PERSPECTIVE MATTERS:
INDIVIDUAL AND SPECIES
MOVEMENT IN SPATIAL CONTEXT

Sam Khosravifard

PERSPECTIVE MATTERS:
INDIVIDUAL AND SPECIES MOVEMENT IN SPATIAL CONTEXT

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Chapter 1

General Introduction

1.1 Introduction

Movement of an organism is a fundamental characteristic of life, defined as a change across many spatial and temporal scales (Baker, 1978; Berg, 1993; Nathan *et al.*, 2008). It is a ubiquitous ecological process influencing most facets of individuals' life: the structure and dynamics of populations, communities, and ecosystems (Holloway and Miller, 2017). The organismal movement and environmental changes have been illuminated by research on anthropogenic habitat fragmentation, changes in land-use patterns and climate, and the introduction of alien (Nathan *et al.*, 2008). A more coherent comprehension of reasons, mechanisms, patterns, and outcomes of organismal movement may assist in restoration of degraded habitats and controlling the spread of pests, invasive alien species and infectious diseases (Wiens *et al.*, 1993; Debinski, Ray and Saveraid, 2001; Holyoak *et al.*, 2008).

Recent advances in movement research have inspired a shift from the Eulerian approach to the Lagrangian approach. The Eulerian approach quantifies population redistribution while the Lagrangian approach quantifies the movement of individuals (Turchin, 1998; Yamada *et al.*, 2003; Smouse *et al.*, 2010). It is essential to differentiate between Eulerian (population), and Lagrangian (individual) approaches, as species distribution models (SDMs) incorporating movement are getting more complex (Holloway and Miller, 2017). In spite of substantial impacts of the geographical distribution of species on movement processes and ecological significance, the incorporation of movement has lagged behind other methodological advancements, particularly in species distribution modelling (Franklin, 2010a; Miller and Holloway, 2015). In the context of SDMs, the accessibility of habitats by species or populations has been considered rather than underlying the process of individuals' movement (Guisan and Thuiller, 2005; Elith *et al.*, 2006; Datry, Bonada and Heino, 2016). Movements of individuals incorporate the most detail concerning movement patterns and environmental interactions, but the focus of SDMs is usually on emergent population or species-level patterns (Tang and Bennett, 2010).

SDMs are still focusing solely on environment-species relationships to predict the occurrence of species and provide a robust spatial ecological framework for studying the geographic distribution of a wide range of organisms. These models are frequently used to address questions on ecological processes involving climate change, invasion risk and biogeographic hypotheses (Peterson *et al.*, 2011). In addition, the range shifts, responding to changing climate or tracking the spread of invasive species, have been addressed by SDM researchers with terms such as 'dispersal limitations', 'dispersal capacities', 'migration rates', and 'spread rates'. These are used interchangeably to refer to the cumulative movement of a species or a population across a broad temporal scale and often across multiple generations (Alagador, Cerdeira and Araújo, 2014; Holloway, Miller and Gillings, 2016). When dispersal has been considered in SDMs, it has usually referred to one of the two simple approaches: unlimited dispersal or no dispersal (Araújo, Thuiller and Pearson, 2006). Ultimate dispersal assumes that movement has no barriers, and distance is not a limiting factor. Thus, any suitable habitat which is present in the study area can become occupied by species. Inversely, no dispersal assumes that suitable habitat is restricted to locations that overlap with the original distribution (Holloway, Miller and Gillings, 2016).

1.2 Movement of individuals

The movement ecology is a prominent paradigm for studying the how and why of movements, along with its repercussions for individuals, communities and ecosystems (Nathan et at., 2008). Ever since the paradigm was presented, the definitions of movement behaviour have been intensely debated throughout the ecological studies (Dingle and Drake, 2007); the terms such as 'dispersal' or 'migration' have created highly controversial discussions across both the scientific and public realms (Milner-Gulland, Fryxell and Sinclair, 2011). Notwithstanding the ongoing debates in ecological studies, there is an increasing interest in grasping and modelling species movement (Nathan *et al.*, 2008), as it is critical in the understanding of other phenomena such as climate change, anthropogenic activities or spread of invasive alien species (Bowler and Benton, 2005).

The term dispersal is frequently used instead of movement in the context of SDMs. The reason mainly is that the accessibility of habitat by species or population has been considered instead of determining process of the movement itself (Bruneel *et al.*, 2018). The movement of individuals consists of the fine-scale displacements and environmental interactions, but the emergent population or species-level patterns are the major focus of SDMs. For SDMs, if include movement, broad-scale movement, like migration or dispersal, has mainly conceptualised (Franklin, 2010b; Bateman *et al.*, 2013; Miller and Holloway, 2015). Despite the differences, dispersal and migration have been frequently and interchangeably used to refer to the same movement behaviour, specifically in response to climate change (Holloway and Miller, 2017).

Detailed movement data, retrieved from telemetry techniques, have enabled researchers to track an individual through time and space. Animal tracking technologies have provided the opportunity to depict free-ranging animals' occurrence at an ever-increasing accuracy (Tomkiewicz *et al.*, 2010). The techniques for studying animal movement have been advanced and flourished since earliest attempts (Roy and Hart, 1963) by using radar (Konrad, Hicks and Dobson, 1968), radio (Schemnitz and Owen, 1969), satellite and global positioning system (GPS) tracking (Nowak, Berthold and Querner, 1990; Biro *et al.*, 2002; Weimerskirch *et al.*, 2002). The relatively recent evolution in biological data acquisition techniques, such as extensive use of the biologgers with GPS, have led to enhanced spatial and temporal resolutions and a better understanding of individuals' movement (Tomkiewicz *et al.*, 2010). Telemetry data are potentially able to reveal unique intuitions in how individuals utilise their overall environment.

Levin (1992) noted that patterns at one level of an organisation could be often understood as the collective behaviour of aggregates of smaller units.

It can be a matter of interest for researchers to record different levels of organisation in the meta-analysis as the focus of SDMs is targeted on population or species-level pattern (Holloway and Miller, 2017). Even so, questions related to dispersal and colonisation pertain to population-level processes, and many of the factors responsible for animal movement operate on an individual scale (Jønsson *et al.*, 2016).

Before incorporating individual movement data to distribution models, it entails to present a general description of SDMs.

1.3 Species distribution models

The distribution of species and communities in space and time has been vigorously studied in ecological research, and so far comprehensive reviews on this topic have been published (Guisan and Thuiller, 2005; Elith and Leathwick, 2009). SDMs have recently thrived in literature and practice (Franklin, 2010b; Bruneel *et al.*, 2018).

Habitat suitability, as an outcome of SDM, is derived from environment-species relationships (Franklin, 2010a). The modelling process can be complex, because of several reasons such as the size of datasets, geographical extent, data quality, sample design, assembly and derivation of mapped environmental predictors, modelling methods, model parameterisation and selection, assessment of model performance, and evaluation of spatial predictions (Wintle, Elith and Potts, 2005; Elith and Leathwick, 2009b; Franklin, 2010a). SDMs have been recently used to make two types of predictions; a) where the species may occur, but there is no record of it or where they might exist if human activities had not wiped them out (Anderson *et al.*, 2009), and b) where species may be found in the future while environment changes (Parmesan and Yohe, 2003). In recent years, researchers in the field of biogeography urged that SDMs need to be dynamic and movement, as one of the dynamic factors, is required to be considered into the modelling to depict vivid and accurate habitat suitability (Guisan and

Thuiller, 2005; Araujo and Guisan, 2006; Holloway and Miller, 2017; Bruneel *et al*., 2018). In the past, the effects of movement were neglected, because there was no inducement to incorporate geographical influences to SDMs and only environmental space was considered to predict geographical distributions of species (Bruneel *et al*., 2018).

1.4 From individuals to species

Availability of three conditions is imperative for presence of a species. These conditions addressed in the BAM framework (Figure 1.1) developed by Soberón and Peterson (2005). Abiotic (A) and biotic (B) conditions in an area must be suitable for a species, as well as accessibility to the area where the species exist, without barriers to movement and colonization (M). The suitable abiotic conditions such as aspects of climate, physical environment, edaphic attributes, etc. coerce physiological limits on species' ability to remain in an area. The biotic factors represent the interactions with other species (e.g. competition or predation). The regions are accessible to move by the species from some original area within a proper timeframe (e.g. via dispersal or migration) (Niamir, 2014). For further information, please see Soberón & Peterson (2005) and Soberón & Nakamura (2009).

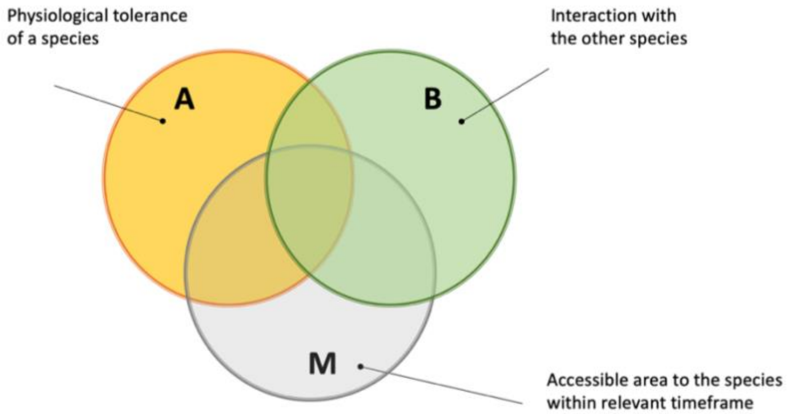

Figure 1. 1 BAM diagram (adopted from Soberón & Peterson 2005).

It is a fundamental question in ecological research that how and why organisms change their spatial position within a certain time (Nathan, 2008). In SDMs, these two attributes are major components, to wit: time and space (Oindo, Skidmore and De Salvo, 2003). But, when movement is considered, it is usually referred to a broad time scale, often across multiple generations (Holloway *et al.*, 2017).

The scale is inherently linked to time and space (Song *et al.*, 2013). The spatial scale can be divided into two types: the grain size or resolution which represents a unit of analysis, and the extent which is the scope of analysis (Seo *et al.*, 2008). The selection of both temporal and spatial scales is motivated by data availability rather than environmental and biological processes and their associated range of influence (Yackulic and Ginsberg, 2016). The importance of scale becomes apparent when the movement of individuals and biotic interactions are considered. This is illustrated in Figure 1.2 as the movement pattern is depicted as different levels of organisation changes from species to individual.

1.5 Research objectives

The overall objective of this dissertation is to improve the performance and transferability of species distribution models by incorporating individuals' movement information, also to further explore transferability of knowledge from the individual level to species level and vice versa. Specifically, this dissertation aims to evaluate the potentials of animal tracking data across spatial and temporal scales, while exploring another dimension across the level of organisation; from individual to species.

This dissertation addresses several underlying ecological theories and recent advancements in methodological approaches that are linked in various ways to assess the applicability of the methods to conservation problems from invasive alien species to collision risk with wind turbines, meaning this dissertation demonstrates the applicability of different compellability in data sources, working at species level data to extreme high-tech individual data.

We hypothesised that understanding the individuals' movement of alien species and accounting for their potential dispersal, along with environmental dynamics improves the accuracy and credibility of models to predict the potential distribution of species over time under climate change (see Chapter 2).

We further expanded our work to assess whether individuals' preferences of landscape correlate with the suitable habitat at species level. The hypothesis underlying this work was whether SDMs, with the use of movement data, can characterise habitat suitability (see Chapter 3).

Having these aspects explored, we realised that often species distributions are being modelled in two dimensions. In contrast, for species with vertical movement ability such as birds and fish, this would impose biases. We hypothesised that considering the vertical movement of individuals improves the accuracy and credibility of individual's range maps.

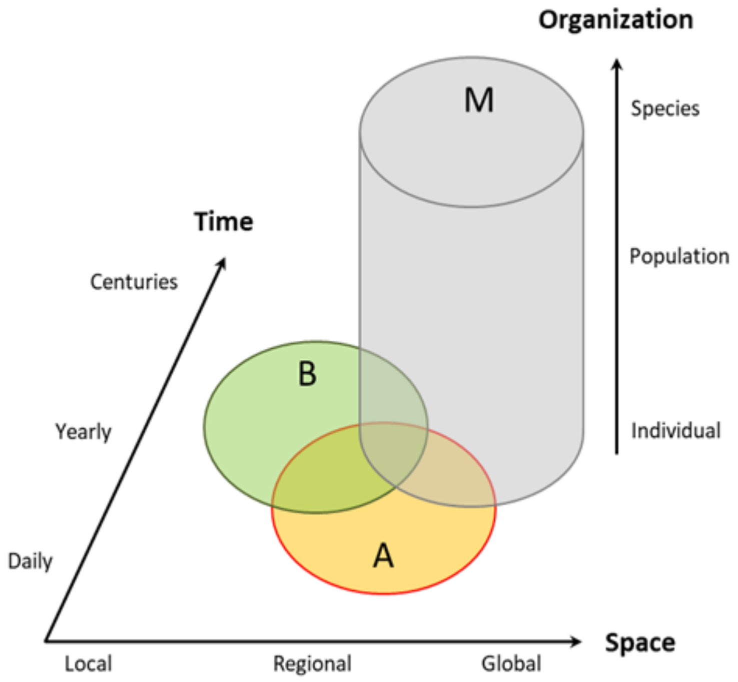

Figure 1. 2 Levels of organization as a new dimension to the BAM diagram; as movement (M) occurs across such spatio-temporal scales, it is depicted that both biotic (B) and abiotic (A) factors are time-dependent. Time is an important construct of shifting both A and B beyond locations deemed accessible to the species.

Thus, we aimed to develop a new approach of 3D modelling which ultimately can provide more reliable guidance for conservation manages (see Chapter 4). To complete our work with movement data, we test a hypothesis on whether movement patterns (i.e. flight types) can be identified using the high-resolution tracking data. This chapter provides evidence that such data contains of sufficient information for the classification which has be neglected (see Chapter 5).

1.6 Outline of the dissertation

This thesis consists of four core chapters. All core chapters have been accepted, are under review or in preparation to be submitted to scientific peer-reviewed journals. Each paper has been presented as a stand-alone Chapter and deals with one specific research question. The structure and content of the manuscripts are largely retained for the purpose of this dissertation.

- Chapter 2: Individuals' dispersal information to delimit prediction of future species geographical range
- Chapter 3: Individuals' movement data to delineate suitable habitats
- Chapter 4: Individual's movement data to estimate space use in volumetric analysis
- Chapter 5: Individual's movement data to identify flight types

While the current chapter sets the scene and provides an overview to the dissertation, Chapter 6, the Synthesis, summarizes and discusses the main findings, and outlines perspectives for future research.

Chapter 2

Individuals' Dispersal Information to Delimit Prediction of Future Species Geographical Range[*]

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[*] This chapter appeared in :

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- Khosravifard S. and Niamir, A. (2015) *Predicting the Potential Invasive Distribution of Raccoon in Iran*, in the proceedings of Internationale Congress for Conservation Biology ICCB2015, Montpellier, France (DOI:10.13140/RG.2.1.1782.8326).
- Khosravifard S. (2014) *Raccoon: The Intrusive Guest in Iran*, a documentary in Farsi (https://youtu.be/G-IpJHJIGng).

Preface

This chapter aims to explore the first hypothesis of the thesis: understanding of the individuals' movement and potential dispersal, along with environmental dynamics improves the accuracy and credibility of models predicting the potential distribution of species under future scenarios. This chapter also intends to support the concepts behind Figure 1.2 (page 9), specifically by addressing the x-axis (space) and the z-axis (organisation) at the same time.

Abstract

Dispersal is a repose to environmental conditions. Climate change might facilitate dispersal and establishment of species, and creates new opportunities for them to become invasive. Growing global evidence demonstrates that not only the invasion of alien species has imposed serious threats to native biodiversity, but it also threatens health and economics. The raccoon (*Procyon lotor*), medium-sized mammal, native to North America, as a result of escapes or deliberate introductions in the mid-20th century, is now distributed across much of mainland Europe and the Caucasus and known as an alien invasive species. The raccoon was observed and reported for the first time in 1991 in the Caspian Hyrcanian mixed forests ecoregion in Iran, near the border of Azerbaijan. Although it has been almost three decades since the first report in the northwest of the country, there are not many official reports nor scientific research on its dispersal and adaptive behaviour. In this study, we provide new evidence on the current distribution range, and predict the potential distribution range and thus invasion risk of the raccoon under climate change in Iran. We trained an ensemble of species distribution models trained in native and European invaded range and transferred it over space and time to Iran in 6 future climate scenarios. We also calculated the potential dispersal range of the raccoon per year and explored potential invasion corridors. Our results show that the raccoon inclines to expand in the forests and rangelands near the Caspian Sea and towards west Iran. Our work provides evidence to conservationists and decision-makers to further focus on the areas where the species will most likely expand, under the future scenarios of the climate change in 2050.

2.1 Introduction

Dispersal, defined as non-regular trips, one-way movements of an individual to a new home range and non-overlapping with the previous one (Santini *et al.*, 2013), is a response to environmental conditions (Holloway and Miller, 2017). Climate change might facilitate dispersal and establishment of species, and creates new opportunities for them to become invasive, or hinder the process and reduce the suitability thus invasion range of the species**.** The response of invasive species to climate change will have ecological and economic implications, too (Hellmann *et al.* 2008). Due to potential impacts of alien species on environmental changes, early detection and rapid response initiatives are suggested a crucial ingredient of integrated programs for dealing with invasive species (Pyšek & Richardson 2010). Therefore, it is essential to understand and predict the impacts of climate change on invasive species.

Reliable information on dispersal and distribution of alien species is crucial for biodiversity monitoring and conservation management (Dornelas *et al.* 2014). Knowledge about the potential distribution of the alien species is also required by conservation managers for better planning in the decision-making of tasks such as bio-security (Catford *et al.* 2012), the identification of entry points (Seebens *et al.*, 2013), the quantification of impacts posed by invasive alien species (Blackburn et al. 2014) or the assessment of the ecological degradation of habitats (Vandekerkhove *et al.* 2013). Growing global evidence demonstrates that not only the invasion of alien species has imposed serious threats to native biodiversity (Usher 1988, Westman 1990, Groom *et al*. 2006, Sinkins & Otfinowski 2012), it also threats health and economics (Scalera *et al*, 2012).

The raccoon (*Procyon lotor*), medium-sized mammal, native to North America, as a result of escapes or deliberate introductions in the mid-20th century, is now distributed across much of mainland Europe and Caucasus (Sherman 1954, Aliev & Sanderson 1966, Michler & Hohmann 2005, Gateway 2008). Although most unintentional introductions of the raccoon in eastern Europe did not reach a viable population in the past (Bartoszewicz *et al*, 2008), the recent investigations showed that the species had a trend of range expansion towards the south and east of the continent. Also, in the western and middle regions of Europe, this carnivore successfully increased in population size (Frantz *et al.* 2005, Canova & Rossi 2009). Today, the population growth and dispersal of the raccoon has become a real concern in the new regions (Ikeda *et al.* 2004, Biedrzycka *et al.* 2014). Although little is known about the potential environmental impacts of the raccoon introduction into Europe (Beltrán-Beck *et al.* 2012), anecdotal evidence suggests that the species may threaten reptiles and amphibians, and may, therefore, impact conservation projects (Kauhala 1996, Frantz *et al.* 2005).

In 1991, for the first time, the raccoon was observed and reported, in the Caspian Hyrcanian mixed forests ecoregion in Iran, near the border of Azerbaijan (Farashi *et al.* 2013). Since then, scattered observation records of this species indicated that the distribution of raccoon is not only confined to the forests and woodlands, but has been extended toward Elburz Range forest-steppe and urban areas in the south and in the east of the ecoregion.

Although it has been a long time since the raccoon was observed and recorded in northwest of Iran, there are not many official reports or scientific research on its adaptive behaviour. In addition, it has been speculated that the raccoon had migrated from Azerbaijan (Farashi & Naderi 2017) and is expanding from west to east. Apart from frequent local media reports, there are few reports or confirmed evidence of the raccoon direct damages to the croplands to the agriculture insurance companies.

The capability of raccoon coping with a variety of environmental conditions due to its opportunistic habits may make another extensive invasion success in Iran too. The old deciduous forests close to watercourses, wetlands or lakes are the raccoon's preferred habitats (Kaufmann 1982). However, this species may also survive and settle in diverse habitats ranging from partly open and marshy ground to urbanized areas where food is available (Sanderson 1987, Zeveloff & Dewitte 2002). The raccoon's adaptability and the food availability (e.g. domestic wastes) in populated and dense rural and urban areas in northern regions of Iran may march up the invasion rate.

In this study, we aim to provide reliable information on the potential invasive dispersal of raccoon in Iran. Therefore, we trained a global ensemble of trained models based on the available species data in native North America and invaded European ranges, and then transferred it over time and space to predict potential invasion range of the raccoon in the mainland of Iran under different climate change scenarios.

2.2 Materials and methods

2.2.1 Study area

Iran is a heterogeneous country with a diverse climate ranging from arid and semi-arid to subtropical along the Caspian Hyrcanian mixed forests, which rarely experience freezing nights and remains humid for the rest of the year. To the west, the Zagros Mountains forest steppe ecoregion supporting Oak-dominant deciduous and Pistachio-Almond forests, experience relatively lower temperature, severe winters with heavy snowfall. The coastal plains of the Persian Gulf and the Gulf of Oman are the Nubo-Sindian desert and semi-desert dominated by Xeric Shrublands with mild winters and very humid and hot summers.

We set 3 geographical extents for the modelling practices; Iran which we obtained the country border from GADM (https://gadm.org/ version 3.6), the native habitat of raccoon in North America (hereinafter called NA), and the invaded range in Europe (hereinafter called EU).

2.2.2 Environmental predictors

To allow for projections over time, the selection of the environmental predictors as input for the SDMs was limited to climatic variables. We obtained the 19 bioclimatic variables for current climate from the WorldClim (Hijmans *et al.* 2005) database averaged over the years 1950–2000 and the future climate averaged over the years 2041–2060. Altogether, 6 different climate scenarios were considered, including the three Generalized Circulation Models (GCM) CCSM4, HadGEM2-AO, and MPI-ESM-LR, and the three Representative Concentration Pathways (RCP) RCP2.6 (i.e. low concentration), and RCP8.5 (i.e. high concentration), representing an anthropogenic radiative forcing of 2.6, and 8.5 watts per square meter across the planet, respectively.

To avoid potential problems that the multicollinearity issue may cause model parameterisation and inference (Naimi & Araújo 2016), all predictors were checked for multicollinearity by calculating the Variance Inflation Factor (VIF). While there is an ongoing debate about the threshold above which correction for multi-collinearity ought to be considered, we took 10 as the threshold value to be considered for multicollinearity (Hair Jr *et al.* 1995, Menard 2002).

2.2.3 Species occurrence data

Since the early 90s that the raccoon was first recorded in Iran, a few official (i.e. confirmed) records were reported by the authorities. However, there are several unofficial records being reported by locals either killed or photographed. With a systematic web search in social networks, news, and media in Farsi and English, we collected over 100 fragmented records of the raccoon in Iran. We took records with solid evidence (e.g. photos and videos), or from locations with multiple records, or with a report by an expert. We also compared our observation list with the previous efforts (Farashi *et al.* 2013, Farashi & Naderi 2017). In the end, we used 48 records of raccoon in Iran in our modelling practices.

We obtained a dataset for occurrence records of raccoon within the native habitat range (i.e. NA), as well as its invaded range in Europe from the Global Biodiversity Information Facility. The North America dataset is consist of more than 10000 occurrence records (GBIF 2020) and the Europe dataset (i.e. EU) contains 7500 occurrences (GBIF 2020). Since the species occurrence records included species presences only and most of the modelling methods required a binary, absence-presence, data structure, pseudo-absence occurrences were generated randomly in the extent of the training data.

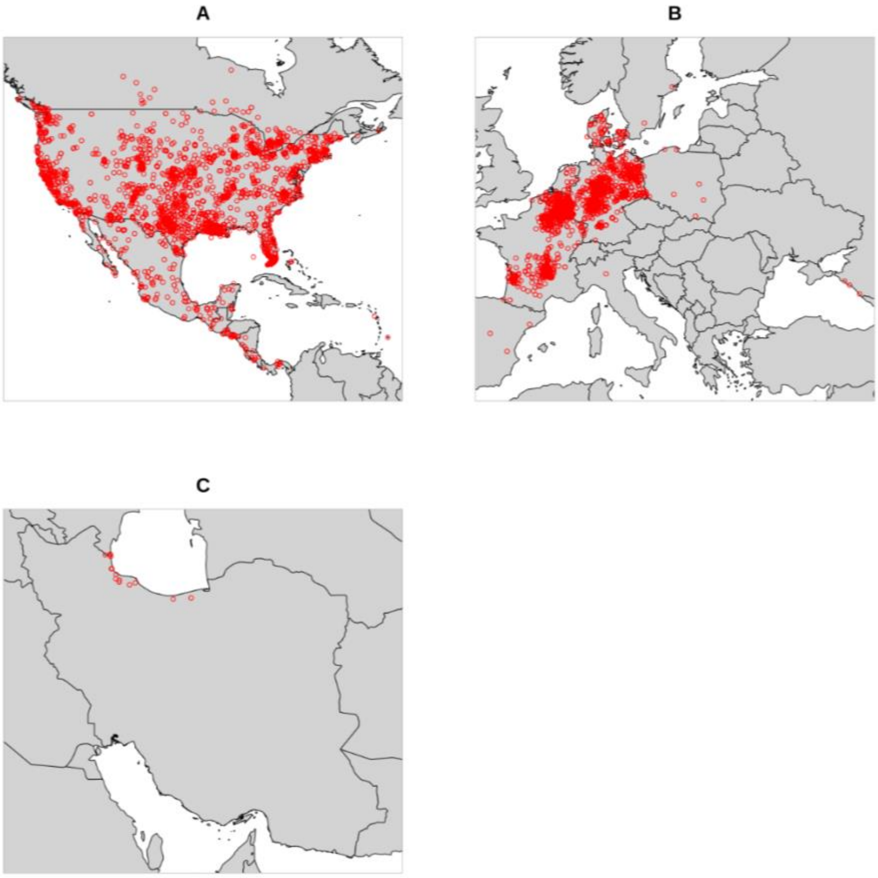

Figure 2. 1 Distribution of Observation Records A) in the Native Habitat North America (NA), B) in the European Invaded Habitat (EU), and C) in Iran.

2.2.4 Species distribution models

The diversity of species distribution models has been constantly growing over the last few decades. While there has been considerable praise for each of them (Drake *et al.* 2006, Elith *et al.* 2006, Merow *et al.* 2014) the selection of an appropriate method for studies on distribution modelling requires extra attention which might result in a significantly different outcome, and often not possible to judge which of the algorithms will perform best. There are, however, recommendations on how to employ multiple modelling methods (i.e., a model ensemble) which combine different models and provide information about the overall output and the uncertainty around it (Seoane *et al.* 2005, Araújo & New 2007). To this end, we set up an ensemble approach consist of 4 modelling methods; Generalized Linear Models (GLM; McCullagh & Nelder 1989, Beale & Lennon 2012), Generalized Additive Models (GAM; Hasties & Tibshirani 1990), Boosted Regression Trees (BRT; Friedman 2001), and Random Forests (RF; Breiman 2001). To identify the current realized distribution range of raccoon in Iran, we employed MaxEnt (Phillips *et al.* 2006). We keep the parameters of the MaxEnt as default, except the regularization multiplier were set to 3 to further increase the fit to the current presence occurrences.

2.2.5 Model evaluation

We evaluated performance of the SDMs with their discrimination power. The discrimination power of an SDM is its ability to recognize a distinction between 'presence' versus 'absence' (Hosmer & Lemeshow 2000). The area under the curve (AUC) of the receiver operating characteristic (ROC) plot was computed in order to assess the discrimination power of the models for each data set. A ROC curve plots sensitivity values (i.e. a true positive fraction) on the *y*-axis against 1 − specificity values (i.e. a false positive fraction) for all the thresholds on the *x*-axis. Sensitivity is the probability that the model correctly predicts an observation while, specificity is the probability that a known absence site is correctly predicted. The plot in ROC space of sensitivity versus specificity displays how well an algorithm classifies instances as the threshold changes. The AUC is a single measure of a model's discrimination power, which provides a threshold-independent measure across all the possible classification thresholds for each model (Fielding & Bell, 1997). We randomly split the data, 70% of which were used to train the models and the remaining 30% of which were used to measure their discrimination power.

We assessed the calibration (Hosmer & Lameshow, 2000) of the models using Miller's calibration statistic (Miller et al., 1991; Pearce & Ferrier, 2000) for the global ensemble of the trained models. Miller's calibration statistic evaluates the ability of a distribution model to correctly predict the proportion of species occurrences with a given environmental profile. It is based on the hypothesis that the calibration line – perfect calibration – has an intercept of zero and a slope of one. The calibration plot shows the model's estimated probability (x-axis) against the mean observed proportion of positive cases (y-axis) for equally sized probability intervals (number of intervals = 10). We then calculated the Root Mean Square Error (RMSE) of the calibration plot (Armstrong & Collopy, 1992) for the ensemble using calibration function in Naimi & Araújo (2016).

2.2.6 Species dispersal

We estimated an annual dispersal range for the raccoon using the empirical model developed by Santini *et al* (2013). They proposed a linear model for applicative purposes representing the relationship between dispersal distance and body size or home range area (Santini *et al*. 2013);

$$\text{Mean dispersal} = 5.78 \times B^{-0.03} \times H^{0.19} \qquad \text{(Equation 2-1)}$$

where *B* is the body size in kilogram and *H* is home range.

There is a wide range of values reported for the body size and the home range of the raccoon in their native and invaded area. We assumed the home range area of 0.4 square kilometre based on IUCN red list of threated species (Timm *et al* 2016), and the body size of 3 kilogram following the Atlas of Mammals of Iran (Karami et al. 2016). The annual dispersal range of 4.38 kilometre is a conservative estimate as our inputs were. This means that we assumed expansion of about 43 kilometres in every decade around the current geographical range through the potential habitat corridors.

2.2.7 Experimental settings

Our aim was to train a reliable ensemble model based on the native and the invaded range (i.e. NA + EU) for the current climatic condition that can predict the potentially suitable habitat of raccoon in Iran. Then to transfer the trained model over time to investigate the potential suitable habitat of raccoon in the near future under climate change. Finally, by comparing the current realized suitable habitat and the future potential habitat, considering the land cover and accessibility, and taking into account the dispersal (i.e. invasion) speed, we prepared an invasion path and discussed priorities of conservation actions for raccoons in Iran. The procedure to implement our work was as follows:

1. Accounting for multicollinearity. We first calculated the VIF, and 9 out of 19 bioclimatic variables had values less than 10 and were taken into the modelling procedure (Table 2.1).
2. Train and evaluate SDMs in NA. We set up an ensemble based on a set of trained models using occurrence records obtained from GBIF as presences, and pseudo-absences sampled randomly from NA. We trained and evaluated them through 100 runs of subsampling, each draws 30% of training data as test dataset. We set our ensemble based on a weighted averaging, using AUC statistic with threshold criterion maximum sensitivity plus specificity.
3. Transfer the NA model to EU. We used the points obtained from GFIB for the invaded range in Europe to evaluate the performance of the ensemble trained in the native extent (i.e. NA) in the invaded extent (i.e. EU). We further investigated the extremes in the bioclimatic variables in EU that the NA model were unable to discriminate. We evaluated the performance of the ensemble with its discrimination capacity.

4. Train a global model. We used the observations from the native (i.e. NA) and the invaded (i.e. EU) extents to train a "global ensemble of trained models" for the raccoon and evaluated the performance of the ensemble with its discrimination capacity and calibration.
5. Transfer the ensemble to IR. The global ensemble of trained models of raccoon was transferred to IR to predict potentially suitable habitat of the raccoon in Iran. We used independently collected observation records to evaluate the prediction of the model.
6. Transfer over Time. We also transferred the ensemble of trained models in IR over time to predict potentially suitable habitat of the raccoon in Iran under climate change scenarios. We calculated the maximum and minimum invasion potential map for Iran in 2050.
7. Realized distribution in Iran. We trained MaxEnt (i.e. presence-only) models using the collected observation records to predict the realized distribution (i.e. current geographical range) of the raccoon in Iran. We used the maximum sum of sensitivity and specificity as the threshold to generate a binary map of realized distribution (Liu *et al.* 2013). Then we cropped the potential distribution with the binary map.
8. Estimated dispersal range in 2050. We calculate 4.38 km as the potential dispersal range per year and therefor draw a buffer of 175 kilometres (i.e. 4.38 km/yr in 40 years) around the current realized distribution of the raccoon to identify and discuss the potential invasion paths.

All models were executed in the R environment v.3.4.4 (R Development Core Team, 2018) using the *sdm* (Naimi & Araújo 2016), *dismo* (Hijmans *et al.* 2013), *raster* (Hijmans *et al.* 2015), sp (Pebesma & Bivand 2005), maptools (Bivand & Lewin-Koh 2013) and, usdm (Naimi 2015) packages.

2.3. Results

2.3.1 SDMs for the native habitat

We built an ensemble of distribution models for raccoon in its native habitat with about 10000 observation records and 9 bioclimatic variables; Mean Diurnal Range, Temperature Annual Range, Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter, Mean Temperature of Warmest Quarter, Precipitation of Driest Month, Precipitation Seasonality, Precipitation of Warmest Quarter, and Precipitation of Coldest Quarter. See Table 2.1 for predictors details and Figure 2.1A for the distribution points.

Among all of the 4 models that we employed in our ensemble approach, the RF models overperformed others with the mean AUC of 0.97 (StDev=0.08) followed by the GAM and the BRT with mean AUC of 0.87 (StDev=0.11) and 0.78 (StDev=0.07), and the GLM models were performed with the lowest mean AUC of 0.75 (StDev=0.14). The ensemble model performed with the mean AUC of 0.94 (StDev=0.01) discriminating the suitable from the unsuitable habitat of the raccoon in NA (i.e the native habitat in North America). See Figure 2.2A. When we transferred the NA model over space to EU (i.e. the invaded extent in Europe) it performed slightly better than a random model with mean AUC 0.59 (StDev=0.08) mainly due to low sensitivity. But when we set up another ensemble of distribution models for raccoon using the occurrences in NA plus occurrences in EU (n=8000) the discrimination capacity improved to mean AUC value of 0.84 (StDev=0.05). Thereafter, we will refer to this model as our “global model” (see Figure 2.2B). The calibration plot of the global model stretched the completed extent of the suitability range revealing the goodness of fit of the model to correctly predict the proportion of species occurrences over time and space. The root mean square error (RMSE) of the global model was 0.09, slightly underestimating the suitability of habitat in low suitability values and slightly overestimating the high suitability values.

2.3.2 Transfer the global model over space and time

We transferred the global model over space to predict the habitat suitability of raccoon in Iran using 9 climatic predictors. On average the AUC of the global model in IR was 0.69 (StDev=0.18). The global model was successful to predict higher probability value to locations with observation records (i.e. high specificity) but failed to discriminate areas with no records of the raccoon (i.e. low sensitivity). This might be due to the fact that the climate condition in the other areas is still suitable for the raccoon but due to lack of access or biotic conditions has not been invaded yet. The potential distribution of raccoon in Iran shows that the tiny line of Hyrcanian mixed forest in the south of the Caspian Sea has the highest climate suitability, followed the Zagros mountain forest-steppe (see Figure 2.2C). We also transferred the global model over time to predict the habitat suitability of the raccoon in 2050 over a variety of climate scenarios and calculate the changes in the probability values (Figure 2.3).

2.3.3. Realized geographical range and dispersal corridors

To model the realized distribution, the area that raccoon actually lives, we trained MaxEnt models using all of the 48 observation records as described in the "experimental settings". To convert the gradient of occurrence to a binary map of realized distribution range, we calculated the threshold of Maximum Sensitivity plus Specificity and assumed area with values above the threshold, as the current realized geographical range of raccoon in Iran (Figure 2.2D). Comparing the geographical range with the potential habitat suitability under climate change revealed that climatic suitability in the realized distribution of raccoon in Iran decreases over all of the Generalized Circulation Models (GCM) and Representative Concentration Pathways (RCP). In contrast, the suitability of habitat for the raccoon in the Zagros Mountain Forest Steppe increased in all GCMs and over all RCPs.

We cropped the future potential distribution habitat suitability maps in the buffer of 175 kilometres, assuming the maximum range of dispersal by 2050.

Table 2.1 Environmental variables used in SDMs

Predictors Code	Predictors Name	VIF Value in NA	Range in NA	Range in EU	Range in EU not covered in NA	Range in EU+NA	Range in IR	Range in IR not covered in EU+NA
Bio 2	Mean Diurnal Range	2.55	60 - 213	43 - 107	43 - 60 *	43 - 213	64 - 175	all covered
Bio 7	Temperature Annual Range (BIO5-BIO6)	3.57	11.9 – 50.8	18.4 – 32.4	all covered	11.9 – 50.8	19.3 – 44.8	all covered
Bio 8	Mean Temperature of Wettest Quarter	3.87	-11.5 – 33.1	-10.1 – 20.6	all covered	-11.5 – 33.1	-6.7 – 25.4	all covered
Bio 9	Mean Temperature of Driest Quarter	5.63	-16.1 – 32.2	-10.2 – 22.8	all covered	-16.1 – 32.2	-9.7 – 36.5	32.2 – 36.5
Bio 10	Mean Temperature of Warmest Quarter	4.12	5.0 – 35.7	0.9 – 23.4	0.9 - 50 *	0.9 – 35.7	7.1 – 36.5	35.7 – 36.5
Bio 13	Precipitation of Wettest Month	3.25	7 - 551	52 - 225	all covered	0.7 – 55.1	1.1-27.1	all covered
Bio 14	Precipitation of Driest Month	7.47	0 - 152	19 - 166	152 - 166 *	0 - 166	0 - 42	all covered
Bio 15	Precipitation Seasonality	5.29	6 - 133	7 - 47	all covered	6 - 133	29 - 137	13.3 – 13.7
Bio 18	Precipitation of Warmest Quarter	4.65	1 -728	135 - 575	all covered	1 - 728	0 - 261	0 - 1

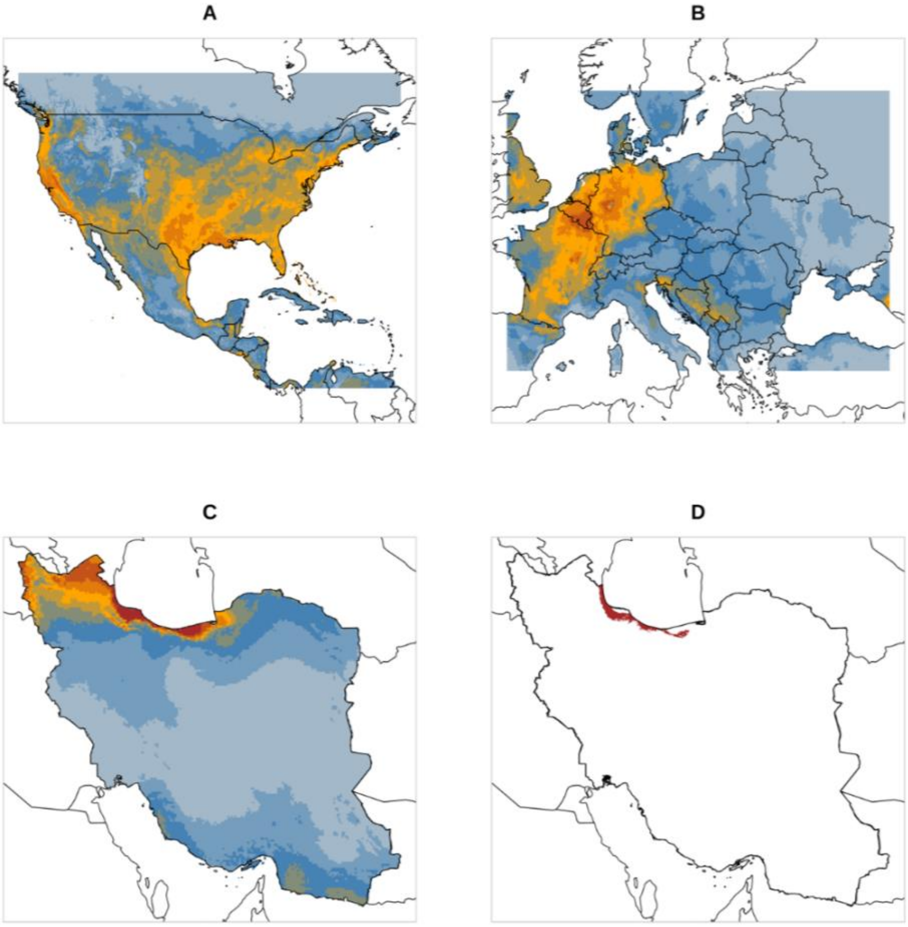

Figure 2. 2 Potential distribution of Raccoon; A) in NA (i.e. the native habitat in North America) based on the SDMs trained by species occurrence records in NA, B) in EU (i.e. the invaded European habitat) based on the SDMs trained by species occurrence records in NA + EU, and C) in IR (i.e. the invaded habitat in Iran) based on the SDMs trained by species occurrence records in NA + EU. The dark orange illustrates relatively most suitable and the dark blue illustrated relatively least suitable habitats. The panel D shows the current realized distribution range of Raccoon in Iran in dark orange.

Then, we compare the suitability of habitat in future with the present conditions and removed areas that either are not suitable or the habitat suitability will significantly decrease by 2050, thus remains areas that could act as potential dispersal corridors.

2.4 Discussions

Our work provided new evidence on the current and future status of geographical range of the raccoon in Iran. The predictions successfully identified the worldwide occurrence records of the raccoon, including native (i.e. North America) and invaded regions (Europe), used in this study and demonstrated high probability values of areas predicted by previous studies such as Italy, Austria and Germany (Fischer *et al.* 2015, Mori *et al.* 2015, Farashi & Naderi 2017, Duscher *et al.* 2018). In addition, our realised distribution model illuminated the current distribution of this species, which is in line with the previous research carried out by Farashi et. al (2017), explaining the raccoon's population inclined to expand in the forests and rangelands near the Caspian Sea and some parts of west Iran. However, unlike the previous study, our realised model showed no signal of the raccoon's distribution in the central parts of the country, this might be due to complementary calibration of our models for the European extent.

Hellmann *et al.*, 2008 argued that a species, to become invasive, needs to overcome new conditions. First, a species must pass major geographical obstacles to reach to a new location. Then, the species must survive in and adapt to the new environmental conditions at the arrival site. Third, a species must obtain critical resources, remain alive in interaction with natural enemies, and likely form mutualistic relationships at the new location. Finally, the species must extent geographical distribution, establishing populations in new sites. This scenario will less likely being applicable for the raccoon in Iran under the current climate conditions. Although the habitat conditions (i.e. old deciduous forests close to water) and food resources availability (i.e. wild plants, fruits berries, small rodents, frogs, eggs and domestic wastes in rural and urban areas) may provide advantages for the raccoon's distribution in the northern parts of Iran, the Elburz Mountain, at the southern edge of the current raccoon's range, is a great geographical obstacle for the species to pass and reach to new sites. However, the anthropogenic assistance (e.g. trade or unintentional transportation) may enable the raccoon to stretch out its distribution.

The "Animal Rights activists" and press have been alerted the increasing population size and the growth of trades and interests to keep the species as a pet (Khosravifard 2007, Animal Rights Watch 2015). This may alter the current distribution of this alien species in Iran.

The raccoon's habitat suitability calculated over the variety of climate scenarios in the year of 2050, illustrated that from north to south of the Zagros mountains may become a destination and new location for the species. This new scenario along with the deliberate or undeliberate introduction of the raccoon should be considered in conservation and management plans.

Despite the anecdotal evidence suggests that climate change is most likely to substantially increase the impact of current invasive species since many of them already spread a range of environmental conditions (Qian & Ricklefs 2006), our study illustrated that the future climate change scenarios are not in favour of the raccoon's distribution expansion. Considering the abiotic variables (i.e. temperature and precipitation), which influence the raccoon's potential distribution, may slow down the future expansion of raccoon's range. This might provide conditions to have the population increased or maybe overpopulated in human settlements due to accessibility and abundance of food.

In Europe, the population growth of the raccoon is out of control because of increasing population trends, range expansion and no efficient management strategy. However, no ecological impacts have still been reported through an evidence based approach (Salgado 2018). Although negative impacts of raccoon on native biodiversity is not yet reported and unknown in Iran, management and conservation plans are needed to prevent any possible or unforeseen threats. The prevention through legislation on pet trade, education and awareness raising campaigns are suggested as the most efficient strategy for the raccoon's geographically expansion (Tollington *et al.* 2017).

To eradicate newly established population, early detection (using sign surveys and camera trapping) and rapid response (by trapping) may be carried out as measurable objectives (e.g. keeping the raccoon's population at low density) are considered. Control is a long-term management strategy, expensive and requiring stable funding. Our study would assist conservationists and managers to focus on the areas where the species would most likely occur. This may ultimately lead to a thrift for developing and executing management plans.

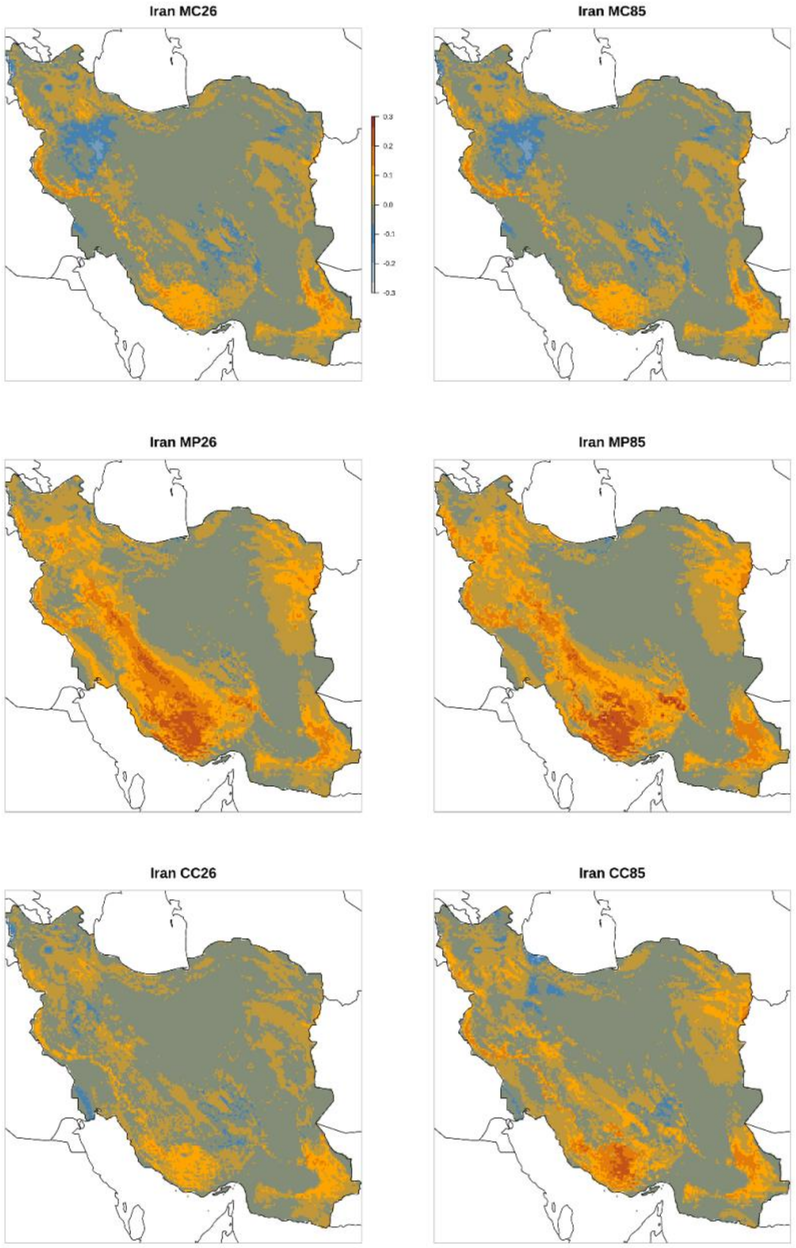

Figure 2. 3 Changes in the potential habitat suitability of Raccoon in Iran under climate change scenarios. The gradient from light to dark orange illustrates increased relative habitat suitability and the gradient from light to dark blue illustrated decreased relative habitat suitability.

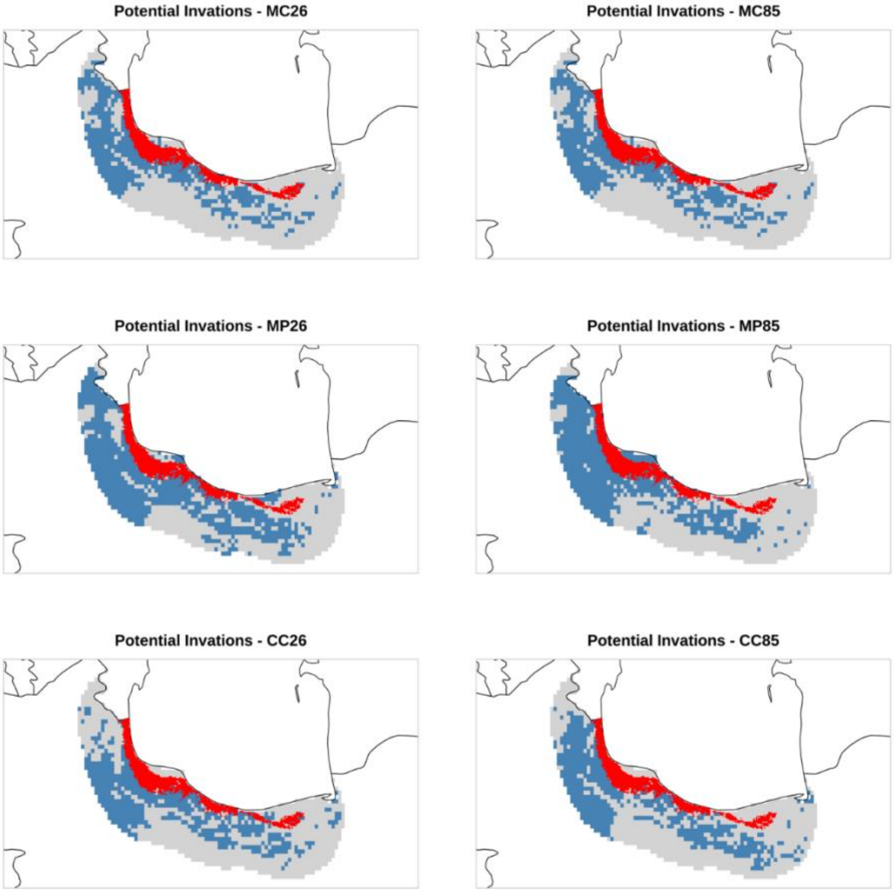

Figure 2. 4 Potential invasion corridors (in dark blue) of Raccoon in Iran under climate change. The current realized distribution range of Raccoon in Iran in red. The panels show the extent of the potential dispersal range (~175 kilometres) in year 2050. The grey areas are either not suitable or the habitat suitability will a significant decrease over time.

Postface

The chapter demonstrated when accounting for individual's movement capacity and their dispersal range, it could improve the understanding of potential distribution of the species over time and under climate change and guide conservation actions. In the next chapter, we go one step further to using individual movement data to inform species distribution models.

Chapter 3

Individuals' Movement Data to Delineate Suitable Habitats[*]

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[*] This chapter is based on:
Khosravifard, S., Skidmore, A.K., Venus, V., Munoz, A.R., Toxopeus, A.G., & Naimi, B. Using Individuals' Movement Data to Characterize Species Distribution (in preparation to submitted to Diversity and Distributions journal).

Preface

This chapter is an expansion of the previous one exploring whether the individual's movement data can characterize habitat suitability for species distribution. Also, this chapter demonstrates the capacity of individuals' movement data addressed the third hypothesis of this thesis; whether SDMs with the use of movement data can characterise habitat suitability.

Abstract

Many studies have endeavoured to reveal the relationships between species movement and environmental variables. Despite some increasing efforts to monitor and collect species movement data, the incorporation of these data in species distribution models (SDMs) has lagged. SDMs are used as powerful tools for conservation biogeography and known as a robust spatial and ecological framework for studying and evaluating the relationship between environmental features and the distribution of organisms. In the past, the effects of movement were neglected. Only spatial locations of species and environmental variables were considered to predict geographical distributions. The availability of high-resolution tracking data allows ongoing monitoring of individual species and potentially provides opportunities to divulge how the individuals utilize their overall environment at a higher level of precision. This study examines how SDMs, with the use of movement data, can characterize habitat suitability and how they are comparable with the commonly used data sources. This chapter shows that the spatial concordance between the outcomes of SDMs, derived from static (i.e. GBIF) and movement data (i.e. Movebank) which the latter can be considered as a reliable source for SDMs.

3.1. Introduction

SDMs are known as a powerful spatial and ecological framework for studying and evaluating the relationship between environmental features and distribution of organisms or biological phenomena (Franklin 2010b) such as invasion risk of undesired species or vector-borne disease (Franklin, 2010a; Holloway *et al.*, 2017). In addition to being frequently used to address questions regarding ecological processes involving climate change and biogeographical hypotheses, SDMs have been also utilized to test conceptual issues related to their effective implementation, such as uncertainty (Naimi *et al.*, 2011), effects of scale (Elith and Leathwick, 2009a), and semantics (McInerny and Etienne, 2012; Peterson and Soberón, 2012). Although the impact of movement on geographic distribution has been known for a long time, incorporation of movement data into SDMs has been considered (Gschweng *et al.*, 2012; D'Elia *et al.*, 2015; Pinto *et al.*, 2016). In the past, the effects of movement were neglected, as most SDMs have still focused on environmental-species relationships. Only spatial locations of species and environmental variables were considered to predict the geographical distributions of species (Bruneel *et al.*, 2018).

The movement of organisms is an essential element of almost any ecological and evolutionary process that operates across various spatial and temporal scales, influencing most forms of organisms' lives (Nathan *et al.*, 2008). With the emergence of tracking and GPS devices, the animal movement has become a focal point of many studies and been increasingly investigated (Careau *et al.*, 2006; Holyoak *et al.*, 2008; Alarcón and Lambertucci, 2018). Some of these studies have endeavoured to reveal the relationships between species movement and environmental variables (Hooten *et al.*, 2014). Notwithstanding the attempts along with the ecological importance, the incorporation of movement in species distribution models (SDMs) has lagged (Holloway and Miller, 2017; Bruneel *et al.*, 2018).

The availability of high-resolution tracking data allows ongoing monitoring of individual species (Dambach and Rödder, 2011), which potentially provides opportunities to divulge how the individuals utilize their overall environment at an ever-increasing accuracy (Nathan *et al.*, 2008). The movement data, retrieved from recently advanced telemetry techniques, are reliable as the accuracy is generally high (Frair *et al.*, 2010; Tomkiewicz *et al.*, 2010). Thus, high-resolution telemetry data can be considered as a source for SDMs. Furthermore, the online and often free available animal tracking data, even in high temporal and spatial resolution, provide the possibility to model the distribution of mobile species in dynamic environments (Franklin 2010b).

The diversity of species distribution models has been constantly growing over the last few decades. While there has been considerable praise for each of them (Drake, Randin and Guisan, 2006; Elith *et al.*, 2006; Duan *et al.*, 2014; Merow *et al.*, 2014), the selection of an appropriate method for studies on distribution modelling requires extra attention which might result in a significantly different outcome.

The distributional area of a species is a complex expression of its ecology and evolutionary history (Brown, 1995). To overcome this complexity, Soberón and Peterson (2005) developed a heuristic scheme illustrating three factors deemed prominent in defining species distribution: Biotic (B), Abiotic (A) and Movement (M) (BAM diagram, Figure 3.1). Abiotic factors refer to physiological tolerances regarding aspects of climate, physical environment, edaphic conditions, etc., where a species can survive. Appropriate biotic factors represent the interactions of a species with other species (e.g. competition, predation). Movement is defined as a specific area in time accessed by a species (Soberón and Peterson, 2005; Soberón and Nakamura, 2009). The influence of abiotic and biotic factors has been established in SDMs, but more research is required to employ movement for projection the current or future distribution of a species (Holloway, Miller and Gillings, 2016). Until now, the movement has been mainly conceived as temporally and spatially coarse-scale processes like migration or dispersal (Miller and Holloway, 2015). Although 'migration' is defined as a movement between two habitats (or destinations) on a predictable basis (Hansson, Akesson and Åkesson, 2014), in SDM studies both migration and dispersal have been often used interchangeably referring to the same behaviour which is a response to changes in the environment (Holloway and Miller, 2017).

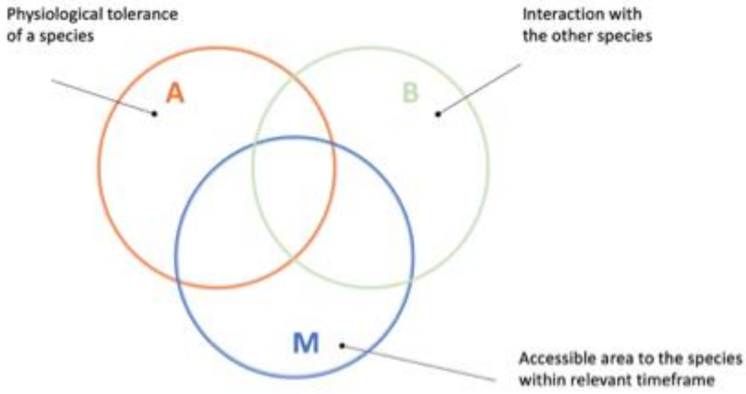

Figure 3. 1 BAM diagram (adopted from Soberón & Peterson 2005)

Combining SDM with other approaches and data like fossil record and of modern genetic studies has been suggested to improve methods for forecasting species distribution and evaluating the impact of environmental changes on the distribution at large spatial scales (Botkin *et al.*, 2007). This study examines how SDMs with the use of movement data can characterize habitat suitability and how they are comparable with the commonly used data sources. The key question of this study is how and to what extent SDMs can benefit by incorporating the movement data into the modelling procedure.

3.2 Material and methods

3.2.1 Data acquisition

This study was mainly conducted with the use of two different and freely available species data sources: Movebank and GBIF. Movebank is a free, online database of animal tracking data hosted by the Max Planck Institute for Ornithology. It is an international project with over 11,000 users, including researchers and conservationists around the globe (https://www.movebank.org/). Also, different sensor types of data including natural marks, bird ring, GPS, radio transmitter, solar geolocator and Argos doppler shift are available from the Movebank repository.

GBIF (the Global Biodiversity Information Facility) is an open-source data research platform funded by the world's governments. The aim of this platform is to provide anyone access to data about all types of life on Earth. Common standards and open-source tools, provided by GBIF, enable data-holding institutions around the world to share information about when and where species have been recorded. This information obtained from many sources, including everything from museum specimens collected in the 18th and 19th centuries to geotagged smartphone photos shared by amateur naturalists in recent days and weeks (https://www.GBIF.org/).

From both repositories, we retrieved data of the following species: Wild Turkey (Meleagris gallopavo) (GBIF, 2019a; Margadant, 2019), Montagu's Harrier (Circus pygargus) (Trierweiler *et al.*, 2014; GBIF, 2019b), and Great White Pelican (Pelecanus onocrotalus) (GBIF, 2019c; Efrat, Hatzofe and Nathan, 2019). We downloaded about 978,000 and 25811 occurrence records of Wild Turkey from GBIF and Movebank datasets, respectively. Also from GBIF and Movebank repositories, we downloaded 158,600 and 45,400 occurrence records of Montagu's Harrier, and nearly 41,000 and 188,000 occurrence records of Great White Pelican, respectively.

The major concern in data acquisition was related to the movement data derived from Movebank. We downloaded the datasets containing a minimum of 20,000 GPS fixes with at least 15 individuals for each of the three species. We generated pseudo-absence records distributed randomly over the entire study area.

We delineated the study area for each species by selecting the regions that are likely to be accessible for the species. To do so, we used the avian biogeographical regions dataset (Rahbek *et al.*, 2012) and selected the regions where the occurrence of species where located.

3.2.2 Environmental predictors

We obtained the widely used 19 bioclimatic variables as predictors in SDMs from the CHELSA dataset Version 1.2 with a spatial resolution of 2.5 arc minutes (Karger et al., 2017). These variables that represent the current climate (averaged over the years 1970–2000) were resampled, aggregated, and harmonized to the same spatial resolution.

3.2.3 Species distribution models

There are some recommendations recently to employ multiple modelling methods (i.e., a model ensemble) to increase model robustness (Guisan and Thuiller, 2005; Araújo and New, 2007). To this end, we set up an ensemble approach (Araújo and New 2007), consisting of 7 modelling methods: Generalized Linear Models (GLM; McCullagh 1989), Boosted Regression Trees (BRT; Friedman 2001), Random Forests (RF; Breiman 2001), Multivariate Adaptive Regression Splines (MARS; Friedman 1991), MAXENT (Csiszár 1985, Phillips *et al.* 2006), Bioclim (Busby 1991; Naimi and Araújo, 2016) and Maxlike (Royle *et al.*, 2012).

3.2.4 Experimental design

The procedure to implement our work was as follow:

1. To avoid the issue of multicollinearity between two and more variables, we used the variance inflation factor (VIF) to detect collinearity (Naimi *et al.*, 2014). We took 10 as the threshold which a greater value of that is a signal showing the model has a collinearity problem (Hair Jr *et al.*, 1995; Menard, 2002). The variables had values greater than 10 were taken out from the modelling procedure
2. We trained an ensemble model using occurrence records obtained from GBIF as presences and the generated pseudo-absences. We used a subsampling procedure (with 10 replications) to draw 30 percent of records randomly as the test dataset. For each replication,

we trained 7 models (GLM, BRT, RF, MARS, MAXENT, Bioclim and Maxlike), and evaluated their performance on the test dataset, using area under the receiver operating characteristic curve (AUC) (Fielding & Bell, 1997) and true skill statistics (TSS) (Allouche *et al.*, 2006). We generated the ensemble of species distribution models by averaging the predicted values from the individual models, weighted by AUC statistic. We repeated the same procedure using the Movebank dataset.

3. We compared the species distribution maps, generated separately using GBIF and Movebank data and binarized using a threshold that maximised TSS by calculating the similarities (agreement) and differences including the total proportion of suitable and unsuitable habitats derived from both datasets for each species. The results were illustrated as the map to visualise the consistency and difference between the outputs of the models based on the two datasets.

All analysis were implemented in the R environment v.3.4.4 (R Development Core Team, 2018) using the packages of sdm (Naimi & Araújo 2016), dismo (Hijmans *et al.* 2013), raster (Hijmans *et al.* 2015), sp (Pebesma & Bivand 2005), maptools (Bivand & Lewin-Koh 2013), and usdm (Naimi 2015).

3.3. Results

We built ensembles of the 7 distribution models for Wild Turkey, Montagu's Harrier and Great White Pelican using GBIF and Movebank datasets. The ensemble models for these species depicted in Figure 3.2. After VIF calculation, to generate the models, 9, 10 and 11 bioclimatic variables were used for Wild Turkey, Montagu's Harrier and Great White Pelican, respectively. The predictor codes and names along with relevant values are summarized in the Table 3.1.

For Wild Turkey, the RF model using GBIF data overperformed others with AUC, followed by Maxent, MARS, BRT, GLM, Bioclim, and Maxlike. Moreover, the highest value of TSS showed by RF, followed by Maxent, MARS, BIOCLIM, BRT, GLM, and MAXLIKE.

For Movebank dataset, the AUC of GLM, RF, MARS, and Maxent models showed perfect discrimination by a score of 1. These models outperformed BRT, Bioclim, and Maxlike. RF, MARS, and Maxent had the highest value of TSS and then GLM, MAXLIKE, BRT, and BICLIM. For Montagu's Harrier, the AUC and TSS values of models incorporating GBIF data are close to the models using Movebank data.

Finally, for the Great White Pelican, the maximum of AUC and TSS were 0.94 and 0.92 obtained from Maxent and RF models using the GBIF dataset while the minimum value of AUC and TSS showed by MAXLIKE and BRT, respectively. The maximum of AUC and TSS using Movebank data for great white pelican showed by RF and MAXLIKE had the minimum of AUC and TSS (see details in table 3.2 and 3.3, and Figure 3.3).

The ensembles derived from GBIF and Movebank datasets were in 0.92 of the total agreement for wild turkey meaning the total suitable and unsuitable habitats predicted as such with the use of both datasets are the same, comparable (Figure 3.4 a). The agreement index for Montagu's harrier on suitable and unsuitable habitats derived from GBIF and Movebank datasets was 0.87. Also, the utmost areas predicted as unsuitable habitats from the GBIF dataset, were identified as such when the Movebank dataset incorporated (Figure 3.4 b). For great white pelican, comparing ensembles of the 7 models showed a total agreement of 0.83 between suitable and unsuitable habitats derived from GBIF and Movebank datasets (Figure 3.4c).

Table 3.1 Environmental variables used in SDMs

Predictor Code	**Predictor name**	**Wild turkey**		**Montagu's harrier**		**Great white pelican**	
		VIF GBIF	VIF Move	VIF GBIF	VIF Move	VIF GBIF	VIF Move
Bio2	Mean diurnal range	0.06	0.0008	0.04	0.07	0.04	0.05
Bio4	Temperature seasonality	0.1	0.01	0.07	0.3	0.24	0.13
Bio7	Temperature Annual Range	-	-	0.24	0.12	-	-
Bio8	Mean temperature of wettest quarter	0.01	0.051	0.05	0.05	0.01	0.03
Bio9	Mean temperature of driest quarter	0.04	0.08	0.15	0.06	0.17	0.10
Bio10	Mean temperature of warmest quarter	0.15	0.07	-	-	0.07	0.13
Bio13	Precipitation of wettest month	0.04	0.002	0.02	0.03	0.02	0.05
Bio14	Precipitation of Driest Month	-	-	0.01	0.02	0.02	0.18
Bio15	Precipitation seasonality	0.04	0.007	0.03	0.03	0.02	0.004
Bio17	Precipitation of Driest Quarter	-	-	-	-	0.03	0.3
Bio18	Precipitation of the warmest quarter	0.05	0.01	0.02	0.12	0.02	0.11
Bio 19	Precipitation of coldest quarter	0.02	0.12	0.24	0.02	0.02	0.008

3.4 Discussion

Our study explored the capacity of movement data in characterizing the habitat suitability. The spatial concordance between the outcomes of SDMs, derived from static (i.e. GBIF) and movement data (i.e. Movebank) demonstrated that the latter can be considered as a reliable source for SDMs. However, the results varied among the models and species.

The selection of statistical methods was one of the most substantial facets of this study. The difference in outputs derived from the statistical methods has long been noted as an important issue (Guisan and Zimmermann, 2000) and uncertainties have been identified in the results of different statistical methods (Graham *et al.*, 2008; Elith and Graham, 2009; Naimi *et al.*, 2014).

We tested several statistical models (GLM, BRT, RF, MARS, MAXENT, Bioclim, and Maxlike) incorporating presence/pseudo-absence data to compare whether the results varied. The discrimination power (i.e. AUC) did not show substantial differences in the models incorporated static and movement

data. It may relate to the nature of absence data which characterized environments in the study region (Hijmans and Elith, 2017).

Additionally, we compared ensembles incorporated static and movement data by outcome agreement index, and in general the concordance is substantial for each species. However, visual comparison between ensembles shows utmost areas predicted as unsuitable habitats with the use of static data, were identified as such when movement data incorporated (Figure 3.4). This might be interpreted as the effect of pseudo-absence data, but it can be biased and incomplete as discussed in the literature on detectability (e.g. Kéry, Gardner and Monnerat, 2010).

As a non-migratory bird and native in North America, wild turkey has a limited distribution. Its movement data also is confined to a portion of the native habitat. However, habitat suitability derived from GBIF dataset shows a vast range of distribution, which may be due to presence data of the birds escaped from captivity or introduced to other parts of the world. The constraint in geographical range of movement data can be perceived the reason of the vastness of false negative areas (Figure 3.4a). However, the extent of true negative areas showing considerable similarity between the outcomes of both datasets might be an effect of non-presence data generated in the models.

Table 3.2 The AUC of 7 SDMs incorporated static and movement data

Models Species		GLM	BRT	RF	MARS	MAXENT	BIOCLIM	MAX-LIKE
Wild Turkey	GBIF	0.85	0.89	0.98	0.94	0.94	0.91	0.81
	Movebank	1	0.99	1	1	1	0.94	0.98
Montagu's harrier	GBIF	0.89	0.90	0.99	0.95	0.96	0.93	0.77
	Movebank	0.88	0.89	0.99	0.94	0.95	0.92	0.84
Great white pelican	GBIF	0.84	0.85	0.99	0.92	0.94	0.87	0.82
	Movebank	0.98	0.97	1	0.99	0.99	0.98	0.91

Table 3.3 The TSS of 7 SDMs incorporated static and movement data

Models Species		GLM	BRT	RF	MARS	MAXENT	BIOCLIM	MAX-LIKE
Wild Turkey	GBIF	0.63	0.66	0.91	0.78	0.79	0.68	0.62
	Movebank	0.99	0.94	1	1	1	0.88	0.97
Montagu's harrier	GBIF	0.64	0.68	0.93	0.77	0.80	0.71	0.61
	Movebank	0.65	0.70	0.93	0.78	0.81	0.73	0.63
Great white pelican	GBIF	0.59	0.58	0.92	0.70	0.74	0.63	0.61
	Movebank	0.94	0.89	0.99	0.95	0.95	0.94	0.79

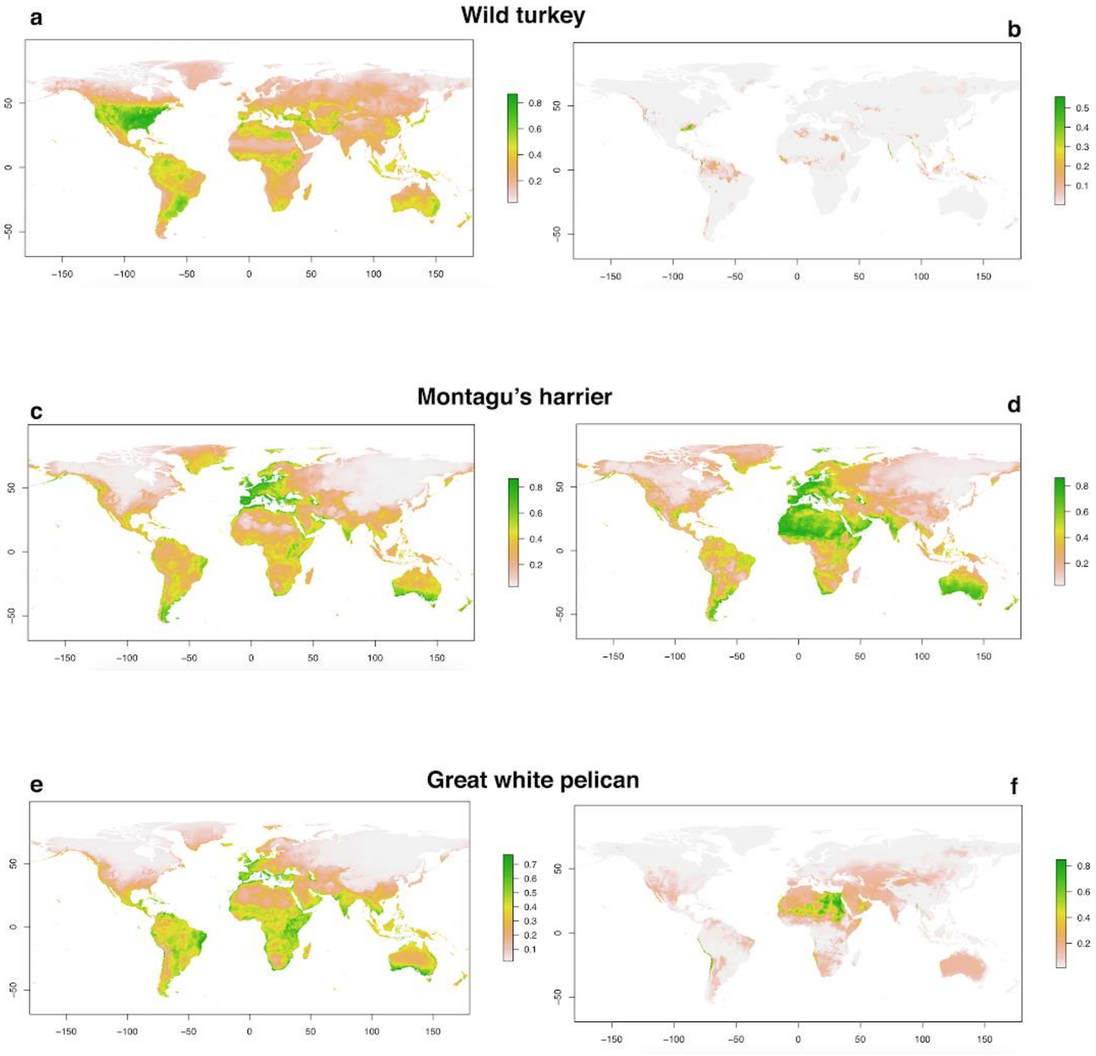

Figure 3. 2 Habitat suitability for three species derived from GBIF (a, c, and e) and Movebank (b, d, and f) datasets.

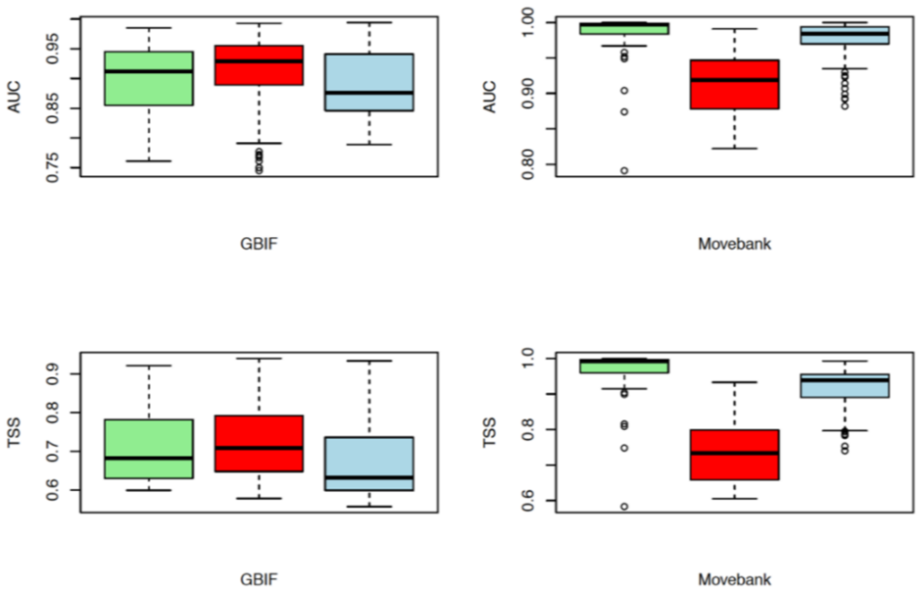

Figure 3. 3 Comparing AUC and TSS between SDMs incorporated GBIF and Movebank data for wild turkey (green), Montagu's harrier (red), and great white pelican (blue).

The high value of agreement also occurred in the ensembles of Montagu's harrier (Figure 3.3 b): showing a great portion of true negative areas from both datasets. On the other hand, the false negative areas depicts a failure in discrimination of suitable habitat by movement-derived models. Furthermore, the unsuitable areas derived from static-ensemble is discriminated as opposite by movement data, as there are coordinate positions showing the presence of the species in the region. Finally, comparison of the predicted suitable habitats (true positive areas) for great white pelican shows limited similarity in geographical distribution (Figure 3.4.c). This may be because the GBIF dataset lacks presence data of that migratory bird, but Movebank includes it. Therefore, the movement data can be also considered as a complementary independent source in SDMs.

It should be considered that 'movement' used here reflects its usage in recent SDM applications and refers to cumulative and collective movement of the three bird species across a broad time scale, not to the daily movement of a single individual. In addition, incorporating movement data in SDMs is essential to identify changes in collective distribution over time, especially in the context of climate change.

Our study is one step forward to have more insight into incorporating movement data in distribution modelling. The 'BAM' framework within the SDM concept is becoming increasingly popular to identify the factors impacting the geographic distribution of species (Holloway, Miller and Gillings, 2016). Through this framework, movement, which enables species to access the potential habitats (e.g. via dispersal or migration), is important, but understudied yet. The importance of incorporating movement data in SDMs predicting habitat suitability cannot be overstated, as the results of SDMs which disregard movement is subject to high levels of uncertainty. More studies are needed to focus on uncertainty for future refinement of models. In addition, it is noteworthy that areas beyond the dispersal capacity may be projected as a low habitat suitability caused by the lack of presence observations instead of unsuitable abiotic and biotic conditions (Barve *et al.*, 2011). Therefore, more telemetry data of a species would ultimately lead to more realistic estimate of suitable habitat. It may provide opportunity to investigate how using movement paths can be incorporated in SDM (Holloway, Miller and Gillings, 2016). This is the first study that has compared the discrimination capacity of the methods of incorporating movement data in SDM, and as such should serve as a foundation for studies aimed at predicting dispersal alongside species' future distributions under climate change scenarios.

Understanding the environmental preferences of species and movement in a suitable habitat or in a new landscape is important for conservation policy and practices (Doherty and Driscoll, 2018). The spatial dynamics of a species in the context of conservation planning and practices underline areas of use and connectivity (Baguette *et al.*, 2013). However, this line of study in SDM

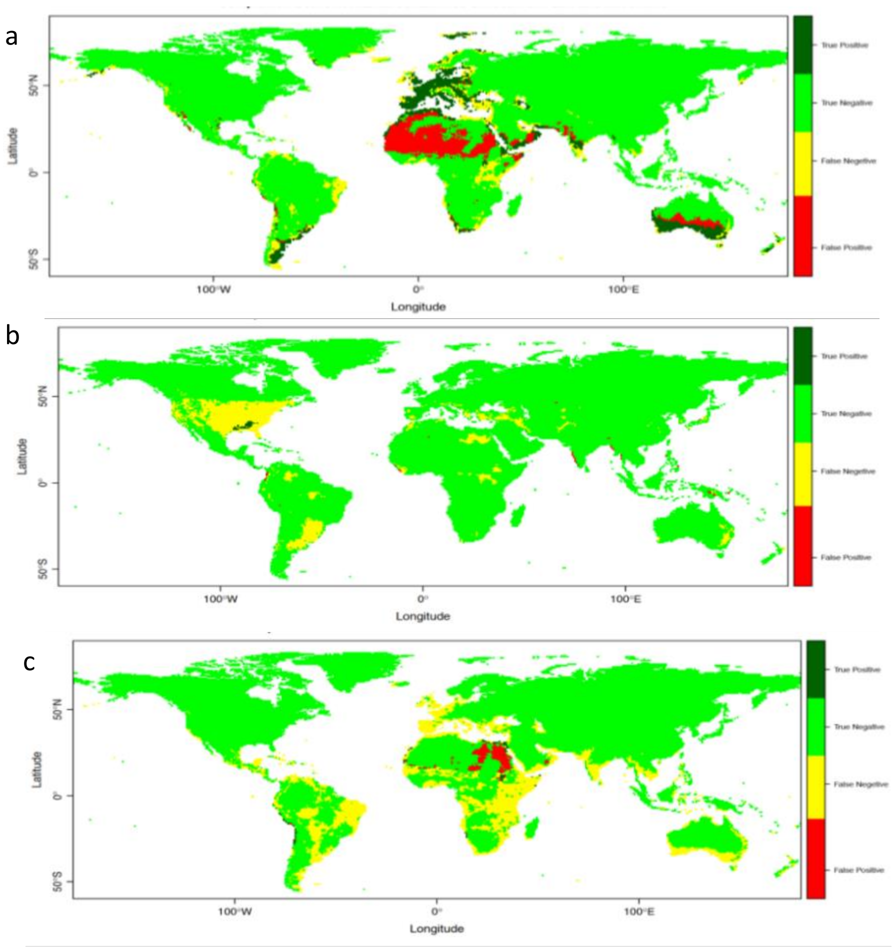

Figure 3. 4 Comparison between suitable and unsuitable habitats derived from GBIF and Movebank data for a) wild turkey, b) Montagu's harrier, and c) great white pelican. Dark green (true positive): SDMs predicted suitable habitats using both datasets. Light green (true negative): unsuitable habitats derived from GBIF datasets, recognized as such when Movebank datasets were incorporated. Yellow (false negative): SDMs discriminated suitable habitats incorporating GBIF datasets, but unsuitable from Movebank datasets. Red (false positive): areas predicted as unsuitable habitats from GBIF and suitable from Movebank dataset.

has lagged behind the availability of technology (Holloway and Miller, 2017). Considering the rocketing volumes of movement data collected at the individual levels (Block *et al.*, 2011; Bruneel *et al.*, 2018), the development of methods to integrate independent and different sources of data is of high value in wildlife management and conservation.

Birds, like other mobile species, inhabit dynamic three-dimensional spaces rather than fixed, point-based and spatially well-aligned habitats. Thus, all physically accessible space should be considered as potential habitat (Bruneel *et al.*, 2018). To develop efficient conservation practices, it is crucial to know the position and time of species presence, especially when a threat may occur (Wilcove 2010). This will be further discussed in the next chapter.

Postface

This chapter explained the capacity of individuals' movement data for characterizing habitat suitability. It also discussed the importance of knowing where a species might occur for conservation purposes. The next chapter further develops this work by using individual movement data to understand better an individual's use of space in volumetric analysis.

Chapter 4

Individual's Movement Data to Estimate Space Use in Volumetric Analysis[*]

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[*] This chapter is based on:
Khosravifard, S. Skidmore, A.K., Naimi, B., Venus, V., Munoz, A.R. & Toxopeus, A.G. 2020. Identifying Birds' Collision Risk with Wind Turbines Using a Multidimensional Utilization Distribution Method Wildlife Society Bulletin. 44(1), pp.191–199.

Preface

This chapter explores the fourth hypothesis of the thesis related to the use of individual movement data to estimate the utilization distribution in three-dimensional space. It hypothesises that vertical movement data can improve the accuracy and credibility of the home range estimation.

Abstract

Renewable energy now plays a key role in reducing greenhouse gas emissions. However, the expansion of wind farms has raised concerns about risks of bird collisions. We have therefore studied different methods used to understand if birds' flight occurs over wind turbines and found kernel density estimators outperform other methods. Previous studies using kernel utilization distribution (KUD) have considered only the two horizontal dimensions (2D). However, if altitude is ignored, an unrealistic depiction of the situation may result because birds move in three dimensions (3D). We have quantified the 3D space use of the Griffon vulture (Gyps fulvus) and, for the first time, their risk of collision with wind turbines in an area in the south of Spain. The 2D KUD showed a substantial overlap of the birds' flight paths with the wind turbines in the study area, whereas the 3D kernel estimate did not show such overlap.

Our aim was to develop a new approach using 3D kernel estimation to understand the space use of soaring birds; these are killed by collision with wind turbines more often than any other bird types in southern Spain. We determined the probability of bird collision with an obstacle within its range. Other potential application areas include air fields, plane flight paths and tall buildings.

4.1 Introduction

Wind farms have received public and government support as a clean source of renewable energy because they do not cause air pollution as does the burning of fossil fuels (Stigka *et al.* 2014, Yuan *et al*. 2015). The use of wind energy is therefore expanding rapidly worldwide. The Global Wind Energy Council reported that 2015 was another record-breaking year for the wind energy industry (Global Wind Energy Council, 2016).However, wind farms may be causing a large numbers of fatalities to flying animals (De Lucas *et al.* 2012a, Zimmerling & Francis 2016), affecting a large area of potentially suitable soaring-habitat around them (Marques *et al*. 2019). Therefore, the expansion of wind farms has raised concerns about their negative impact on habitats and wildlife populations.

Relatively high collision fatality rates have been recorded at several large wind farms in locations with many birds and show that turbines pose a risk, especially to large raptors and other soaring birds. The Griffon vulture is one of the raptors frequently killed by collision with wind turbines in southern Spain (Olea and Mateo‐Tomás 2014, De Lucas *et al*. 2012a , De Lucas *et al*. 2008, Barrios and Rodríguez 2004). For instance, Carrete *et al.* (2012) found 342 dead Griffon vultures during a 10-year period (January 1998–March 2008) in an area of 34 wind farms with 799 turbines in the province of Cádiz, southern Spain.

To develop efficient conservation practices, it is necessary to know where and when a threat of collision may occur (Wilcove 2010). The two most common approaches, namely home range and utilization distribution, have been used to depict and portray animal movements and their space use (Kie *et al.* 2010, Monsarrat *et al.* 2013, Rutz & Hays 2009, Tomkiewicz *et al*. 2010). The home range is the area "traversed by an individual [animal] in its normal activities of food gathering, mating and caring for young" (Burt 1943), whereas the utilization distribution reflects the animal's spatial use probability density (Van Winkle 1975). Recently, the home range has been viewed as one attribute of the animal's utilization distribution. Animal space use has been quantified using different methods such as minimum convex polygon (Mohr 1947), bivariate normal method (Jennrich & Turner 1969), grid square method (Macdonald, Ball & Hough 1980, Siniff & Tester 1965), population utilization distribution (Ford & Krumme 1979), and kernel density (Worton 1995). Several methods have recently been developed for the time-explicit estimation of animal space use, such as the dynamic Brownian bridge movement model (Kranstauber *et al.* 2012) and bivariate Gaussian bridges (Kranstauber *et al*. 2014). The kernel density estimator method has low bias (Seaman & Powell 1996, Worton 1995), and greater flexibility in handling complex location patterns (Worton 1989) and in assuming location independence (Benhamou & Cornélis 2010, Fieberg 2007).

So far, most studies estimating animal home ranges or utilization distributions have only considered the two horizontal dimensions (Cagnacci *et al.* 2010, Fleming *et al*. 2015, Katajisto and Moilanen 2006, Powell and Mitchell 2012). If altitude—the third dimension—is neglected, an unrealistic depiction of reality may be attained for species moving in three-dimensional (3D) space, such as birds, bats, fish, or climbing species (Belant *et al.* 2012, Monterroso *et al*. 2013). However, few studies have quantified space use patterns in 3D. For instance, Koeppl *et al.* (1977) presented a model based on an ellipsoid of a particular size, shape, and orientation in space. It was one of the first models used to compute home range in 3D. Hindell *et al.* (2011) quantified the 3D space use of five different species (two mammals and three bird species). They highlighted that the highest concentrations of locations of southern elephant seals occurred within the 1000 m bathymetric contour.

Simpfendorfer *et al.* (2012) calculated the utilization distribution of European eels (Anguilla anguilla) using 2D and 3D kernel density. They emphasized that the 2D analysis overestimated the amount of movement overlap between individuals by 13-20%. Recently, Cooper *et al.* (2014) studied the 3D space use and overlap of American Redstarts (Setophaga ruticilla) using a direct observation method for data collection and kernel density estimator. Their study was confined to observing focal territories throughout each sampling period, with birds located visually and the altitude estimated by observers. The number of locations for each observed bird was also limited. Nevertheless, their findings concurred with a former study on the overestimation by 2D analysis compared to the 3D method. They also found that American Redstarts may avoid areas of overlap, presumably to limit interactions with neighbours.

Here we describe how we collected locations of an individual Griffon vulture with the use of a bio-logger, quantified the bird's 2D and 3D utilization distributions, and, for the first time, its collision risk with wind turbines using KUD. We demonstrate that volumetric analysis (3D) is more informative than planar analysis (2D) in utilization distributions. We show that neglecting the third dimension would provide incomplete depiction of the aerial species' space use, whereas 3D kernel estimators can not only be used to improve our understanding of the bird's movements, but they can also be considered as a way to determine wildlife collision risk with an obstacle in the territory or home ranges in conservation plans.

4. 2 Materials and methods

4.2.1 Study area

The study area was located in the natural park of El Estrecho, in Tarifa (southern Spain); it lies on the northern shore of the Strait of Gibraltar (Figure 4.1); 36°07′-36°06′ N, 5°45′-5°46′ W). This area is the most southern protected area in Europe. It is a maritime-terrestrial park along 54 km of coastline in Andalusia and it is an Important Bird Area (BirdLife International 2017, Guerra García *et al*. 2009). In this area, Ferrer *et al.* (2012) reported the highest collision rates ever published for birds (1.33/turbine/year) with the Griffon vulture being the most frequently killed species (0.41 deaths/turbine/year). There are several Griffon vulture colonies in the area, consisting of approximately 320 breeding pairs in total. We focused on colony at an escarpment running north-south, 4 km from the Strait of Gibraltar; with approximately 65 breeding pairs (Del Moral 2009). Our analysis is constrained to the space used by one tagged Griffon vulture; the space encompassed an area of 152 km2 and included 20 wind farms with 269 operational turbines. The turbine specifications are shown in table 4.1.

Table 4.1 Wind turbine data: model name, ID-number, hub height, blade length and total height (in meters)

Model	Colour on	ID-number of turbine	Hub height	Blade length	Total height
ECOTECNIA ECO-74	●	34	70	35.5	105.5
ENERCON E-70	●	20	84	33.5	117.5
GAMESA G-80	●	30	67	40	107
GAMESA G-87	●	11	78	42.3	120.3
MADE AE-56	●	43	60	27.25	87.25
MADE AE-59	●	55	60	28.75	88.75
VESTAS V-72	●	4	78	36	114
VESTAS V-80	●	6	78	40	118
VESTAS V-90	●	66	80	44	124

4.2.2 The species and tracking system

A Griffon vulture was captured using a foot-snare trap. The bio-logger was attached as a backpack using a harness made of teflon ribbon with one strap fitted across each wing and another strap below the crop (Kenward 2000). The capture and release took place on September 11, 2010. Distinctive yellow patagial markers, with a unique combination of numbers and letters (i.e. 9FJ) were also attached to both wings. This method was shown to be harmless to the bird and led to no detectable changes from its normal behaviour (Reading *et al.* 2014). Our Griffon vulture was a male, sub-adult, and with a body mass of about 7 kg.

We used the Bird Tracking System developed at the University of Amsterdam (Bouten *et al*. 2013). The key features of this bio-logger are solar rechargeable batteries, light weight (45 grams, <0.6% of body mass), two-way data-communication, four-megabyte flash memory (capable of storing 60,000 GPS fixes), and a GPS tag with high resolution temporal intervals from 3 to 7,200 seconds. This bio-logger had a biometric pressure sensor and it transferred the GPS data (with 3D coordinate positions) to a base station. It could be programmed remotely using the BirdTracking software (http://www.uva-bits.nl/). The positional and altitude mean errors were 1.13 m and 1.42 m as shown by a test of stationary bio-loggers GPS in open space (Bouten *et al*. 2013). We used the GPS fixes and their properties to quantify the Griffon vulture's 3D movement in order to determine the overlap of air space use between the bird and the wind turbines.

We retrieved the GPS fixes of our Griffon vulture for 18 months (February 2012–July 2013). This data comprised 169,778 locations at 5-minute intervals.

The procedures of this research, including the bird trapping and bio-logger tagging were conducted with permission from the Consejería de Medio Ambiente of the Junta de Andalucía (Regional Council for the Environment).

4.2.3 Data analysis

As the Griffon vulture is a diurnal species, only data points during daytime (i.e. from dawn till dusk) were considered and stationary locations (speed < 4 m/s) were filtered out. The remaining 12,611 locations were used to quantify KUDs (50% and 95%) in 3D. 50% KUDs are most commonly calculated to depict the core activity space, while 95% KUDs are used to describe its extent (e.g. Benhamou & Cornélis 2010). The multivariate kernel density estimate is defined by:

$$\hat{f}_h(x) = n^{-1}\sum_{i=1}^{n} h^{-d}K\left(\frac{x_1 - X_{i1}}{h_1}, \dots, \frac{x_d - X_{id}}{h_d}\right)$$

(Equation 4-1)

where x = (x1, x2, …, xd) is an independent and identically distributed sample of a random variable X, h is the bandwidth, and K is the kernel function of dimensions d.

We used a plug-in bandwidth selector to estimate the smoothing factor matrix. This method provides adequate results in the utilization distribution estimation and requires less intensive computation compared to other methods, such as least squares cross-validation (LSCV) or the reference method.

We quantified monthly 2D and 3D KUDs (50% and 95%) for the Griffon Vulture using the "ks" package (Duong 2007) in R Statistical environment (version 3.2.3, www.r-project.org, accessed 5 September 2016). At the location of each turbine, we extracted the value of probability density generated by the 2D kernel function. In a similar fashion, we extracted the density values generated by the 3D kernel, but this time the total height of a turbine (i.e. turbine height plus blade length) was considered. This is the sum of the turbine's height, the length of a blade, and the land elevation determined using a digital elevation model (DEM).

In addition, we consider the value for the probability density in both 2D and 3D KUD as a proxy of the plausible collision risk. Then we used the Mann-Whitney-Wilcoxon test to examine any significant differences in the extracted values. In 2D and 3D KUD, values above the third quartile (i.e. the highest 25% of the values) were selected as a proxy for plausible collision with high risk. The frequency distribution of plausible risk pertaining to the turbines was calculated to determine which turbines might be relatively dangerous in the course of data gathering.

4.3 Results

The 2D KUD of our tagged Griffon vulture showed that all the wind turbines are located in the core and extended home range, where the KUD values were relatively high and may explain the birds' relatively frequent collisions with the turbines (Figure 4.2). The values extracted from the 2D KUD were significantly higher than for the 3D model at the turbine locations (Mann-Whitney-Wilcoxon Test $p < 0.001$).

The 3D kernel estimation of the Griffon vulture's occurrence covered a large space use (Figure 4.3): 50% and 95% KUD were estimated to be 476 km3 and 11120 km3, respectively. The values extracted from the 3D kernel estimation showed a high probability density in the winter and early spring of 2012 and of 2013.The results showed that there was no sign of collision risk in May and June in both years because the Griffon vulture was not then in the vicinity of the turbines. However, the concentration of collision risk increased in March and April of both years (Figure 4.4).

In 3D space, just three turbines had a relatively high risk (i.e. above the third quartile) in 12 out of 17 months, whereas seven turbines appeared to have such a risk in 2D space. The maximum number of turbines that had a relatively high risk in 3D and 2D space were 55 and 62, respectively.

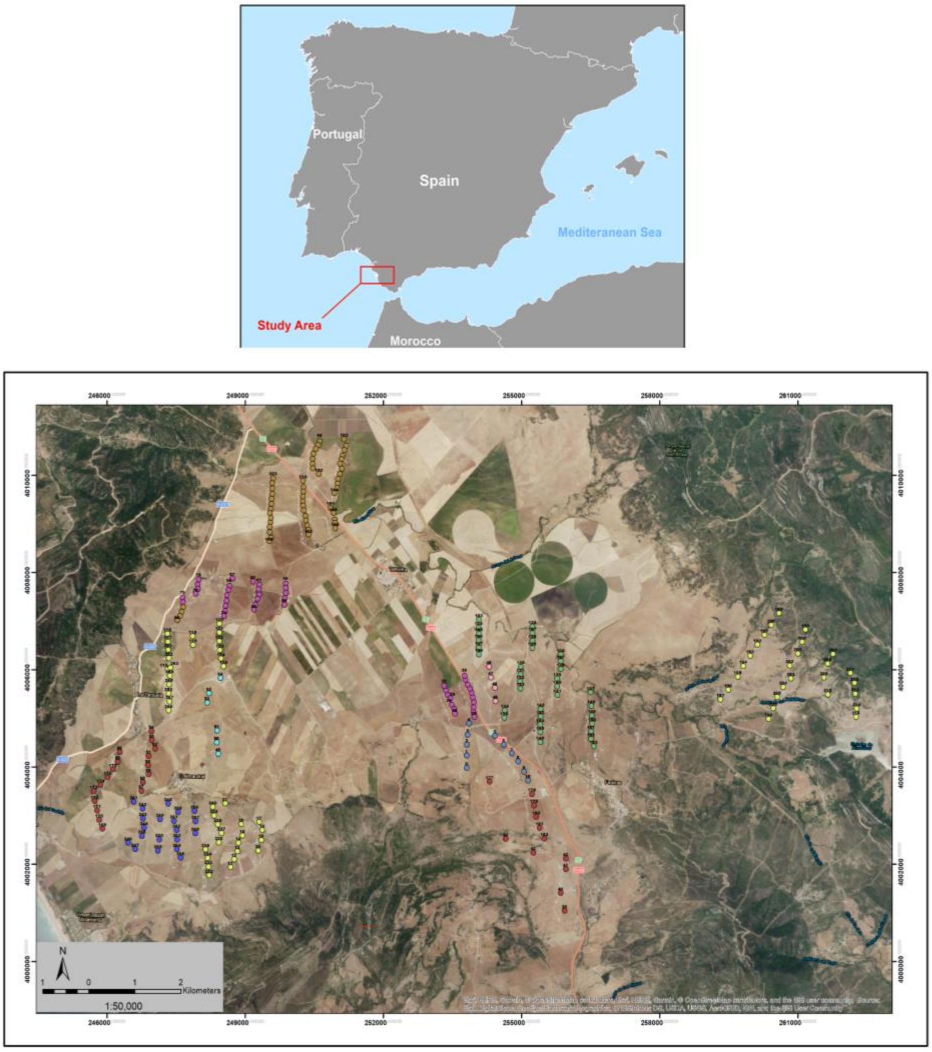

Figure 4. 1 The study area is part of the El Estrecho natural park in Tarifa (southern Spain) and lies on the northern shore of the Strait of Gibraltar. The Griffon vulture colony (red square) is located at an escarpment close to wind turbines (colourful circles with numbers, each colour represents a group of identical turbines).

The high risk occurred in one month for 3D and in three months for 2D space use (Figure 4.5). The turbines located in the southern part of the study area, in the vicinity of the Griffon vulture colony, had a relatively high risk of collision in both the 3D and 2D analyses (Figure 4.6).

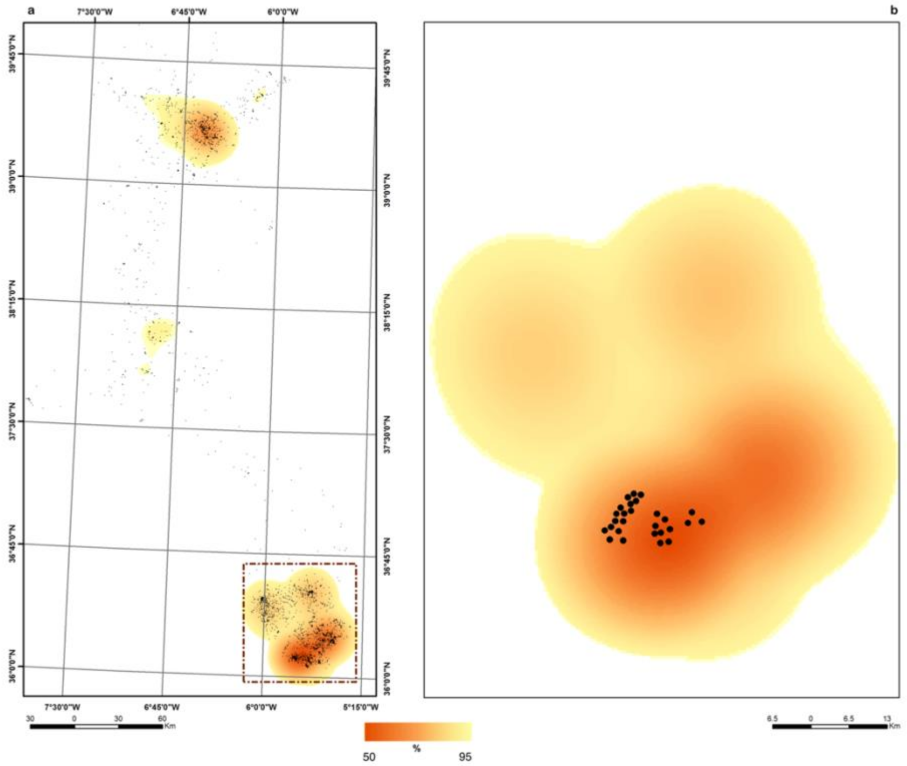

Figure 4. 2 The activity space of our tagged Griffon vulture estimated by 2D kernel utilization distribution (KUD) for 17 months (February 2012 to July 2013). Panel (a) demonstrates the bird's entire activity space use, while panel (b) depicts the portion where wind turbines are located (black circles represent a portion of entire turbines).

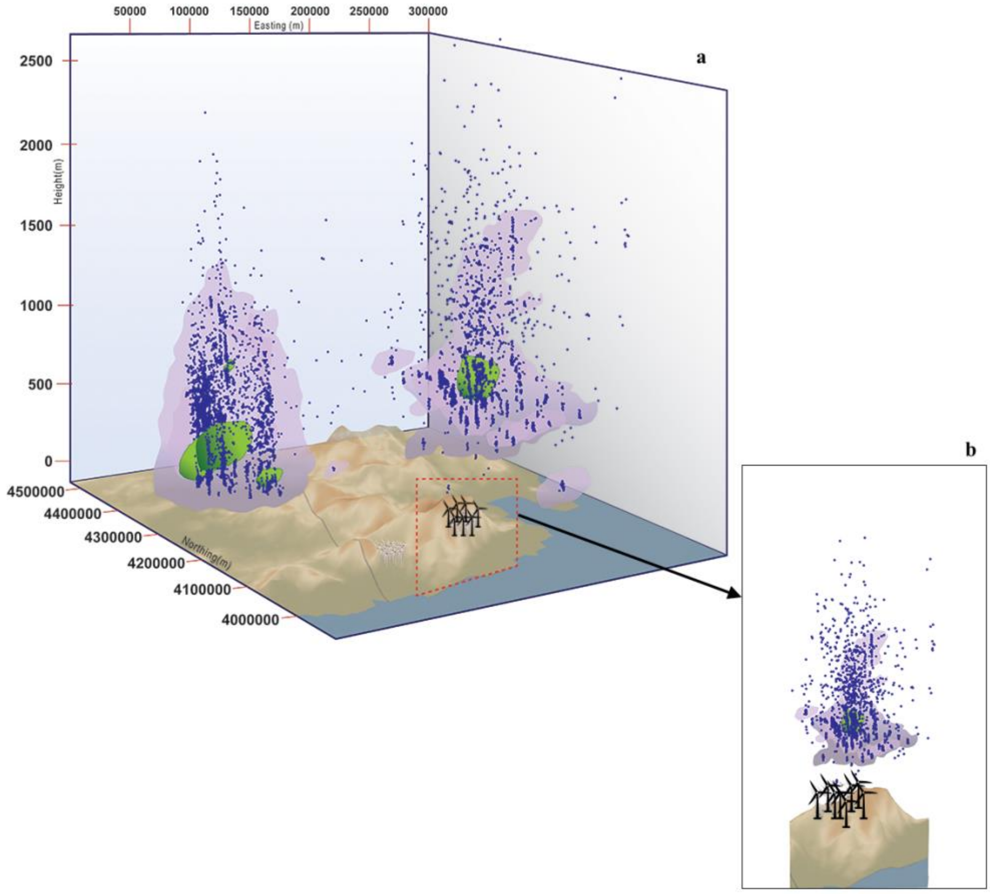

Figure 4. 3 (a) Representation of 3D KUD of a Griffon vulture for 17 months (February 2012 to July 2013). The green and purple shapes indicate 50% and 95% KUDs. The digital elevation model DEM) is illustrative. Panel (b) reveals that, in 3D space use, there is no overlap between the birds' space use and the wind turbines.

4.4 Discussion

We have used kernel utilization distribution (KUD), for the first time, to understand the plausible collision risk between wind turbines and bird occurrence. Our results demonstrate the advantage of 3D KUD for modelling the birds' 3D space use and, in particular, the comparative risk of a bird colliding with a turbine. Although 2D analyses are useful to summarize information on the location of individuals (Simpfendorfer *et al.* 2012), volumetric analyses (i.e. with altitude added as a third dimension) provide a more detailed depiction of species occurrence. Using a 3D KUD, we show that the most dangerous times and highest risk turbines can be identified. This information can be used to reduce the mortality rate caused by bird collisions with turbines and offers leads to wildlife managers on how to minimize the probability of such collisions (Belant *et al.* 2012).

So far, the probability of collision has been studied by analysing a range of complex factors such as the species' flight behaviour, topography, and weather (De Lucas *et al.* 2008). Those studies were conducted with the aim of reducing the birds' mortality rate at wind farms, particularly of raptors (Barrios and Rodríguez 2004, Bellebaum *et al.* 2013, DeVault *et al.* 2005, Drewitt and Langston 2008, Tellería 2009).

However, 3D space use was not considered so far and we show that this has a major impact on the results. A trial mitigation measure was instigated by Regional Council for the Environment in 2008-2009, that power companies selectively stopped some wind turbines when raptors were observed in their vicinity. This measure reduced the Griffon vulture fatality rate by 50% (De Lucas *et al.* 2012a). The trial also demonstrated that the distribution of Griffon vulture mortality was not uniform, which is consistent with our results from the 3D KUD approach.

In Europe, an environmental impact assessment (EIA) is required prior to the construction of new wind farms. The anticipated impact of the development on a site's bird population is included in the EIA (Environmental Impact Assessment Directive 97/11/EC). Ferrer *et al.*

(2012) ascertained that risk assessment studies had erroneously assumed a linear relationship between the frequency of observed birds and fatalities. They concluded that the correlation between predicted and actual fatalities can be improved by changing the scale of studies and concentrating on the location of each proposed turbine. Our findings, with the focus on the location of the turbines, support this conclusion and offer a new tool for performing such calculations. Specifically, the proxy of plausible collision risk per turbine can be estimated by deriving the values generated by 3D KUD. This 3D model can assist wind farm developers to calculate the risk

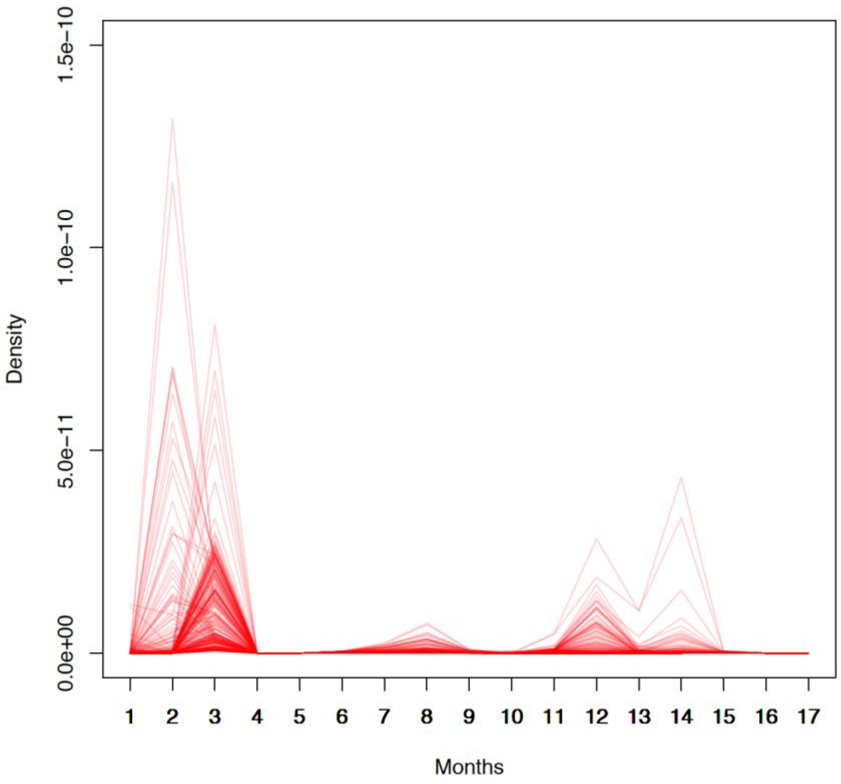

Figure 4. 4 The value of probability density extracted from 3D KUD at the location of the wind turbines shows a relatively high space activity in the winter and early spring of 2012 and 2013.

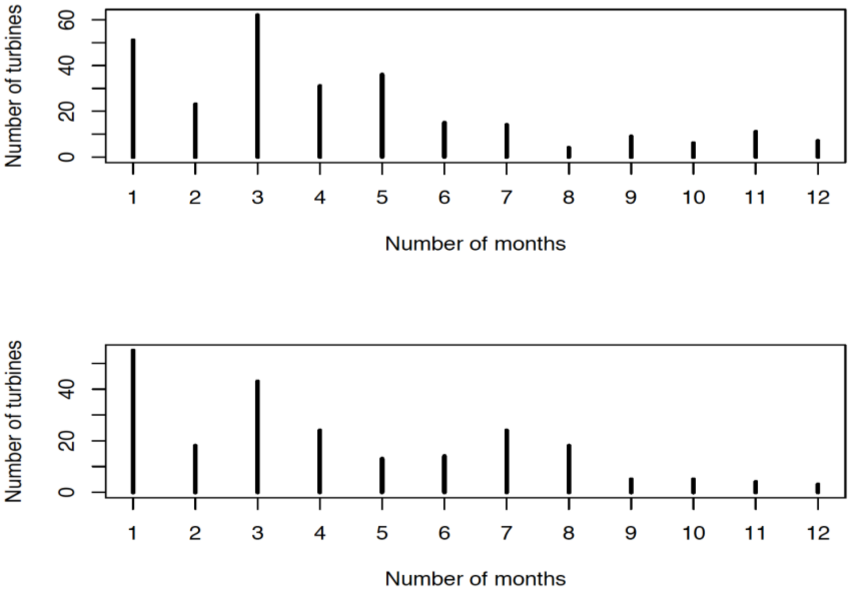

Figure 4. 5 Distribution of the number of turbines and relative months of plausible collision with a relatively high risk in 2D- (above) and 3D-space (below).

of installing a turbine at a specific location. Our 3D approach could also be used during the post-construction and operational phases of wind farms, helping management to predict periods of high risk and reduce the number of bird collisions by selectively curtailing certain wind turbines.

We purposely used recorded movement data for a tagged Griffon vulture rather than simulated data to depict the real situation. Since Griffon vultures have similar flight and foraging behaviour (Bosè and Sarrazin 2007, Mateo-Tomás & Olea 2011, Xirouchakis and Andreou 2009), the results may be generalized to other individuals. Although this new application of 3D KUD, as presented here, can be used for identifying collision risk between obstacles and species in 3D space, some aspects of the method need to be investigated further. For example, more research into producing easily interpretable results with confidence measures is needed. In addition, spatiotemporal

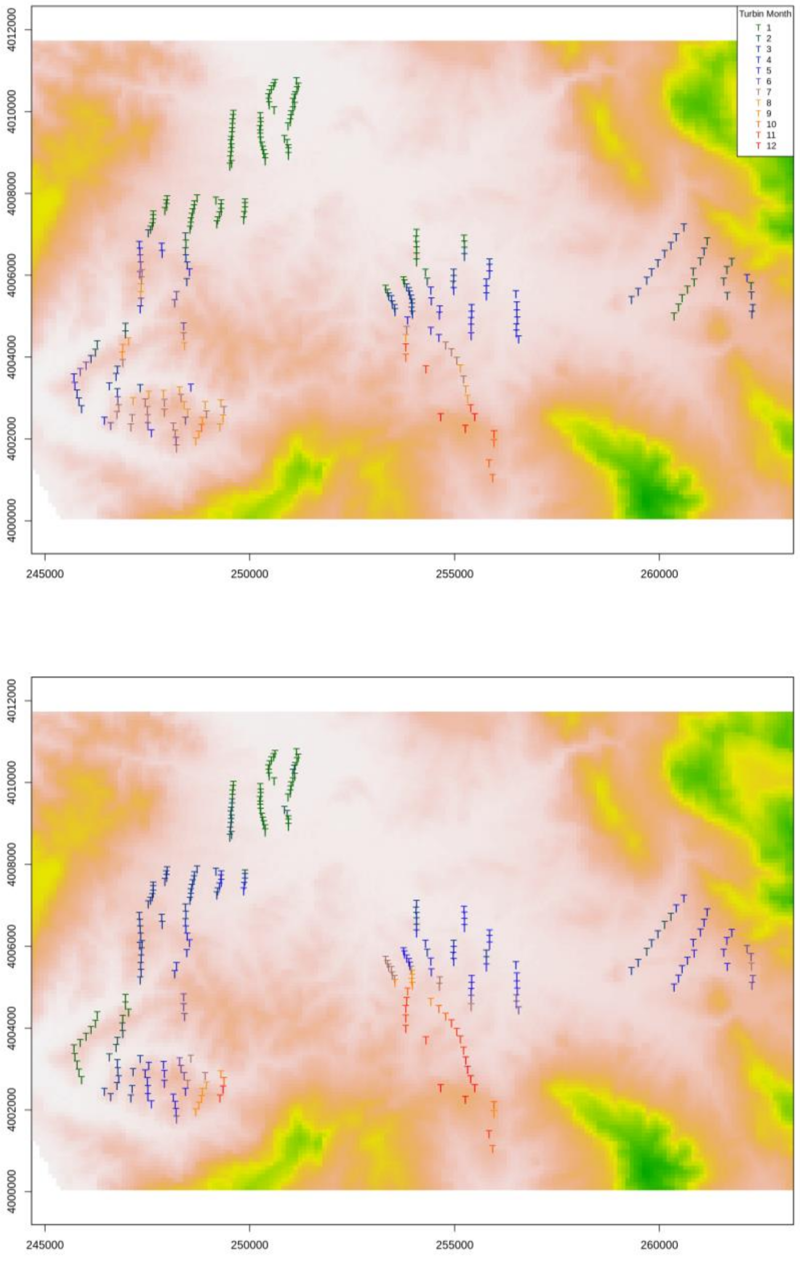

Figure 4. 6 Location of the turbines and the number of months with a high collision risk in 2D (above) and 3D space use (below).

autocorrelation in movement data is an important issue since this yields an underestimation of an individual's space use (Fleming *et al.* 2015). So far, in animal movement research, many studies have focused on autocorrelated data in 2D (Fieberg 2007, Fleming *et al.* 2017), whereas 3D data studies might well be required. We expect this new application of 3D KUD to offer exciting opportunities for exploring the process of volumetric analysis in animal movement research, such as spatial autocorrelation in estimating risk and the need to develop methods for 3D kernel density estimators.

4.5 Acknowledgments

Our bird behaviour studies are supported by the UvA-BiTS virtual lab, with contributions from the Netherlands eScience Center, SURF Foundation, and LifeWatch-NL. We thank members of the Migres Foundation, especially Miguel González, for his technical support during the fieldwork. We thank Aidin Niamir for valuable technical support in analysis and Jackie Senior for editing the manuscript.

Postface

The chapter showed that incorporating the vertical movement data to space use analysis improves the accuracy and credibility of home range maps. It also proved that the 3D volumetric analysis a realistic depiction of species occurrence. This chapter discussed that the approach could be used for conservation purposes to reduce the collision rate of species with a human-made obstacle. The next chapter explores movement (i.e. flight) types with the use of high-resolution data.

Chapter 5

Individual's Movement Data to Identify Flight Types[*]

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[*] This chapter is based on:
Khosravifard, S., Venus, V., Skidmore, A.K., Bouten, W., Munoz, A.R. & Toxopeus, A.G. 2018. Identification of Griffon vulture's flight types using high resolution tracking data. *International Journal of Environmental Research* 12, 313-325

Preface

This chapter aims to complete our work with movement data. It explores the last hypothesis of this thesis testing whether movement patterns (i.e. flight types of a soaring bird) can be classified using the movement data. This chapter provides further insight into movement and flight behaviour.

Abstract

Being one of the most frequently killed raptors by collision with wind turbines, little is known about the Griffon vulture's flight strategies and behaviour in a fine scale. In this study, we used high-resolution tracking data to differentiate between the most frequently observed flight types of the Griffon, and evaluated the performance of our proposed approach by an independent observation during a period of 4 weeks of fieldwork. Five passive flight types including three types of soaring and two types of gliding were discriminated using the patterns of measured GPS locations. Of all flight patterns, gliding was classified precisely (precision = 88%), followed by linear and thermal soaring with precision of 83 and 75%, respectively. The overall accuracy of our classification was 70%. Our study contributes a baseline technique using high-resolution tracking data for the classification of flight types, and is one step forward towards the collision management of this species.

5.1 Introduction

Flight and foraging behaviour, and migration of the Griffon vulture (Gyps fulvus, Hablizl, 1783) have been well studied (Bildstein *et al.*, 2009; Duriez *et al.* 2014, García-Ripollés, *et al.*, 2011; Houston, 1974) (see appendix). However, little is known about the fine-scale flight and motion capacity of this species, which is on the top list of most frequently killed raptors by collision with wind turbines in southern Spain (Barrios & Rodríguez, 2004).

Flight type plays an important role in collision risk with wind turbines, especially when associated with hunting and foraging strategies of big raptors (Marques *et al.*, 2014). Hoover and Morrison (2015) highlighted that soaring flight, which needs strong wind and occurs in rotor swept zone of wind farm, is a factor explaining the high collision rate of raptors.

The motion capacity of an individual is its ability to move in various ways or modes either by its own locomotion or by externally vectored via physical means (e.g. winds, water flow, etc.) or by other organisms (e.g. wingless flower mites traveling on foraging bees) (Holyoak *et al.*, 2008). Generally, a movement paradigm was introduced as the interplay amongst the four basic mechanistic components: external factors affecting movement, internal state (i.e. why move?), navigation capacity (i.e. where and when to move?) and motion capacity (i.e. how to move?) (Holyoak *et al.*, 2008; Nathan *et al.*, 2008). A more detailed understanding of the motion capacity of flying birds has been developed in many ornithological studies (Cone, 1962; Dhawan, 1991; Pennycuick, 1971, 1972; Tucker, 1998; Videler, 2005). Soaring and gliding are the two most common types of flight among raptors and have been at the centre of many studies since the first attempt to understand raptors' flight behaviour in 1913 (Dhawan, 1991). However, a major challenge underlying studies of movement type is of a methodological nature, related to data collection and the methods used to classify the movement patterns.

With respect to data collection, researchers have traditionally used direct observation as a method to monitor birds, as well as to elucidate and describe flight phenomena (C J Pennycuick & Scholey, 1984). Bildstein and colleagues (2009), for example, used this method during the autumns of 2004 to 2007 to determine Griffon vultures' flight types during migration. Not losing sight of an animal is the most challenging part of this traditional type of research (Pennycuick, 1973), but this has now been solved by telemetry techniques. These methods provide practical insight into wildlife movements (for instance see Harel *et al.*, 2010, Bouten *et al.* 2013 and López-López *et al.* 2013).

Techniques for studying free-living birds' behaviour have advanced and flourished since these earlier attempts (Roy & Hart, 1963). Since then, technologies including radar (Konrad, Hicks, & Dobson, 1968), radio (Schemnitz & Owen, 1969), satellite and Global Positioning System (GPS) tracking (Biro *et al.*, 2002; Nowak *et al.*, 1990; Weimerskirch *et al.*, 2002) have been deployed. Recent advances in telemetry techniques, such as extensive use of bio-loggers with GPS, have enabled spatiotemporal data to be collected on vertebrates with ever-increasing accuracy as well as density of data points (Tomkiewicz *et al.*, 2010).

Much research has been conducted via the classification of movement patterns to solve the difficulties of dealing with large datasets and their interpretation (e.g. Guting *et al.*, 2010). These methods, however, have been used mainly to analyse movement in two dimensions (i.e. x and y) (Giannotti and Pedreschi 2008; Güting & Schneider, 2005; Long & Nelson, 2013)and mostly at coarse temporal resolution (i.e. daily or hourly movements) to determine home range, dispersal and migration routes (Calenge *et al.*, 2009; Kranstauber *et al.*, 2012; López-López *et al.*, 2013; Mandel *et al.* , 2008; Smouse *et al.*, 2010).

Research to date indicates that the Griffon vulture exhibits mainly passive flight types (i.e. various kinds of soaring and gliding) by using air currents, as well as occasional flapping when necessary (Bildstein *et al.*, 2009; Dhawan, 1991). Moreover, using accelerometer data, Halsey *et al.* (2009) proved that the species rarely flaps except during take-off or landings in non-migratory movement. Since soaring birds such as the Griffon vulture are not capable of maintaining constant altitude by flapping flight alone (Newton, 2010; Shepard *et al.*, 2011) and it has also been shown by Bildstein *et al.* (2009) that the flapping rate in the Griffon vulture is very low (i.e. mean of 1.2 flaps per 30 seconds), we made a basic assumption in this study that the flapping rate during daily flights can be considered negligible in non-migratory movement.

Our study utilised collection methods using GPS-logger technology. Based on the high-resolution tracking data only, we developed and tested a baseline method to differentiate passive flight in three spatial dimensions (i.e. x, y and z) to classify these flight types of the Griffon vulture. This study is one step forward to have more insight into flight behaviour which may play a role in collision risk.

5.2 Materials and methods

5.2.1 Study area and species

Our study area in southern Spain is part of the natural park El Estrecho, in Tarifa, Andalucía region, and is located on the northern side of the Strait of Gibraltar (36°07′ – 36°06′ N, 5°45′ – 5°46′ W). The Strait of Gibraltar is the shortest sea crossing between Europe and Africa and is a well-known migratory bottleneck for soaring birds (Bildstein & Zalles 2000). In this area, Ferrer *et al*. (2011) reported the highest collision rates ever published for birds (1.33 deaths/turbine/year) with the Griffon vulture being the most frequently killed species (0.41 deaths/turbine/year). An escarpment with north-south direction, 4 km away from the Strait of Gibraltar, is a location of Griffon vulture's colony, consisting of approximately 65 breeding pairs (Del Moral, 2009) The population is surrounded by several other breeding colonies, consisting of approximately 320 pairs so the area is persistently used by vulture during their local movements (De Lucas *et al*., 2012) and is encompassed by 25 wind farms, consisting of 491 operating turbines. Figure 5.1 shows the study area, location of wind turbines and the colony.

A Griffon vulture was captured using a foot snare. The bio-logger was attached to it as a backpack using a harness made of teflon ribbons with one strap fitting across each wing and another strap below the crop (Kenward, 2000). The capture and release took place on September 11, 2010. Also, distinctive yellow patagial markers, with unique combination of numbers and letters (i.e. 9FJ) were attached to both wings. This method was proved to be harmless to the bird with no changes in its normal behaviour (Reading *et al*. 2014). The captured Griffon vulture was a male, sub-adult, and with a body mass of about 7 kg.

Collison risk may also be influenced by behaviour associated with a specific sex or age. Although it is reported that young vultures were not especially vulnerable to collisions compared with the other age classes (Barrios & Rodríguez. 2004; Marques *et al*. 2014), de Lucas *et al*., 2012 demonstrated that among 117 killed vultures by collision with turbines, 74.36% (87) were juveniles and 25.64% (30) were matures and adults. Additionally, to the best of our knowledge, no information has been published about correlation between sex and collision rate of the Griffon vulture.

5.2.2 Tracking device

We used the Bird Tracking System developed at the University of Amsterdam (Bouten *et al.*, 2013). The key features of its bio-logger are rechargeable solar batteries, low weight style (45 grams, <0.6% of a Griffon vulture's body mass), two way data-communication, four megabytes flash memory (capable of sorting 60,000 GPS fixes) and the GPS tag with high resolution temporal intervals from 3 seconds up to 7,200 seconds (see http://www.uva-bits.nl for more information). In this study, we used GPS fixes and their properties to differentiate between the flight types.

5.2.3 Collecting data from a free-ranging vulture

Tracking data were retrieved for 27 days between May and July 2013. This period was a part of breeding season of the bird. During this time, we also undertook fieldwork observations independent of the tracking dataset. We used a camera recorder synchronized to Universal Time Coordinated (UTC) time with Garmine eTrex Summit GPS along with direct visual observations to note the times and flight types simultaneously. The observations were made by two observers during daylight hours with the aid of 10x42 binoculars and a 20-60X telescope spot. We conducted a filed survey to select the observation locations with a wide angle of view in almost centre of the escarpment: one up and the other down on the cliff with almost 360° and 270° angle of view, respectively. To motivate the Griffon vulture to fly, carrion was dumped on the ground. Additionally, observation points were selected to provide a wide field of view of the tagged bird with the yellow patagial markers on the dorsal and ventral surfaces of wings.

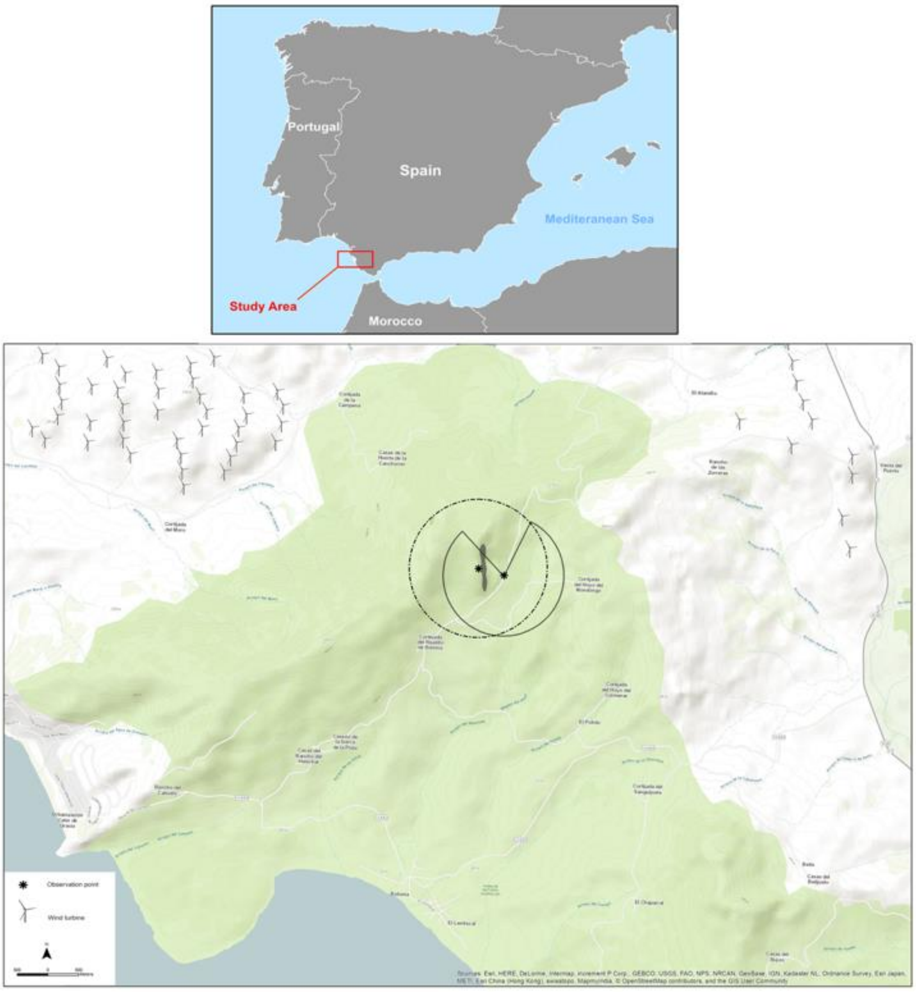

Figure 5. 1 The Study Area in province of Cádiz, south Spain: the grey polygon (bottom) is the location of colony site and the asterisk symbols show the location of observers. The observers' angle of view is shown in solid and dashed line.

5.2.4 Data preparation

Although we had set the measurement interval of the GPS tracker to three-seconds, the retrieved datasets consisted of various intervals. Therefore, to prepare the final dataset, we extracted 11 days of collection data with a three-second interval, yielding 66,766 data points. The instrument recorded several properties for each point including time, geographic coordinates, altitude, and instantaneous velocity in three directions (x, y and z). Based on this raw data we calculated the distance, cumulative distance, average altitude, altitude difference and direction of motion between all successive GPS fixes. To discriminate between flying and non-flying modes, we considered speed of movement and calculated the first non-static points with a speed >4 m/sec (Nathan *et al*., 2012).

5.2.5 Flight types

This paper focuses on five different types of passive flights namely: thermal soaring, linear soaring, slope soaring, gliding, and spiral gliding. Figure 5.2 illustrates all the flight types.

Thermal soaring is characterized by a circular flight in the course of which birds gain altitude in thermal columns using tight curves as close as possible to the centre (Pennycuick, 1973; Pennycuick, 2008; Videler, 2005). The term *linear soaring* was introduced by Pennycuick (1972). It refers to an almost straight flight without circling when thermal currents are strong and abundant (Videler, 2005). Although this term was introduced to describe long distance flight, we have here applied the term to straight flight with a minimum length of 350m in order to discriminate it from slope soaring. *Slope soaring* is a flight type often exhibited by Griffon vultures along their nesting or roosting cliffs. Generally, slope soaring takes place at low altitude. Birds repeat this type of flight parallel to the cliff. This type of flight lasts until they detect a thermal or other air current (Barrios & Rodríguez, 2004; Pennycuick, 1972). It is performed in a shape that can be likened to a figure of eight. *Gliding* refers to flight with wings spread (or folded) in a downward or straight direction (Dhawan, 1991; Pennycuick, 1971; Pennycuick, 2008). *Spiral gliding* is used to reduce altitude in an almost spiral-like pattern, and in slow downward motion towards the ground or to the nesting site. The term spiral gliding is not commonly used in the ornithology literature; it was borrowed from a study that focused on the flight behaviour of seeds dispersed by the wind (see: Minami and Azuma, 2003).

5.2.6 Flight classification

To discriminate between linear flight patterns (i.e. linear soaring and gliding) and non-straight flight patterns (i.e. thermal soaring, slope soaring and spiral gliding), we calculated the radius of curvature parameter by using a minimum of three successive GPS fixes. To further differentiate patterns within each flying type, we applied the laws of motion, as defined in physics, based on the following parameters: distance, altitude, speed and angle of direction.

For the space curve (like a non-straight flight pattern), the radius of curvature is the length of the curvature vector. To calculate the radius of curvature, we combined the flight distance and speed within non-straight flight patterns. In this regard, speed was smoothed with a running mean over three successive GPS fixes.

The curvature *k* is defined as:

$$k = \frac{\Delta\phi}{\Delta s} = \frac{\phi_{i+1}-\phi_i}{s_{i+1}-s_i} \qquad \text{(Equation 5-1)}$$

Where ϕ denotes the tangential angle and s is the arc length. In three-dimensional space, the space curve *r(t)* for the tangent vector $\hat{T}$ is defined as:

$$\hat{T} \equiv \frac{\frac{\Delta r}{\Delta t}}{\left|\frac{\Delta r}{\Delta t}\right|} = \frac{\frac{\Delta r}{\Delta t}}{\frac{\Delta s}{\Delta t}} = \frac{\Delta r}{\Delta s} \qquad \text{(Equation 5-2)}$$

According to the Frenet-Serret formula, in differential geometry, keeping $\hat{T}$ as the tangent vector and $\hat{N}$ is the normal vector (Coxeter, 1969) then we have:

$$\dot{\hat{r}} = \hat{T} \qquad \text{(Equation 5-3)}$$

$$\hat{\hat{r}} = k\widehat{N} \qquad \text{(Equation 5-4)}$$

When $\hat{\hat{r}}$ changes constantly, it will show a circular flight (such as thermal soaring). However, if $\hat{\hat{r}}$ fluctuates by showing increasing and decreasing magnitude, the flight can be considered to be slope soaring with its radius of curvature going up and down.

Another parameter that assisted in discriminating between non-straight flights was altitude, which constantly increases in thermal soaring and decreases in spiral gliding. However, it remains almost steady during the slope-soaring movement ($z \sim 0$).

Flights with a radius of curvature > 350m were considered straight flights. To determine whether a flight pattern was soaring or gliding, regardless of whether it was straight or non-straight, the altitude of five successive GPS fixes (over a period of 15 seconds) were also considered. In this regard, soaring or gliding were characterized when the majority of the fixes ($n \geq 3$) were either ascending or descending, respectively. Figure 5.3 shows the steps we took in building and evaluating our differentiation of Griffon vulture flight types.

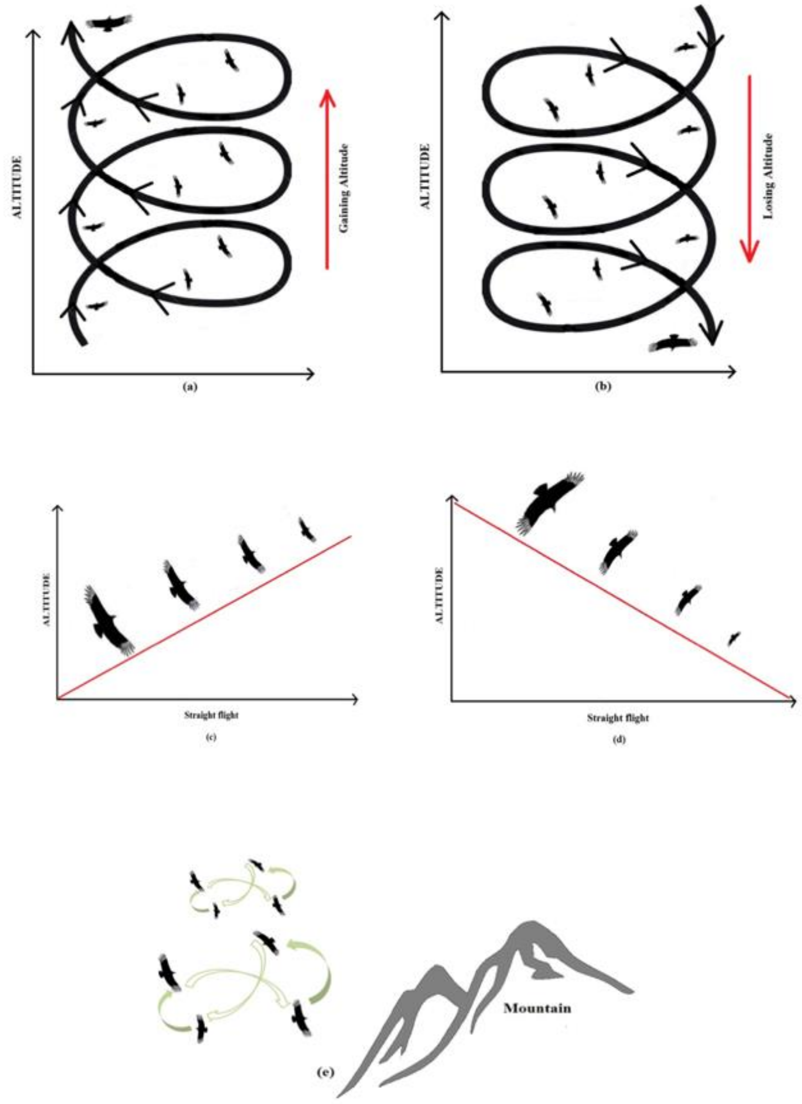

Figure 5. 2 Thematic illustration of the Griffon vulture's different flight patterns (a) thermal soaring, (b) spiral gliding, (c) linear soaring, (d) gliding, (e) slope soaring.

5.2.7 Evaluation of flight pattern differentiation

An independent observation dataset was gathered during the fieldwork and used to evaluate predicted flight patterns. For this purpose, we collated and compared records based on the field observations and extracted 1146 seconds of flight synchronized with the final dataset. Considering each interval between two successive GPS points is 3 seconds, the length of recording consisted of 382 segments in total, matched with the dataset. It consisted of 54, 104, 109, 23 and 92 segments for linear soaring, gliding, thermal soaring, spiral gliding and slope soaring respectively.

Validated results are presented in the form of a confusion matrix, (for example see: Kohavi and Provost, 1998) giving the number of cases that were correctly classified as positive (i.e. predicted flight pattern), as well as the number correctly identified as negative (other flight patterns). The cases where a negative sample was misclassified as positive, and vice versa, are called false positive and false negative, respectively. The performance of the identified flight patterns was evaluated based on indicators, namely precision, true positive rate, true negative rate, the accuracy of each flight pattern, and the overall accuracy, as well as the kappa value (Weiss and Provost, 2001) (see below for definitions).

Precision is defined as the proportion of the predicted cases that were correct. The true positive rate indicates that the percentage of a flight pattern matches

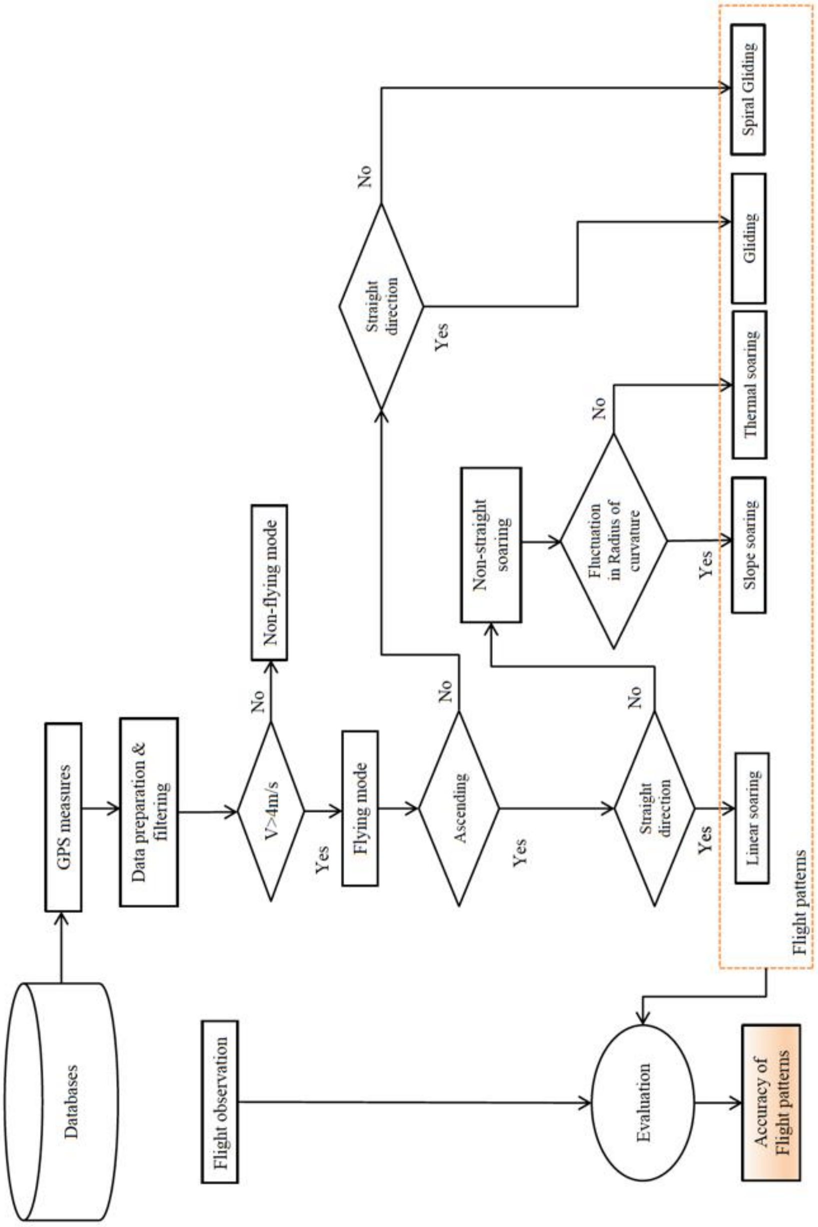

Figure 5. 3 Study workflow of the Griffon vulture's flight patterns and evaluation of the classification.

what is also observed from the data, while the true negative rate expresses the proportion of other flight patterns that are correctly predicted as that class. The accuracy of each flight pattern is the proportion of predictions (positive or negative) that are correct. Overall accuracy is calculated by the total number of correct classifications divided by the total number of samples. Finally, the kappa value is used to measure the agreement between predicted and observed classes, while correcting for an agreement that might occur by chance (Stehman, 1997; Viera & Garrett, 2005). The confusion matrix (Table 5.1, above) shows the number of segments belonging to each flight pattern. For instance, in the first row, 41, 0, 7 and 6 are number of segments corresponding to each flight pattern classified as linear soring, gliding, thermal soaring, spiral gliding and slope soaring, respectively. The numbers in diagonal line (in bold) are those segments that were correctly classified as positive.

5.3 Results

The evaluation method indicated a substantial agreement between the predicted and observed Griffon vulture's flight types (Table 5.1, below). The estimated kappa value (0.61±0.06) is intended to illustrate the agreement between two groups of predicted and actual flights. The overall classification accuracy was 70%. Of all flight patterns, gliding had the highest precision (88%), while linear and thermal soaring had a precision of 83% and 75%, respectively. The lowest values of precision were present for spiral gliding (34%) and slope soaring (53%).

The flying and stationary modes were clearly distinguished. The variation of instantaneous speed > 4 m/s, as a main proxy of the flying mode, is demonstrated in figure 5.4. This figure also shows that the stationary mode is more frequent than flying mode in the period of our study.

Table 5.1 Summary statistics of confusion matrix for Griffon vulture's flight patterns. The columns and rows (top) show the predicted and observed flight patterns, respectively. Numbers are representatives of segment. The numbers in bold are corresponding segments of each flight pattern which were correctly classified as positive. Summary statistics of the classification's performance (bottom) for all flight classes, overall performance of the classification.

Observed Flight pattern	**Predicted flight pattern**					Total Observation
	Linear Soaring	Gliding	Thermal Soaring	Spiral Gliding	Slope Soaring	
Linear Soaring	**41**	0	7	0	6	54
Gliding	0	**81**	0	12	11	104
Thermal Soaring	5	0	**89**	0	15	109
Spiral Gliding	3	0	0	**16**	4	23
Slope Soaring	0	11	22	18	**41**	92
Total predicated	49	92	118	46	77	382

	Classification's performance indicators					
Behaviour	Precision	True positive rate	True negative rate	Accuracy	*Kappa*	*Overall Accuracy*
Linear Soaring	83.67%	75.92%	97.56%	92.73%		
Gliding	88.04%	77.88%	90.04%	88.74%		
Thermal Soaring	75.42%	81.60%	89.37%	85.50%		
Spiral Gliding	34.78%	69.56%	91.64%	87.86%		
Slope Soaring	53.24%	44.56%	87.58%	75.41%		
					0.61	*70.15%*

Although, thermal and linear soaring, as well as gliding, were classified correctly to a high degree of the estimated precision, some misclassifications of flights also occurred. Linear soaring was mostly misclassified as thermal soaring. Gliding was also misidentified as slope soaring, while spiral gliding was misclassified as either gliding or slope soaring. Finally, slope soaring was mixed up with thermal soaring, gliding, and linear soaring. Slope soaring and spiral gliding had the lowest values of the true positive rate. The highest true positive rate (81%) was achieved for thermal soaring at 81% and was slightly better than that for linear soaring or gliding. The true negative rates were excellent for all flight patterns.

The lowest and highest values of true negative rate were achieved for slope soaring (85%) and linear soaring (97%) respectively. The predicted accuracy measures, and the proportion of positives or negatives were excellent for all flight patterns. Linear soaring (92%) and slope soaring (75%) were the most and least accurate flight types, respectively.

Examples of the different flight types in three dimensions are visualized in Figure 5.5 a and b, demonstrating variation of flight behaviour in different altitude and with the use of thermal soaring the bird reached up to 1400 m above sea level. Additionally, Figure 5.5 c and d shows a scheme of radius changes as the bird flew along the curve.

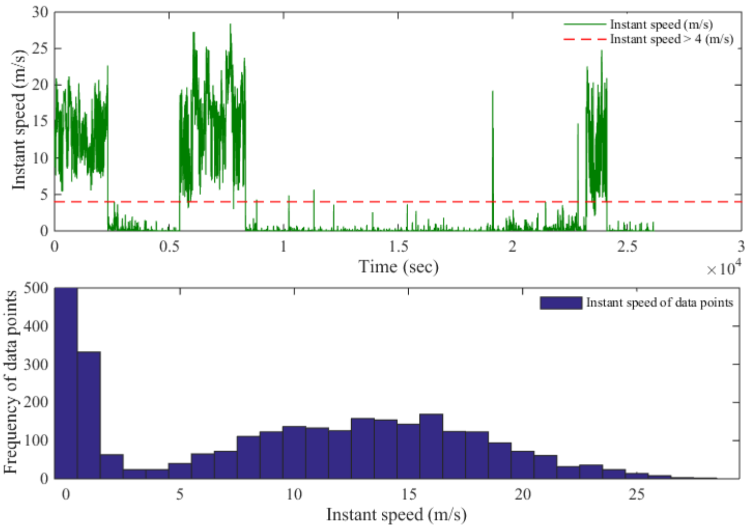

Figure 5. 4 Variation and frequency of instant speed in the dataset: (a) instantaneous speed > 4 m/s (red dashed line) is the main proxy to identify flying mode, and (b) frequency of flying and static modes in the dataset.

5.4 Discussion

Our study differentiated five passive flight types of the Griffon vulture including linear soaring, thermal soaring, slope soaring, gliding and spiral gliding. To our knowledge, this is the first reported differentiation of a raptor's flight patterns by using tracking data. Our results show differences between flight patterns in terms of accuracy, precision, true positive rate, and true negative rate. Each class shows over 75% performance in accuracy. Due to the unbalanced structure (the ratio of positive and negative cases, the predicted flight and other flight pattern) in most of the observed data, other measures of the classification's performance, such as precision and true positive rate, are more informative (Kubat *et al.*, 1998; Martiskainen *et al.*, 2009). The classification precision was high for linear and thermal soaring as well as for gliding.

The lower precision values seen for spiral gliding and slope soaring indicate that the classification method can be problematic in predicting positive cases (predicted flight pattern) correctly. Most cases of confusion involved slope soaring. This may be because it could be the most complex flight pattern, or because it closely resembles other patterns. Part of the difficulty could lie in the sampling rate of the flight type, which might have been too low to discriminate slope soaring well enough. This is in fact supported by the Nyquist Theorem (also known as the sampling theorem), according to which the minimum sampling rate must be twice the highest frequency contained in the flight pattern (Grenander 1959).

Our results reveal the highest percentage of misclassification is seen for spiral gliding, due to the inadequate number of samples (Bohrer *et al.*, 2012; Kubat *et al.*, 1998; Mellone *et al.*, 2015) in our current dataset. Since only two fieldworkers were assigned to collect the observational dataset in a limited time, there may also have been some human error during sightings or recording the bird’s flight behaviour and this might have affected the dataset.

The true positive rate was high in the three flight patterns of linear soaring, thermal soaring and gliding. This implies that fewer negative cases (predicted other flight pattern) were falsely classified in those flight patterns; in other words, the true positive rate shows these three flight types were more often correctly identified than slope soaring and spiral gliding. The excellent values (85% and higher) of the true negative rate in all the flight types also shows that the negative cases were correctly classified for those flight patterns. The value of kappa (0.61±0.06) shows a substantial classification agreement, which could be interpreted as demonstrating the method’s success.

For the above flight types, data with finer temporal resolution (e.g. a one second interval) of GPS fixes might be useful for making a more precise and accurate classification. In this experiment, although we set the measurement interval of the GPS tracker to three seconds, the retrieved dataset consisted of unequal intervals. By filtering out the coarse temporal resolution, some gaps in the dataset decreased the consistency of the data. Due to the varying success in classifying the flight types, it might be worthwhile to include various parameters (e.g. time window) in the classification process. More specifically, including other parameters (e.g. aspect ratio or wing loading) would entail considering the traits of each flight pattern. Another point that could improve classification performance is the further optimization of different flight characteristics (e.g. horizontal vs. vertical speed).

Since we can assume birds' flight types are affected by the environmental conditions (Shamoun-Baranes *et al.*, 2004) when gathering data in different seasons, there may be an opportunity to observe and digitally capture more flight types, particularly those that were seen less often during the period of this study. We speculate that the Griffon vulture spent more time in non-flight mode, because we performed the study during the breeding season; the birds would have been in parental mode and more vigilant than at other times of the year in order to protect their chicks from bad weather and predators (Xirouchakis & Mylonas, 2007).

5.5. Conclusion

This study investigated the flight types of the Griffon vulture using high resolution GPS data and we provide evidence that such data contains sufficient information to recognize Griffon vulture's flight types. In movement ecology research, our study makes a useful contribution by providing a new baseline technique using GPS sensor data to classify a bird's flight type as a part of its motion capacity. However, more studies are needed to refine the properties employed in this classification method, including the testing of other types of sensory data (e.g. accelerometer data) or the use of different analytical parameters. Collision risk of the Griffon vulture was mediated by flight behaviour and it is suggested that a detailed research on flight behaviour is needed at precise location where the turbines are installed (Barrios & Rodríguez, 2004), so our study is one step forward to solve the collision dilemma.

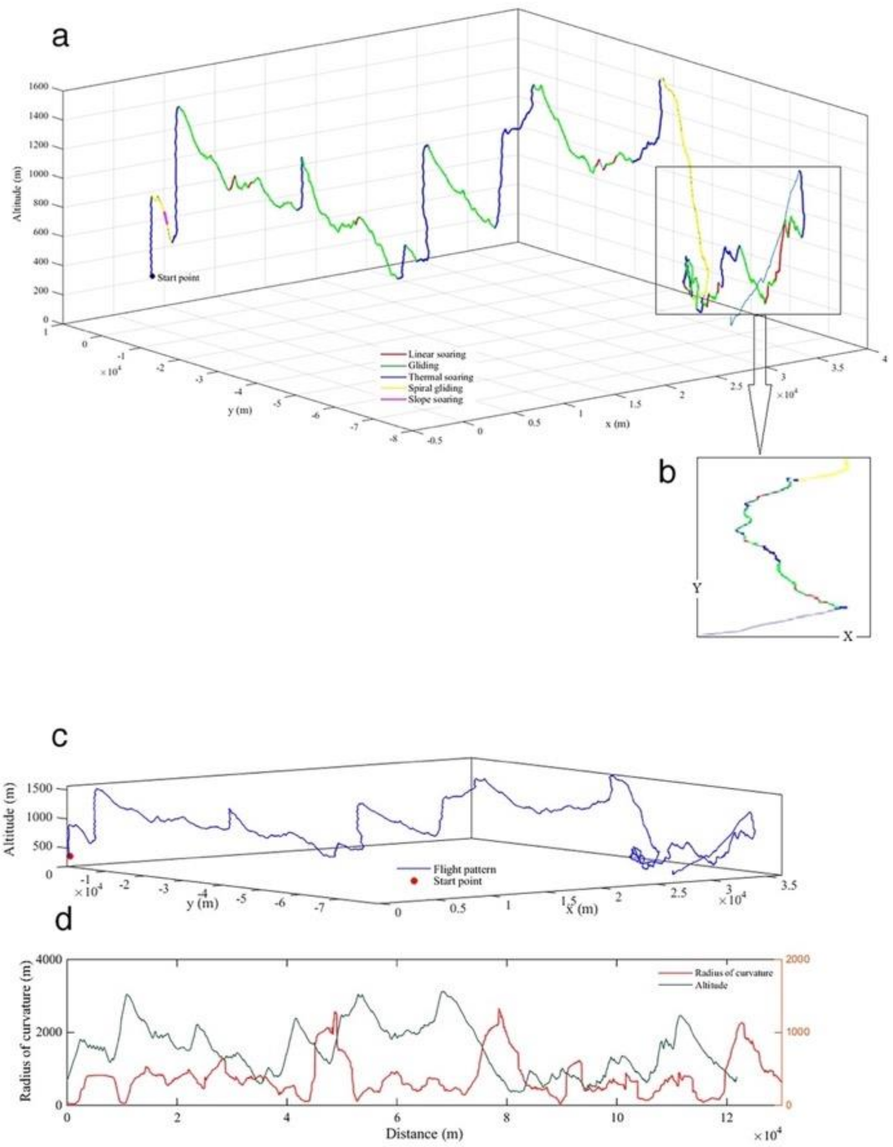

Figure 5. 5 Scheme of the Griffon vultures flight patterns in three-dimensions, and (b) in two-dimensions segregated using the concept of motion in physics. (c) Scheme of the Griffon vulture's flight patterns in three-dimensions, and (d) its relative radius of curvature (red line) and altitude (green line) during the flight.

5.6 Acknowledgement

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5.7 Ethical Approval

The experimental procedures of this study, including bird trapping and GPS tagging, were approved by the Consejería de Medio Ambiente of the Junta de Andalucía, who provided permissions for this research through the licence to capture and mark raptors to Antonio-Román Muñoz (Regional Licence: 65029 Consejería de Agricultura, Pesca y Medio Ambiente, Junta de Andalucía; National Licence 650038, Ministerio de Agricultura, Alimentation y Medio Ambiente).

Postface

This chapter demonstrated that movement pattern could be derived from high resolution tracking data. It further developed understanding of movement (i.e. flight) with the use of movement data. It was one step forward to have more insight regarding flight behaviour which may play a role in conservation plans and practices.

Appendix

Details of studies pertaining to movement and foraging of Griffon vulture.

Subject	Method	Major findings	References
Flight and foraging behaviour	Electrocardiogram, GPS and accelerometers	Heart rate increased three-fold during take-off and landing compared to baseline level. 10 minutes after initial flapping phase, home range in soaring and gliding dropped to the baseline level that was lower than theoretically possible.	(Duriez et al., 2014)
	GPS tracking	Change in size of home range in different seasons and also amongst individuals. Vultures prefer a feeding station compared to the rest of the habitat with unpredictable food resources.	(Monsarrat et al., 2013)
	GPS and accelerometers	Despite high variability in food deprivation periods, flight speed, straightness of flight and the proportion of active flights do not vary in relation to food deprivation.	(Spiegel et al., 2013)
	GPS and tri-axial accelerometer	Classifying behavioural modes using machine learning classifiers with 80- 90% accuracy.	(Ran Nathan et al., 2012)
	GPS satellite telemetry	Traditional stock-raising areas are the Griffon vultures' main range. Overall foraging rage is 1719 km^2 as Minimum Convex Polygon, with 4078 km^2 and 489 km^2 as 95% and 50% kernel contours respectively.	(García-Ripollés, et al., 2011)
	GPS and tri-axial accelerometer	Hungry individuals (fasted > 4 days) spent more time flying, travelled longer distances, and their paths were less straight than well-fed ones.	(Harel et al., 2010)
	Radio telemetry and direct observation	Griffon vultures spend 7.6 hour/day on food searching, mean distance from colony to feeding area is 8.4 km, mean foraging radius is 15 km, foraging ranges, based on direct observations are 206-851 km^2 and 195-527 km^2 using the adaptive kernel method. The range based on radio tracking is 390-1300 km^2.	(Xirouchakis & Andreou, 2009)
	Tri-axial accelerometer	Griffon vultures use legs before taking off and after landing. Mean overall dynamic body acceleration for flying up and down a hill were 1.396±0.114 and 0.889±0.123 respectively.	(Halsey et al., 2009)
	Direct observation	Finding food directly or relying on following other birds, food searching is concentrated on large ungulate herds, gaining altitude with lower density of ungulates in a herd.	(Houston, 1974)
Migration flying characteristics	Direct observation	Higher rate of flapping when crossing water than land, flapping rate and attempts to cross water are influenced by time and weather conditions, passage over a water body is limited by Griffon vulture's over-water flapping-flight abilities.	(Bildstein et al., 2009)
	Satellite tracking	A Griffon vulture changed migration direction from south to north and its longest flight distance in a day was 80 km.	(Berthold et al., 1991)

Chapter 6

Synthesis

6.1 Introduction

Biodiversity is undergoing significant and often rapid changes worldwide. Understanding the species dynamic underlying such a quick change would bring a better insight for decision-makers and conservation managers. In this thesis, we mainly focused on this concept that the species shifts and individual movements are inherently linked. We argued that similar to time and space, the organization has a continuous and interlinked range from individuals to species. See Figure 1.2, Chapter 1.

In this thesis, we conducted four studies supporting our proposed concept. We demonstrated that invasion is a well-known concept at the species level, but it roots to the capacity of individuals' movement and habitat preferences (see Chapter 2). In the next chapters of this thesis, we tackled a methodological approach to inform species distribution models with individual movement data (Chapter 3), and to accommodate the three dimensions of space in habitat studies (see Chapter 4). We also focused on movement types of an individual in response to their physical environment (see Chapter 5). In this chapter, we summarized our findings and provide some suggestions for future studies.

It is well-studied that movement of species, a complex and continuous ecological process (Long and Nelson, 2013), is often in response to short-term goals such as reproduction, maintenance, feeding, survival and escaping threats (Holyoak *et al.*, 2008). Rather than fixed and well-aligned habitats, mobile specie occupy dynamic and three dimensional spaces (Belant *et al.*, 2012). Hence, all physical and reachable spaces might be potential habitats, as it is inherently assumed in the telemetry technique that tagged organisms use the spaces between sampling locations (Bruneel *et al.*, 2018). Since movement is a time-dependent and essential process in shaping the distributions of species, it should be considered as a compulsory aspect of any studies projecting the current or future distributions of species (Holloway and Miller, 2017).

Also, movement can be a confounding parameter to estimate when future distribution and invasion rate of an alien species is considered (Miller and Holloway, 2015). Invasive movements violate the standard assumption of SDMs which is species are in equilibrium with their environment (Holloway and Miller, 2017). The occurrence data of invasive species including native and invaded regions (or post-established areas if there are any) can be advantageous for modelling new distributional areas. This was applied, tested and discussed in chapter 2.

The scale of movement is usually limited to spatial or temporal attributes, but levels of organization (i.e. individual, population or species) should be included (Oindo *et al.*, 2003; Franklin, 2010; Song *et al.*, 2013).Considering the availability of movement data and recent advances in movement research (Turchin, 1998; Smouse *et al.*, 2010), it has been an opportunity for researchers to incorporate fine-scale temporal and spatial movement of individuals in species distribution modelling. Although a number of studies have been conducted using the individuals' locations retrieved from telemetry as the response in SDM (Edrén *et al.*, 2010; Gschweng *et al.*, 2012; D'Elia *et al.*, 2015), integrating multiple scales of movement within SDM needs to be continued (Bruneel et al., 2018). The incorporation of movement has been further discussed in Chapter 3.

Species movements are often modelled in two dimensions (2D)(Long and Nelson, 2013; Khosravifard *et al.*, 2018) while this approach would impose biases for species moving in three dimensions (3D) such as birds and fish (Belant *et al.*, 2012). Recently, some studies have started to provide 3D analysis of species movement. For example, Simpfendorfer *et al.* (2012) calculated the utilization distribution of European eels (Anguilla anguilla) using 2D and 3D kernel density. Three-dimensional movement modelling has also been used to track burrowing behaviours of worms (Bastardie *et al.*, 2003) and movement paths of captive fish (Zhu and Weng, 2007) (please see Chapter 4 for further info).

Moreover, classification of movement patterns have been often considered in 2D (see Chapter 5) and mostly at coarse temporal resolution (i.e., daily or hourly movements) to determine home range, dispersal and migration routes (Mandel *et al.*, 2008; Calenge *et al.*, 2009; Smouse *et al.*, 2010; Kranstauber *et al.*, 2012; López-López *et al.*, 2013). Using high-resolution spatiotemporal movement data may assist researchers to differentiate movement patterns. This has been further discussed in Chapter 5.

6.2. Dealing with data scarcity

It is crucial for biodiversity monitoring and conservation management to have reliable information on the distribution of alien species (Dornelas *et al.* 2014). However, they are often non-existent, unavailable or challenging to gather. The approach presented in Chapter 2 is a technique to predict distribution of species when the data are limited.

In such cases when little is known about the distribution of an alien species and the available data are insufficient, information of its native range and post-established region may be of assistance. It was explored the current and future distribution of an alien species in a new distributional region, based on the extensive information on the native and invaded ranges (Chapter 2).

By using the information of native and post-established region, we went through a procedure to illuminate and explain the distribution of raccoon, a non-native species, in Iran. Unlike the native habitat range in North America and post-established region in Europe, the occurrence data of raccoon in Iran were limited to some observations and reports. Thus, the three geographical ranges, namely native, post-established and newly invaded habitats (i.e. Iran) were set for the modelling.

The predictions successfully identified high probability values of the raccoon's distribution in the current climate condition. As hypothesized in Chapter 2, individual's movement and dispersal capacity, along with environmental dynamics enhanced the accuracy and credibility of models predicting the potential distribution over time. By transferring the trained model over time, we investigated the potentially suitable habitat of the species in Iran under climate change scenarios in the future. Considering the land cover and dispersal speed, we compared the current realised habitat to the future potential habitat. As a result, the raccoon may access from north to south of the Zagros mountains in the year of 2050. That would be a new area for the species. This prediction may turn to an undeniable fact in the future when occurrence data of the raccoon would be scientifically gathered and documented.

Having access to new areas is the first obstacle for alien species, but it doesn't necessarily mean that the species is already or becomes invasive in the future. The existence of some conditions is needed to make an alien species invasive; survival, adaptability and acquiring resources are other challenges that an alien species should overcome to establish a population in new sites (Hellmann *et al.*, 2008). In the future, it should be studied whether the conditions exist or not for the raccoon. Although the raccoon population growth is out of control in Europe since the earlier reports in the 1950s, just anecdotal evidence suggests the species may threaten reptiles and amphibians (Kauhala 1996, Frantz *et al.* 2005). Hence, we can infer that it is too early to have consolidated judgment about the status of raccoon in Iran whether it becomes an invasive or not. However, the outcome of Chapter 2 may be used in conservation plans and would assist conservationists to consider the areas where the alien species would most probably occur.

6.3. Species movement data fulfil the occurrence gap

A number of studies have tried to determine the relationships between species movement and environmental predictors (Hooten *et al.*, 2014). In spite of substantial impacts of geographical distribution of species on movement process and ecological significance, the incorporation of movement has lagged behind other methodological and conceptual advancement, particularly, in species distribution modelling (Franklin, 2010a; Miller and Holloway, 2015). Since the movement data are available, shouldn't they be used in SDMs? Do SDMs incorporated movement data of individuals define geographical distribution of species? And how well the outcome might be? These questions were answered in Chapter 3. We used three birds' datasets from two different and freely available sources: GBIF, the commonly-used data source, and movement data from Movebank. Although, the results varied among the models, they showed a spatial concordance between the outcomes of SDMs, derived from static and movement data.

This was a clear response to the aforementioned questions: movement data can be potentially used as a source to estimate habitat suitability. The results were promising and one step forward to consider and use the movement data in SDMs. It should be mentioned that the outcome of this chapter was limited to the three datasets of three different species: one native and non-migratory, and two migratory birds. More telemetry data of a species would ultimately lead to more realistic estimate of suitable habitats. It may provide opportunity to investigate how using movement paths can be incorporated in SDMs. More studies are needed to focus on a variety of species, as well as uncertainty for future refinement of models.

Since having insight of the environmental preferences of species and movement in a suitable habitat or a new landscape is important for conservation policy and practices (Doherty and Driscoll, 2018), this chapter is one step forward to consider different and independent sources of data, instead of commonly used ones, in habitat modelling.

6.4. Species space use in three dimensions

Animal movement in the context of modelling usually is considered in 2D. Like SDMs, home range and utilization distribution are two other methods often quantified by researchers in 2D (Fleming *et al.*, 2015; Holloway and Miller, 2017). If we estimate home range or utilization distribution ignoring the altitude, the results would consist of bias; an unrealistic depiction may be attained for the mobile species living in 3-dimensional space, such as birds, bats, fish or climbing species (Belant *et al.*, 2012).

To have a better understanding of space use of those species, volumetric analysis is more informative than planer analysis. This was tested in Chapter 4 by estimating space use of a soaring bird (i.e. Griffon vulture). We estimated a 3D kernel utilization distribution (KUD) presenting a better insight of plausible collision risk between wind turbines and the bird. The results showed that 3D KUD was beneficial method for quantifying the space use (Khosravifard *et al.*, 2020). Therefore, this method can be considered as an assistance for wind farm developers to calculate the relative risk of installing turbines. However, more studies are needed to quantify the actual risk of turbines.

To calculate the risk, pre-construction data of target species is a must-have. It is suggested that data gathering and monitoring would continue after pre-construction period and last during the post-construction, and operational phases of wind farms. The 3D KUD could be used and helping management to forecast periods of high risk and decrease the number of bird collisions by selectively ceasing certain wind turbines.

One important issue, which was not included in the scope of Chapter 4, is spatiotemporal autocorrelation in movement data. It might provide an underestimation of individual's space use (Fieberg, 2007; Fleming *et al.*, 2015) and should be considered for future studies.

6.5. Classification of flight movement types

The classification methods of movement patterns have been often considered in 2D (Giannotti and Pedreschi, 2008; Güting, Behr and Düntgen, 2010) like SMD (Holloway and Miller, 2017), home range and utilization distribution (Katajisto and Moilanen, 2006; Powell and Mitchell, 2012). Mostly, those classification methods have focused on at coarse temporal resolution (e.g. daily or hourly movement) (Calenge *et al.*, 2009; Kranstauber *et al.*, 2012).

The high-resolution tracking data can provide opportunity to have a better understanding of movement patterns. As hypothesized in Chapter 5, that kind of data are sufficient enough to differentiate flight types of a soaring bird. It was classified and tested five passive flight types of the Griffon vulture in the Chapter 5. Although this Chapter was one step forward to have more intuition regarding flight behavior which may play a role in analysis the collision risk (Khosravifard *et al*, 2018), it relied solely on GPS tracking data set measurement interval to three seconds. However, unequal intervals were retrieved which constructed a disadvantage of some gap in the dataset. The disadvantage might be reduced or eliminated in future studies by including various parameters such as time window, aspect ratio, wind loading or other types of sensory data into the classification method.

Nevertheless, Chapter 5 provided the evidence that high-resolution tracking data consists of sufficient information to differentiate passive flight types of soaring birds.

6.6. Management implications

Movement of animals has always intrigued humans since hunting was a chance of survival. In the modern era, this curiosity shifted towards a better understanding and knowledge for managing and protecting wildlife populations. Minimization in size and weight, as well as growth in the use of new tracking devices, not only have made movement research glamorous, enabled researchers to investigate across a variety of scales. In the contemporary epoch of the "golden age of bio-logging" (Wilmers et al., 2015) and biotelemetry, it is possible to gather estimates of movement at ever-increasing accuracy even for small and cryptic species. Concurrently, human activities change natural areas that ultimately cause reducing natural habitats and inducing range shifts. Therefore, it entails acquiring baseline data and knowledge on movement patterns, new ranges, and space uses for management and policy decisions. The absence of basic data, information or knowledge on distribution, foraging, dispersal and migration, as well as home range and space use of wildlife can be serious obstacles to status assessment, conservation plans, reintroduction and restoration projects. We have presented new information on the distribution of a species (Chapter 2), different approaches to use data (Chapter 3 and 5) and the method (Chapter 4) that may be of interests to wildlife managers, conservation practitioners and decision-makers.

New distributional areas, where native and non-native species exist, may need special consideration for protection or rehabilitation to keep the new populations under control. In the case of non-native species, it may forge more concerns that require a multi-faceted approach to deal with the new situation caused by the presence of the species. For instance, the impacts of the non-native species on native species, habitat, economy, and health may raise a red flag for local people, decision-makers and conservationists. Predictions of new ranges where non-native species may occur is an advantage for conservation planners and practitioners to be prepared before the species reach to the new areas. It may require protection of native animals and plants, humans, farms, buildings, and constructions against the non-native species. The geographical distribution of the raccoon in Iran predicted in Chapter 2 can be a notification that Zagros, the mountainous region, may be a destination of the species. It should be studied whether the raccoon is a threat to the Luristan newt (*Neurergus kaiseri*), an endemic and vulnerable species to the central Zagros mountains (IUCN SSC Amphibian, 2016). Also, the impact of the raccoon population on agriculture requires intensive investigation.

As the field of movement ecology seeks increasingly detailed information on the spatiotemporal movement of mobile species, novel approaches on tracking data would open new windows for wildlife managers and conservationists. Data at individual level may inform conservation assessments for dynamic management or to increase protected areas for better enclose the range and extent of animal movement. Our outcome in Chapter 3 provides the opportunity to develop efficient and dynamic conservation practices, as animals are tracked. In other words, tracking animals and predicting new distributional areas can be executed concurrently. It gives the conservation planners an insight of location and time that a target species may occur.

Having a false understanding of species occurrence may lead to a wrong conservation decision. To estimate utilization distribution and home range, usually, two horizontal dimensions are considered and the vertical aspect is neglected. Therefore, an unrealistic image of reality may be obtained for species like birds that move in three-dimensional space. We have demonstrated that considering the vertical movement of individuals can improve the credibility of utilization distribution. This approach would give a better intuition to conservationists and wildlife managers while developing or practising conservation plans.

Additionally, relatively high-risk obstacles can be identified through a volumetric analysis when the target species move in three-dimensional space. In the matter of wind turbine, relatively high-risk turbines can be selectively stopped to reduce the probability of collision between birds, especially raptors, and turbines. This new approach also was presented in Chapter 4.

A range of methods is available to aid conservation planning and environmental decision-making. Still, plans and decisions concerning species' movement require detailed information and a specific way of thinking. A complex phenomenon like movement involving uncertainties may create confusion for managers. The new approach we presented in Chapter 5 described another form of the use of data. Based on the high-resolution tracking data only, baseline method showed to differentiate passive flight in three spatial dimensions. It is asserted that collision risk between birds and wind turbines and mortality was attributed by flight behaviour (Barrios et al., 2008). Our new approach is one step forward to have more insight into flight behaviour and how they vary in details. Also, it can be useful for developing bird avoidance strategies which need a real perception of the movement of individuals.

6.7. Conclusion and recommendation

So far, a number of studies have commenced using the locations retrieved from telemetry techniques (e.g. Pinto 2016 *et al.*). However, the concept of movement used in recent distribution modelling applications often refers to the cumulative, collective movement of species or populations across a broad time scale, not to the daily movement of a single individual. With the emergence of high temporal resolution movement data from advanced tracking devices, daily or hourly movement of individuals should be (re)considered in SDM. This may provide a better insight into the interaction of the target species with others and with the environment accessible for the species within a relevant timeframe. At a finer scale, integration of classified movement (i.e. locomotion) into distribution modelling may also provide more informative results which ultimately assist with a better understanding of biotic factors to have a more accurate estimation of habitat suitability. As the BAM concept presented in Chapter 1, determination and delineation of the biotic interaction is one of the essential requirements for the presence of a species. Movement data, therefore, can be used to describe the distribution and configuration of suitable areas. Moreover, the assumption of abiotic and abiotic homogeneity behind the BAM concept may be revisited when movement data is incorporated in the distribution modelling, as species move in an inhomogeneous environment.

Although movement data creates a new avenue in the SDM framework, new conceptual issues related to this data structure, such as precision, autocorrelation, and idiosyncratic preferences should be considered. Moreover, movement doubtlessly occurs across fine and broad spatial and temporal scales, then the integration of multiple ‘’’’scales of movement into SDM can be considered for further studies.

Another issue that should be addressed in future research is to delineate the definition of movement and to differentiate between dispersal and migration. These terms, as described before, are used interchangeably in distribution modelling (Alagador, Cerdeira and Araújo, 2014; Miller and Holloway, 2015).

Also, spatial dynamics of a species are crucial in conservation planning and management, as they underline regions including habitats, migration corridors and connections areas (Pinto *et al.*, 2016). Therefore, moving beyond static distributional modelling is imperative as demonstrated in this thesis. The realization of suitable spatial distribution of species is not the final step of spatial conservation, but is a fundamental step towards it. Hence, the approach proposed here, which is using different data sources including native and invaded range to predict invasion rate (Chapter 2), movement in SDMs (Chapter 3), the vertical position (i.e. z dimension) in home range (Chapter 4) and high spatiotemporal tracking data to delineate movement (Chapter 5), offers considerable promise for increasing the reliability of model outputs used to inform conservation management.

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Summary

Movement is a fundamental characteristic of life that has been defined as a change across many spatial and temporal scales. It is also a ubiquitous ecological process which influences the structure and dynamics of populations, communities, and ecosystems. Movement has always been at the center of many observations, investigations and studies since the very first attempt to understand where a species may go. Naturalists have investigated the mysteries of movement since the writings of Aristotle (4th century B.C.) searched for common features unifying animal movements. He tried to explain movement such as flight through air and motion of animals in water in general terms on the basis of casual observations. Since then, researchers have traditionally used direct observation as a method to monitor wildlife. The direct observation has also been used to elucidate and describe movement phenomena. Not losing sight of an animal is the most challenging part of this traditional type of research, but this has now been solved by deploying telemetry techniques radar, radio, satellite and Global Positioning System (GPS) tracking. Recent advances in telemetry techniques, such as extensive use of bio-loggers with GPS, have enabled spatiotemporal data to be collected on animals with ever-increasing accuracy. Also, recent advances in movement research have inspired a shift in the study at species-level or population-level patterns to individual-level patterns.

This dissertation aims to contribute to the understanding of the movement phenomenon at individual-level pattern. The availability of movement data and recent advances in movement research are key factors to improve our understanding of animals' movement at individual levels.

Although the techniques for studying animal movement have been advanced and flourished since earliest attempts, the incorporation of movement studies in other methodological advancements, particularly in species distribution modelling (SDM) has lagged behind. In the context of SDMs, the accessibility of habitats by species or populations has been considered rather than underlying the process of individuals' movement.

Part of my dissertation is dedicated to providing evidence that including the individuals' movement of a species and accounting for their potential dispersal, along with environmental dynamics improves the accuracy and credibility of models to predict the potential distribution of species over time under climate change. Also, I illustrate the capacity of individuals' movement data which can be considered as a reliable source for species distribution modelling.

A common hypothesis is that when including the vertical movement of individuals improves the accuracy and credibility of the individual's range maps. Another part of this dissertation provides evidence for this hypothesis and puts it to use in the utilization distribution model. I incorporated the vertical movement data to the 2D space use analysis and proved that the 3D volumetric analysis is a realistic depiction of species occurrence. To develop efficient nature conservation practices, it is necessary to know where and when wildlife may occur. This approach would give a better information to conservationists and wildlife managers while developing or practising conservation plans.

A complex phenomenon like movement involving uncertainties may create confusion for managers. In this dissertation, I also presented the use of movement data to classify different types of movement (i.e. flight). I am confident that application of movement data in wildlife management and conservation practices will continue to expand and improve.

Samenvatting

Beweging is een fundamenteel kenmerk van het leven dat is gedefinieerd als een verandering over vele ruimtelijke en temporele schalen. Het is ook een alomtegenwoordig ecologisch proces dat de structuur en dynamiek van populaties, gemeenschappen en ecosystemen beïnvloedt. Sinds de allereerste poging om te begrijpen waar een soort naartoe kan gaan, heeft beweging of verplaatsing van een dier altijd centraal gestaan bij veel waarnemingen, onderzoeken en studies. Naturalisten hebben de mysteries van beweging onderzocht sinds de geschriften van Aristoteles (4e eeuw voor Christus) waarin hij zocht naar gemeenschappelijke kenmerken die de bewegingen van dieren verenigden. Hij probeerde bewegingen zoals door de lucht vliegen en de beweging van dieren in het water in algemene termen uit te leggen op basis van terloopse observaties. Sindsdien gebruiken onderzoekers van oudsher directe observatie als een methode om dieren in het wild te volgen, en om hun bewegings- of verplaatsingsgedrag op te helderen en te beschrijven. Het niet uit het oog verliezen van een dier is het meest uitdagende onderdeel van dit traditionele type onderzoek, maar dit is nu opgelost door telemetrietechnieken in te zetten zoals radar, radio, satelliet en Global Positioning System (GPS) tracking. Recente ontwikkelingen in telemetrietechnieken, zoals het uitgebreid gebruik van bio-loggers met GPS, hebben het mogelijk gemaakt om ruimtelijk-temporele gegevens over dieren te verzamelen met een steeds grotere nauwkeurigheid. Ook hebben recente ontwikkelingen in het bestuderen van bewegingspatronen geleid tot een verschuiving in onderzoek op soort- of populatieniveau naar patronen op individueel niveau.

Dit proefschrift heeft tot doel om inzicht in de toepasbaarheid van verschillende formaten in databronnen te verbeteren, voor zowel data op soortniveau als ook extreem hightech data op individueel niveau. De toenemende beschikbaarheid van bewegingsgegevens en de recente ontwikkelingen in bewegingsonderzoek zijn sleutelfactoren om onze kennis in het bewegingsgedrag van dieren op individueel niveau te verbeteren.

Hoewel de technieken voor het bestuderen van de beweging van dieren sinds de eerste pogingen veel verder zijn ontwikkeld en toegenomen, is de integratie van bewegingsstudies met andere methodologische ontwikkelingen, met name het modelleren van soortenverspreiding (SDM), achtergebleven. In de context van SDM's is de toegankelijkheid of bereikbaarheid van het leefgebied van een soort of populatie belangrijker gevonden dan het proces van individuele bewegingen.

Een deel van mijn proefschrift is gewijd aan het leveren van bewijs dat incorporatie van de bewegingsgedrag van een soort door individuen en het verklaren van hun potentiële verspreiding, samen met de omgevingsdynamiek, de nauwkeurigheid verbetert en geloofwaardigheid vergroot van modellen om de potentiële verspreiding van soorten in de tijd te voorspellen, ook onder klimatologische verandering. Ook toon ik aan, dat bewegingsgegevens van individuele dieren kunnen worden beschouwd als een betrouwbare data bron voor het modelleren van de verspreiding van soorten.

Een veel voorkomende hypothese is dat wanneer de verticale beweging van individuen is inbegrepen, het de nauwkeurigheid en geloofwaardigheid van de verspreidingskaarten van het individu verbetert. Een ander deel van dit proefschrift levert bewijs voor deze hypothese en gebruikt het in het modelleren van de verspreiding van dieren. Ik heb de verticale bewegingsdata verwerkt in de 2D analyse van ruimtelijk gebruik en heb bewezen dat de 3D-volumetrische analyse een realistische weergave is van het voorkomen van soorten. In dit proefschrift presenteerde ik ook een methode om het gebruik van bewegingsgegevens om verschillende soorten bewegingen (d.w.z. vluchten) te classificeren. Om efficiënte natuurbeschermingspraktijken te ontwikkelen, is het noodzakelijk om te weten waar en wanneer dieren in het wild kunnen voorkomen. De benadering zoals beschreven in dit proefschrift zal natuurbeschermers en natuurbeheerders betere informatie kunnen geven bij het ontwikkelen of toepassen van natuurbeschermingsplannen.

Een complex fenomeen zoals beweging of verplaatsing bij dieren met hun onzekerheden kan voor managers verwarring scheppen. Ik ben er daarom van overtuigd dat het toepassen van bewegingsgegevens bij het beheren van wild en natuurbehoud in het algemeen zal blijven groeien en verbeteren.