1. A BRIEF HISTORY OF THE STUDY OF BIRDS' MOVEMENTS

The rich variety of movement modes seen among microorganisms, plants, and animals has fascinated mankind since time immemorial (Nathan 2008). Particularly, the mysterious disappearance of some bird species called the attention of numerous naturalists from ancient times, but especially since the 20th century. First records of bird migration were made 3,000 years ago by Hesiod, Homer, Herodotus and Aristotle (Lincoln 1979) and even in the Bible it is possible to find references to these concerns. In the biblical texts there are several references to the periodic movements of birds, as in the Book of Job, where the inquiry is made: "Doth the hawk fly by Thy wisdom and stretch her wings toward the south?" (Lincoln 1979). The prophet Jeremiah (7th century B.C.), for instance, described the temporal consistency in migratory patterns of birds (Nathan 2008) and in the ancient biblical texts is written: "The stork in the heavens know her appointed time; and the turtledove, and the crane, and the swallow, observe the time of their coming" (Lincoln 1979). Anecdotally, the flight of quail that saved the Israelites from starvation in their wanderings through the Sinai wilderness is now recognized as a vast migration between their breeding grounds in Eastern Europe and western Asia and their winter home in Africa.

Among observers whose writings are extant, Aristotle (4th century B.C.) was one of the first to discuss the subject of bird migration: he observed the sudden appearance of swallows in spring and concluded that these birds should remain all winter buried in the mud to reappear with the good weather. Although his explanation of the swallows is well known, Aristotle ascribed hibernation not only to swallows, but also to storks, kites, doves and other birds (Lincoln 1979). He believed the disappearance of many species of birds in the fall was due to their passing into a torpid state where they remained during the cold season, hidden in hollow trees, caves, or in the mud of marshes. But on the other hand, Aristotle himself noted cranes traveling from the steppes of Scythia to the marshes at the sources of the Nile, and pelicans, geese, swans, rails, doves, and many other birds passing to warmer regions to spend the winter.

In the earliest years of the Christian era, the Roman naturalist Pliny the Elder, repeated in his *Historia Naturalis* most of what Aristotle said on migration and added comments of his own concerning the movements of starlings, thrushes and European blackbirds. It was not until early in the nineteenth century that migration was accepted as an explanation for the winter disappearance of birds from northern latitudes (Lincoln 1979). In1804, the American Naturalist John James Audubon tied a string around the legs of many birds nesting in his neighbourhood. He wondered whether migrating birds returned to the same place each year. In the following spring, Audubon was ecstatic to see that his banded bird had returned to its original nesting site. This was a huge finding in the early nineteenth century, when very little was guessed about bird migration and, even today, there is "The National Audubon Society" (a U.S. conservation organization and one of the world's oldest). A few decades after Audubon´s observation, in 1878, Elliott Coues listed the titles of no less than 182 papers dealing with the hibernation of swallows.

For many years, some of the largest and most interesting routes and patterns were unveiled with the oldest, simplest and most frequently used method of studying migration in the past: by direct observation. Size, colour, song, and flight of different species aided the amateur as well as the professional in determining when birds are migrating: data was sorted tediously after compiling and comparing literally thousands of observations on whether a species was or was not seen in a given locality at a particular time of year. Direct observation has contributed much to our knowledge of migration (Lincoln 1979), but the notable limitations and some of the biases in visual tracking techniques soon would lead to the development of more effective methods for the study of the movements of wildlife.

The first method used to try to quantify birds' movements was ringing (figure 1). Although similar methods had been employed in the past (for example, falconers in the Middle Ages would fit plates on their falcons with seals of their owners), the use of metal rings with codes deployed on birds' legs was first used (with some scientific purpose) by H.C.H. Mortensen in 1889, who tagged several starlings (*Sturnus vulgaris*) with numbered rings in Denmark to see if those birds returned to the area in subsequent years. However, this method provides limited information on birds' movements, as only tagging and capturing sites and dates are known, but tracks or movements in limited areas could not be known. The increasing need for both ecologists and managers to know several aspects of birds' ecology in order

Figure 1. Since its inception in 1889, bird ringing quickly evolved into a standard research technique used in all parts of the world. Although increasingly sophisticated method helps to understand the movements of wild animals, ringing has not fallen into disuse due to its low price, to its technical simplicity and its applicability in certain studies. Furthermore, it is the only technique that allows the identification of each bird (as each metal ring carries a unique code), and some data such as largest known longevity (recorded in a shearwater that was recovered 50 years after her ringing) may only be obtained with this kind of labels. In the picture above we see a Bluethroat (*Luscinia svecica*) being ringed.

to propose proper conservation schemes and actions promoted a particular interest to develop some methods to unravel some of these issues. Thus, the next step were marks that could be read at longer distances. Amongst these, the most used and known are plastic coloured rings. Simple one-colour rings could be used to identify cohorts, areas, years, etc., but no individual sights could be achieved. Hence, adding a code (letters, numbers or a combination of the two) makes it possible to identify the ringed birds individually. Again, these tags provide only restricted and limited observational data and the use of a spotting scope is needed to obtain some readings. Wing-tags are other plastic tags that could be observed at longer distances and when the bird is flying; thus, they are expected to provide more data that plastic rings on legs, despite the shortcomings being essentially the same. In any case, ringing has been the most used method to track birds for a long time and it has provided very insightful and interesting data on their movements (Fiedler 2009).

Over the years, a more sophisticated approach to study birds' movements was born with the use of remote sensing, based on the use of transmitters. The most used technology until a few decades ago was terrestrial radiotelemetry, based on a VHF radio transmitter, whose pulsed emissions could be recorded with a special receiving device that could be distant up to a few kilometres from the transmitter (e.g. Kenward 2001). From the advent of remote control of wildlife with VHF transmitters until today, modern movement research has obtained a broad range of specialized scientific approaches, each developed to explore a different type of movement by a specific group of organisms (Nathan 2008):geolocators, GPS transmitters, data loggers, PPT devices, AVEDs or UASs, WildLink Radio transmitters, temperature sensors VHF or PIM devices, among many others, all of them with Lithium and silver batteries or Solar Cell distributed as a collar, harness or with the possibility of being implanted. A huge list of possibilities with one pitfall: there is a trade-off between the weight of the transmitters and both the battery duration and the maximum distance at which signals can be received, with both these features increasing with the size (i.e., weight) of the transmitter device.

In general, it is considered appropriate that the supplementary load that can be deployed on a bird should not exceed 3-5% of its weight (Caccamise & Hedin 1985). Currently, the smallest radiotracking tags are light enough to be deployed on a honey bee (Roach 2008) and thus, basically all birds can be tracked using this technology. But usually, small birds are tagged with radio tags lasting only a few days or even hours because longer lasting batteries would represent an increase in the weight of the VHF that is unaffordable for smaller birds. In any case, in larger birds a heavier radio tag can be used and therefore, larger birds can be tracked for long and from longer distances than small birds. Besides, radiotracking technology has the shortcoming that tagged birds are only "found" when they are close to the researchers tracking them, but no information can be recorded if the animal moves several kilometres from the study area that is being monitored. Therefore, it precludes obtaining accurate data on bird migration as birds may move hundreds of kilometres in only a few hours (except in a few cases; Bowlin *et al.* 2005).

For these reasons, more recently, and in order to track the migration and wintering grounds of small birds, researchers are increasingly using devices operating through satellites, so that it is no longer necessary to follow the animal in the wild. However, these labels require larger batteries to send the data to the satellite and its miniaturization is more expensive than other technologies. Other recent devices, such as geolocators (or light-locators), have the advantage of recording light intensity as well as sunrise and sunset time; one photoreceptor coupled to a clock serves to calculate latitude from the duration of daylight and longitude from sunrise and sunset time (see e.g. Fiedler 2009). This technology could be quite light (currently the smaller ones are ca. 1-gram) and thus, it makes it possible to track movements of small birds like passerines (e.g. Stutchbury *et al.* 2009). However, they also have important disadvantages; for example, tagged birds need to be recaptured to connect the geolocators to the computer in order to download the data (and sometimes on-clock failures prevent obtaining data; e.g. Rodríguez *et al.* 2009) and large errors in locations usually appear (mean errors of 185-200 km; Phillips *et al.* 2004; Shaffer *et al.* 2005), especially during the equinoxes, which prevents the obtention of data on the latitude of tagged birds.

In brief, the development of new technologies for monitoring wildlife has evolved in the midst of in a constant conflict between four key determinants: easier data reception mode, increasing data quality and reduction of size and prices. The use of telemetry to study movements in the wild, from the smallest organisms (such as the study of the movement of the virus associated with birds, see FAO 2007) until studies of larger wild animals as the Whale Sharks (Eckert & Stewar 2001) has become a fundamental tool that now not only allows us to analyse the movement of wildlife but it also provides information on some environmental parameters,linking them to spatio-temporal movements. There is a growing recognition of the need to understand and predict the movement of individual organisms, as one of the most fundamental features of life on Earth and a crucial component of almost any ecological and evolutionary process, including major problems associated with habitat fragmentation, climate change, biological invasions, and the spread of pests and diseases.