZ, P., LIMIÑANA, R., URIOS, V. 2013c. Summer pre-breeding movements of Eleonora's Falcons *Falco eleonorae* revealed by satellite telemetry: implications for conservation. *Bird Conservation International*, 23: 487-494

MELLONE, U., DE LA PUENTE, J., LÓPEZ-LÓPEZ, P., LIMIÑANA, R., BERMEJO, A., and URIOS, V. 2015a. Seasonal differences in migration patterns of a soaring bird in relation to environmental conditions: a multi-scale approach. *Behavioral Ecology and Sociobiology*, 69: 75–82.

MELLONE, U., LIMIÑANA, R., LÓPEZ-LÓPEZ, P., and URIOS, V. 2015b. Regional and age-dependent differences in the effect of wind on the migratory routes of Eleonora's Falcon. *Current Zoology*, 61: 428–434.

MEYBURG, B.-U., MEYBURG, C., BĚLKA, T., ŠREIBR, O., and VRANA, J. 2004a. Migration, wintering and breeding of a lesser spotted eagle (*Aquila pomarina*) from Slovakia tracked by satellite. *Journal of Ornithology*, 145: 1–7.

MEYBURG, B.-U., GALLARDO, M., MEYBURG, C., and DIMITROVA, E. 2004b. Migrations and sojourn in Africa of Egyptian vultures (*Neophron percnopterus*) tracked by satellite. *Journal of Ornithology*, 145: 273-280.

MONSARRAT, S., BENHAMOU, S., SARRAZIN, F., BESSA-GOMES, C., BOUTEN, W., and DURIEZ, O. 2013. How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers. *PloS ONE*, 8: e53077.

MOORE, G.E. 1965. Cramming More Components onto Integrated Circuits. *Electronics Magazine*, 38: 114–117.

MORALES, J. M., HAYDON, D. T., FRAIR, J., HOLSINGER, K. E. and FRYXELL, J. M. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, 85: 2436–2445.

MORALES, J. M., MOORCROFT, P. R., MATTHIOPOULOS, J., FRAIR, J. L., KIE, J. G., POWELL, R. A., MERRILL, E. H. and HAYDON, D. T. 2010. Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365: 2289 – 2301.

MOSS, E. H., HIPKISS, T., ECKE, F., DETTKI, H., SANDSTRÖM, P., BLOOM, P. H., KIDD, J. W., THOMAS, S. E., and HÖRNFELDT, B. 2014. Home-range size and examples of post-nesting movements for adult Golden Eagles (*Aquila chrysaetos*) in boreal Sweden. *Journal of Raptor Research*, 48: 93 – 105.

MOURITSEN, H., HUYVAERT, K. P., FROST, B. J., and ANDERSON, D. J. 2003. Waved albatrosses can navigate with strong magnets attached to their head. *Journal of Experimental Biology*, 206: 4155 – 4166.

MÜLLER, M. S., MASSA, B., PHILLIPS, R. A., and DELL'OMO, G. 2014. Individual consistency and sex differences in migration strategies of Scopoli's shearwaters *Calonectris diomedea* despite year differences. *Current Zoology*, 60: 631-641.

MÜLLER, M. S., MASSA, B., PHILLIPS, R. A., and DELL'OMO, G. 2015. Seabirds mated for life migrate separately to the same places: behavioural coordination or shared proximate causes? *Animal Behaviour*, 102: 267 – 276.

MURRAY, D. L., and FULLER, M. R. 2000. A critical review of the effects of marking on the biology of vertebrates. In, Boitani, L., and T.K. Fuller (eds.) *Research Techniques in Animal Ecology: Controversies and Consequences*, pp. 15–64. Columbia University Press, New York.

NAGY, M., ÁKOS, Z., BIRO, D., and VICSEK, T. 2010. Hierarchical group dynamics in pigeon flocks. *Nature*, 464: 890 – 893.

NAGY, M., VÁSÁRHELYI, G., PETTIT, B., ROBERTS-MARIANI, I., VICSEK, T., and BIRO, D. 2013. Context-dependent hierarchies in pigeons. *Proceedings of the National Academy of Sciences*, 110: 13049 – 13054.

NATHAN, R. 2008. An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences*, 105: 19050-19051.

NATHAN, R., GETZ, W. M., REVILLA, E., HOLYOAK, M., KADMON, R., SALTZ, D., and SMOUSE, P. E. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, 105: 19052-19059.

NATHAN, R., SPIEGEL, O., FORTMANN-ROE, S., HAREL, R., WIKELSKI, M., and GETZ, W. M. 2012. Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *The Journal of Experimental Biology*, 215: 986 – 996.

NEWMAN, S. H., IVERSON, S. A., TAKEKAWA, J. Y., GILBERT, M., PROSSER, D. J., BATBAYAR, N., NATSAGDORJ, T., and DOUGLAS, D. C. 2009. Migration of whooper swans and outbreaks of highly pathogenic avian influenza H5N1 virus in eastern Asia. *PLoS ONE*, 4: e5729.

NEWMAN, S. H., HILL, N. J., SPRAGENS, K. A., JANIES, D., VORONKIN, I. O., PROSSER, D. J., YAN, B., LEI, F., BATBAYAR, N., NATSAGDORJ, T., BISHOP, C. M., BUTLER, P. J., WIKELSKI, M., BALACHANDRAN, S., MUNDKUR, T., DOUGLAS, D. C., and TAKEKAWA, J. Y. 2012. Eco-virological approach for assessing the role of wild birds in the spread of avian influenza H5N1 along the Central Asian Flyway. *PLoS ONE*, 7: e30636.

NEWTON, I. 2014. Is bird ringing still necessary? *British Birds*, 107: 572–574.

NORRIS, D. R., MARRA, P. P., KYSER, T. K., SHERRY, T. W., and RATCLIFFE, L. M. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B*, 271: 59 – 64.

NORRIS, D. R., and MARRA, P. P. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor*, 109: 535–547.

NOWAK, E., BERTHOLD, P., and QUERNER, U. 1990. Satellite tracking of migrating Bewick's Swans. *Naturwissenschaften*, 77: 549-550.

OKES, N. C., HOCKEY, P. A., PICHEGRU, L., VAN DER LINGEN, C. D., CRAWFORD, R. J., and GRÉMILLET, D. 2009. Competition for shifting resources in the southern Benguela upwelling: seabirds versus purse-seine fisheries. *Biological Conservation*, 142: 2361 – 2368.

OPPEL, S., DOBREV, V., ARKUMAREV, V., SARAVIA, V., BOUNAS, A., KRET, E., VELEVSKI, M., STOYCHEV, S., and NIKOLOV, S. C. 2015. High juvenile mortality during migration in a declining population of a long-distance migratory raptor. *Ibis*, 157: 545–557.

OTIS, D. L. and WHITE, G. C. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *The Journal of Wildlife Management*, 63: 1039-1044.

OUWEHAND, J., AHOLA, M. P., AUSEMS, A. N. M. A., BRIDGE, E. S., BURGESS, M., HAHN, S., HEWSON, C. M., KLAASSEN, R. H. G., LAAKSONEN, T., LAMPE, H. M., VELMALA, W. and BOTH, C. 2016. Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. *Journal of Avian Biology*, 47: 69–83.

PATRICK, S. C., and WEIMERSKIRCH, H. 2014. Personality, foraging and fitness consequences in a long lived seabird. *PloS ONE*, 9: e87269.

PATRICK, S. C., BEARHOP, S., GRÉMILLET, D., LESCROËL, A., GRECIAN, W. J., BODEY, T. W., HAMER, K. C., WAKEFIELD, E., LE NUZ, M., VOTIER, S.C. 2014. Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos*, 123: 33 – 40.

PATTERSON, T. A., THOMAS, L., WILCOX, C., OVASKAINEN, O. and MATTHIOPOULOS, J. 2008. State–space models of individual animal movement. *Trends in Ecology and Evolution*, 23: 87-94.

PENG, R.D. 2011. Reproducible Research in Computational Science. *Science*, 334: 1226–1227.

PENNYCUICK, C. J., FAST, P. L., BALLERSTÄDT, N., and RATTENBORG, N. 2012. The effect of an external transmitter on the drag coefficient of a bird's body, and hence on migration range, and energy reserves after migration. *Journal of Ornithology*, 153: 633-644.

PÉREZ-GARCÍA, J. M., MARGALIDA, A., AFONSO, I., FERREIRO, E., GARDIAZÁBAL, A., BOTELLA, F., and SÁNCHEZ-ZAPATA, J. A. 2013. Interannual home range variation, territoriality and overlap in breeding Bonelli's Eagles (*Aquila fasciata*) tracked by GPS satellite telemetry. *Journal of Ornithology*, 154: 63 – 71.

PÉRON, C., and GRÉMILLET, D. 2013. Tracking through life stages: adult, immature and juvenile autumn migration in a long-lived seabird. *PLoS ONE*, 8: e72713.

PETERSEN, M. R., BYRD, G. V., SONSTHAGEN, S. A., and SEXSON, M. G. 2015. Re-colonization by common eiders *Somateria mollissima* in the Aleutian Archipelago following removal of introduced arctic foxes *Vulpes lagopus*. *Journal of Avian Biology*, 46: 538–549.

PFEIFFER, T., and MEYBURG, B. U. 2015. GPS tracking of Red Kites (*Milvus milvus*) reveals fledgling number is negatively correlated with home range size. *Journal of Ornithology*, 156: 963–975.

PHIPPS, W. L., WILLIS, S. G., WOLTER, K., and NAIDOO, V. 2013. Foraging ranges of immature African white-backed vultures (*Gyps africanus*) and their use of protected areas in southern Africa. *PLoS ONE*, 8: e52813.

PIMM, S. L., ALIBHAI, S., BERGL, R., DEHGAN, A., GIRI, C., JEWELL, Z., JOPPA, L., KAYS, R. and LOARIE, S. 2015. Emerging Technologies to Conserve Biodiversity. *Trends in Ecology and Evolution*, 30: 685 – 696.

PINAUD, D., and WEIMERSKIRCH, H. 2005. Scale-dependent habitat use in a long-ranging central place predator. *Journal of Animal Ecology*, 74: 852 – 863.

PORTUGAL, S. J., HUBEL, T. Y., FRITZ, J., HEESE, S., TROBE, D., VOELKL, B., HAILES, S., WILSON, A. M., and USHERWOOD, J. R., 2014. Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature*, 505: 399-402.

POTTS, J. R., MOKROSS, K., and LEWIS, M. A. 2014. A unifying framework for quantifying the nature of animal interactions. *Journal of The Royal Society Interface*, 11: 20140333.

PROSSER, D. J., TAKEKAWA, J. Y., NEWMAN, S. H., YAN, B., DOUGLAS, D. C., HOU, Y., XING, Z. H. I., ZHANG, D., LI, T., LI, Y., and ZHAO, D. 2009. Satellite-marked waterfowl reveal migratory connection between H5N1 outbreak areas in China and Mongolia. *Ibis*, 151: 568 – 576.

PROSSER, D. J., CUI, P., TAKEKAWA, J. Y., TANG, M., HOU, Y., COLLINS, B. M., YAN, B., HILL, N. J., LI, T., LI, Y., and LEI, F. 2011. Wild bird migration across the Qinghai-Tibetan plateau: a transmission route for highly pathogenic H5N1. *PloS ONE*, 6: e17622.

QUILLFELDT, P., VOIGT, C. C., and MASELLO, J. F. 2010. Plasticity versus repeatability in seabird migratory behaviour. *Behavioural Ecology and Sociobiology*, 64: 1157–1164.

RAMOS, R., SANZ, V., MILITÃO, T., BRIED, J., NEVES, V.C., BISCOITO, M., PHILLIPS, R.A., ZINO, F. and GONZÁLEZ-SOLÍS, J. 2015. Leapfrog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel (*Bulweria bulwerii*). *Journal of Biogeography*, 42: 1651 – 1664.

RATCLIFFE, N., HILL, S. L., STANILAND, I. J., BROWN, R., ADLARD, S., HORSWILL, C. and TRATHAN, P. N. 2015. Do krill fisheries compete with macaroni penguins? Spatial overlap in prey consumption and catches during winter. *Diversity and Distributions*, 21: 1339 – 1348.

REYNOLDS, A. M., CECERE, J. G., PAIVA, V. H., RAMOS, J. A., and FOCARDI, S. 2015. Pelagic seabird flight patterns are consistent with a reliance on olfactory maps for oceanic navigation. *Proceedings of the Royal Society B*, 282: 20150468.

ROBINSON, W. D., BOWLIN, M. S., BISSON, I., SHAMOUN-BARANES, J., THORUP, K., DIEHL, R. H., KUNZ, T.H., MABEY, S., and WINKLER, D. W. 2009. Integrating concepts and technologies to advance the study of bird migration. *Frontiers in Ecology and the Environment*, 8: 354-361.

RODRÍGUEZ, A., RODRÍGUEZ, B. and NEGRO, J.J. 2015. GPS tracking for mapping seabird mortality induced by light pollution. *Scientific Reports*, 5: 10670.

RODRÍGUEZ-RUIZ, J., DE LA PUENTE, J., PAREJO, D., VALERA, F., CALERO-TORRALBO, M. A., REYES-GONZÁLEZ, J. M., ZAJKOVÁ, Z., BERMEJO, A. and AVILÉS, J. M. 2014. Disentangling Migratory Routes and Wintering Grounds of Iberian Near-Threatened European Rollers *Coracias garrulus*. *PLoS ONE*, 9: e115615.

RODGERS, A. R., CARR, A. P., BEYER, H. L., SMITH, L., and KIE, J. G. 2007. HRT: Home Range Tools for ArcGIS—Version 1.1: Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

ROPERT-COUDERT, Y. and WILSON, R. P. 2005. Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment*, 3: 437-444.

ROPERT-COUDERT, Y., KATO, A., WILSON, R. P., and CANNELL, B. 2006. Foraging strategies and prey encounter rate of free-ranging Little Penguins. *Marine Biology*, 149: 139 – 148.

RUTZ, C., and HAYS, G. C. 2009. New frontiers in biologging science. *Biology Letters*, 5: 289-292.

SCHICK, R. S., LOARIE, S. R., COLCHERO, F., BEST, B. D., BOUSTANY, A., CONDE, D. A., HALPIN, P. N., JOPPA, L. N., MCCLELLAN, C. M., and CLARK, J. S. 2008. Understanding movement data and movement processes: current and emerging directions. *Ecology Letters*, 11: 1338 – 1350.

SAINO, N., RUBOLINI, D., AMBROSINI, R., ROMANO, M., SCANDOLARA, C., FAIRHURST, G. D., CAPRIOLI, M., ROMANO, A., SICURELLA, B., and LIECHTI, F. 2015. Light-level geolocators reveal covariation between winter plumage molt and phenology in a trans-Saharan migratory bird. *Oecologia*, 178: 1105 – 1112.

SENNER, N. R., HOCHACHKA, W. M., FOX, J. W. and AFANASYEV, V. 2014. An exception to the rule: Carry-over effects do not accumulate in a long-distance migratory bird. *PLoS ONE*, 9: e86588.

SERGIO, F., TANFERNA, A., DE STEPHANIS, R., JIMÉNEZ, L. L., BLAS, J., TAVECCHIA, G., PREATONI, D., and HIRALDO, F. 2014. Individual improvements and selective mortality shape lifelong migratory performance. *Nature*, 515: 410 – 413.

SERGIO, F., TAVECCHIA, G., TANFERNA, A., LÓPEZ JIMÉNEZ, L., BLAS, J., DE STEPHANIS, R., MARCHANT, T. A., KUMAR, N. and HIRALDO, F. 2015. No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. *Journal of Applied Ecology*, 52:1665-1675.

SHADE, A., and TEAL, T. K. 2015. Computing Workflows for Biologists: A Roadmap. *PLoS Biology*, 13: e1002303.

SHAFFER, S. A., TREMBLAY, Y., WEIMERSKIRCH, H., SCOTT, D., THOMPSON, D. R., SAGAR, P. M., MOLLER, H., TAYLOR, G. A., FOLEY, D. G., BLOCK, B. A., and COSTA, D. P. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences*, 103: 12799-12802.

SHAMOUN-BARANES, J., VAN LOON, E. E., PURVES, R. S., SPECKMANN, B., WEISKOPF, D. and CAMPHUYSEN, C. J. 2011. Analysis and visualization of animal movement. *Biology Letters*, p.rsbl20110764.

SHEPHARD, J. M., RYCKEN, S., ALMALIK, O., STRUYF, K., and ERP-VAN DER KOOIJ, L. 2015. Migration strategies revealed by satellite tracking among descendants of a population of European white stork (*Ciconia ciconia*) reintroduced to Belgium. *Journal of Ornithology*, 156: 943 – 953.

SHOJI, A., ARIS-BROSOU, S., CULINA, A., FAYET, A., KIRK, H., PADGET, O., JUÁREZ-MARTÍNEZ, I., BOYLE, D., NAKATA, T., PERRINS, C.M., and GUILFORD, T. 2015. Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. *Biology Letters*, 11: 20150671.

SIGNER, J. and BALKENHOL, N. 2015. Reproducible home ranges (rhr): A new, user-friendly R package for analyses of wildlife telemetry data. *Wildlife Society Bulletin*, 39: 358–363.

SOKOLOV, L. V. 2011. Modern telemetry: new possibilities in ornithology. *Biology Bulletin*, 38: 885-904.

SOUTULLO, A., CADAHÍA L., URIOS V., FERRER, M., and NEGRO J. J. 2007. Accuracy of lightweight satellite telemetry: a case study in Iberian Peninsula. *Journal of Wildlife Management*, 71: 1010–1015.

SOUTULLO, A., URIOS, V., FERRER, M., and LÓPEZ-LÓPEZ, P. 2008. Habitat use by juvenile Golden Eagles *Aquila chrysaetos* in Spain. *Bird Study*, 55: 236-240.

SOUTULLO, A., LÓPEZ-LÓPEZ, P., CORTÉS, G. D., URIOS, U., and FERRER, M. 2013. Exploring juvenile golden eagles' dispersal movements at two different temporal scales. *Ethology Ecology & Evolution*, 25: 117–128.

SPINA, F. 1999. Value of ringing information for bird conservation in Europe. *Ringing and Migration*, 19: 29-40.

STANLEY, C. Q., MACPHERSON, M., FRASER, K. C., MCKINNON, E. A., STUTCHBURY, B. J. M. 2012. Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE*, 7: e40688.

STRANDBERG, R., KLAASSEN, R. H., HAKE, M., OLOFSSON, P., and ALERSTAM, T. 2009a. Converging migration routes of Eurasian hobbies *Falco subbuteo* crossing the African equatorial rain forest. *Proceedings of the Royal Society B*, 276: 727–733.

STRANDBERG, R., KLAASSEN, R. H., HAKE, M., and ALERSTAM, T. 2009b. How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. *Biology Letters*, rsbl20090785. doi:10.1098/rsbl.2009.0785

STUTCHBURY, B. J. M., TAROF, S. A., DONE, T., GOW, E., KRAMER, P. M., TAUTIN, J., FOX, J. W., and AFANASYEV, V. 2009. Tracking long-distance songbird migration by using geolocators. *Science*, 323: 896 – 897.

TIAN, H., ZHOU, S., DONG, L., VAN BOECKEL, T. P., CUI, Y., WU, Y., CAZELLES, B., HUANG, S., YANG, R., GRENFELL, B. T., and XU, B. 2015. Avian influenza H5N1 viral and bird migration networks in Asia. *Proceedings of the National Academy of Sciences*, 112: 172 – 177.

TOMKIEWICZ, S.M., FULLER, M.R., KIE, J.G. and BATES, K.K. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365: 2163 – 2176.

TRACEY, J. A., SHEPPARD, J., ZHU, J., WEI, F., SWAISGOOD, R. R., and FISHER, R. N. 2014. Movement-Based Estimation and Visualization of Space Use in 3D for Wildlife Ecology and Conservation. *PLoS ONE*, 9: e101205.

THAXTER, C. B., ROSS-SMITH, V. H., BOUTEN, W., CLARK, N. A., CONWAY, G. J., REHFISCH, M. M., and BURTON, N. H. 2015. Seabird–wind farm interactions during the breeding season vary within and between years: A case study of lesser black-backed gull *Larus fuscus* in the UK. *Biological Conservation*, 186: 347-358.

THIEBOT, J. B., BOST, C. A., DEHNHARD, N., DEMONGIN, L., EENS, M., LEPOINT, G., CHEREL, Y. and POISBLEAU, M. 2015. Mates but not sexes differ in migratory niche in a monogamous penguin species. *Biology Letters*, 11: 20150429.

THORUP, K., FULLER, M., ALERSTAM, T., HAKE, M., KJELLÉN, N., and STRANDBERG, R. 2006. Do migratory flight paths of raptors follow constant geographical or geomagnetic courses? *Animal Behaviour*, 72: 875-880.

TRIERWEILER, C., MULLIE, W. C., DRENT, R. H., EXO, K. M., KOMDEUR, J., BAIRLEIN, F., HAROUNA, A., BAKKER, M., and KOKS, B. J. 2013. A Palaearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel. *Journal of Animal Ecology*, 82: 107 – 120.

TRIERWEILER, C., KLAASSEN, R. H., DRENT, R. H., EXO, K. M., KOMDEUR, J., BAIRLEIN, F. and KOKS, B. J. 2014. Migratory connectivity and population-specific migration routes in a long-distance migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences*, 281: 20132897.

USHERWOOD, J. R., STAVROU, M., LOWE, J. C., ROSKILLY, K., and WILSON, A. M. 2011. Flying in a flock comes at a cost in pigeons. *Nature*, 474: 494 – 497.

VANDENABEELE, S. P., WILSON, R. P., and WIKELSKI, M. 2013. New tracking philosophy for birds. *Frontiers in Ecology and the Environment*, 11: 10 – 12.

VAN DIJK, J. G. B., KLEYHEEG, E., SOONS, M. B., NOLET, B. A., FOUCHIER, R. A. M., and KLAASSEN, M. 2015. Weak negative associations between avian influenza virus infection and movement behaviour in a key host species, the mallard *Anas platyrhynchos*. *Oikos*, 124: 1293–1303.

VAN HEEZIK, Y., SMYTH, A., ADAMS, A., GORDON, J. (2010). Do domestic cats impose an unsustainable harvest on urban bird populations?. Biological Conservation, 143(1): 121 – 130.

VAN WIJK, R. E., KÖLZSCH, A., KRUCKENBERG, H., EBBINGE, B. S., MÜSKENS, G. J. D. M. and NOLET, B. A. 2012. Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos*, 121: 655–664.

VANSTEELANT, W.M.G., BOUTEN, W., KLAASSEN, R.H.G., KOKS, B.J., SCHLAICH, A.E., VAN DIERMEN, J., VAN LOON, E.E. and SHAMOUN-BARANES, J. 2015. Regional and seasonal flight speeds of soaring migrants and the role of weather conditions at hourly and daily scales. *Journal of Avian Biology*, 46: 25 – 39.

VARDANIS, Y., KLAASSEN, R. H., STRANDBERG, R., and ALERSTAM, T. 2011. Individuality in bird migration: Routes and timing. *Biology Letters*, 7: 502–505.

VIDAL-MATEO, J., MELLONE, U., LÓPEZ-LÓPEZ, P., DE LA PUENTE, J., GARCÍA-RIPOLLÉS, C., BERMEJO, A., and URIOS, V. (*in press*). Wind effects on the migration routes of trans-Saharan soaring raptors: geographical, seasonal and interspecific variation. *Current Zoology*

VISWANATHAN, G. M., AFANASYEV, V., BULDYREV, S. V., MURPHY, E. J., PRINCE, P. A., and STANLEY, H. E. 1996. Lévy flight search patterns of wandering albatrosses. *Nature*, 381: 413 – 415.

WAKEFIELD, E. D., PHILLIPS, R. A., and MATTHIOPOULOS, J. 2009. Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series*, 391: 165-182.

WAKEFIELD, E. D., BODEY, T. W., BEARHOP, S., BLACKBURN, J., COLHOUN, K., DAVIES, R., DWYER, R. G., GREEN, J. A., GRÉMILLET, D., JACKSON, A. L., and JESSOPP, M. J., 2013. Space partitioning without territoriality in gannets. *Science*, 341: 68-70.

WAKEFIELD, E. D., CLEASBY, I. R., BEARHOP, S., BODEY, T. W., DAVIES, R. D., MILLER, P. I., NEWTON, J., VOTIER, S. C. and HAMER, K. C. 2015. Long-term individual foraging site fidelity-why some gannets don't change their spots. *Ecology*, 96: 3058 – 3074.

WEBSTER, M. S., MARRA, P. P., HAIG, S. M., BENSCH, S., and HOLMES, R. T. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution*, 17: 76-83.

WEIMERSKIRCH, H., BERTRAND, S., SILVA, J., MARQUES, J. C., and GOYA, E. 2010. Use of social information in seabirds: compass rafts indicate the heading of food patches. *PLoS ONE*, 5: e9928

WEIMERSKIRCH, H., CHEREL, Y., DELORD, K., JAEGER, A., PATRICK, S. C., and RIOTTE-LAMBERT, L. 2014. Lifetime foraging patterns of the wandering albatross: life on the move! *Journal of Experimental Marine Biology and Ecology*, 450: 68-78.

WEIMERSKIRCH, H., DELORD, K., GUITTEAUD, A., PHILLIPS, R. A., and PINET, P., 2015. Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. *Scientific Reports*, 5: 8853.

WHITE, G. C., and GARROTT, R. A. 1990. *Analysis of Wildlife Radio-tracking Data*. Academic Press, San Diego, USA.

WIKELSKI, M., KAYS, R. W., KASDIN, N. J., THORUP, K., SMITH, J. A., and SWENSON, G. W. 2007. Going wild: what a global small-animal tracking system could do for experimental biologists. *Journal of Experimental Biology*, 210: 181-186.

WIKELSKI, M., and KAYS, R. 2015. Movebank: Archive, analysis and sharing of animal movement data. www.movebank.org

WIKELSKI, M., ARRIERO, E., GAGLIARDO, A., HOLLAND, R. A., HUTTUNEN, M. J., JUVASTE, R., MUELLER, I., TERTITSKI, G., THORUP, K., WILD, M., ALANKO, M., BAIRLEIN, F., CHERENKOV, A., CAMERON, A., FLATZ, R., HANNILA, J., HÜPPOP, O., KANGASNIEMI, M., KRANSTAUBER, B., PENTTINEN, M-L., SAFI, K., SEMASHKO, V., SCHMID, H., and WISTBACKA, R. 2015. True navigation in migrating gulls requires intact olfactory nerves. *Scientific Reports*, 5: 17061.

WILCOVE, D. S., and WIKELSKI, M. 2008. Going, going, gone: is animal migration disappearing. *PLoS Biology*, 6; e188.

WILLEMOES, M., STRANDBERG, R., KLAASSEN, R. H., TØTTRUP, A. P., VARDANIS, Y., HOWEY, P. W., THORUP, K., WIKELSKI, M., and ALERSTAM, T., 2014. Narrow-front loop migration in a population of the common cuckoo *Cuculus canorus*, as revealed by satellite telemetry. *PloS ONE*, 9: e83515.

WILLEMOES, M., BLAS, J., WIKELSKI, M., and THORUP, K. 2015. Flexible navigation response in common cuckoos *Cuculus canorus* displaced experimentally during migration. *Scientific Reports*, 5: 16402.

WILLIAMS, H. J., SHEPARD, E. L. C., DURIEZ, O. and LAMBERTUCCI, S. A. 2015. Can accelerometry be used to distinguish between flight types in soaring birds? *Animal Biotelemetry*, 3:45.

WILSON, R., DUCAMP, J., REES, W., CULIK, B., and NIEKAMP, K. 1992. Estimation of location: global coverage using light intensity. In, I.G. Priede and S.M. Swift (eds.) *Wildlife Telemetry: Remote Monitoring and Tracking of Animals*, pp. 131–134. Ellis Horwood Ltd, Hemel Hempstead, UK.

WILSON, R. P., WHITE, C. R., QUINTANA, F., HALSEY, L. G., LIEBSCH, N., MARTIN, G. R., and BUTLER, P. J. 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology*, 75: 1081-1090.

WILSON, R. P., and VANDENABEELE, S. P. 2012. Technological innovation in archival tags used in seabird research. *Marine Ecology Progress Series*, 451: 245 – 262.

YAMAÇ, E., and BILGIN, C.C. 2012. Post-fledging movements of Cinereous Vultures *Aegypius monachus* in Turkey revealed by GPS telemetry. *Ardea*, 100: 149 – 156.

YAMAMOTO, T., TAKAHASHI, A., SATO, K., OKA, N., YAMAMOTO, M., and TRATHAN, P. N. 2014. Individual consistency in migratory behaviour of a pelagic seabird. *Behaviour*, 151: 683-701.

ŽYDELIS, R., LEWISON, R. L., SHAFFER, S. A., MOORE, J. E., BOUSTANY, A. M., ROBERTS, J. J., SIMS, M., DUNN, D. C., BEST, B. D., TREMBLAY, Y., and KAPPES, M. A. 2011. Dynamic habitat models: using telemetry data to project fisheries bycatch. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20110330. doi:10.1098/rspb.2011.0330.

BOX 1. Glossary.

Accelerometer: electronic device that measures acceleration over time. Acceleration sensors are usually included in dataloggers and usually record data in multiple axes (i.e., typically in three axes X,Y,Z). Sensor output can change due to two causes: changing orientation of the device and accelerated translational movement of the device. Raw acceleration data must be converted to physical units (e.g. m/s^2) using mathematical formulae.

Archival data logger (or datalogger): an electronic device attached to or implanted in animals that registers and stores information in an on board memory. Depending on their size, battery capacity and species tracked, dataloggers must be recovered for data retrieval. In most advanced devices data can be remotely transmitted via satellite, GPRS/GSM phone network or through a wireless link to a base station connected with a special antenna.

Argos location: The ARGOS system allows calculating a transmitter's location using the Doppler Effect on transmission frequency, which is the only available position information for small PTTs not including GPS sensor (e.g. < 5g). Location is calculated using two location processing algorithms: Least squares analysis and Kalman filtering, which provides more positions and better accuracy. Regardless of the number of messages received during a satellite pass, an estimated error is calculated by Argos. This allows a classification of location classes (LCs) depending on their nominal accuracy as follows: LC3 < 250 m; LC2 = 250 m – 500 m; LC1 = 500 m – 1500 m; LC0 > 1500m; LCA, LCB = No accuracy estimation; LCZ = invalid location (Argos 2015).

ARGOS system: a global satellite-based location and data collection system dedicated to studying animal movement. It allows any mobile object equipped with a compatible transmitter to be located across the world by means of a network of six satellites. Data recorded in Platform Transmitters Terminals (PTTs) are transmitted to one of these satellites, stored on the on-board recorder and retransmitted to the ground each time the satellite passes over one of the three main receiving stations. Processing centres process all received data and make available information to users.

Behavioural segmentation (or behavioural annotation): to identify movement trajectories' simplest functional units (i.e., behavioural modes) and annotate them to each location. Drawing an analogy, a behavioural mode is to the movement trajectory what a gene is to the DNA sequence (Nathan et al., 2008). There are several computational tools and mathematical algorithms that do this in an unsupervised manner (e.g., binary clustering, Bayesian estimation methods, state-space models, etc).

Biologging (or biotelemetry): use of miniaturized animal-attached tags for recording and/or relaying data about animal's movements, behaviour, physiology and/or environment. This term embraces different types of sensors including those aimed at recording fast-tracking GPS position, accelerometry, conductivity, light-level information, heart rate, neuro-loggers, body temperature, video recording and even exchange of information with other nearby tags and base stations.

Conventional tracking (or ground tracking, radio-tracking, VHF tracking): individual ground-based tracking system based on the emission of short-range very high frequency (VHF) radio signals which are received by an array of systems including antennas mounted on towers, vehicles (cars, airplanes, boats…), or handled by persons. Position is estimated by triangulation and the main disadvantage is that the receiver must be close to the transmitter (usually within a few kilometers of distance). Due to the low cost of the equipment and its basic technology it has been the conventional tracking system used for decades.

Environmental data annotation (or path annotation): a system to add external information (i.e., environmental data) and/or internal information (physiological) to animal tracking data. The result is an annotated path which includes additional data to each geographic location of the moving organism.

Geolocator (or global location sensing/GLS logger, light-level logger, light-sensing geolocator): small recording data loggers that include a light sensor, which measures solar irradiance, and an accurate real-time clock to determine the time of sunrise and sunset. The estimated geographical position is obtained by calculating the length of the day which indicates latitude, and the time of solar noon, which indicates longitude.

GPRS: acronym of General packet radio service. An extension of the Global System for Mobile Communications consisting of a packet oriented mobile data service on the 2G and 3G cellular communication systems. In contrast to circuit switched data, which is usually billed per connection time, GPRS usage is typically charged based on volume of data transferred.

GPS: acronym of Global Positioning System. Satellite-based navigation system developed in the United States that provides location and time information in all conditions with global coverage on the earth.

GSM: acronym of Global System for Mobile Communications.A digital mobile telephony system that is widely used in Europe and other parts of the world for data transmission.

ICARUS: acronym of “International Cooperation for Animal Research Using Space”. International initiative aimed at observing global migratory movements of small animals through a satellite system installed in the Russian module of the International Space Station (ISS) (www.icarusinitiative.org). This system is equipped with powerful processing capability to detect and distinguish the weak signals of small tags (< 5g) that are in the reception area of receive antennas installed in the ISS. Tags record archival data including GPS position, accelerometer and temperature.

ODBA: overall dynamic body acceleration. A measure of dynamic acceleration induced about the centre of an animal's mass as a result of its movement. This measure is derived from recordings of acceleration in the three spatial dimensions by an accelerometer. ODBA is considered as a calibrated proxy for rate of oxygen consumption ($\dot{V}O2$) and hence animal’s metabolic rate (i.e., energy expenditure) (Wilson et al., 2006).

PTT: acronym of Platform Transmitter Terminal. Equipment used for measurement through a set of sensors and one-way transmitting communication.

Telemetry: a word derived from the combination of two Greek words: tele (τῆlε) and metron (μετρον), which mean remote measurement of data.

Tracking (or individual tracking): methodological technique aimed at following and determining where an animal is located spatially. For the aims of this paper, I refer only to remote telemetry to track animal movement.

TABLE 1

Main topics in which individual-based tracking methods have made significant contributions in ornithology (or are expected to do so in the future). The reference list shows some examples to illustrate addressed topics and includes only information on birds tracked by remote telemetry (examples using radio-tracking and ringing methods are not shown).

[Principales temas en los que los métodos de seguimiento individual han contribuido a realizar importantes aportaciones en ornitología (o se espera que así lo hagan en el futuro). La lista de referencias muestra algunos ejemplos para ilustrar los asuntos tratados e incluye información solo de aves seguidas mediante telemetría remota (se han excluido ejemplos en los que se hubiera utilizado radio-seguimiento o anillamiento científico).]

Topic	**Questions and future challenges**	**References**
Migratory routes and wintering areas	Description of novel migratory routes (i.e., short- and long-distance migrations). Analysis of migratory patterns and strategies (i.e., routes, directions, speed, timing, altitude, diurnal/nocturnal migration, loop migration, differential/partial migration, leapfrog migration, transcontinental and trans-oceanic migration, migratory divides, population-specific migration routes). Identification and characterization of wintering areas. Winter ecology of migratory species (e.g., habitat selection and trophic ecology).	Martell et al., 2001; Meyburg et al., 2004a, 2004b; González-Solís et al., 2007; Gschweng et al., 2008; Gill et al., 2009; López-López et al., 2009; Egevang et al., 2010; García-Ripollés et al., 2010; Klaassen et al., 2010; Mellone et al., 2012a, 2013a, 2013b; Rodríguez-Ruiz et al., 2014; DeLuca et al., 2015 ; Ramos et al., 2015

Migratory connectivity	Analysis of the links between breeding and nonbreeding areas. Measurement of the strength of migratory connectivity (i.e., strong, weak/diffuse). Effects of migratory connectivity on individual breeding success and population dynamics. Behavioral and evolutionary effects. Conservation implications.	Webster et al., 2002; Bächler et al., 2010; Robinson et al., 2009; Cresswell 2014; Rodríguez-Ruiz et al., 2014; Trierweiler et al., 2014; Ouwehand et al., 2016
Carry-over effects	How individuals' decisions, previous history and experience explain current and future performance over the annual cycle. Detailed analysis of key vital stages throughout the annual cycle (e.g. migration, wintering, breeding). Analysis of the interplay between environmental and intrinsic factors in determining carry-over effects. Impacts of environmental change on individuals' migratory performance and populations.	Norris et al., 2004; Norris and Marra 2007; Harrison et al., 2011; Arlt et al., 2013; Daunt et al., 2014; Senner et al., 2014; Saino et al., 2015; Shoji et al., 2015
Lifetime tracking	Individual monitoring throughout the bird's lifetime. Description and analysis of variations in tracks' characteristics and movement patterns over different life-history stages. Analysis of the role of experience on migratory performance.	Sergio et al., 2014; Weimerskirch et al., 2014; Flack et al., 2015; Kays et al., 2015
Behavioural flexibility	Analysis of the degree of flexibility or consistency in birds' behaviour. Repeatability in migratory routes and timing. Examination of annual	Alerstam et al., 2006; Quillfeldt et al., 2010; Vardanis et al., 2011;

	schedules of migration and route fidelity. Evaluation of the role of individuality and personality in animal behaviour (i.e., behavioural plasticity) and its consequences on fitness.	Stanley et al., 2012; Dias et al., 2013; Conklin et al., 2013; López-López et al., 2014a; Müller et al., 2014; Yamamoto et al., 2014
Ecological barriers	Effects of geographical and meteorological barriers on movement (e.g., migration, altitudinal movements). Identification of migration corridors, barriers and main migration flyways. Migration patterns (e.g., detours, narrow-front migration, wide-front migration, sea-crossing, mountain-crossing).	Gill et al., 2009; Strandberg et al., 2009a; López-López et al., 2010; Hawkes et al., 2011; Mellone et al., 2011; Willemoes et al., 2014; Adamík et al. 2016
Stopover ecology	Identification of stopovers along migration routes. Detailed analysis of birds' ecology in stopovers (e.g., foraging and refueling tactics). Conservation of stopover sites.	Shaffer et al., 2006; Guilford et al., 2009; Chevallier et al., 2011; van Wijk et al., 2012; Kessler et al., 2013; Shephard et al., 2015
Environmental conditions	Analysis of the effects of external conditions on birds' behaviour. Relationship between global patterns of productivity (e.g. primary productivity, upwelling currents, temperatures, etc.) and movements (i.e., "green wave" hypothesis). Testing the effects of prevailing winds,	Klaassen et al., 2010, 2011; Mandel et al., 2011; Mellone et al., 2012b, 2015a, 2015b; Péron and Grémillet 2013; Trierweiler et al., 2013; Kölzsch et al., 2015; Vansteelant et al., 2015;

	atmospheric pressure and other meteorological conditions on migratory performance.	Bridge et al., in press; Vidal-Mateo et al., in press;
Foraging ecology	Detailed study of foraging movements, identification of feeding locations and food provisioning. Evaluation of different theoretical models of food searching behaviour (e.g., central place foraging theory, Brownian movement, correlated random walks, Lévy flight/walk, first-passage time analysis). Analysis of spatial foraging consistency, foraging site fidelity and complex foraging strategies (e.g. dual-foraging). Evaluation of different flight modes (e.g. flapping flight vs. soaring-gliding flight), energy consumption and foraging ecology.	Jouventin and Weimerskirch 1990; Viswanathan et al., 1996; González-Solís et al., 2000; Magalhães et al., 2008; Pinaud and Weimerskirch 2005; Dean et al., 2012; López-López et al., 2013a; Focardi and Cecere 2014; Patrick et al., 2014; Hernández-Pliego et al., 2015; Wakefield et al., 2015
Space use	Delineation and quantification of home range size. Evaluation of different methods for estimating home range (i.e., kernel density estimators, minimum convex polygons, dynamic Brownian bridge, local convex hull, etc.). Analysis of habitat use, habitat selection and its influence on breeding performance. External and internal drivers of animal movement across geographical gradients.	Soutullo et al., 2008; Wakefield et al., 2009; Kie et al., 2010; Kranstauber et al., 2012; López-López et al., 2014c; Domenech et al., 2015; Pfeiffer and Meyburg 2015

Social interactions	Analysis of how intraspecific and interspecific interactions affect movement. Roles of social networks and hierarchy in movement behaviour (e.g. leadership in flocking behaviour). Development of mechanistic models of territorial interactions. Use of social information in colonial species. Tracking of cohort of individuals of the same guild.	Nagy et al., 2010, 2013; Weimerskirch et al., 2010; Usherwood et al., 2011; Potts et al., 2014; Müller et al., 2015
Population dynamics	Spatially-explicit analysis of the mechanisms of population regulation (e.g., individual experience, territory quality, territoriality, density-dependence effects). Niche segregation, niche partitioning and analysis of intraspecific and interspecific competition in colonial birds.	Masello et al., 2010; López-López et al., 2013b; Pérez-García et al., 2013; Wakefield et al., 2013; Moss et al., 2014; Thiebot et al., 2015
Dispersal	Dispersal studies, post-fledging movements and site fidelity. Obtaining spatially explicit information of key events of the life-cycle (i.e., natal, breeding dispersal and recruitment). Inter-connexion between different populations in meta-populations. Identification and delineation of dispersal areas.	Cadahía et al., 2008,2009,2010; Kays et al., 2011; Yamaç and Bilgin 2012; Soutullo et al., 2013; López-López et al., 2014b; Bentzen and Powell 2015
Disease transmission	Transmission routes of pathogens and disease-dynamics along migration routes. Study of outbreaks of emergent diseases (e.g. avian influenza). Detailed tracking of vectors of disease	Prosser et al., 2009, 2011; Newman et al., 2009, 2012; Adelman et al.,

	transmission. Surveillance of the population ecology of zoonotic hosts, pathogens or vectors.	2014; Tian et al., 2015; van Dijk et al., 2015
Physiology	Recording of physiological parameters (e.g. heart rate, body temperature, blood pressure, respiration) and their interaction with locomotor activity. Use of body acceleration to estimate energy expenditure (e.g., ODBA). Analysis of physiological rhythms at different spatio-temporal scales. Managing of sleeping habits, starvation and dehydration during migration.	Grémillet et al., 2005; Ropert-Coudert et al., 2006; Wilson et al., 2006; Mandel et al., 2008; Wilson and Vandenabeele 2012; Liechti et al., 2013; Dominoni et al., 2014; Duriez et al., 2014; Portugal et al., 2014
Orientation and homing	Disentangling the mechanisms of bird orientation and navigation (e.g., magnetic field, celestial cues, sun compass, polarized light, landscape features and odour cues). Experimental analysis of homing mechanisms in captive birds. Contribution to the development of optimal migration models and detailed understanding of migration routes (e.g. orthodromes, geographic loxodromes, magnetoclinic routes, magnetic loxodromes). Comparison between orientation mechanisms in captive birds and free-ranging birds.	Mouritsen et al., 2003; Bonadonna et al., 2005; Alerstam 2006; Biro et al., 2006; Åkesson and Hedenström 2007; Dell'Ariccia et al., 2008; Guilford et al., 2011; Horton et al., 2014; Reynolds et al., 2015; Wikelski et al., 2015; Willemoes et al., 2015
Conservation	Identification of critical mortality hotspots along migration routes and their impact on population dynamics. Environmental impact assessment of major threats for endangered species and obtaining	Strandberg et al., 2009b; van Heezik et al., 2010; Grecian et al., 2012; Mellone et al., 2013;

	spatially explicit information of where mortality occurs (e.g., electrocution, wind-farms, illegal hunting, poisoning, light pollution). Impact of introduced species on native species. Evaluation of the performance of protected areas and delineation of new ones (e.g. Marine Important Bird Areas). Obtaining unbiased mortality estimations to feed capture-recapture demographic models.	Phipps et al., 2013; Klaassen et al., 2014; Braham et al., 2015; Oppel et al., 2015; Thaxter et al., 2015
Management actions	Evaluation of the effectiveness of different management actions for bird conservation and their impacts on movement behaviour (e.g., reintroduction programmes, removal of non-native species, supplementary feeding).	Margalida et al., 2013; Monsarrat et al., 2013; Gil et al., 2014; López-López et al., 2014c; Gooch et al., 2015; Petersen et al., 2015
Exploitation of natural resources	Analysis of the interactions between bird movements and exploitation of natural resources (e.g., fisheries, game species). Impact of fisheries bycatch on marine pelagic birds. Movement of species of economic interest and sustainable harvesting.	Brothers et al., 1998; Okes et al., 2009; Pichegru et al., 2009; Žydelis et al., 2011; Caudill et al., 2014; Ratcliffe et al., 2015; Weimerskirch et al., 2015

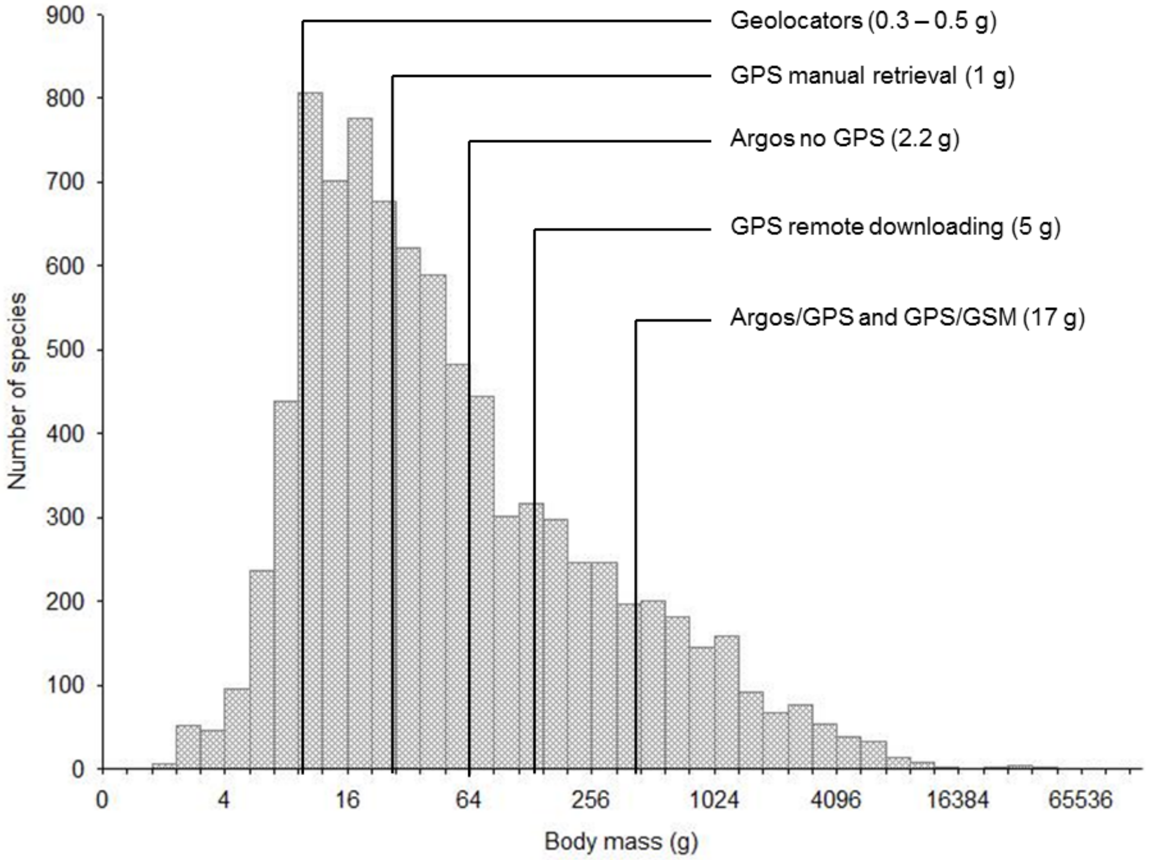

Fig. 1.- Histogram of bird body masses and possible tracking devices according to the 3%-body-weight rule. This figure has been adapted and updated from Bridge et al., (2011) and Kays et al., (2015). Note that body mass (g) in the X-axis is shown in $\log_2$ scale. Bird body masses of 8654 species were obtained from Dunning (2007).

[Histograma de los pesos corporales y posibles dispositivos de seguimiento que se pueden utilizar de acuerdo con la regla del 5% del peso corporal. La figura ha sido adaptada y actualizada a partir de Bridge et al., (2011) y Kays et al., (2015). Nótese que la masa corporal (g) en el eje X se muestra en escala $\log_2$*. El peso corporal de 8654 especies de aves fue obtenido de Dunning (2007).]*

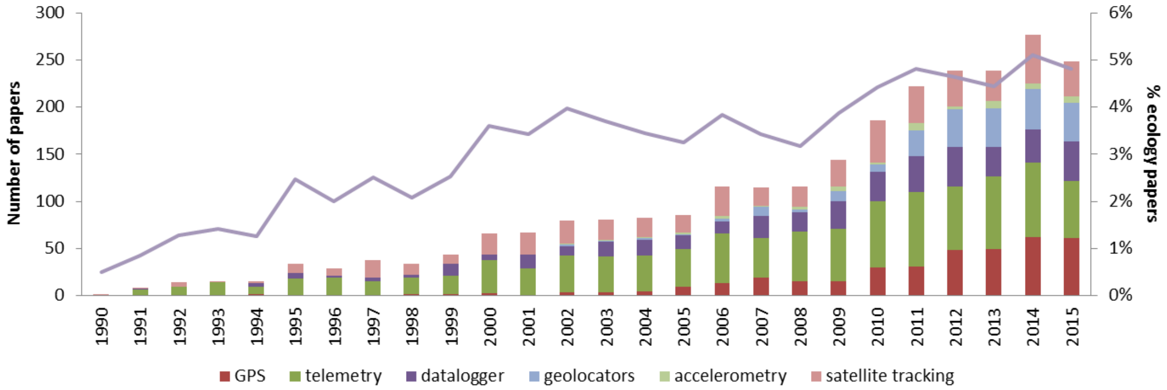

Fig. 2.- Number of papers published per year referring to individual tracking systems for birds. Information was obtained based on a literature survey by using the ISI Web of Science database. The purple line shows the number of published papers on individual tracking as a percentage of all papers published in the field of Ecology. Search terms are available in Appendix 2.

[Número de artículos publicados por año referentes a sistemas de seguimiento individual en aves. La información fue obtenida a partir de una búsqueda bibliográfica en la base de datos del ISI Web of Science. La línea morada muestra el porcentaje de artículos publicados sobre seguimiento individual con respecto al número total de artículos publicados en el campo de la Ecología. Los términos de búsqueda están disponibles en el Apéndice 2.]

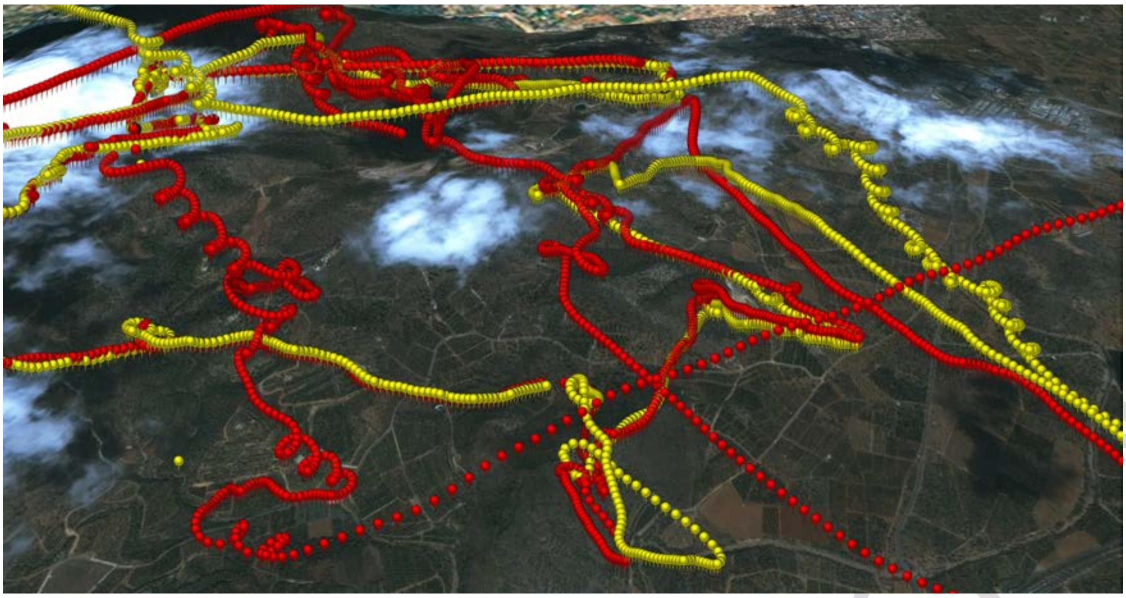

Fig.- 3. Example of two individual tracks of a pair of Bonelli's eagles (*Aquila fasciata*) recorded by high-resolution GPS/GSM telemetry in Spain (López-López & Urios, unpubl. data). Each point corresponds to a GPS location and shows how male (red) and female (yellow) soar together a two-hour time window. For this particular study, dataloggers were programmed to record one GPS location and tri-axial accelerometer measurements (sampling rate = 33.3 Hz for each axis) every five minutes according to a basic configuration throughout the year. Furthermore, dataloggers record a GPS location every second during certain time periods of 15 minutes in length called "super busts". As a result, high-resolution GPS telemetry is allowing in-depth analysis of the behavior of these birds in their territory.

[Ejemplo de dos "tracks" individuales de una pareja de águilas perdiceras (Aquila fasciata) *en España gracias a telemetría GPS/GSM de alta resolución (López-López & Urios, datos inéditos). Cada punto corresponde a una localización GPS y muestra cómo el macho (rojo) y la hembra (amarillo) ciclean juntos en una ventana temporal de dos horas. En concreto, para este estudio los dataloggers fueron programados para obtener una posición GPS y medidas del acelerómetro tri-axial (frecuencia de muestreo = 33 Hz en cada eje) cada cinco minutos de acuerdo con la programación básica para todo el año. Además, los dataloggers recogen una localización GPS cada segundo durante determinados períodos de tiempo de 15 minutos de duración denominados "super*

ráfagas”. De este modo, la telemetría GPS de alta resolución está permitiendo llevar a cabo un análisis en profundidad del comportamiento de estas aves en su territorio.]

APPENDIX 1

Marketing companies of individual tracking devices for birds. The smallest size of the tracking device commercially available is shown (prototypes not included). The number of locations, battery-expectancy and operating/data downloading distance may vary considerably among tracking devices, based in part on duty cycle configuration and attachment system on birds, hence devices of similar size may have different performance.

[Empresas comercializadoras de aparatos de seguimiento individual para aves. Se muestra el tamaño mínimo de los dispositivos comercialmente disponibles (no se incluyen prototipos). Aviso importante: el número de localizaciones, duración de la batería y la distancia a la que se pueden descargar los datos puede variar considerablemente entre dispositivos de seguimiento, configuración individual y sistema de colocación en las aves, por tanto dispositivos de tamaño similar pueden tener un rendimiento diferente.]

Company name	website	Argos (no GPS)	Argos/ GPS	GPS/GSM dataloggers	GPS-remote downloading dataloggers	geolocators
Microwave Telemetry Inc.	http://www.microwavetelemetry.com	2.2g	17g	25g	no	no
North Star Science and Technology, LLC	http://www.northstarst.com/	5g	22g	55g	no	no
e-obs digital telemetry	http://www.e-obs.de	no	no	48g	10g	no
Cellular Tracking Technologies	http://www.celltracktech.com/	no	no	23g	no	no
Telonics Inc.	http://www.telonics.com/	15g	no	137.5g	no	no
UvA-bits	http://www.uva-bits.nl/	no	no	18.5g	7.2g	no
Ecotone Telemetry	http://www.ecotone-telemetry.com/	no	no	17g	5g	no
TechnoSmArt	http://www.technosmart.eu/	no	no	no	17g (3.5g***)	no
Migrate Technology Ltd.	http://www.migratetech.co.uk/	no	no	no	no	0.3g
Biotrack*	http://www.biotrack.co.uk/	100g	3.5g**	no	no	0.39g

PathTrack Ltd.	http://www.pathtrack.co.uk/	no	no	no	5g (1g****)	no
Blueoceanix Technology Co., LTD	http://blueoceanix.en.ec21.com/	no	no	45g	no	no

* commercial partners of Sirtrack Ltd. (http://sirtrack.co.nz/) and Lotek Wireless (http://www.lotek.com/)

** up to 30 locations (PinPoint technology)

*** 3.5 g device is an archival location logger that must be retrieved at the end of its deployment. Expected battery duration is up to 3-5 days.

**** The 1 g device is an archival location logger that must be retrieved at the end of its deployment. It provides 80 locations on average during lifetime.

APPENDIX 2

Search terms used for the literature survey in ISI Web of Science. Search conducted in SCI-EXPANDED database and time period 1950 – 2015 in all cases. Search date: December 2015. *[Términos de búsqueda utilizados para la búsqueda bibliográfica en el ISI Web of Science. Búsqueda realizada en la base de datos SCI-EXPANDED para el período temporal 1950 – 2015 en todos los casos. Fecha de búsqueda: diciembre de 2015.]*

Search #	**Search term**	**Results**
1	Search term: (ecology) Refined by: (ECOLOGY OR MARINE FRESHWATER BIOLOGY OR ZOOLOGY OR ENVIRONMENTAL SCIENCES OR EVOLUTIONARY BIOLOGY OR BIODIVERSITY CONSERVATION OR MULTIDISCIPLINARY SCIENCES)	74664
2	Search term: (satellite track*) AND (bird*) Refined by: (ORNITHOLOGY OR ECOLOGY OR MARINE FRESHWATER BIOLOGY OR ZOOLOGY OR OCEANOGRAPHY OR BIODIVERSITY CONSERVATION OR ENVIRONMENTAL SCIENCES OR MULTIDISCIPLINARY SCIENCES OR COMPUTER SCIENCE THEORY METHODS OR BIOLOGY OR BEHAVIORAL SCIENCES OR EVOLUTIONARY BIOLOGY)	543
3	Search term: (accelerom*) AND (bird*) Refined by: Categorías de Web of Science: (BIOLOGY OR MARINE FRESHWATER BIOLOGY OR MULTIDISCIPLINARY SCIENCES OR ECOLOGY OR ZOOLOGY OR EVOLUTIONARY BIOLOGY OR PHYSIOLOGY OR ORNITHOLOGY)	51
4	Search term: (GPS AND bird*)	380
5	Search term: (geoloc*) AND (bird*)	231
6	Search term: (telemetry) AND (bird*)	989
7	Search term: (logger) AND (bird*)	413