Ardeola 63(1), 2016, 103-136 DOI: 10.13157/arla.63.1.2016.rp5

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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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. Hence we can claim that ornithology has entered 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 future. To this end, I first provide a brief overview of individual tracking systems for birds. I then discuss current challenges for tracking birds with remote telemetry, including technological challenges (i.e., tag miniaturisation, 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 be answered 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 extraordi-

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narios 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 cells through microscopes, the use of x-ray diffraction to discover 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 (Benson, in press). As happened some decades ago with genomics, proteomics, metabolomics and other "–omics", ecology has entered the so called era of "big data" (Hampton *et al.*, 2013). The study of animal movement, an important aspect of ecology, is no exception.

Animal movement, and particularly bird movement, has long caught the attention of naturalists and scientists since the time of Aristotle. As a consequence, there is a vast amount of information gathered across different taxa and geographic regions that has been the subject of analysis of many scientific disciplines. In order to provide a conceptual framework to integrate all this information, some scientists 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, to recent graduates in the fields of biology or environmental sciences and especially to young scientists wishing to start their careers in the emerging field of movement ecology. It reflects my personal point of view of the 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. I then discuss current challenges for tracking birds with remote telemetry, including technological and scientific challenges. I also highlight future prospects for this research field including a set of scientific questions that have been answered by means of remote telemetry data or are expected to be answered in the future. Finally, I discuss some ethical aspects of animal tracking with particular focus on bird trapping, attachment methods, tag mass to body mass ratios and the 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), involves methodological techniques aimed at following and determining where an animal is located spatially on Earth. Individual tracking has a long tradition in ornithology, principally in the form of 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; Hays *et al*., in press), to give a few examples. A comprehensive description of major achievements in animal ecology attributable to bird ringing is, however, beyond the scope of this paper. I would kindly ask the reader to excuse me for this omission.

For present purposes, hereafter I refer to the study of individual tracking using remote telemetry methods (Box 1). 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).

Box 1. Glossary

Accelerometer: an 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 information available 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; Benson, in press). 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

Box 1. Glossary (cont.)

triangulation and the main disadvantage is that the receiver must be close to the transmitter (usually within a few kilometres). 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 that 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 day length 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 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 (VO2) 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 purposes of this paper, I refer only to remote telemetry to track animal movement.

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 most bird species (fig. 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 researcher needing to locate the signal (Börger, 2016). Hence, questions that so far had remained unsolved, such as where long-distance migrants spent their winters, and concerning 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 revolutionised 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 times 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, their main disadvantages are that geolocators must be retrieved to download data, and so are only useful for easily recaptured species exhibiting high site-fidelity, and that their 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 first available in the late 1990s and have become more popular in recent years mainly due to their capability to incorporate new sensors along with GPS location, these including accelerometers and 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' requests, has made near-real-time monitoring of animals possible. Currently available commercial dataloggers allow the collection of up to several thousand locations per day due to their high frequency of data acquisition (1 Hz = 1 location/second) and larger 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 a "golden age" during which the current generation of scientists will witness unprecedented exciting discoveries (Wilcove and Wikelski, 2008; Kays *et al*., 2015).

BIRD TRACKING IN THE CONTEXT OF SCIENTIFIC PUBLISHING

Bird movements have long held great interest for ornithologists. Consequently, the number of published papers using individual-based tracking technologies for birds has increased considerably in recent years (Holyoak *et al*., 2008). For example, according to a

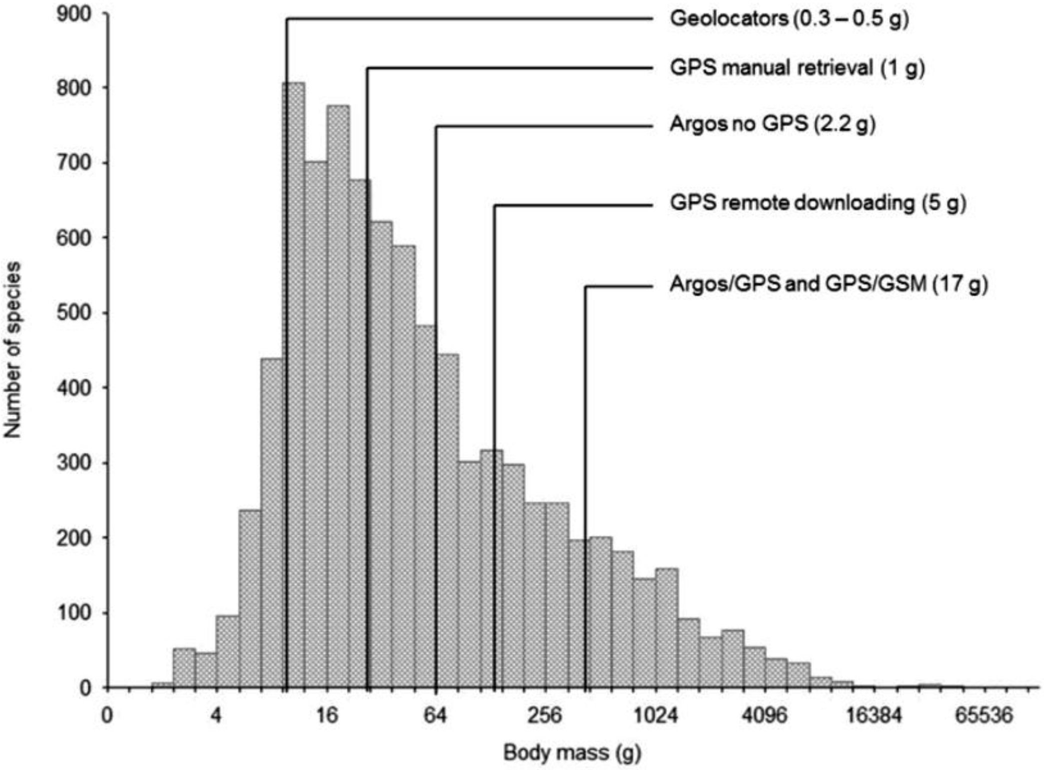

FIG. 1.—Histogram of bird body masses and possible tracking devices according to the 3%-body-weight rule. This figure has been adapted and updated from Bridge *et al.* (2011) and Kays *et al.* (2015). Note that body mass (g) on the X-axis is shown in $\log_2$ scale. Bird body masses of 8,654 species 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 3% 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 8.654 especies de aves fue obtenido de Dunning (2007).]*

literature survey for the period 1950-2015, the first papers about satellite tracking, data-loggers, 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 (fig. 2). In parallel, scientific publishing has experienced an exponential increase in the last decades (Bornmann and Mutz, 2015). However, whereas ecology papers have increased on average by 7.0% per year, those involving individual-based tracking technologies for birds have increased on average by 17.6% per year (i.e., by 2.52 times over the same period) (fig. 2). This clearly shows that modern individual-based tracking technologies have made significant contributions to many important topics in ornithology, or are expected to do so in the future (table 1), building on knowledge gained by other methods, such as ringing and conventional radio-tracking.

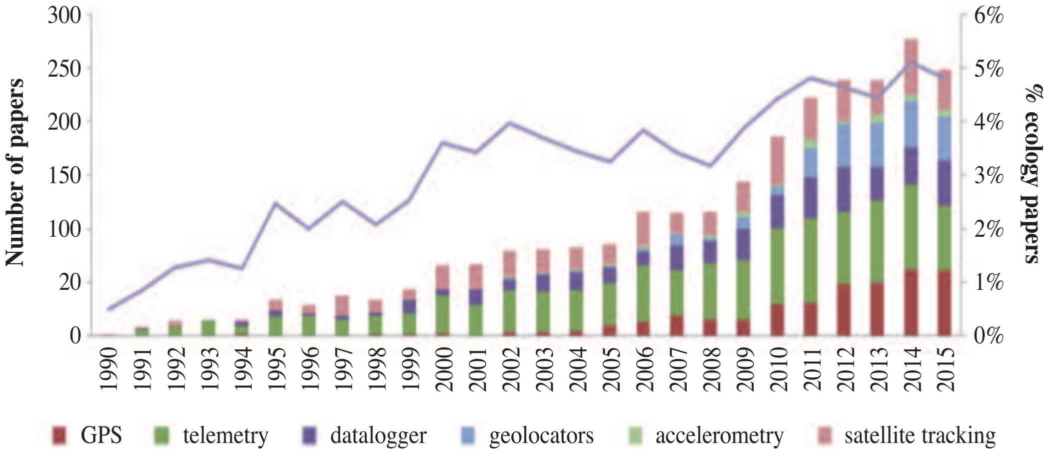

FIG. 2.—Number of papers published per year referring to individual tracking systems for birds. Information is based on a literature survey by using the ISI Web of Science database. The purple line shows the number of published papers on individual tracking as a percentage of all papers published in the field of ecology. Search terms are available in Supplementary Electronic Material: Table S2.
[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 Material Suplementario Electrónico: Tabla S2.]

CURRENT CHALLENGES OF BIRD TRACKING

Technological challenges

Since Gordon E. Moore, co-founder of Intel Corporation, stated his famous law in 1965 based on the observation that the number of transistors in a dense integrated circuit doubles approximately every two years (i.e., Moore's law) (Moore, 1965), electronic devices have undergone a dramatic miniaturisation process during the last five decades. Like mobile phones and computers, animal tracking technologies have downsized by 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 (fig. 1; Supplementary Electronic Material: table S1). Obviously, there is a trade-off between the operational life of tracking devices, maximum number locations recorded per day, temporal and spatial resolution, battery size and weight. Thus, 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 one location per second (fig. 3), also including additional information from

TABLE 1

Main topics to 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 only includes 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 temas 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 characterisation 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 non-breeding areas. Measurement of the strength of migratory connectivity (i.e., strong, weak/diffuse). Effects of migratory connectivity on individual breeding success and population dynamics. Behavioural 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 (e.g., migration, wintering, breeding) throughout the annual cycle. 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.

TABLE 1 (cont.)

Topic	Questions and future challenges	References
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 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.	Alerstam *et al*., 2006; Quillfeldt *et al*., 2010; Vardanis *et al*., 2011; 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 at stopovers (e.g., foraging and refuelling 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, atmospheric pressure and other meteorological conditions on migratory performance.	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; Bridge *et al*., in press; Vidal-Mateo *et al*., in press.

TABLE 1 (cont.)

Topic	Questions and future challenges	References
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, in press; 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.

TABLE 1 (cont.)

Topic	Questions and future challenges	References
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-connection 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 transmission. Surveillance of the population ecology of zoonotic hosts, pathogens or vectors.	Prosser *et al*., 2009, 2011; Newman *et al*., 2009, 2012; Adelman *et al*., 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, polarised 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 spatially explicit information of where	Strandberg *et al*., 2009b; van Heezik *et al*., 2010; Grecian *et al*., 2012; Mellone *et al*., 2013; Phipps *et al*., 2013;

TABLE 1 (cont.)

Topic	Questions and future challenges	References
Conservation (*cont.*)	mortality occurs (e.g., electrocution, wind-farms, illegal hunting, poisoning, light pollution). Impact of invasive 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.	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.

other activity sensors, and are able to send data packages through the GSM network (e.g., Lanzone *et al*., 2012) or by 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 transmitter size together with increasing the number of incorporated bio-logging sensors (Cooke *et al*., 2004; Rutz and Hays, 2009). Cutting-edge tracking devices, unlike traditional tracking methods such as metal rings or conventional radio-tracking, are very expensive: from several hundred to several thousand euros. There is thus an enormous commercial market behind tracking technologies, leading companies to strive vigorously to develop ever-smaller transmitters with higher capacities at competitive prices (see some examples in table S1). Future transmitters will have higher internal storage capacities and longer battery lifetimes (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 en-

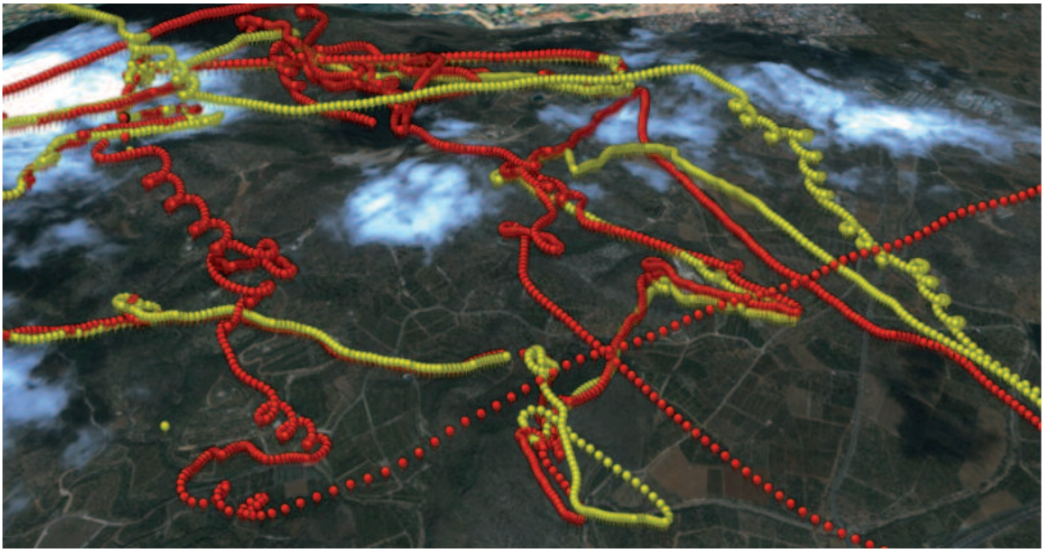

FIG. 3.—Example of two individual tracks of a pair of Bonelli's eagles *Aquila fasciata* recorded by high-resolution GPS/GSM telemetry in Spain (López-López and Urios, unpubl. data). Each point corresponds to a GPS location and shows how male (red) and female (yellow) soar together a two-hour time window. 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 behaviour of these birds within 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 and 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.]*

terprises, 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 (ISS), are under development (Wikelski *et al*., 2007). This initiative aims to revolutionise current tracking systems, mimicking conventional radio-tracking by pointing antennas towards Earth from near-Earth orbit in the ISS. This will permit radio transmitters attached to small animals, from birds to insects, to be located anywhere 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 succeeds, this could facilitate a quantum leap in our knowledge of animal movement.

Data archiving and data processing

As a result of the 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 at a relatively low frequency (e.g., usually every week or every ten days from the Argos system) and could easily be 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 that are freely available on the Internet allow long-term data archiving in an off-site 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 emphasise 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 (see, for example, seaturtle.org and seabirdtracking.org). This facilitates participation in collaborative work to help scientists to address wider scientific questions, and also attracts public interest. 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 at 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 sizes and the high dimensionality of big data (Fan *et al.*, 2014). To overcome this problem needs the development of new sophisticated data-management tools to analyse movement data (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 biology programmes, as well as to create multidisciplinary teams in which ornithologists take part in 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 visualise 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. 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 into the analysis of bird movements.

Spatial and temporal autocorrelation

Animals move great distances over long periods following highly variable individual routes (e.g., López-López *et al*., 2014a). For example, bird movements may vary from the ballistic trajectories recorded during migration (i.e., following a nearly constant direction at high speed), 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: i.e., their location at time t + 1 is dependent on their location at time t (Otis and White, 1999), which is moreover stochastic and often subject to severe observational error (Patterson *et al*., 2008). Dealing with both uncertainty and spatiotemporal autocorrelation 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 it necessary to use one or other set of analytical tools (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 by high-resolution GPS telemetry, making formerly very useful analytical tools somewhat obsolete. For example, current dataloggers (at least those available for larger birds, see fig. 1 and table S1) record GPS locations with 1 Hz frequency and so it 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 a bird's path, to the analysis of its true trajectory (Benson, in press). 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, such as cognitive processes and memory effects, that cause this spatiotemporal autocorrelation (Boyce *et al*., 2010).

Environmental data annotation

No-one would study fish or cetacean movements without taking into account the movement of ocean currents. Correspondingly, analysing bird movement data without considering environmental conditions would also be meaningless. For their locomotion birds must push against a fluid, either air (most species) or water (e.g., penguins, 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, i.e., the "environmental data annotation process", is thus necessary to understand bird behaviour (Mandel *et al*., 2011). However, this represents an analytical challenge due to the different spatio-temporal 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., with respect to wind currents, temperature, thermal uplift, air pressure, and other measures recorded by remote sensing technologies). Nevertheless, 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 essential. Hence, 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 substantial input from the researcher and are thus subject to a 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 remains a challenge (Hays *et al*., in press).

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, such as "ks" (Duong, 2015) and "mkde" (Tracey *et al*., 2014) R-packages, have been developed to generate novel movement-based kernel density estimators, there are very few examples of movement analysis that consider 3D in the analysis of space use and quantification of utilisation distributions (Keating and Cherry, 2009; Cooper *et al*., 2014; Cleasby *et al*., 2015). Modelling bird movements in three dimensions (or even in four dimensions, thus also considering time) is hence a promising field of research, especially for the analysis of animal interactions both in space and time. In addition, we need better computer visualisation 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

The complex behaviour exhibited by birds is the outcome of the sum of animal-environment interactions and animal-animal interactions, both at intraspecific and interspecific levels. There is vast body of ecological literature on the study of the relationship between animals and their environment (e.g., on habitat selection, resource use, environmental niche analysis, etc.). However, the role of intra- and interspecific interactions and how they affect bird movements and ultimately determine their use of space remains poorly understood. Traditionally, most studies of 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 such interesting topics such as the 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 promising fields of research (Potts *et al.*, 2015).

Ethical aspects

Studies using individual-based tracking systems are based on an underlying basic assumption that bird behaviours are not altered (or are insignificantly altered) by the effect of transmitters. However, this basic assumption has rarely been tested and is arbitrary to a degree (Caccamise and Hedin, 1985; Barron *et al.*, 2010; Constantini and Møller, 2013). There is a sizable literature on the effects of transmitters on birds, yet the results are inconclusive (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 the sample sizes in most studies reporting deleterious effects are 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 effects on bird behaviour (e.g., Vandenabeele *et al.*, 2013; Blackburn *et al.*, 2016).

There is a 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) (fig. 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 great 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., the tracking project should not be permitted if the effects of the combination of a transmitter and method of attachment are unknown or are suspected of harmful effects in related or morphologically similar species. 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 the aerodynamics of different groups of species and the resulting possible drag effect (e.g., Pennycuick *et al.*, 2012). Trial studies with common non-endangered species could be a good chance to check the 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 requires 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, a scientist should clearly justify why tracking a given species is needed and should state the main goals of the project and how these goals are only achievable by using individual-based tracking technologies. Currently, the cost of transmitters is decreasing rapidly, making them more accessible to everyone. Consequently, some public administrations, NGOs, land managers, and amateur groups have found tracking birds an entertaining hobby that feeds numerous public profiles in social media (e.g., Facebook, project websites, etc.) without any intention of addressing clear questions supported by sound scientific projects. In my opinion, the simple curiosity to know where animals move does not itself justify trapping and tracking birds. 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 bird movements since the time of Aristotle. Fast-developing technologies are allowing cutting-edge studies that reveal an unprecedented level of detail about animal movements. 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 does not itself constitute a separate scientific discipline, no-one doubts the importance of movement and its essential role in ecology and behaviour (Benson, in press). Individual tracking technologies are usually criticised for their elevated cost, which results in small sample sizes and thus a limited capacity for ecological inference (Hebblewhite and Haydon, 2010). Nevertheless, a promising future for the study of animal movement is assured by the continual improvements in current tracking technologies and the increasing number of companies commercializing remote-tracking devices. Current challenges include 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 how to put the information derived from telemetry into the general framework of the theoretical body of ecological knowledge.

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 disturbance (tolerable in most cases) and, accordingly, a great responsibility. Prior to starting a tracking project, researchers should carefully consider the main goals of the study, the convenience of tracking the species in question and whether remote tracking is the best methodology to 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 a golden era in the study of animal movement and we should not miss this opportunity.

ACKNOWLEDGEMENTS.—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, E. García 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.

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SUPPLEMENTARY ELECTRONIC MATERIAL

Additional supporting information may be found in the on-line version of this article. See volume 63(1) on www.ardeola.org

Table S1: Marketing companies of individual tracking devices for birds.

Table S2: Search terms used for the literature survey in ISI Web of Science.

Editor: Emilio Barba