Evaluating the future impacts of climate change on the movement of migratory birds

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Chapter 1

General introduction
Understanding how the projected anthropogenic climate change will influence biodiversity is a major area of concern for biologists. Climate change affects different parts of the world differently, making it particularly challenging to understand the overall influence on migratory species, as they encounter varying extents and types of change in different stages of their journeys, in different parts of the globe. Migratory birds, specifically, will be affected by changes in their breeding, wintering, and stopover areas. Moreover, they can face unexpected conditions *en route*, as air movement patterns in the atmosphere, which are paramount for successful migration particularly for long-distant migrants [1], will be altered as a result of climate change. While projected climatic and weather variables under different climate change scenarios have long been used to understand the effects of this phenomenon on the habitats of migratory birds (e.g. [2, 3]), no previous studies have focused on how the wind-determined migratory route selection of the birds will be altered by climate change. In this research, I used a combination of remote-tracking data, track annotation, and modeling techniques to show how atmospheric conditions, particularly the wind, are important in shaping migratory routes of birds in the present and provide some evidence on how such traditionally optimal routes might be altered under climate change.

1.1 Resources and methods for investigating climate change effects

Earth’s climate has changed drastically throughout the history of the planet, largely due to natural causes. The climate change that we are currently facing however is caused on the most part by human activities that have altered the atmosphere’s energy budget [4]. The high concentrations of greenhouse gases (GHG) such as carbon dioxide and methane emitted through burning of fossil fuels and land use change are
the main causes of this phenomenon. GHGs are transparent to the incoming solar radiation, but block outgoing infrared radiation by absorbing and reemitting it back to the Earth’s surface, thus increasing the amount of energy in the global system. Radiative forcing is the measure used to quantify the influence of a factor in altering the balance of incoming and outgoing energy in the Earth [4]. These forcings trigger many feedbacks occurring through interactions among the components of the climate system: the atmosphere, ocean, land, and cryosphere. By taking into account the physical processes that take place in the climate system and the relationships between the components of the system, various climate models have been developed to predict the response of the system to changing levels of radiative forcing [3]. The future projections of these climate models are used by biologists to make predictions about the influences of climate warming on biodiversity under different scenarios of radiative forcing.

Studying the effects of climate change efficiently requires two types of data source: long-term species data and long-term climate data. Long-term time-series data are very useful sources to study how phenology, demography, life history, and distribution of species are affected by climate change. Probably more such databases exist for birds than all other taxa combined. Sources of long-term data on birds include census data, atlases, ringing, migration stations, bird observation databases, and museum and DNA collections [5]. Long-term climate data are available in various formats and resolutions from local weather stations to mesoscale global or regional reanalysis databases [6]. While these data allow for making comparisons between the past and the present, in order to compare the present with the future, projections of the future conditions are needed.
1.1.1 Projections of future climatic conditions

Climate models are developed by meteorological institutions all over the world. These models, known as General Circulation Models (GCMs), represent the physical processes in the atmosphere, ocean, and land surface and simulate the response of the global climate system to changes in GHG concentrations [4, 7]. The Intergovernmental Panel on Climate Change (IPCC) is the international body responsible for making assessments of these models. IPCC assessments provide rigorous scientific information about climate change for policy makers, scientists, and the general public [4]. In the fifth IPCC assessment report (AR5), projections are based on four Representative Concentration Pathway (RCP) levels, which describe the possible future climates based on future GHG emissions and climate change mitigation efforts. The four levels, namely RCP2.6, RCP4.5, RCP6.0, and RCP8.5, refer to a possible range of radiative forcing values in the year 2100 compared with the pre-industrial values. RCP8.5 corresponds to a business-as-usual scenario of climate change [8].

GCMs use a range of RCPs to make projections about future climate conditions. The output of GCMs is a wide range of variables related to the atmosphere, hydrosphere and cryosphere. The atmospheric data are usually available at the surface level as well as at a number of pressure levels above the surface of the Earth. As GCMs have global coverage and have quite coarse resolution, they are unsuitable to be directly used in local or regional scale studies and particularly in ecological research where many interactions occur at small spatial scales. Downscaling methods extract higher resolution projections of climate parameters of interest from GCMs through the use of Regional Climate Models (RCMs). RCMs are developed using the same or similar schemes and characteristics as GCMs, but take into account additional explanatory
variables, such as regional topography, to make projections of future climate conditions under finer spatial resolutions [7].

Downscaled climate projections are available in various online databases, such as the Coordinated Regional Climate Downscaling Experiment (CORDEX; http://www.cordex.org/), which aims to advance and coordinate the science and application of climate downscaling through global partnerships. All regions of the world are represented in the CORDEX databases and the corresponding data produced by regional RCM developers are mostly available to the public. Not all RCMs are represented in CORDEX however, and some data can only be obtained through direct contact with the individual institutions.

Another global climate database that is very popular among biologists is Worldclim (http://www.worldclim.org/), which provides average monthly climate data for minimum, mean and maximum temperature and precipitation for the past, the present and the future [9]. Although the spatial resolution of the data is very fine (ca. 1 km), the temporal resolution is low and the number of variables provided is limited. While Worldclim data are very useful for distribution modeling and range shift predictions, they do not suit studies related to animal movement, for instance, which require fine scale temporal resolution.

1.1.2 Forecasting species’ spatial response

Forecasting how species are affected by the impacts of climate change on environments and ecosystems can be done through mechanistic or correlative species distribution models (SDMs) [10, 11]. While mechanistic models are based on functional traits and physiological processes that limit distributions [12], correlative approaches focus on relating occurrence data to spatial environmental data. Both
approaches provide congruent results when used to predict the impacts of climate change on species distribution [13] and consist of two general steps: (1) building a model that estimates suitability based on current environmental conditions and (2) applying the model to the future conditions to estimate the areas that will be suitable in the future.

Climate is the principle driver in ecological niche models. The future conditions of climate-related variables are easily attainable through GCM and RCM predictions and are widely used to predict the impact of climate change on the spatial distributions of various taxonomic groups.

1.2 Climate change and migratory birds

Birds are commonly used as model organisms for studying the impacts of climate change on animals. Migratory birds have been of particular importance because they can be severely affected by climate change as they encounter its geographically uneven impacts in different parts of the world. Migratory birds vary in their ability to respond to direct and indirect effects of climate change. This ability is constrained by factors such as lack of genetic variability or phenotypic plasticity, limited dispersal ability, increase in frequency of severe weather conditions, loss or degradation of important habitats, and changes in the influence of competitors, predators and diseases [14]. Generally, short-distance migrants are believed to be better capable to respond to climate change due to their ability to temporally adjust their migration, based on weather and other environmental conditions. Long-distance migrants however, have little plasticity in the timing of their migration, as their migration schedules are endogenously controlled.
Changes in phenology [15], fitness and population dynamics [16], migratory strategies [17, 18] and geographic ranges [2, 3] are among the impacts of climate change on migratory species.

1.2.1 Phenology, fitness, and population dynamics

Phenology refers to the relationship between climate and the timing of various life stages of an organism. As a result of climate warming, many migratory species are arriving earlier to their breeding grounds in spring. This behavior has been associated with rising temperature, which advances the phenology of plants and insects in spring in breeding areas, as well as in stopover and passage sites. Warmer springs also result in more benign weather and improved flight conditions, which can shorten the duration of spring migration [19, 20]. Not all species have been able to respond to the early beginning of spring, however. Some species, particularly those whose migration schedules are under strong endogenous control, do not have the plasticity to respond to changes in temperature by changing the timing of their migration [21]. These species face mismatches between chick-rearing period and food abundance and can face population declines [15, 22]. Population declines can be particularly severe in seasonal habitats where there are short peaks in food availability [23]. Phenological changes can also cause malnutrition and body shrinkage in chicks and reduce their survival rates at later life stages [16].

The direction of change in autumn phenology is less well understood and seems to be very species-specific. In long-distance migrants, the response varies in single brood and multiple brood species. Single brood species that arrive earlier in spring tend to leave earlier in autumn as well, thus shifting their whole life cycle following the advancement of spring. Multiple brood species, however, are more likely to delay their autumn migration to make the most profit from their early arrival in the breeding
areas by laying second and/or third clutches. The response of short-distance migrants to milder conditions in the breeding areas is found to be postponement or even suppression of departure, resulting in a change in the migratory strategy of the population by becoming sedentary [18].

1.2.2 Range shifts

As a result of climate warming, the distribution range of many species worldwide has shifted polewards [24]. Migratory birds are no exception and are in fact expected to be severely affected by shifts in their breeding [2] and wintering [3, 25, 26] areas. Of particular concern are long-distance migrants, especially trans-equatorial migrants, as they will face increases in their migration distance [2, 27] as their breeding and non-breeding areas shift poleward in the northern and southern hemisphere, respectively. The situation for short-distance migrants will be less severe, because breeding and non-breeding areas in the same hemisphere are likely to be affected in the same way. In fact, as winters have become milder, many short-distance migrants are wintering closer to their breeding areas, thus reducing their migratory distances [28].

1.3 The East-Asian flyway for raptors as a case study

Bird migration research in East Asia still remains in its infancy. Long-distance migrating raptors in this region are only beginning to gain attention worldwide, perhaps due to unique characteristics of the East Asian flyways and behavioral adaptations that are not commonly seen in European raptors (e.g. [29]).

Two major migratory flyways are used by raptors in East Asia [30]. The East-Asian Continental flyway is a 7000 km long, mostly overland, route where more than one million raptors of at least 33 species from eastern Siberia, Kamchatka, northern China, Korea and Japan migrate south to South-East Asia. At least 33 species use this flyway
[30]. One dominant species in this flyway is the Oriental honey-buzzard *Pernis ptilorhynchus*, some populations of which are known for their unique seasonal water-crossing behavior over the East China Sea region, which is likely to be facilitated by sea thermals and wind conditions [29, 31]. Grey-faced buzzard *Butastur indicus*, Japanese Sparrowhawk *Accipiter gularis*, and Chinese Sparrowhawk *A. soloensis* are other dominant species, while Rough-legged hawks *Buteo lagopus*, Amur falcons *Falco amurensis*, Merlins *F. columbarius*, Northern hobbies *F. subbuteo*, and Peregrine falcons *F. peregrinus*, and Pied harriers *Circus melanoleucos* also use this corridor. The East Asian Oceanic flyway lies farther East, stretching from northeastern Siberia and Kamchatka, through Kuril Islands, eastern China, Korea, Japan, Taiwan, the Philippines, and for some species further south. This flyway, used by half a million raptors of about 19 species, is the only flyway for raptors that is largely over-water. This flyway is dominated by the Chinese Sparrowhawk and the Grey-faced Buzzard, a soaring raptor which very likely uses sea thermals that commonly form in the trade wind zone [30, 32] to carry out the numerous sea-crossing maneuvers along its migration route [33]. Other species using this flyway include Rough-legged hawks, Eurasian buzzards *B. buteo*, Merlins, Northern hobbies, and peregrine falcons.
Chapter 2

The effects of atmospheric currents on the migratory behavior of soaring birds: a review

Publication:

Abstract

Atmospheric currents influence the choice of migratory routes and flight characteristics of birds as well as their decisions regarding migration onset and stopovers. Among long distance avian migrants, soaring birds are particularly dependent on wind and updrafts to help them complete their journeys. This review focuses on the behavioral adaptations of migratory soaring birds at various scales with regard to these atmospheric phenomena. Soaring landbirds and soaring seabirds have evolved morphological characteristics that make them specialists in soaring flight, thus enabling them to reduce the costs of migration significantly. I introduce the flight strategies of each group and discuss how migratory routes, flight characteristics, and onset and stopover decisions are all adjusted in relation to atmospheric conditions best suited for soaring. In addition, I discuss briefly how this strong dependence on atmospheric conditions makes soaring birds vulnerable to anthropogenic threats, such as wind energy development and climate change.

Keywords: Dynamic soaring, Migratory route, Raptors, Seabirds, Thermal soaring
2.1 Introduction

Atmospheric conditions have considerable influence on various aspects of bird migration, such as migratory routes \[34, 35\], orientation \[36\], flight characteristics \[37, 38\], departure and stopover decisions \[1\], and intensity of migration \[39\]. A bird’s responses to local weather conditions affect the regional and seasonal efficiency of its migration, consequently impacting its reproductive success and population dynamics, thereby generating optimal migratory strategies through natural selection. Air movements (both horizontal and vertical) are particularly important in shaping the migratory behavior of birds. Horizontal winds are within the same order of magnitude as avian flight speeds. Therefore, winds that blow along the migratory track (tailwind) may increase flight speed \[37\], while those blowing from the opposite direction (headwind) or from the side (side-wind or crosswind) may pose major obstacles to migratory movements by reducing ground speed, forcing deviation from the intended flight direction, or temporarily halting migration.

While horizontal winds impact all avian migrants regardless of their phylogeny and morphology \[1\], changes in vertical air movement particularly impact soaring birds, as for them vertical air movements are essential and indispensable facilitators of migration. The vertical air movements that allow birds to gain height while using little energy, are generated by two major phenomena: the upward deflection of horizontal winds against tall structures, topographic features, or waves (i.e. orographic updrafts); and localized columns of rising air generated as the sun warms the Earth’s surface during the day (i.e. thermals).

Soaring flight, also known as soaring-gliding flight, refers to the ability of birds to use atmospheric currents in order to sustain long periods of flight without flapping their
wings, which is the most energetically cost-efficient form of flight [40-42]. Birds soar in upward moving air to gain altitude without spending much energy and complement it with gliding toward their preferred direction. Many large birds depend on soaring flight for their long-distance migratory movements, as they cannot accumulate enough fat reserves to fuel long periods of flapping flight [43, 44]. Examples include seabirds (mostly Procellariiformes) as well as birds that fly predominantly over landmasses and inland water bodies (hereafter landbirds), particularly raptors [Accipitridae, Pandionidae, Falconidae and Cathartidae], storks (Ciconiidae), pelicans (Pelecanidae), anhingas (Anhingidae), and to some extent cranes (Gruidae), herons (Ardeidae), and bee-eaters (Meropidae). Passerines, such as the Common Starling *Sturnus vulgaris*, also occasionally engage in soaring flight [45].

Various reviews have dealt with the effects of atmospheric conditions, particularly horizontal wind, on migratory birds [1, 36, 39, 46, 47]. A decade has passed since the latest review [1], and a wide range of research has been conducted taking advantage of recent advances in telemetry devices [48, 49], wider availability of weather data [50, 51], and the increasing use of modeling techniques [34, 52, 53]. In this review, I bring together studies on the effects of atmospheric currents on migratory birds, but focus on those that have investigated behavioral adaptations of soaring migrants with regard to horizontal and vertical air movements. In each section of this paper, I discuss a different aspect of the migratory behavior of soaring birds, addressing landbirds and seabirds separately. In a concluding section, I briefly summarize the major weather-related anthropogenic changes and developments that may threaten these particular birds in the future.
2.2 Flight strategies

*Landbirds*

The adaptation of migratory birds to specific flight types is determined by biometrical and ecological constraints [40, 54]. Soaring flight is the result of such adaptations in heavier birds with high wing loading (ratio of body mass to wing area), for which the energetic cost of flapping flight is extremely high. The wing morphology of such birds has evolved in such a way as to utilize atmospheric currents very efficiently for soaring and gliding with little cost.

The soaring landbirds include both obligate and facultative species. On the one hand, obligate soarers are the larger and heavier species, with long, broad wings; they depend solely on soaring flight in order to conserve as much energy as possible during long flights [54]. These heavy birds have relatively high wing-loading and thus circle thermals slowly and are confined to using only strong thermals and particularly the stronger parts of each thermal, but have the advantage of being able to glide quickly from one thermal to the next [55]. On the other hand, facultative soarers are lighter and have long, slender wings; they can alternate between soaring and flapping flight depending on air movements. These birds have relatively lower wing-loading, thus although they can climb thermals quickly and even use weak thermals, their gliding speed between thermals is limited. Although both obligate and facultative groups migrate diurnally, when thermals are formed, the latter commence travelling earlier in the day by depending on flapping flight, whereas the former must wait until several hours after sunrise for strong thermals to form [56-58].

The family Accipitridae is the largest group of soaring landbirds and is therefore the main focus of the sections on landbirds in this review. Owing to the previously
mentioned aspects of their morphology, members of the Accipitridae have varying migration tendencies with respect to updrafts, thermals, and wind. Among them, the most dependent on soaring flight, in order from obligate to facultative, are vultures (e.g. *Gyps* spp.) and eagles (e.g. *Aquila* spp.), hawks (*Buteo* spp.), kites (*Milvus* spp.), hawks (*Accipiter* spp.) and honey-buzzards (*Pernis* spp.), and finally harriers (*Circus* spp.) and ospreys (*Pandion* spp.) [32].

Species in the family Falconidae also soar, but among raptors they are the least dependent on soaring flight. Their long pointed wings have high aspect ratios (wing span squared, divided by wing area) that generate low induced drag and consequently their energetic cost of flapping flight is low [59].

Soaring over land is achieved through the use of thermals or orographic updrafts (Fig. 2.1). Thermal soaring migrants gain height while circling in one thermal, then lose height while gliding to the next, repeating this process multiple times along their route [32]. In contrast, slope soaring requires orographic updraft (also known as deflection updraft; [30]). Soaring landbirds can use both these types of soaring flight interchangeably, but slope soaring is a common mode of flight in the Americas, where most mountain ranges are aligned along a north-to-south axis and where strong orographic updrafts form thermal streets. Contorted soaring is a third type of soaring flight used frequently by vultures to subsidize flight, particularly in terrain where there are few thermal and orographic updrafts. Contorted soaring depends on shear-induced turbulence caused when horizontal air flow is interrupted by forest or tree line [60].
Figure 2.1. Soaring flight in landbirds. Landbirds use two soaring modes interchangeably: thermal soaring (left) is facilitated by columns of rising warm air, i.e. thermals, and orographic soaring (right) on updrafts created by upward deflection of horizontal winds.

The predominant flight type used by migratory birds is determined not only by their body mass and wing morphology, but also by their long-distance flight strategy in terms of optimizing their migration by energy or time minimization criteria. Although many avian species may be morphologically capable of adopting soaring flight, for many, particularly smaller species, the slow cross-country speed of such flight makes it unattractive for those birds aiming at maximizing their overall migration speed [40].

**Seabirds**

Seabirds can be classified into four major groups based on their flight type: soarer-giders (small albatrosses and large gadfly petrels), flap-giders (surface-feeding Procellariiformes and small gadfly petrels), glide-flappers (diving and Manx-type shearwaters and storm petrels), and flappers (Charadriiformes, Alcidae and
cormorants (Phalacrocoracidae)) [61]. The flight pattern of each species is determined mostly by biometric characteristics; heavier birds with higher wing-loading and aspect ratio perform more soaring flight and lighter birds use a gradient of soaring and flapping flight [62].

Seabirds use atmospheric currents differently from landbirds in order to achieve low cost flight. Over land, soaring flight predominantly depends on thermals, but strong thermals are usually not generated over the sea surface. The exception to this occurs in the trade-wind zone (5–30° north and south of the equator) where strong “sea thermals” form throughout the year [63]. The Magnificent Frigatebird *Fregata magnificens* has a restricted range within the trade-wind zone where it utilizes a thermal soaring strategy similar to that of landbirds [64, 65].

Winds blow more strongly over the sea surface than over land and they become stronger with elevation due to reduced friction. Such strong winds facilitate two types of soaring flight: dynamic soaring and wave-slope soaring [66, 67]. Dynamic soaring is also known as wind-shear soaring [68] and gust soaring is a special case [69]. The basis of dynamic soaring lies in the difference between the wind speed close to the sea surface and that above the wind-shear boundary, where friction is not a limiting factor [68]. To start one cycle of dynamic soaring, a seabird flies upwind against the weak surface wind gaining height, it then flies above the wind shear, makes a downwind turn and angles its body to maximize the surface area affected by the wind and allows itself to be carried forward at speed (Fig. 2.2).
Figure 2.2. Dynamic soaring in a seabird. One cycle of dynamic soaring begins as a seabird flies upwind, pulling up above the wind-shear layer (1), then encounters a strong gust of wind that allows the bird to increase its airspeed and gain kinetic energy. The bird then banks and turns (2) and descends downwind, flying in the opposite direction, descending back below the wind-shear layer with tailwind support (3), gaining another pulse of kinetic energy. The bird then turns and changes its direction to start the next cycle (4) [67, 68].

In wave-slope soaring, seabirds soar using any updraft derived from wind-wave interactions (similar to orographic updrafts forming along slopes on land). This behavior is particularly common among albatrosses (e.g. Diomedia spp.) and to a lesser extent in giant petrels Macronectes halli and M. giganteus) [62, 70]. Soaring conditions over the sea are generally improved when swell waves (i.e. waves not created by local wind) propagate upwind, as the wind flowing up the wave face creates a substantial updraft. Moreover, a swell wave propagating downwind with
higher speed than the local wind can also produce a similar effect [68, 71]. These modes of soaring restrict seabirds to flying at much lower elevations [72] than soaring landbirds that gain high altitude by circling in thermals.

A combination of dynamic soaring and wave-slope soaring is considered ideal for seabirds in order that they may maximize total energy gain. The energy demand of soaring is almost as low as that expended when sitting on the sea surface [73, 74]. The low energy demand of soaring allows seabirds to perform some of the most impressive avian movements, both during the breeding season, when their foraging trips sometimes exceed thousands of kilometers [75-77], and on their long-distance trans-oceanic migrations [78-80].

2.3 Migratory route selection

_Landbirds_

Avian migrants do not follow the shortest great circle path between their breeding and wintering grounds. In fact, the large-scale movement of birds, particularly on migration, is determined mainly by patterns of air movement in the boundary layer. Air currents shape the most efficient flyways for birds in general [34] and for soaring birds in particular [81]. Although many soaring landbirds generally migrate on a broad front for parts of their migration, their flyways are shaped along topographical features that support the formation of strong thermals and orographic updrafts [30, 32, 41] such as mountain ranges, narrow valleys, and coastal plains, also along thermal streets [42] or sea-breeze fronts [82]. The dependence of soaring birds on updraft and wind conditions is so strong that these variables can be used to predict and simulate their potential migratory routes [83-85]. Major corridors for raptor migration for
example, include the Appalachian Mountains, the Rocky Mountains, the Sierra Madre Oriental, the Talamancan Mountains, and the Andes in the Americas, the Alps in Europe, the Tien Shan and Hindu Kush and the southern Himalayas in Asia, and the escarpments of the Great Rift Valley in East Africa and the Middle East [30].

Large water bodies act as ecological barriers along the migration route of many soaring birds [86]. Whether a species adopts water-crossing behavior or not is determined by its energy consumption during flapping flight [87]. Thermals are weak or absent over water, making soaring flight energetically inefficient or even impossible for soaring birds, particularly obligate soaring species that cannot accumulate enough fat reserves to sustain flapping flight to cross water bodies. Behavioral adaptation of these species favors avoidance of water crossing by taking detours over land and crossing water bodies only at their narrowest parts, such as straits, which may be considered migration “bottlenecks”. Concentrations of many thousands of migrants can be seen at such “bottlenecks” including Costa Rica, Mexico and Panama in the Americas, Falsterbo, Organbíðeská, and Gibraltar in Western Europe, Burgas and Bosphorus in Eastern Europe, Batumi and Himalayas in Central Asia and Malay Peninsula and Tsushima Strait in eastern Asia [30].

While soaring migrants avoid flying over water where possible, migratory trajectories of some soaring birds include considerable water-crossings of various lengths. Most soaring birds that make such crossings are highly dependent on tailwind support [88-91] and possibly sea thermals in the trade-wind zone in East Asia [30, 31]. Falconidae species, including Eleonora’s Falcon *Falco eleonorae*, Sooty Falcon *F. concolor* and Amur Falcon *F. amurensis*, which fly long distances over water, also depend on tailwind assistance [92-95].
The absence of physical barriers over the seas and oceans results in constant wind flows, providing ideal conditions for soaring flight. Although it has long been suggested that wind is important during the migration and at-sea movement of seabirds [78, 96], until recently, the evidence of the role of wind patterns in shaping the migratory routes of seabirds was no more than speculation based on global wind patterns and indirect evidence from the migratory movements of certain species. With advances in tracking technology, it became possible for researchers to study the details of the migratory movements of seabirds, and to reveal their astonishing journeys of tens of thousands of kilometers, facilitated by atmospheric conditions, especially wind [72, 80, 97, 98].

In both the Atlantic and the Pacific oceans, trans-equatorial migrants, including shearwaters, follow general flyways that resemble a figure-eight pattern [80, 97], indicating that they travel in the direction of the prevailing winds, which circulate clockwise in the Northern Hemisphere and counter-clockwise in the Southern Hemisphere. Felícísimo et al. [99] were among the first to explore the role of wind in the spatial and temporal patterns of movements of a migratory seabird (Cory’s Shearwater *Calonectris borealis*), and explain why seabird migration routes are usually longer than the great circle routes connecting their departure and arrival points. Felícísimo et al. [99] found that large-scale migration patterns are driven by spatiotemporal variations in the wind. Calms or strong headwinds resemble a barrier across a transoceanic path. González-Solís et al. [100] further investigated the effects of wind on the migratory routes of soaring seabirds, and found that shearwaters followed low-cost pathways that were 26-52% longer than the shortest distance path. Their findings proved that ‘wind highways’ exist even for seabirds that migrate over...
topographically barrier-free oceans. These studies suggest that the optimum migration route for shearwaters is a compromise between wind-mediated costs and traveling time, perfected as they gain experience about choosing the best route.

The Wandering Albatross *Diomedea exulans* also avoids headwinds by circumnavigating Antarctica during the non-breeding period, essentially making a 10,000 km detour so as to continuously follow westerly winds. In addition to their migratory route, the migration range of albatrosses is also restricted by wind conditions [101].

2.4 Local-scale migratory behavior

*Landbirds*

Atmospheric conditions not only significantly influence the large-scale migratory patterns of soaring birds, but also affect their flight characteristics and decision-making at the local-scale. Soaring birds on migration adjust the timing of departure and stopover, as well as flight characteristics including altitude, speed, and direction, in response to changes in atmospheric conditions.

Although the timing of migration is under strong endogenous control [102], weather is one of the major exogenous factors that trigger the onset of migration in birds [37, 39]. Shamoun-Baranes et al. [103] showed that obligate soaring birds, such as the Lesser Spotted Eagle *Clanga pomarina*, are more likely to be detained in their breeding range when soaring conditions are poor. Vansteelant et al. [104] investigated local aggregations of raptors in the Black Sea coastal convergence zone and found that as cloud conditions limited thermal formation, obligate soaring birds aggregated.
near the coast and avoided taking off. Consequently, weather factors can be used to predict the density of migrating birds at migratory raptor watch sites [39, 105].

Once soaring birds take off and commence migrating, they adjust their flight characteristics according to the quality and availability of updrafts. Flight altitude, for example, is adjusted in relation to intensity and depth of thermals [55]. Soaring birds gain higher altitude until mid-afternoon when thermals are strongest, taking advantage of the opportunity to climb higher over a shorter period of time [54, 106].

Better convective conditions allow soaring birds to travel faster and farther [107-110]. Lanzone et al. [111] suggest that soaring birds are able to minimize their energy expenditure by switching between modes of soaring. For example, as wind speed increases and reduces thermal formation, Golden Eagles *Aquila chrysaetos* fly lower and use less vertical air space, in order to use more orographic uplift. Such adjustments allow for migration over longer periods each day [112], increasing the overall speed of migration. Soaring birds also adjust their gliding airspeed to soaring conditions, actively reducing speed when thermals are scarce in order to avoid switching to flapping flight when possible [113]. Sapir et al. [114] studied the effects of convective conditions on the flight mode of the European Bee-eater *Merops apiaster* using turbulent kinetic energy (TKE) levels as an index of thermal strength, and found that these facultative soaring birds switch between flapping flight at lower TKE levels and soaring flight at higher TKE levels.

Tailwind support may significantly affect the daily distances that birds travel [110, 115, 116]. Against headwinds, obligate soarers are more affected than facultative soarers, as it is more difficult for them to switch to flapping flight to compensate for wind drift [107, 117, 118]. Soaring birds also avoid unsuitable weather events such as
dust storms by changing their flight direction and taking detours [107]. Even so, Turkey Vultures *Cathartes aura* have a remarkable ability to soar even under turbulent winds conditions, perhaps related to their dihedral wing profile and their use of contorted soaring [60, 119].

Stopover decisions by soaring migrants are also influenced by weather conditions. Unfavorable atmospheric conditions can halt the migration of soaring birds. For example, White Storks *Ciconia ciconia*, pause during migration making rest stops when thermal conditions are weak, especially during the mornings and evenings [120]. Similarly, migrating Golden Eagles, when they face no time limits during migration (pre-adult movements in spring and all movements in autumn) pause along their route so as to avoid suboptimal flight conditions [121].

*Seabirds*

Soaring seabirds are also affected by local atmospheric conditions during migration. Since their soaring behavior is facilitated by wind, both the flight altitude and behavior of seabirds change as a function of wind speed and direction [122]. By analyzing simultaneous data from fine-scale wind conditions and aerial movements of Cory’s Shearwaters, Felicísimo et al. [99] showed that the shearwaters make local-scale decisions about flight direction based on wind conditions to achieve low-cost flight. It has been suggested that shearwaters adjust the time of crossing the equator in order to avoid the monsoon westerlies during the summer months [99].

Wind direction also plays a key role in small-scale adjustments to flight direction. Soaring Procellariiformes not only prefer crosswinds because they facilitate dynamic soaring [62, 123], but also travel most frequently in crossing tailwinds and generally avoided headwinds (Adams and Flora [72]. Additionally, Mateos and Arroyo [124]
analyzed the off-shore distances of the most abundant species passing through the Strait of Gibraltar during spring and autumn and found that seabirds approached the coast in response to headwinds, indicating that wind direction and speed co-varied with local patterns of flight trajectories.

Such decision-making by soaring seabirds is not only dependent on wind conditions however, as the birds alternate migratory flight with rest periods for refueling [125, 126]. Such behavior indicates that, especially when not crossing ecological barriers, soaring seabirds choose their local flight characteristics not only according to the most favorable winds, but also by considering the location of foraging areas. When encountering severe weather conditions, however, birds prefer to avoid such areas by circumnavigating them [72].

2.5 Future perspectives

The dependence of soaring birds on atmospheric conditions means that they are at risk from anthropogenic changes and developments. Two of the main areas of concern for future conservation of soaring birds include the development of wind energy facilities and climate change.

The existing and planned wind power generating facilities are all located in regions with strong winds. On-shore wind turbines are often arranged along coasts or mountain ridges, features that are used for lift by soaring birds [127, 128]. These structures put soaring birds at risk of displacement and mortality [129, 130]. Depending on species- and site-specific attributes, different species of soaring birds have different levels of vulnerability to wind energy structures [122, 128, 130-132]. Although avoidance of wind farms by changing migration trajectories has been
observed among raptors [133, 134], adjustments in flight trajectories require deviating from the traditional optimal routes, consequently forcing the birds into conditions that require extra energy expenditure. Off-shore wind farms may have similar negative effects not only on migrating seabirds [135], but also on soaring landbirds that perform water-crossings.

Another anthropogenic phenomenon that may pose a threat to soaring birds (by altering their preferred atmospheric conditions) is global climate change. Global warming is expected to affect the dominant wind patterns, both in strength and direction. Existing literature on the consequences of such changes are mostly limited to the behavior of birds during the breeding season. Weimerskirch et al. [101] showed that in response to the increased intensity of westerly winds in the Southern Ocean, Wandering Albatrosses have shifted their foraging range poleward. Thorne et al. [136] investigated the effects of changes in wind patterns due to El Niño Southern Oscillation (ENSO) on incubating and brooding albatrosses and found that changes in wind speeds during El Niño and La Niña conditions affected habitat accessibility and travel costs for the birds. Climate change-induced alterations in wind conditions may also adversely affect soaring birds outside their breeding season, as their migration routes are determined largely by atmospheric currents. Changes in wind and updraft conditions may impact the ability of birds to use traditional routes; however, to my knowledge, the consequences of such changes on migrating birds have rarely been studied. Simulation models using projected values for weather variables will be helpful tools facilitating our understanding of the likely effects of climate change on avian migratory movements.
Acknowledgments

I would like to thank Daniel N. Suzuki for preparing the figures and Wouter Vansteelandt and an anonymous reviewer for their valuable comments on an earlier version of this review.
Chapter 3

Wind conditions facilitate the seasonal water-crossing behaviour of Oriental Honey-buzzards over the East China Sea

Publication:

Abstract

Migratory raptors rarely fly over stretches of water greater than 25 km, although various species undertake water-crossings of varying lengths, depending mainly on their morphology. Oriental Honey-buzzards fly ca. 680 km over the East China Sea in autumn from breeding areas in Japan to wintering areas in Southeast Asia, but avoid the water-crossing in spring. I investigated the effects of weather on this exceptional migratory behaviour and its seasonality through a Maximum Entropy niche modelling approach. I used data collected through satellite tracking of 31 adult birds as presence points and a set of variables related to wind, precipitation, and convective condition as environmental predictors. Results of modelling showed very different, almost non-overlapping, areas suitable for migration over the East China Sea region in autumn and spring. Suitable migration route in autumn mostly occurred over the sea while suitable areas for spring migration mostly occurred on land, suggesting that circumnavigating the East China Sea is preferable in spring. I found that, at the regional scale, wind conditions facilitate water-crossing behaviour of Oriental Honey-buzzards in autumn, but not in spring. Specifically, suitable tailwind over the sea enables water-crossing in autumn, while in spring, wind support and convective conditions are best over land. My modelling did not identify the importance of convective conditions for autumn migration. However, I expect that at smaller temporal scales, convective conditions would be a considerable facilitator of the water-crossing behaviour in this raptor species.

Keywords: *Pernis ptilorhynchus*, raptor, migration, East Asian flyways, MaxEnt, sea-crossing, tailwind, migratory niche
3.1 Introduction

To migrate successfully, raptors depend on low-cost soaring-gliding flight, only possible by exploiting updrafts and thermals [30, 41]. Raptors thus select their migratory routes along geographical and topographical features that support strong convective conditions, i.e. thermals and updrafts [41, 137]. High energy demands of long powered flight [138] has resulted in a general hesitance in raptors of flying over stretches of water greater than 25 km [30, 39], where thermals are weak [40, 89]. Morphological characteristics of the wing in facultative soaring raptors, such as harriers and falcons, allow them to tackle such ecological barriers by adjusting their flight behaviour to powered flight over water [54, 89, 92, 139, 140]. Many larger raptors however, lack the ability to use flapping flight for long distances and instead circumnavigate large bodies of water [30, 90, 141, 142].

Apart from morphology [59, 87], physiological state of the bird [89], flock size [143], time of day [144], experience [89, 145, 146], historical direction of migration [147] and a tendency to minimize migration time in spring [148] have been associated with water-crossing behaviour in raptors. There is a consensus however, that water-crossing in raptors, whether it be the regular 1500 km ocean-crossing of Eleonora’s Falcons *Falco eleonorae* [92], a facultative soaring bird, or the 150 km journey of the European Honey-buzzard *Pernis apivorus*, an obligate soaring bird, over the Mediterranean Sea [89, 143, 144], depends strongly on selection of optimal weather conditions for traveling over water.

An exceptional water-crossing behaviour by an obligate soaring bird has also been observed in the East Asian flyways, where the Oriental Honey-buzzard *Pernis ptilorhynchus* undertakes journeys of c. 680 km every autumn over the East China Sea on migration from breeding areas in Japan and wintering areas in Southeast Asia.
The birds take a longer route in spring however, detouring over the Korean Peninsula and reaching Japan through Korea/Tsushima Strait (water-crossing of ca. 170 km). From an ecological perspective, this unique behaviour has been attributed to seasonality of prey distribution and availability [149] and possible competition in wintering areas with conspecific and congeneric migrant and resident birds, which makes it more preferable for Oriental Honey-buzzards to minimize the duration of autumn migration [152]. Yamaguchi et al. [31] have suggested that weather conditions over the East China Sea in autumn is responsible for the ability of Oriental Honey-buzzards to cross the sea directly. Although thermal formation over water surfaces is generally weak, sea thermals are rather common in tropical and subtropical waters between 5° and 30° north and south of the equator [63]. The East China Sea is located within this sub-tropical belt and is dominated by north-easterly winds probably due to the Asian monsoon, which, along with the sea thermals, are assumed to facilitate the sea-crossing behaviour of Oriental Honey-buzzards, even though their migratory route is slightly above the northern limit of this belt [31]. These assumptions have not been quantitatively proven, however.

In this study, I investigate the water-crossing behaviour of Oriental Honey-buzzards in the context of ecological niche, assuming that the migratory niche of these birds is determined by suitable weather conditions over the East China Sea region. I therefore adopt a niche modelling approach to show the spatial distribution of suitable weather conditions for migration over the region in autumn and spring.

Although ecological niche modelling is extensively applied in ecology and conservation research [153, 154], its use in avian migration ecology studies has been limited to predicting wintering ranges [155, 156], mostly with an aim to assess the effectiveness of protected area networks [157, 158] and predict future range shifts.
but rarely has it been used for understanding the environmental preferences of species on the wing [160, 161].

I employed a maximum entropy ecological niche approach to (i) identify the most important weather variables that shape the migratory niche of Oriental Honey-buzzards, i.e. the environmental conditions that the birds prefer *en route*, in each season and (ii) understand the differences in weather conditions over the region between autumn and spring to explain the seasonality of water-crossing behaviour. I expected that suitable tailwind over the East China Sea in autumn would explain the seasonality of this behaviour. Moreover, since Oriental Honey-buzzards would not be able to undertake long powered flight, and Yamaguchi et al. [31] suggested that the birds use soaring flight during their flight over the East China Sea, I expected convective conditions to be also an important determinant of migratory niche for the birds.

3.2 Methods

3.2.1 Satellite tracking data

I used satellite tracking data collected by solar-powered platform transmitter terminals (PTTs; North Star Science and Technology LLC, Baltimore, Maryland, USA; Microwave Telemetry Inc. Columbia, MD, USA), which were deployed to the back of 31 adult Oriental Honey-buzzards between 2006 and 2013 in Japan. Four different types of PTTs were used that weighed between 12 and 30 g (+6.7 g harness; 1.44-3.69% of body mass). Locations were collected using the Argos system [162]. Details of capture and deployment methods are described in Yamaguchi et al. [31].
3.2.2 Ecological niche modelling

I used maximum entropy algorithm, MaxEnt [163], a commonly used method for niche modelling using presence-only data and therefore suitable for data collected by satellite tracking [155], to model the potential migratory niche of Oriental Honey-buzzards over the East China Sea at a regional scale. MaxEnt has shown good performance compared to other niche modelling methods [164]. It assumes a uniform distribution (i.e. maximum entropy) *a priori* and by performing a number of iterations, maximizes average probabilities for point localities (i.e. training gain) by adjusting some weights, while taking into account constraints that result from empirical averages of environmental predictors. The resulting weights [165] are used to compute MaxEnt distribution over the area.

3.2.3 Presence points

For the purposes of the modelling, tracking data were filtered based on accuracy, timing and location. I only used satellite tracking points with location classes (LCs) 3, 2, 1 and 0, corresponding to spatial accuracy of < 250 m, 250-500 m, 500-1500 m and slightly above 1500 m, respectively [31].

Following Yamaguchi et al. [31], I defined autumn migration as 11 September to 20 October and spring migration as 1-31 May, corresponding to the time when the birds moved through the focal areas. Another temporal filter that I applied to the data was to only retain bearings recorded at daytime (06:00 a.m. to 18:00 p.m. JST) (Fig. 3.1).

For autumn migration, I excluded all points within Japanese terrestrial borders and retained the points from the first bearing off the coast of Japan onward to China. Because most birds in this season flew over the East China Sea and I was interested in the sea-crossing behaviour, I excluded bearings from after the birds arrived to China.
A small number of complete tracks belonged to individuals that were suspected to have stopped over Jeju Island [31]. I removed these from the analysis in order to focus the study on the direct sea-crossing behaviour.

Points retained for spring included bearings over China, Korea and any point recorded before the first bearing of each bird within Japan.
Figure 3.1. Autumn and spring migration of Oriental Honey-buzzards breeding in Japan. Tracking points were obtained from 31 adult birds between 2006 and 2013 during autumn (top) and spring (bottom) migration. Wind fields are visualized using $u$ and $v$ values obtained from National Center of Environmental Protection (NCEP) reanalysis data archives (www.cdc.noaa.gov/cdc/data.nmc.reanalysis.html) and averaged over daytime for each migration season. Japan’s Mesoscale Model was not used.
due to its limited geographic extent. In autumn, the birds set off from Japan’s Kyushu Island (A), cross the East China Sea (B) and reach China (C). In spring, they fly over land through China and the Korean Peninsula (D) and cross the Korea/Tsushima Strait (E) to return to Japan. This seasonal difference in migratory route is likely caused by seasonal differences in weather conditions over East China Sea, which facilitates sea-crossing in autumn, but not in spring. Squares over the East China Sea region represent the extent used in this study. The location of Jeju Island is also shown (F).

To account for unequal contribution of individuals to the models and to reduce pseudoreplication, for individuals with more than five tracking points in the dataset, I randomly sampled five points with the condition that selected points that were recorded on the same day were located at least 50 km apart. For the individuals that were represented with less than or equal to five tracking points, I retained all points, except for pairs of points that were recorded on the same day and were < 50 km apart, in which case one point was randomly selected and removed. Thus the final training set for autumn and spring included 64 points for 22 individuals and 86 points for 20 individuals, respectively.

3.2.4 Predictor variables

I extracted weather data from the Japan Meteorological Agency’s Mesoscale Model (MSM; http://database.rish.kyoto-u.ac.jp/arch/jmadata/data/gpv/netcdf). As of the year 2006, the spatial resolution of the database is 7.5 arc minutes latitude and 6 arc minutes longitude corresponding to about 15 km and 12 km on the surface of the Earth, respectively. Temporal resolution of the data is 3h. I downloaded meridional (v), zonal (u), and vertical (omega) components of the wind at 850 mb pressure level
(corresponding to an average geopotential height of 1.5 km and the average flight height of Oriental honey buzzards on migration) and hourly precipitation (mm) at the surface level. Temperature data were downloaded at 850, 900, 925, 950 and 1000 pressure levels to calculate vertical temperature gradient as a proxy for thermal convection [110]. The same temporal filters that were used for the tracking data were also applied to the weather variables. The following variables were computed separately for autumn and spring to be used for modelling.

*Horizontal and vertical wind components*

Wind is the most important weather variable affecting birds on migration (for a review, see [1]), influencing, among other aspects, the optimality of migration route [38, 86] and overall speed of migration [107, 166]. I incorporated both horizontal (tailwind and side-wind) and vertical (omega) components of the wind in the modelling. Omega is defined as the vertical motion in the atmosphere, with negative and positive values relating to upward and downward air motion, respectively. Wind data downloaded from MSM, including u, v and omega, were averaged for daytime over the 40 days of autumn migration and 31 days of spring migration for each 7.5 × 6 arc minute grid cell. To achieve a fine resolution suitable for modelling, I interpolated each variable using a thin plate spline (TPS) approach [167] to a grid with a cell size of 72 arc seconds, approximately corresponding to 2 km on the surface of the Earth. This cell size corresponded with the lowest accuracy of location classes of satellite tracking points (LC 0; ca. 1.5 km). I then calculated tailwind and side-wind using the interpolated u and v values. Tailwind and side-wind were calculated in R environment v 3.1.3 [168] using the ‘RNCEP’ package [169] by
considering the mean direction of flight over the East China Sea region as 212° and 133° in autumn (from south-west Japan to eastern China) and spring (from Korean Peninsula, over the Korea/Tsushima Strait to Japan), respectively. Negative and positive values of side-wind correspond to wind blowing from right and left of the direction of flight, respectively.

Vertical velocity values approach zero when they are averaged over a large spatial or temporal scale [137, 170]. To compensate for this possible loss in the impact of vertical velocity in the models, apart from the average omega layer prepared as a proxy for vertical velocity, I also prepared a layer of minimum omega for each season. As negative values of omega correspond to upward air movement, I determined the minimum value of omega in each cell during the migration season in each year. The minimum values were then averaged over the eight years and interpolated as explained above.

*Thermal convection*

I followed Chevallier et al. [110] for determining an indicator for thermal convection in each grid cell over the study area. In this method, temperature gradient (°C/100m) is used as a proxy for thermal convection and is calculated as the mean of temperature gradients between given pressure levels. I calculated four temperature gradients between 1000, 950, 925, 900 and 850 pressure levels and averaged them over all pressure levels. Unlike Chevallier et al. [110] however, I did not convert the resulting values (ranging from 0 to 1) to thermal energy classes, but retained this variable as a continuous one.

I incorporated this measure of thermal gradient into the model both as average thermal convection over the eight years in each cell and also as maximum thermal
convection for each cell (for the same reason as stated for the minimum omega variable).

Precipitation

I incorporated precipitation in the models as the maximum hourly precipitation per cell during the migration season. My aim was to determine whether birds on migration avoided areas with frequent heavy rain.

3.2.5 Model construction

I used Pearson correlation coefficients to evaluate the co-linearity of variables in each season. To limit co-linearity to < 0.7, I dropped average thermal convection from the autumn model due to high correlation with side-wind.

I implemented MaxEnt in ‘dismo’ package [171] in R environment v 3.1.3 [168] to model the ecological niche of Oriental Honey-buzzards on migration over the East China Sea region (120°-132° E and 28°-41° N; also see Fig. 3.1). To get more interpretable results on the direction of contribution of each environmental predictor in the final model, I limited features used in model fitting to linear, quadratic and product. A maximum iteration of 1000 times was set to ensure convergence.

Background data, or pseudo-absences, a necessary input for presence-only modelling methods, are often sampled automatically by MaxEnt, under the assumption that every pixel in the specified range has the same probability of being selected as a background point and thus representing a pseudo-absence [172]. However, because training dataset contained only a portion of the initial tracking dataset, pseudo-absences selected by MaxEnt could be selected from cells containing tracking points.
which were left out of the training set during the data sampling stage. To account for
the potential bias in automatically selected background points, I randomly selected
5000 points from the whole region, except at satellite tracking points that were
filtered temporally.

I evaluated the predictive performance of the models and the probable overfitting by
using a K-fold cross-validation procedure [172]. For each season, the dataset was
randomly split into 10 partitions and modelling was run 10 times, each time excluding
the tracking points in one partition from the training data, while the remaining
partition was used as testing data to assess model performance. Importance of each
variable, in the form of regularized training gain of the model with only that variable,
was evaluated using a Jackknife procedure.

As an additional step, I carried out randomization tests to better understand the
differences between land and sea regions in terms of the most important variables
identified through MaxEnt modelling. I defined land as all landmasses in the study
region, apart from Japan. Because not the whole extent of waterbodies in the region is
located along the migratory route of Oriental Honey-buzzards, I considered ‘sea’ to be
the area between China and Japan, defined as all cells falling within the extent of the
autumn niche model ( > 0.5 suitability). Random samples of points over land and sea
(\( n = 29 \) for each season), located at least 50 km apart, were used as inputs for
randomization tests.

3.3 Results
Ecological niche models predicted considerably different areas suitable for Oriental
Honey-buzzard migration over the East China Sea region in autumn and spring. The
models showed strong discriminatory power with area under the curve (AUC) values
of 0.89 and 0.87 for autumn and spring, respectively. Variables side-wind and tailwind for autumn (Table 3.1) and variables tailwind, average thermal convection, and side-wind (Table 3.2) for spring contributed the most to the final model for each season.

Autumn migration model predicted the most suitable areas for migration to be over the East China Sea towards China, while no area over the land was identified as suitable (Fig. 3.2). Areas of high suitability predicted for spring migration were almost the opposite of that of autumn and were mostly located over land China and the Korean Peninsula, over Korean/Tsushima Strait and into Japan. Small patches of moderately suitable areas for migration were also located over the East China Sea (Fig. 3.2).

Response curves for autumn migration model showed that strong side-winds both from left and right of the migration heading reduced suitability for migration (blowing approximately from the NW and SE, respectively), while weak negative side-wind (blowing from the right of the migration track) was preferred, probably due to its effect on shaping the southwest-ward route. Tailwinds with strengths of about 2-4 m/s contributed substantially to suitability of an area for migration (Fig. 3.3).
Figure 3.2. Predictions of MaxEnt models for potential migratory niche of Oriental Honey-buzzard over the East China Sea region in autumn (a) and spring (b). Black dots show the tracking points included in the model for each season.
Spring migration was also found to be dependent on wind, as side-wind from the right was shown to have a positive effect on suitability for migration (Fig. 3.4) and tailwinds with strengths of up to 3 m/s had a positive effect. Areas with high average thermal convection were also found to have positive influence on defining the spring migratory niche (Fig. 3.4).

In the cross validation runs, the predictive powers of the models were high for both autumn (AUC = 0.81-0.92) and spring (AUC = 0.65-0.92), indicating that the overall predictive power of the models for migratory niche of the Oriental Honey-buzzard is acceptable and not prone to over-fitting.

Results of randomization tests showed that there is significant difference ($P \leq 0.001$) between land and sea regions in terms of side-wind and tailwind in autumn and in terms of tailwind, side-wind, and average thermal convection in spring (Table 3.3).
Figure 3.3. Response curves for the autumn model. The relationship between the probability of presence of Oriental Honey-buzzards and predictor variables used for modelling the autumn migratory niche over the East China Sea region is shown. Each curve shows the effects of one predictor on probability of presence while other variables are held at their mean sample value. X-axis represents the range of values of the predictor variable at presence and background points. Negative and positive values of side-wind correspond to wind blowing from right and left of the direction of flight, respectively.
Figure 3.4. Response curves for the spring model. The relationship between the probability of presence of Oriental Honey-buzzards and predictor variables used for modelling the spring migratory niche over the East China Sea region is shown. Each curve shows the effects of one predictor on probability of presence while other variables are held at their mean sample value. X-axis represents the range of values of the predictor variable at presence and background points. Negative and positive values of side-wind correspond to wind blowing from right and left of the direction of flight, respectively.
Table 3.1. Variable contribution, in the form of permutation importance and training gain, in autumn migratory niche model of Oriental Honey-buzzard over the East China Sea region.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Permutation importance (%)</th>
<th>Training gain with only variable (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Side-wind</td>
<td>64.8</td>
<td>72.63</td>
</tr>
<tr>
<td>Tailwind</td>
<td>22</td>
<td>52.96</td>
</tr>
<tr>
<td>Average omega</td>
<td>8.4</td>
<td>0.01</td>
</tr>
<tr>
<td>Minimum omega</td>
<td>3.8</td>
<td>0.26</td>
</tr>
<tr>
<td>Maximum precipitation</td>
<td>1</td>
<td>2.66</td>
</tr>
<tr>
<td>Maximum thermal</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 3.2. Variable contribution, in the form of permutation importance and training gain, in spring migratory niche model of Oriental Honey-buzzard over the East China Sea region.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Permutation importance (%)</th>
<th>Training gain with only variable (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tailwind</td>
<td>46</td>
<td>32.73</td>
</tr>
<tr>
<td>Average thermal</td>
<td>20.9</td>
<td>21.97</td>
</tr>
<tr>
<td>Side-wind</td>
<td>20.5</td>
<td>40.01</td>
</tr>
<tr>
<td>Minimum omega</td>
<td>7.5</td>
<td>24.07</td>
</tr>
<tr>
<td>Maximum precipitation</td>
<td>3.7</td>
<td>4.37</td>
</tr>
<tr>
<td>Average omega</td>
<td>0.7</td>
<td>13.65</td>
</tr>
<tr>
<td>Maximum thermal</td>
<td>0.7</td>
<td>21.99</td>
</tr>
</tbody>
</table>
Table 3.3. Results of randomization tests comparing mean values of the most important variables in niche modelling between ‘sea’ and ‘land’ areas in the study region. ‘Land’ was defined as the land over China and the Korean Peninsula, but not Japan. ‘Sea’ was defined as all cells falling within the extent of the autumn niche model (> 0.5 suitability).

<table>
<thead>
<tr>
<th>Season</th>
<th>Variable</th>
<th>Sea ( (n=29) )</th>
<th>Land ( (n=29) )</th>
<th>( P )-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>SD</td>
<td>mean</td>
<td>SD</td>
</tr>
<tr>
<td>Autumn</td>
<td>Side-wind</td>
<td>-0.50</td>
<td>0.49</td>
<td>-2.70</td>
</tr>
<tr>
<td></td>
<td>Tailwind</td>
<td>2.30</td>
<td>0.51</td>
<td>-0.38</td>
</tr>
<tr>
<td></td>
<td>Tailwind</td>
<td>1.52</td>
<td>0.25</td>
<td>2.95</td>
</tr>
<tr>
<td>Spring</td>
<td>Average thermal</td>
<td>0.30</td>
<td>0.03</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>Side-wind</td>
<td>-1.11</td>
<td>0.30</td>
<td>-2.81</td>
</tr>
</tbody>
</table>
3.4 Discussion

Ecological niche models of Oriental Honey-buzzards migrating over the East China Sea region showed that wind is the most important variable defining the migratory niche and is the main reason for the considerable spatial difference in migratory route between autumn and spring. In autumn, Oriental Honey-buzzards face a choice of flying overland where headwinds prevail (Fig. 3.1; Table 3.3) or fly over the sea, where, as my analyses showed, they can avoid side-wind and use wind support in the form of tailwind. The importance of tailwind in the water-crossing behaviour of Oriental Honey-buzzard had also been suggested by Yamaguchi et al. [31], who showed visualizations of migration tracks along wind fields. This behaviour is in agreement with the “optimal use of wind” hypothesis [38] which states that a bird follows a route where it can avoid head- and lateral winds, while making use of tailwind. Avoidance of strong side-winds is especially expected from obligate soaring raptors, such as my study species and its close relative the European honey-buzzard [107], due to their limited ability to overcome side-winds by switching to flapping flight. As Meyer et al. [89] have pointed out, when wind support is lacking over land, it is less energy-demanding for migrating raptors to fly over a water surface than take a significantly longer detour over land. Furthermore, flying in the best angle relative to the wind reduces the energy required for maintaining minimum power speed and compensating for drift and therefore maximizes the progress of the birds toward their intended destination [1, 173]. Tailwind assistance is also known to facilitate overwater flight of other raptors such as European Honey-buzzards [174, 175] and Eleonora’s Falcons [92].
Given the strong dependence of obligate soaring birds on thermal convection [30], I expected convective conditions to be also important in facilitating water-crossing in Oriental Honey-buzzards. Moreover, Yamaguchi et al. [31] mention that thermal formation is common over the East China Sea in autumn by suggesting that satellite-tracked Oriental Honey-buzzards adopted soaring flight to make the crossing. However, even though average thermal convection contributed substantially to the spring model, the autumn model did not capture the importance of any of the variables indicative of convective conditions over the East China Sea (i.e. omega and thermal convection). This is not surprising however, considering that vertical air movements are small scale meteorological events that lose their importance when estimated over large scales [137]. The temporal scale of the weather data that I used (i.e. 3 hours) was not ideal for estimation of vertical air velocity, especially when averaged over the migration season. I am therefore unable to make conclusions about whether Oriental Honey-buzzards dominantly use soaring or flapping flight during their long water-crossing. Although the use of weather data with 3-hr resolution has been successful in showing the effect of thermal convection on migration of raptors [31, 107, 137], the most promising approach for estimating the instantaneous depth and intensity of thermals and their use by birds would be to monitor the birds using 3D accelerometers [176] and high frequency GPS-loggers [170]. Observations conducted by such devices not only allow for distinguishing flight type, but also provide a reliable high-resolution proxy for weather conditions in general and thermal activity in particular during flight [170, 177]. Such methods would also be very useful in future studies exploring whether and how the decisions made by some individuals to stop over Jeju Island on autumn migration is related to weather conditions.
I found that in spring, the best conditions for migration occur over the land. Thermal convection and tailwind is stronger over land (Table 3.3), making it preferable for the buzzards to avoid sea-crossing. Considering that mean values of tailwind over land and sea are both positive in spring (Table 3.3), it is apparent that avoidance of water-crossing is not due to dominance of headwinds over the East China Sea (also see Fig. 3.1). I therefore suggest that it is the strength of the wind, rather than its direction, that acts as a limiting factor for water-crossing in this season (also see wind fields in Fig. 3.1). These findings do not support the initial suggestions made by Higuchi et al. [149] as they first reported the unique water-crossing behaviour of Oriental Honey-buzzard, that headwind over the East China Sea in spring might be the cause of avoidance of water-crossing. In addition to low wind strength, unstable wind direction may also prevent Oriental Honey Buzzards from crossing the East China Sea in spring. By investigating the wind over the East China Sea at a finer temporal scale, Yamaguchi et al. [31] showed that wind direction over the East China Sea is not stable in spring, resulting in higher risks of water-crossing. The coarse scale of my analysis did not allow capturing such highly variable wind conditions over the region however.

Rather unexpectedly, local Japanese birdwatchers told us that some Oriental Honey-buzzards arrive at Kyushu Island from the direction of the East China Sea in spring, suggesting that they undertake water-crossing in this season as well (T. Deguchi, personal communication). Although I did not observe such behaviour in any of the tagged birds, I have identified small moderately suitable patches for migration over the East China Sea in spring (Fig. 3.2), which could explain the route taken by those
individuals. The number of tagged birds in my study might not have been enough to represent all types of migration strategies within this species.

Another point to consider about the spring migration route circumnavigating the East China Sea, is the fact that the migration tracks, located inland China, can be interpreted as the birds not having attempting to cross the East China Sea on their return way to the breeding ground in Japan (Fig. 3.1). Agostini and Mellone [152] argue that this distance from the East China Sea coast can indicate that the birds are not avoiding water-crossing in spring, but rather not considering it at all simply because they have more time for spring migration than for autumn, when they supposedly prefer to minimize the timing of migration due to possible competition with congeneres and conspecifics in wintering grounds. my findings, however, clearly show that rather pre-dominantly, weather and specifically wind pattern, is responsible for the unsuitability of conditions over the East China Sea for water-crossing in spring and is therefore resulting in the seasonality of migration route. Moreover, wind is generally considered to be the most important factor in shaping detours in bird migration routes [86]. I therefore suggest that the deviation of spring migration route from the East China Sea coast, which also could have served as a guide for the birds to arrive to Japan, might have been developed over time, by birds that attempted to cross the sea, but avoided it after reaching the coast in China and finding the conditions unsuitable, and consequently followed a route over land to return to their breeding ground in Japan. The experience gained by these birds about the best overland route over China, with regards to the strength of thermals and updrafts as well as food availability and navigational cues on land, might have gradually resulted in shifting the spring migration route away from the East China Sea coast. Previously,
such flexibility in migration route has been observed in Bald Eagles *Haliaeetus leucocephalus* [178] and Sharp-shinned Hawks *Accipiter striatus* [179] in North America, which changed their migration behaviour as a response to prey populations. More insight into this hypothesis can be achieved by studying the route selection of juveniles and immature birds in spring. Because juvenile birds generally tend to follow their innate direction of migration [30, 146, 148], their spring migration route may provide further insight into whether this assumed shift in spring migration route has been favoured through natural selection and is present in the population’s genetic makeup or if it is communicated through social interactions. Unfortunately, however, there has only been one juvenile Oriental Honey-buzzard tagged in Japan, which, as reported by Higuchi et al. [149], did not undertake spring migration and remained in the wintering grounds, a behaviour that is very likely typical of juveniles [180]. No data was received from this young bird after the first spring.

3.5 Concluding remarks

The East Asian flyways for migratory raptors [30] include some of the least studied raptor species. Due to the geography of these flyways, raptors adopt water-crossings of various lengths on migration each season. As the results suggest, the ability of these species to make such crossings can be highly dependent on weather conditions *en route*, indicating that any changes in the weather system in this region, due to climate change, can have serious effects on these birds as it will carry over to the next stages of their life cycle or threaten their survival on migration. It is necessary therefore to further investigate the migratory behaviour of the Oriental Honey-buzzard and other raptors on
the East Asian flyways and determine their vulnerability to future weather conditions in
the region.

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Chapter 4

Climate change alters the optimal wind-dependent flight routes of an avian migrant

Publication:

Abstract

Migratory birds can be adversely affected by climate change as they encounter its geographically uneven impacts in various stages of their life cycle. While a wealth of research is devoted to the impacts of climate change on distribution range and phenology of migratory birds, the indirect effects of climate change on optimal migratory routes and flyways, through changes in air movements, are poorly understood. Here I predict the influence of climate change on the migratory route of a long-distance migrant using an ensemble of correlative modelling approaches, and present and future atmospheric data obtained from a regional climate model. I show that changes in wind conditions by mid-century will result in a slight shift and reduction in the suitable areas for migration of the study species, the Oriental honey-buzzard, over a critical section of its autumn journey, followed by a complete loss of this section of the traditional route by late century. These results highlight the need for investigating the consequences of climate change-induced disturbance in wind support for long-distance migratory birds, particularly species that depend on the wind to cross ecological barriers, and those that will be exposed to longer journeys due to future range shifts.

Keywords: Regional climate model, niche modelling, ensemble forecasting, flyway, optimal route, Crested honey-buzzard.
4.1 Introduction

Global climate change is projected to have severe impacts on migratory species, as they might face alterations in their breeding, wintering and stopover areas, as well as *en route* [181]. Migratory birds are already responding to climate warming through geographic range shifts [182], as well as changes in phenology [15, 183], migratory strategies [18], fitness [16], and demography [184]. Unsurprisingly, temperature and precipitation are the most commonly used variables in research on the impacts of climate change on migratory birds, as they determine the general suitability of habitats and breeding success. Variables related to air movement have also been considered in a handful of studies, but mostly due to their correlation with the timing of spring arrival of migratory birds [185-188]. Atmospheric currents, especially wind, play a significant role in shaping migratory routes and facilitating long-distance flight [1, 34, 38], particularly for species whose morphology and flight characteristics result in higher dependence on air movements for route selection, such as soaring raptors [81, 189]. Thus, alterations in the pattern and strength of winds and other forms of air movement as a consequence of climate change can subsequently influence the efficiency and spatial distribution of optimal migratory routes of birds. Attempts at predicting such influences remain very limited in the scientific literature, however.

Predicting the response of natural phenomena to climate change is possible through General Circulation Models (GCMs), which estimate the future values of climate variables by taking into account physical atmospheric and oceanic processes. Correlative niche models are commonly used to address the spatial changes in distribution range of migratory birds in the face of climate change as defined by GCMs.
[11]. Although the migratory niche of a bird, defined as the environmental conditions that birds prefer en route, can be modelled using correlative approaches [91], to my knowledge no studies have used such methods to make predictions about optimal migratory routes under climate change scenarios.

In this study, by using an ensemble of correlative modelling approaches and atmospheric data for the present and future, I investigated the potential changes in the optimal migratory route of the Oriental honey-buzzard *Pernis ptilorhynchus*, an East Asian soaring raptor, over a critical section of its autumn migration.

4.2 Methods

I used two regression-based (GLM, generalized linear model; GAM, generalized additive model) and two machine-learning-based algorithms (GBM, generalized boosted model; MaxEnt, maximum entropy) to build an ensemble model of the migratory niche of Oriental honey-buzzards over the East China Sea region (116°-133° E and 26°-42° N) in autumn. I focused on this relatively small section of the autumn journey as it is characterized by a c.a. 680 km non-stop flight over the East China Sea between south-western Japan and China and is very likely to be shaped solely by atmospheric conditions [31, 91]. Such independence of biotic interactions (e.g. prey availability and competition) and dispersal restraints can increase the reliability of a niche model and its transferability across time and space [10].

I modelled the contemporary relationship between honey-buzzard migration routes and wind conditions based on en route locations derived from satellite-tracking of 31 adult birds (2006-2013). Training points were taken from Nourani et al. [91] and background points were selected as described therein. Explanatory variables included eastward
(wind-u) and northward (wind-v) components of the wind and planetary boundary layer height (BLH) as a proxy of convective conditions, with higher BLH corresponding to stronger convective conditions [55, 107]. I used 80% of the satellite telemetry locations for model development and 20% for testing the models. Models were evaluated using a 10-fold cross-validation procedure and true skills statistic (TSS) and area under the receiver operating characteristic curve (AUC) metrics were calculated for classification accuracy. I used models with AUC > 0.8 and TSS > 0.7 to generate an ensemble model following a weighted (proportional) average approach [190]. I then projected the niche model to the values of explanatory variables averaged for the present (2006-2013) and the middle (2046-2055) and the end (2091-2100) of this century. Projections to future conditions were done separately for two scenarios of climate change. All analyses were done using biomod2 package [191] in R environment v 3.3.1 [168].

All projections of atmospheric variables for the period of autumn migration (from 11 September to 20 October; [31]) and averaged for the present (2006-2013) and two periods in the future (mid-century: 2046-2055; late century: 2091-2100), were obtained from HadGEM3-RA Regional Climate Model (RCM) developed by National Institute of Meteorological Research in South Korea through the CORDEX-East Asia database (https://cordex-ea.climate.go.kr/). This RCM provides projections under two climate change scenarios, Representative Concentration Pathways (RCPs) 4.5 and 8.5, which I used in this study. RCPs are greenhouse gas concentration trajectories as adopted in the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC) [4]. The RCP4.5 scenario assumes a peak in greenhouse gas emissions around 2040, followed by a decline, while RCP8.5 scenario (i.e. the business-as-usual scenario)
assumes that emissions continue to rise throughout the 21st century [8]. Wind variables were downloaded at the 850 mb pressure level with a 6-hour temporal resolution. This pressure level corresponds with the average flight height of the birds [31]. Furthermore, it was the lowest pressure level data available from the above-mentioned RCM. Only daytime data was used for model building as birds complete this section of migration during the day. BLH was downloaded at daily intervals (at 12:00 UTC). All variables were interpolated to 0.02-degree cell size before averaging.

Model projections for conditions exceeding the limits experienced during model building are not reliable [11, 192]. Biomod2 identifies areas in the future data where values are outside the range of those of the current conditions and presents them as a clamping mask. These areas should be interpreted with caution or removed from the final model.

4.3 Results

The modelling algorithms used for building an ensemble model of the migratory niche of Oriental honey-buzzards over the East China Sea region in autumn had high discrimination capacity and accuracy (Table 4.1). The final ensemble model was successfully cross-validated (Table 4.1) and correctly predicted most observations (sensitivity= 97.7%; specificity= 89.5%). Eastward and northward winds had very similar average importance in the ensemble model. Boundary layer height had the smallest effect in model building (Table 4.1; for response curves see Fig. S1).

Table 4.1. Average performance (AUC and TSS) and variable importance (and standard deviation, SD) calculated for individual algorithms and the ensemble model.

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<table>
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<th>Algorithm</th>
<th>Model performance</th>
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<td>GBM</td>
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<td>GAM</td>
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<td>MaxEnt</td>
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<td>Ensemble</td>
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Visualizations of projecting the niche model to the current and future conditions showed dramatic changes in the suitability of autumn migration route over the region under both scenarios. Based on the contemporary atmospheric conditions, suitable locations for migration between Japan and China occur over the East China Sea (Fig. 4.1). The mid-21st century will see a slight northward shift in suitable areas, with a considerable reduction in the area and connectivity of the highly suitable areas (Fig. 4.2a and 4.2b), with more severe conditions under the RCP4.5 scenario. At the end of the century, however, the model identified suitable areas to the east of the Korean Peninsula under RCP4.5 (Fig. 4.1c) and a small patch of moderate suitability under RCP8.5 (Fig. 4.1d), all of which lie outside the traditional route and cannot provide a complete route from Japan to China.
Figure 4.1. Ensemble model projection for the regions of suitable atmospheric conditions during the autumn migration of Oriental honey-buzzards in the present (2006-2013). Black dots represent *en route* locations of Oriental honey-buzzards marked with satellite transmitters (2006 – 2013) used for model-building. The dashed ellipse indicates the location of Goto Islands, where the birds depart at the start of their autumn migration.

Areas identified as having values outside the range used for training the model, as shown by the clamping masks (Fig. 4.2), were predicted as unsuitable by the model. See Fig. S2 for a comparison of monthly averages of wind speed over the East China Sea region, calculated for the traditional route in the three time periods.
Figure 4.2. Ensemble model projections for the regions of suitable atmospheric conditions during the autumn migration of Oriental honey-buzzards for (a) mid-century (2046-2055) under RCP4.5 scenario, (b) mid-century (2046-2055) under RCP8.5 scenario, (c) late century (2091-2100) under RCP4.5 scenario, and (d) late century (2091-2100) under RCP8.5 scenario. Black dots represent en route locations of Oriental honey-buzzards marked with satellite transmitters (2006 – 2013) used for model-building. Dark grey patches show areas identified by clamping masks as having values outside the range used for training the model.
4.4 Discussion

I have shown that predicted alterations in atmospheric conditions caused by climate change have the potential to adversely affect the suitability of traditional avian migratory routes. The ecological consequences of such changes for Oriental honey-buzzards can be severe as I approach the end of the century, particularly because the projections did not reveal alternative routes at the modeled altitude and dates for the birds to migrate from Japan to China.

4.4.1 Mid-century conditions

As Oriental honey-buzzards start their migration from Goto Islands of Japan (Fig. 4.1) toward China, they depend highly on thermals and tailwind to complete the sea-crossing [31, 91]. Wind conditions over Goto Islands are expected to remain somewhat suitable by mid-century under both climatic scenarios. The overlap between the current and the mid-century suitable locations for migration over the East China Sea region makes it likely for the birds to gradually shift their route to fly over the more suitable areas. Such behavioural adjustments, by learning from individual experience or by observing others, can happen relatively quickly [193, 194]. It has been previously shown that birds, including soaring raptors, have high phenotypic plasticity of migratory routes [195, 196]. However, it remains unclear whether Oriental honey-buzzards have the necessary adaptive potential relative to the speed of climate change. Satellite-tracking of one juvenile bird indicates that in this population of Oriental honey-buzzards, juveniles migrate separately from adults [149], suggesting strong endogenous control on the choice of migratory route and limited possibility for cultural transmission of new suitable routes. It is therefore highly probable that many individuals following their
innate migratory route would attempt to cross the sea at areas that are no longer suitable and would perish at sea, as they are unable to perform flapping flight over such a long distance in the absence of tailwind. Thus, the population of the Oriental honey-buzzard breeding in Japan is very likely to face new environmental conditions that will require an adaptive response, which may imply processes of severe natural selection, if routes are kept as in the present.

The connectivity of suitable areas in mid-century compared to the current conditions will be reduced under both scenarios. Conditions under the RCP4.5 scenario are particularly concerning because the areas identified as suitable do not extend all the way to China. Such reductions and large gaps between suitable migration areas indicate higher energetic costs of crossing the sea, due to the need for the birds to switch to flapping flight where conditions are not suitable, and potentially an increase in the duration of migration over the region. The resulting poor migratory performance can lead to delayed arrival in South-east Asian wintering grounds, where the birds face high competition with other raptors [152]. Moreover, the associated carry-over effects can further affect the individuals negatively.

Our results showed more severe conditions under the optimistic RCP4.5 scenario than the most pessimistic scenario, RCP8.5. It is important to note that the relationship between wind and increased greenhouse gas concentration is complex and, in my study area, depends on the global circulation patterns under each scenario, particularly over the Pacific Ocean. As changes in wind conditions from RCP4.5 to RCP8.5 are not unidirectional (Fig. S2), I did not observe a clear reduction in suitability when moving from RCP4.5 to RCP8.5. Moreover, the strong variability of wind can be responsible for
the results. By averaging data over longer periods of time than I used in this study, it
might be possible to remove the strong variability in wind patterns (I. Takayabu,
Personal communication). I urge future studies to consider this when deciding on the
appropriate time periods for studying wind conditions.

4.4.2 Late century conditions

By the end of this century, the region is likely to lose its suitability for autumn
migration of Oriental honey-buzzards altogether. Under RCP8.5, this is likely to be due
to the weaker winds (Fig. S2). Under RCP4.5, however, winds will be stronger (Fig. S2),
even more so than the maximum wind speed in the present conditions, hence the
clamping mask over the region (Fig. 4.2c). Projections show that such high wind speeds
will not be suitable for the birds to migrate over the East China Sea.

The loss of suitability of the traditional route shown by my results can severely affect
this population of Oriental honey-buzzards. However, migratory birds are able to assess
atmospheric conditions, particularly wind, to decide the best time for departure [197]. It
can therefore be expected that Oriental honey-buzzards will delay their departure due to
unsuitability of atmospheric conditions. It has been suggested that autumn conditions
will start later due to climate change, indicating the possibility that suitable wind
conditions over the region can occur later in the year, leading to a temporal adjustment
of Oriental honey-buzzard over the region. The overall changes in wind patterns over
the traditional route do not clearly suggest a delay of autumn conditions however (see
Fig. S2). Moreover, although such temporal adjustments can save the population from
extinction, the birds will bear the costs of delayed arrival in wintering grounds. Another
possibility for the population to survive would be to adjust their migratory strategy, by
either becoming sedentary (see [194, 198]) or switching to an overland route through the Korean peninsula and China while fuelling their migration by adopting a stop-and-forage strategy. Again, it remains unclear whether the population will be able to adapt to such changes through phenotypic adjustments or evolutionary response over such a short period of time.

4.4.3 Concluding remarks

The present study is one of the first attempts at investigating the greatly overlooked, but potentially severe, indirect effects of climate change on migratory routes of birds through alteration of atmospheric conditions. These results are not to be considered as the definite future for the Oriental honey-buzzards in the region, however, as my analyses were restricted to a single RCM and a single pressure level (i.e. altitude). The use of an ensemble of climate models can improve the outcome of projections [199] and considering various altitudes allows for a more thorough understanding of changes in atmospheric conditions. Although many General Circulation Models are available and cover a range of variables at different altitudes and under all RCPs worldwide, I advise against using them directly in ecological studies as they have low spatial resolutions and require downscaling to suit the small scale of animal movement. RCMs provide such downscaled data and it is important to note that the characteristics of data provided by many RCMs are decided based on the needs of the end-users (e.g. ecologists). I therefore encourage ecologists to make contact with RCM developers in their region for collaboration and to negotiate their specific data requirements.

Atmospheric conditions are the facilitators of migration in many long- and short-distance migrants worldwide [1, 34]. Investigating how climate change can disturb wind
support for migratory species is crucial, particularly for species that depend on the wind to cross ecological barriers such as waterbodies and deserts (e.g. [200, 201]) and those that are predicted to be exposed to longer journeys due to range shifts caused by climate change [182].

Although my study covered only a small portion of the autumn migratory route of the study species, it is important to note that due to the uneven impacts of climate change in different parts of a single migration journey [202], local-scale and high resolution studies are required to address these issues efficiently. Additionally, modelling the complete routes of long-distance migratory birds, or parts that include flying over land (e.g. the spring migration of Oriental honey-buzzards [29]), will involve challenges, as birds in such circumstances are not only affected by atmospheric conditions, but also by changes in landuse and biotic interactions. Therefore, apart from atmospheric conditions, changes in the quality and distribution of suitable stopover and refuelling areas need to be accounted for as they might also alter the migratory routes of birds and lead to deviations from optimal wind-defined traditional routes.

Additionally, it is important to gain better knowledge of flexibility and adaptive response of migratory species to a range of wind conditions. This can be studied by taking advantage of among-year variations in wind conditions by monitoring the migratory behaviour of individuals in different years using high-resolution tracking.

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Supplementary material

Figure S1. Average response of each algorithm to explanatory variables. The x-axis defines the variable range and the y-axis delineates the model response. Wind variables are presented in meters per second and boundary layer height in meters.
Figure S2. Monthly averages for wind speed (m/s) in the present, mid-century and late century. Wind speed for all time periods were calculated over the area that was identified as suitable in the contemporary conditions (i.e. the traditional route for migration of Oriental honey-buzzards over the East China Sea). This area corresponds to areas with a higher suitability of 0.5 in Fig. 4.1.
Chapter 5

Raptor migration in an oceanic flyway: the role of geographic and atmospheric conditions in shaping the migratory route of Grey-faced buzzards in East Asia

Publication:

Manuscript under preparation
Abstract

Morphological and behavioral adaptations in migratory raptors that enable them to efficiently carry out soaring flight over land also limit their ability to perform powered flight, hence the strong reluctance of most migratory raptors to fly over water. Exceptions can be found in the East Asian Oceanic flyway for raptors, where various raptor species have specialized in migrating by island-hopping, flying over water for distances of up to 200 km between islands. In this study, I used satellite telemetry data collected for Grey-faced buzzards *Butastur indicus* to investigate the atmospheric and geographic variables responsible for the suitability of this migratory route. By assuming that the birds try to minimize water-crossing, I used habitat connectivity approaches to find an optimal route that would connect the breeding and wintering grounds through the islands and therefore minimize flight over water. I then compared this optimal route with the observed routes obtained from satellite tracking and found differences between them. I therefore employed a step selection function to better understand the route selection and found that deviations in the birds’ observed route from the optimal route can be explained by taking into account the strength of wind support and cross-wind over the flyway. These results confirm the role of wind in shaping the East Asian flyways of long-distance raptor migrants. I also compared present and future wind conditions over the region to provide a general picture of how wind support will be affected by climate change by the end of the century.

Keywords: *Butastur indicus*, step selection function, mixed-effects conditional logistic regression, climate change, island-hopping.
5.1 Introduction

Many species of raptors accomplish their long-distance migrations exclusively by soaring flight [30, 32, 41, 189]. Morphological adaptations of raptors enable them to effortlessly soar on thermals and orographic updrafts [189]. However, these morphological characteristics restrict their ability to perform long bouts of powered flight, as would be necessary over ecological barriers, particularly waterbodies, where thermal formation is rare in most latitudinal zones [87, 189]. To avoid such circumstances, many raptors prefer to make detours around waterbodies or cross them at their narrowest points [86, 89]. It is not surprising therefore that most raptor migration flyways are mainly overland [30]. However, remarkable exceptions exist in East Asia, where the world’s only oceanic flyway for raptors is located. The East Asian Oceanic flyway for raptors (Hereafter the oceanic flyway) stretches from northeastern Siberia and Kamchatka, through Kuril Islands, eastern China, Korea, Japan, Taiwan, to East Asian countries such as the Philippines and Indonesia. This flyway is dominated by the Chinese Sparrowhawk Accipiter soloensis and the Grey-faced Buzzard Butastur indicus which use the southern two-thirds of the flyway by an island-hopping strategy, characterized by numerous water-crossings between islands [30].

The oceanic flyway has been little studied and the specific geographic, atmospheric, and biotic characteristics that make it suitable for raptor migration are not well known. A quick glance at the map of the region would indicate that the existence of a large number of islands along a north-south axis enables raptors to migrate through it without facing the dangers of water-crossing. However, a closer look will make it clear that the distances between the islands is not very small after all. In fact, some islands are over 200 km apart, which suggests that other factors must be responsible for suitability of this route for migration of raptors.

Wind and other forms of air movement facilitate water-crossing in raptor species [91, 92, 144]. In the trade-wind zone, 5° to 30° north and south of the equator, sea thermals might
facilitate over water soaring flight for raptors [31, 32]. It is possible therefore, that atmospheric variables including wind and updraft conditions are responsible for shaping the Oceanic flyway [33]. In this study, I investigated remote tracking data collected for Grey-faced buzzards migrating from mainland Japan to the Ryukyu Islands and the Philippines to understand whether the existence of islands, i.e. the possibility of migration by island-hopping, alone is responsible for selection of this route or if atmospheric conditions are also at play. I hypothesized that, considering the long distances between the islands, atmospheric currents, in the form of wind support and updrafts, are partly responsible for the suitability of this migratory route.

5.2 Methods

5.2.1 Satellite telemetry data
I used satellite-tracking data collected in 2007-2009 for autumn migration of the Grey-faced buzzards captured in breeding areas in various prefectures of mainland Japan as well as in wintering areas in Okinawa prefecture. Platform transmitter terminals (PTTs) weighed less than 4.5% of the average body weight of the birds. I investigated autumn migrations using data from 16 individuals.

I also deployed GPS-UHF (Ecotone Telemetry) devices on six adult birds in spring 2015 in two field sites in Nagasaki and Fukuoka prefectures. The devices weighed less than 5% of the birds’ total mass. The tags were set to record data every 15 minutes. However, none of the birds returned to the field sites the next year and due to the type of tags, they were not traceable. One possibility is that the birds fell victim to the heavy poaching in northern Philippines. For this study, I was therefore limited to use the above-mentioned satellite-tracking data.
5.2.2 Least-cost path analysis

By assuming that the birds try to minimize the distance that they need to fly over water, I generated an optimal route that would connect the neighboring islands and reduce water-crossing. I used gdistance package [203] in R environment [168] for the least-cost path analysis. I used the inverse of a distance-to-land layer as a conductance surface to find the shortest path (i.e. the least-cost path) that would connect the start and end points of Grey-faced buzzard tracks that started in Kyushu Island and ended in the Philippines.

5.2.3 Step selection function

*Generating case-control steps*

I modeled migratory route selection of the Grey-faced buzzards over the region using step selection functions (SSF) [204]. In this method, the straight-line segment connecting successive tracking points is considered as one step (i.e. observed step) and a number of alternative steps from the same starting point is generated. This case-control design is then analyzed using a conditional logistic regression approach, which allows taking into account stratification in the analysis [205].

Before selecting the alternative steps, it is important to thin the observed points to reduce autocorrelation. My dataset was rather sparse, but I made sure that the data points used for the analysis were at least one hour apart. For each observed step (n= 600), I generated 100 random steps. Length and turning angle of random steps were drawn from the frequency distribution of those of the observed steps.

*Annotation of steps with environmental data*

I considered distance to coast (NASA), eastward and northward components of the wind, cloud cover, and boundary layer height as a proxy for convective conditions, to build the step
selection function. All observed and random steps were annotated using the Env-DATA track annotation service of Movebank (https://www.movebank.org/), using bilinear interpolation. All atmospheric variables were taken from ECMWF. Pressure level data were downloaded at 850 mb level. Additionally, a categorical variable distinguishing land and sea areas was prepared for the extent of the study area.

After obtaining data from Movebank, I calculated wind support and crosswind along each step. Such calculations require heading (the angle of travel) as an input. For each step, I calculated the heading as the angle from the starting point (i.e. observed point of the previous step) to the end point in each alternative step.

**Statistical analysis**

All variables were checked for multi-collinearity (r > 0.7) before analysis, and no variables were correlated. Mixed-effects conditional logistic regression was carried out in mclogit package [206] in R [168]. Groups of matched case and control steps were entered as strata in the model and individual birds set as a random effect.

I used a backward stepwise selection by removing variables that had low contribution to model building one by one. The model that yielded the lowest AIC was selected as the best model. The predictive ability of the SSF was assessed using a k-fold cross-validation method suitable for the case-control design of the study [207] with 30 repetitions.

5.2.4 Wind roses

In order to compare the wind conditions over the flyway in the present and future, I summarized the frequency distribution of wind direction and speed over the flyway for the two periods. I prepared averaged values of each variable for the peak of autumn migration season (Sep-Oct) for the entire extent of the study area (15°-43° N and 111°-140° E) for the
present (arbitrarily set to 2006-2015) and the future (late century: 2090-2100). Because my aim was to compare the present and future conditions of the migratory route, I used average monthly values of present, mid-century and late century from a Regional Climate Model (HadGEM3-RA Regional Climate Model (RCM) developed by National Institute of Meteorological Research in South Korea) downloaded from the CORDEX-East Asia database (https://cordex-ea.climate.go.kr/). The future data were downloaded under the business-as-usual scenario (RCP8.5) of climate change. I drew wind roses using wind data within the longitudinal range of Grey-faced buzzard autumn migration (see [81]).

5.3 Results

The optimal route that I generated using least-coast path analysis connected Japan’s Kyushu Island to the Philippines by passing through the Ryukyu Islands and Taiwan (Fig. 5.1). This optimal route deviated from the actual tracks recorded for this population of the Grey-faced buzzards (Fig. 5.1). For instance, unlike what the optimal route suggests, the birds in my study did not pass over Taiwan to reach the Philippines.
Figure 5.1. The optimal route with minimum water-crossing from Kyushu Island to the Philippines (in red). Note that this supposedly optimal route deviates from the actual path of the birds as shown by satellite telemetry (black dots).

5.3.1 Step selection function

Step selection function identified the most important variables that determine the route selection of Grey-faced buzzards migrating from Kyushu Island to the Philippines. In the final model that yielded the lowest AIC, distance to land had the highest influence in route selection, followed by crosswind and an interaction between distance to land and wind support (Table 5.1). The random effect of individuals was not found to be significant. Cross-
validation indicated that the model was a useful predictor of route selection in Grey-faced buzzards, as the distribution of observed rs was higher than expected by chance alone. (K-fold values (n=30): observed 0.34 (0.28-0.40), expected -0.26 (-0.44 - 0.003))

Table 5.1 Results of the step selection function

<table>
<thead>
<tr>
<th>Covariate</th>
<th>β ± SE</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance to coast</td>
<td>-1.745</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Wind support</td>
<td>0.019</td>
<td>0.254</td>
</tr>
<tr>
<td>Crosswind</td>
<td>-0.035</td>
<td>0.030</td>
</tr>
<tr>
<td>Distance to coast * wind support</td>
<td>0.046</td>
<td>0.003</td>
</tr>
<tr>
<td>Distance to coast * crosswind</td>
<td>-0.017</td>
<td>0.265</td>
</tr>
<tr>
<td>Mixed effect (individual)</td>
<td>1.081e+12</td>
<td>0.725</td>
</tr>
</tbody>
</table>

5.3.2 Comparison of present and future wind conditions

Wind roses indicated easterly and northeasterly wind direction over the Grey-faced buzzard route in all three time periods. Wind speeds at the present conditions had an average and maximum of 2.8 m/s and 7.3 m/s, respectively. Average and maximum wind speeds were calculated as 3.0 m/s and 8.1 m/s for mid-century and 2.7 m/s and 7.6 m/s for late century, respectively (Fig. 5.2).
Figure 5.2. Wind conditions (speed and direction) over the southern part of East Asian Oceanic flyway for the Grey-faced buzzard in the present, mid-century and late century (business-as-usual scenario of climate change). Wind roses were drawn separately for two latitudinal zones along the flyway (horizontal dashed lines) and were limited to the longitudinal range used by the birds (vertical dashed lines).
5.4 Discussion

Geographic and atmospheric variables are critical for successful migration of long-distance migratory raptors. Prominent geographic features such as islands help raptors, and many species of migratory birds for that matter, in navigation [32]. Soaring raptors need specific atmospheric conditions in order to carry out soaring flight, including suitable updrafts and winds [41, 189]. Islands are therefore also attractive to migratory soaring raptors as thermals are generally stronger over land [208]. Migratory flyways that raptors use are the representations of the best of geographical and atmospheric conditions [30, 81], established over evolutionary history of raptor species. The East Asian Oceanic flyway has been little studied in these aspects, but my results indicate that this flyway too has been shaped by suitable geography and atmospheric conditions.

The most important determinant of suitability of this flyway, as indicated by data from Grey-faced buzzard satellite-tracking, is the existence of islands along the flyway from Kyushu Island to the Philippines. The birds can use such prominent geographic formations as leading lines for navigation purposes [30]. Islands can also be important for providing suitable refueling opportunities between long water-crossings [209]. Moreover, thermal conditions over land are generally better than over the sea and can give the birds a boost in updrafts for more efficient soaring [208]. Although I showed that the location of islands is important in shaping the migratory route of Grey-faced buzzards, due to the coarse resolution of my data, I could not determine whether the birds that winter in the Philippines use islands as stopovers and how the thermal conditions over the islands affects their flight type.

Apart from the role of geographic features in shaping the migratory route, wind conditions also influence the suitability of the route and explain the deviations from an optimal route generated by only considering the islands. I found that both wind support and crosswind significantly affect route selection in the Grey-faced buzzards. Birds respond to both wind...
support and crosswind when selecting the appropriate migratory route (e.g. [208]). The importance of wind support, i.e. tailwind, is in increasing the speed of migration, while crosswinds are important in navigation [30].

Although I expected the birds to use sea thermals on migration [30, 32], I was not able to find the effects of such updrafts on the route selection in this analysis. The reason for this can be the coarse scale of the tracking data that I used, which hampered my efforts to identify the small-scale response of the birds to updraft conditions.

I also investigated the wind conditions on the flyway, where the dominant wind direction is easterly and northerly, indicating that the birds do not face headwinds along their flyway. Comparisons of the present wind conditions with those of the mid-century and late century did not show a notable difference in the direction and speed of the wind over the flyway. However, the temporal and spatial resolution of data used to draw wind roses were rather coarse. The small differences detected by the wind roses might be significant when investigated at a finer resolution for birds en route, for instance by an individual-based modeling approach.

5.5 Conclusion

Our attempts at identifying the geographic and atmospheric variables in shaping the East Asian Oceanic flyway provided a general picture of the factors that lead to the suitability of this flyway for raptor migration. I was not able, however, to provide fine-scale information on the birds’ flight type and the importance of thermals, as well as details on navigation and response to wind drift. I suggest future studies to use GPS-GSM or GPS-PTT devices, with a suitable weight, which enable researchers to locate the birds remotely and determine the reasons for unsuccessful migration.
Acknowledgements

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Chapter 6

General discussion
I started this thesis to answer an intriguing question about the effects of climate change on migratory birds’ routes and flyways. To do so, I intended to use remote tracking data, from both satellite-tracking and GPS-loggers, for two long-distance raptor migrants in East Asia.

At the time of starting my PhD research, it had been shown in previous studies that both Oriental honey-buzzard *Pernis ptilorhynchus* and Grey-faced buzzard *Butastur indicus* depend on atmospheric currents to complete their migrations, indicating that their route selections depended on atmospheric conditions. I started my PhD project trying to show this dependence quantitatively. Throughout this project, I focused on sections of the migratory route and flyway that include long bouts of water-crossing. The reason for this is related to the dependence of raptor species on atmospheric conditions to fly over water. Therefore, by showing that their route selection over such areas depends on wind and other atmospheric variables, it is rather straightforward to project the route choice criteria to the future. In situations where the migratory route includes flying over both land and sea, there is a possibility, depending on the species, that the birds might make stops over land, and their route selection might depend on the location of suitable stop-over sites that provide good prey and little competition. Projecting route selection to future conditions in such cases will be complicated, because not only atmospheric conditions, but also landuse and biotic interactions play a role in route selection. Unfortunately, future predictions of the latter two are not easily accessible. The East Asian raptor migration flyways have great potential for research on the influence of climate change on migratory routes and flyways of raptor species as they contain water-crossings of hundreds of kilometers long, making it possible to project route selection by only considering atmospheric conditions.

In this chapter I provide a summary of my PhD research as well as discuss the findings, where they fall within the broader scientific research, and their implications for future studies.
6.1 Regional scale: migration of Oriental honey-buzzard over the East China Sea region

One of the first things that stand out when looking at the migratory route of the oriental honey-buzzard, also known as the crested honey-buzzard, migrating from Japan to South-East Asia is the ca. 700 km water-crossing that the birds perform over the East China Sea. This is indeed strange, because raptor species are known for their reluctance to water-crossing (Chapter 2). I investigated this seasonal behavior by looking at a number of atmospheric variables along the birds’ migratory route over the East China Sea region (Chapter 3). By using a niche modeling approach [163], I found that this behavior is related to wind conditions indeed and is possible because of the wind support that exists over the sea in autumn, but is missing in spring (Chapter 3). These results are in agreement with the “optimal use of wind” hypothesis [38] and matches well with the findings of other studies that show the importance of wind support for water-crossing by raptors [92, 174, 175].

I expected thermal convection to be also significant in the suitability of the route for Oriental honey-buzzards, as it had been pointed to in previous studies [31]. I found that thermal convection contributes to the spring niche model, but no effect was found for autumn. This is probably due to the fact that my satellite-tracking data had very coarse resolution, which led to my inability to capture the importance of thermals in the models.

This was one of the first times that a niche modeling approach was used to model the suitability of the route of migratory species. One useful aspect of such models is that they can be applied to novel conditions of the explanatory variables [11, 210]. In this case, the model was projected to future conditions of the wind and boundary layer height (Chapter 4). This approach needs to be applied with care, however, depending on where the future data comes from. It is advisable to use an average of climate model data, which was unfortunately not available to me.
To project the niche model to future conditions of the wind over the East China Sea region, I downloaded downscaled data for wind and boundary layer height variables for mid-century and late century from a regional climate model, under two scenarios of climate change. The results were rather dramatic in that the suitability of the migratory route over the East China Sea, which allows the birds to fly ca. 700 km over the sea from Japan to China, will be considerably reduced by mid-century and will be completely lost by the end of the century. This was true under both scenarios of climate change. However, rather unexpectedly, the results of the more optimistic scenario (RCP4.5; i.e. greenhouse gas emissions peak around 2040, then decline) were more severe for the birds than the most pessimistic, business-as-usual, scenario (RCP8.5; i.e. greenhouse gas emissions continue to rise throughout the 21st century). This was due to the complicated nature of wind, which depends on the global circulation patterns over the Pacific region. It could also be caused by the uncertainty surrounding wind as an explanatory variable. I considered the wind conditions for each period in 10-year intervals, which might not have been enough to remove the uncertainty. I urge future studies to take into account longer time periods when working with the wind as an explanatory variable.

After showing how the future suitability of the route will differ from the present conditions, it was then time to think about how the birds will respond to these changes. I made some speculations about various ways in which the birds could adapt or adjust their migratory behavior and strategies to the new conditions (Chapter 4). Various bird species have responded to climate change in different ways, for example by adjusting their departure times [197] or becoming sedentary [194, 198]. Although similar speculations can be made about the Oriental honey-buzzard, they cannot be proven with facts as yet. This is because the Oriental honey-buzzard is not a very well-known species and its biology and ecology are not studied in detail. Therefore, the flexibility of the birds in responding to atmospheric variables,
and consequently, how flexible they can be in their route selection under climate change remains unknown.

6.2 Flyway scale: Grey-faced buzzards in the East Asian Oceanic flyway for raptors

The Grey-faced buzzard populations that breed in Japan fly southward to winter in the Ryukyu Islands, Taiwan or the Philippines. This route is characterized by a good number of islands that can provide navigation opportunities for the birds that use this flyway. Raptors along this flyway are assumed to engage in an island-hopping strategy to complete their migration. The great distance between some of the islands however makes it probable that the birds not only depend on the islands, but also on some sort of atmospheric support for their migration. I showed in Chapter 5 that it is indeed true.

I used a step selection function to investigate the route selection of Grey-faced buzzards using satellite-tracking data. I found that route selection along this flyway is determined by distance to land (i.e. the existence of islands), as well as the conditions of side-wind and wind support. The existence of islands along the flyway can be helpful for navigation [30], refueling [209], or to provide a thermal boost [208]. Due to the little knowledge that exists about Grey-faced buzzards’ migratory behavior however, I cannot say for certain whether the birds use these islands as stopover sites or to gain uplift. Moreover, I expected an effect of thermal convection too, due to the fact that some parts of the flyway that Grey-faced buzzards use are located in a zone with sea-thermal activity [30, 32].

I intended to look deeper into the migratory behavior and show, at a small scale, how the birds are able to travel from one island to the next and whether they use the islands as stopover sites or merely for navigation purposes. To do this, I fitted six Grey-faced buzzards with GPS loggers in breeding areas in Japan (in April 2015). Previous tracking attempts have
shown that Grey-faced buzzards have high fidelity to breeding sites and retrieving the data should have been easy once the birds returned to breeding territories the next spring. However, the birds tagged for this study did not return to breeding areas the next breeding season. Due to the type of the tags, which require downloading all the data through a base station, I could not locate the missing birds nor confirm the reason for their failure to return to the breeding grounds. This unfortunately meant that I was not able to collect any of the GPS-tracking data. I was therefore unable to investigate the small-scale behavior and their response to wind and thermal convection.

The suitability of this flyway in the future remains unclear, apart from my attempts at comparing present and future conditions of the wind along the flyway (Chapter 5). Based on averaged regional climate model data over the southern part of the flyway, wind strength and wind direction over the southern part of the flyway will not undergo considerable changes by the end of the century. However, this needs to be investigated in future studies under finer spatial and temporal scale. Individual-based models would be a suitable approach to carrying out such analysis. On the one hand, Lower wind speeds can reduce the overall speed of migration over the flyway, which can have negative effects on the birds as they may face competition in wintering grounds. Stronger winds in a less than optimal direction, on the other hand, can blow the birds off course and lead to higher energy expenditure to compensate for wind drift.

6.3 Notes on using future weather and climate data in the research on migratory birds

Atmospheric variables are widely used in studies concerning migratory birds. There are various sources where such data can come from [6]. A great variety of variables have been used to answer a wide range of ecological questions. Future predictions of these atmospheric
variables are available and are used by ecologists, mostly as monthly averages (e.g. from the WorldClim database at http://www.worldclim.org). Using data at smaller temporal scales is less common in research on climate change and birds, as these are not easy to obtain. It is possible to download such data directly from general circulation models (GCMs), but the spatial resolutions will be coarse and downscaling is required. Some researchers, mostly physicists, carry out their own downscaling before using the data [211, 212]. For biologists, however, downscaling meteorological variables might not be straightforward. It is best then, in my experience during my PhD, to obtain downscaled data from regional climate models (RCMs). Such models are developed in many countries nowadays and many of them are available online (e.g. from http://www.cordex.org). It would be best if biologists obtained data from multiple regional climate models and used an average of model predictions. This was unfortunately not possible in my study and I had access to data from a single RCM for all my analyses of future conditions. The main aim of many RCM developers is to provide suitable data based on the needs of the end-users. I therefore suggest that researchers contact the developers of RCMs within their study region and communicate their specific needs. For example, the pressure level, RCPs, and variables for which data are normally produced are usually negotiable, although producing the data can be time-consuming.

6.4 Conclusions

The question of how climate change will impact bird migration has received much attention in past decades. We now know, for instance, that climate change can lead to earlier arrivals to breeding areas [15, 213] and shifts in geographic ranges [2, 3, 214]. It is important however to consider, not only the spatial and temporal aspects of migration at the departure and destination sites, but also the route through which the birds are required to fly to complete these migrations. For many birds, the suitability of these routes is determined by the wind and any changes in wind conditions could lead to changes in the birds’ ability to complete their
migration over the routes. This is very true especially for species that depend on atmospheric conditions to fly over ecological barriers, such as seas and deserts. My PhD project was one of the first attempts at doing this and shows how severe the impacts of climate change on migratory routes and flyways can be. It is important therefore to pay more attention to the wind as a predictor variable and investigate how the migratory birds can be affected by, and how they can respond to, alterations in atmospheric conditions.
Summary

Atmospheric variables have great impact on the evolution of migratory behaviors in birds. Temperature and precipitation determine geographic distributions, timing of life-cycle events and the overall breeding success and population size. Wind and other variables related to air movement affect migratory birds’ ability to navigate and, at a larger scale, shape their migratory routes and flyways. As biologists became aware of the significance of climate change and its potential influence on the global circulation patterns, they started to make predictions about how changes in atmospheric variables will affect migratory birds. In this thesis, I focus on a less studied aspect of climate change and migratory birds. That is, the effect of climate change on the routes and flyways of migratory birds through alterations in, mainly, wind patterns. My study systems for doing this research are two long-distance soaring raptor migrants in East Asia. I start off by providing a review of the way atmospheric currents affect migratory behavior of soaring birds (Chapter 2). I then use satellite-tracking data collected for Oriental honey buzzards *Pernis ptilorhynchus* to show the importance of weather, and particularly wind, in the route selection of this species over a critical section, a ca. 700 km water-crossing over the East China Sea (Chapter 3). I then project the findings from the current suitability of the East China Sea region for the migration of Oriental honey-buzzards to the future, under two scenarios of climate change (Chapter 4). I show that, as climate change progresses towards the end of the century, the suitability of this section of migratory route will be reduced significantly due to changes in wind conditions. I also investigate the impact of current and future wind conditions on the migratory route of Grey-faced buzzard *Butastur indicus*, a species that dominates the East Asian Oceanic flyway for raptors (Chapter 5). For this species, which has an island-hopping strategy, I show that the existence of islands in a north-to-south axis, which is along the general direction of migration, and the occurrence of wind support and little crosswind are responsible for the suitability of
this flyway for raptor migration. I further explore the conditions of the wind along the flyway in the future and, at the scale of my investigation, find no considerable changes in wind speed and direction by the end of the century.

My finding that the optimal traditional migratory routes and flyways of long-distance raptor migrants can be affected by changes in wind conditions under climate change is of high relevance for research in migration ecology of birds. Wind support is a crucial component of migration for many birds and it is important for researchers to start looking into how changes in wind variables will impact these birds, particularly those that depend on wind to complete migration over ecological barriers. Using future wind data in ecological research is rather new, but it is doable and I have tried to provide some suggestions and examples to pave the way for future studies.
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