From thermal to flyway: how weather shapes the soaring migration of European Honey Buzzards Pernis apivorus at multiple scales

Vansteelant, W.M.G.

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at multiple scales

Wouter M.G. Vansteelant
From thermal to flyway:
how weather shapes the soaring migration
of European Honey Buzzards *Pernis apivorus*
at multiple scales
This PhD project was carried out in the Computational Geo-Ecology group of the Institute for Biodiversity and Ecosystem Dynamics (IBED) at the University of Amsterdam. Part of the funding for the Honey Buzzard studies was provided by the Natura 2000 program at the province of Gelderland (Chris Rövenkamp & Jan van Diermen) that initiated the Honey Buzzard project. Tracking studies in this dissertation project were facilitated by infrastructures for e-Science, developed with support of the NLeSC (www.esciencecenter.com) and LifeWatch, carried out on the Dutch national e-infrastructure with support of SURF Foundation. ECMWF data were provided by KNMI and the ESA FlySafe initiative within the framework of the Integrated Applications Promotion (IAP) Programme. Data from the migration surveys at Batumi, Republic of Georgia, was provided by Batumi Raptor Count (www.batumiraptorcount.org). Hawk Mountain Sanctuary (Pennsylvania, USA) supported WMGV during the starting phase of his research concerning raptor migration in Georgia through a Conservation Leadership Internship.

Cover: Honey Buzzards soar over Batumi, Georgia. August 2014. © Folkert de Boer

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From thermal to flyway: how weather shapes the soaring migration of European Honey Buzzards *Pernis apivorus* at multiple scales

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Wouter Marc Gerard Vansteelant
geboren te Roeselare, België
Promotiecommissie:

Promotor: Prof. dr. ir. W. Bouten Universiteit van Amsterdam
Copromotor: dr. J.Z. Shamoun-Baranes Universiteit van Amsterdam
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prof. dr. H. Hooghiemstra Universiteit van Amsterdam

Faculteit: Faculteit der Natuurwetenschappen, Wiskunde en Informatica
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Chapter 1

Introduction
Understanding how animals respond to their environment, and how they adapt to change, is a grand challenge in current biology [1–3]. For migrating birds, weather conditions are a vital component of the environment, and so unravelling how they respond to weather conditions at multiple scales is an important research avenue in current migration ecology [4–6]. It has been no easy task to determine to what extent weather conditions shape migratory journeys, especially not in the case of long-distance migrants which wander vast distances across the globe, far beyond the view of human observers. However, as we entered the digital age, the advent of animal telemetry has opened up tremendous new opportunities for ecologists to study the flight behaviour and movement patterns of wild birds in great detail, and across multiple scales, ranging from local foraging movements to the world’s longest animal migrations [7–9]. In this research, I will combine visual observations with high-resolution GPS-tracking research in order to gain a deeper understanding of how soaring birds have adapted to the atmospheric processes which govern weather conditions along their migratory journeys. In order to do this, I will use a recently proposed framework for integrating meteorology in migration research [5].

1.1 INTEGRATING METEOROLOGY IN MIGRATION RESEARCH

When animals move they base their decisions on how they perceive their environment at multiple scales [10]. An animal’s movement trajectory depends primarily on the motivation and the objectives of the animal to move, its motion capacity and its navigational abilities. On the other hand, animal movements are constrained by environmental circumstances such as weather conditions which affect its internal state, the bioenergetics of motion and its navigational abilities. Atmospheric processes may therefore affect migrating birds in many ways (Fig 1.1).

Local weather conditions influence the instantaneous flight behaviour of migrating birds, and such effects will accumulate across the journey, thus determining the regional and seasonal efficiency of migration (Fig 1.1, center left column). Migration timing and body condition at arrival may ultimately carry-over to
Fig. 1.1 How atmospheric processes at varying spatiotemporal scales influence instantaneous flight behaviour and regional and seasonal patterns in bird migration, ultimately carrying-over to population dynamics and the evolution of migratory behaviour [5, Fig 1].

individual reproductive success and population dynamics (Fig 1.1, right-most column) through which natural selection for the most efficient migration strategies will take place. Consequently, when we relate the flight direction and flight speed of a migrating bird to local weather conditions in site-specific studies, we should remain aware that the local response to weather is part of a migration strategy which has evolved in response to the broad range of weather conditions which a bird encounters along its entire migration route. Moreover, the weather conditions which birds encounter along a given flyway are shaped by relatively predictable seasonal and regional circulation patterns, and birds may adopt regional and seasonal strategies with respect to such circulation patterns [6,11,12]. This is especially
likely to take place in long-lived species, which may learn complex migration routes through experience over the years [13,14].

An additional complication in the study of weather and migration is that different species adopt a wide range of migration strategies, varying in the extent to which birds feed during migration, the use of strategic stop-over sites, the use of stepping-stones and bottleneck-sites to circumvent geographical barriers, the degree of sociality during migration, as well as the mode of flight and the flight speed they adopt during travel. In other words, the motivation, objectives, navigational abilities and motion capacity of a migrant are highly species-specific, and so is the scale at which a bird will adjust flight behaviour and adapt migration strategies in relation to weather conditions [5,6,10,15]. Biologists have long struggled with the complex challenge of unravelling animal behaviour in relation to environmental influences, especially out of controlled conditions in the lab [1,2,10,16]. Fortunately, ecologists have recently acquired the technological tools that are needed to study how weather shapes bird migration strategies from the scale of local flight behaviours to entire journeys [5,7,8].

1.2 THE ROLE OF TECHNOLOGY IN THE STUDY OF BIRD MIGRATION

The notion that birds like cranes, turtledoves and storks escape the northern winter by travelling to warmer climates has been around since the ancient Greeks [17], and the existence of a ‘migratory instinct’ was introduced in ornithology as early as 1702 [18]. However, it took until the late 19th century before migration became the commonly accepted explanation for the seasonal appearance and disappearance of birds. It is easy to imagine why it took so long for naturalists to imagine that small birds like passerines could migrate, given that many species travel to remote regions, far outside the reach of human observers. Alternative explanations for long-distance migration, such that birds hibernate or transmute during winter, could only fully be dismissed once tangible evidence for migration appeared. Some of the earliest evidence came in the form of the infamous Pfeilstorch, a White Stork *Ciconia ciconia* which returned to Germany in spring 1822 impaled by African
tribal spear [18]. Studies on the influence of weather on migrating birds would only start appearing at the dawn of the 20th century, when the advent of bird ringing and binoculars facilitated identification and observation of birds in the field [19–21].

1.2.1 Site-specific studies on the role of weather in migration

Some of the earliest publications on the influence of weather on migrating birds involved reports of mass-mortality of migrants due to extreme weather events, and by collision with lighthouses and other man-made structures [21–24]. Systematic attempts at investigating the influence of weather on the timing and abundance of migrating birds later involved the study of visible migration, at geographical hotspots for diurnally migrating soaring birds, and by systematic counts or mist-netting in stop-over areas [20,25,26]. However, bird migration research only really started booming after the end of World War II. The war had brought forth surveillance radar technology which could be used to study the flight directions and speeds of migrants in the wild [27,28]. This was especially important for the study of nocturnal migrants which could otherwise only be studied by moon-watching or using infra-red camera’s [20,23,29]. Moreover, the relative tranquillity of the 1950’s and ’60’s in western Europe and North America meant that there was more time for science, and field observers enjoyed notable improvements in personal transportation and communication [23,29–32]. These advancements, together with the rise of commercial air travel in the 1960’s, opened up an exciting period of discovery during which the composition and timing of bird migration at some of the world’s biggest migration hotspots were being described for the first time [33–37].

While surveillance radar technology had caused a notable advance in the study of weather and migration, birds cannot be identified to species level using surveillance radar and radars tend to detect flocks rather than individual birds [23,29]. Therefore, the development of tracking radar, with which one can track the speed and orientation of specific individuals, was one of the most important developments for the study of weather and bird migration during the 20th century [23,38–41]. The technique was pioneered in Switzerland [42,43] and has been used to describe flight
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strategies of migrant birds throughout various parts of the world ever since [38,44–46].

Numerous studies correlated visual and radar observations on the magnitude and timing of migration as well as flight speed and flight direction with local weather conditions [23,38,46,47]. In addition, several early works considered how large-scale weather systems may affect migration, thereby correlating timing of migration with the passage of cold-front and low- or high-pressure zones [23,25,29]. Large-scale atmospheric indices and weather maps are still being used in contemporary studies using counts of visible migration [48,49], and the same holds for field estimates and measurements of local weather conditions [50,51]. However, integrating information about the flight behaviour of migrating birds observed across multiple sites is not a trivial task. The ecological implications of a given set of meteorological conditions cannot readily be compared between any two locations because they depend on the climatological context of any given location [23,43]. For example, an approaching cold front will have different effects depending on the direction it is coming from, and how this relates to the average weather pattern in that location [43]. Also, many observers have reported on the relation between weather and bird migration at islands and coastlines, where the intensity of (passerine) migration tends to be correlated to adverse conditions such as fog and rain, while we know that migrants are more numerous in fair weather when they travel inland [20,23,45]. Nevertheless, researchers have long been constrained to study migration within a site-specific context, due to lack of tools with which to study birds across larger scales.

1.2.2 Adopting a bird’s perspective through telemetry

While radio-tracking of wild birds became possible in the late 1960’s [52], the true revolution for migration research occurred during the 1980’s, when satellite-based navigation systems entered the public domain [53,54]. The first satellite-based telemetry devices were rather large and heavy and could only be fitted to larger mammals. However, in 1987 a Bald Eagle *Haliaeetus leucocephalus* could be tracked for up to 8 months using a Platform Transmitter Terminals (PTT) that
operated via the Argos Satellite System [55,56]. Argos-based devices determine positions on the globe using Doppler shifts in radio signals, offering limited spatial accuracy, but when solar-powered Argos-devices appeared in the mid 1990’s it became possible to record daily movements over sufficiently long periods in order to map entire migratory journeys. The problem of accuracy was finally also solved by the introduction of GPS (Global Positioning System) at the start of the new millennium [53,54,57].

Of course, studies using new technologies tend to be biased towards larger species as it takes time for tracking devices to be miniaturized to the extent that they can fit on even the smallest of migrants. However, as the pace of innovation continues to accelerate, the components needed to build tracking devices become ever smaller, cheaper and energy-efficient, paving the way towards a global tracking system for animals big and small [8,9,57,58]. Today, researchers are integrating radio- and satellite-based tracking technologies with other sensors such as heart-rate monitors [59,60], accelerometers [61,62] and even video cameras [63–65] in order to monitor any aspect of avian flight imaginable, ranging from physiology and bioenergetics of flight to the very weather conditions which a bird encounters on the wing.

1.2.3 Quantifying weather influences for telemetry studies

There is a great variety of online meteorological data resources which capture atmospheric processes at varying spatiotemporal scales and which can readily be combined with field observations or telemetry data. Weather station data may still suffice to study flight behaviour of migrant birds in a local or regional context. However they do not allow a reliable annotation of migration tracks with weather data. Numerical simulations of atmospheric processes can fill this gap to a great extent. Such models may be used to predict atmospheric turbulence and flows at a resolution of meters and seconds, such as in large-eddy simulations [66], or at a resolution of minutes-days in mesoscale (i.e. regional) atmospheric models. Unfortunately, such models require extensive calibration, they are mainly used by expert meteorologists, and their data output is rarely available online, so that it is not surprising that they have rarely been used in migration research so far [67–70].
Moreover, applying these models across entire migration routes is computationally very expensive, and requires intensive collaboration between meteorologists and IT-specialists.

Fortunately, meteorological research centres also provide global weather data at a resolution of a few tens of kilometres and over time steps of three to six hours, and which are easily accessible to ecologists in order study flight behaviour over entire migration flyways. These are so-called reanalysis models, which simulate 3D circulation patterns resulting from large-scale, synoptic atmospheric processes. They are calibrated with measurements from weather stations, sounding balloons, weather aircraft and remote sensing data (e.g. ECMWF) [71] and can be used to obtain good approximations of the actual weather conditions encountered during flight at relatively high altitude above the ground. Various authors have used these models in previous studies of weather influences on various aspects of bird migration such as flight speed and direction [72,73], flight altitude [74], stop-over decisions [75,76], and selection of migration routes [77] at regional and continental scales. Moreover, there are various open access tools and other bird tracking systems which enable users to annotate migration tracks with weather data from these reanalysis models [62,78,79].

1.3 WEATHER AND SOARING MIGRATION

Resolving how migrating birds adapt to weather conditions at multiple scales remains an important scientific challenge which can be addressed in all earnest using tracking technology. So far, tracking studies which consider flight behaviour in relation to weather conditions along entire migration routes have mainly been conducted for larger birds, and at a resolution of entire travel days [11,13,80–84] down to hourly -rarely shorter- travel segments [72,77,85–88]. These are often soaring species, which have also been studied intensively through site-specific observations using tracking radar [44,46,89–96]. In this dissertation, I will use field observations of weather and bird migration as well as advanced tracking techniques
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and global atmospheric reanalysis models in order to determine how weather shapes the migration of a long-distance soaring migrant from thermal to flyways.

It is outside the scope of this introduction chapter to provide an extensive review of the influences of weather on migrant birds using other flight modes than thermal soaring during migration. Others have provided recommendable reviews on the influence of weather on migration [12,38,47]. Instead, I will briefly summarize the current state of our knowledge about the role of weather specifically for the case of thermal soaring migration here, followed by more detailed literature reviews concerning those aspects of migration which I studied in each of the following chapters (chapters 2-5).

1.3.1 Soaring migration

While the energetic cost of flight increases with body size, soaring allows birds to use atmospheric currents in order to subsidize the energy required for flight [97–100]. Soaring flight is thus the predominant migratory flight mode in many large birds [93,101]. Large birds which are not capable of soaring flight usually migrate much shorter distances than those who can, simply because large birds cannot accumulate enough fat reserves to sustain longer trips [101,102]. Soaring birds may use columns of warm rising air, called thermals, in order to gain lift [45,89,103], and sometimes they can even continue gliding for long distances in thermal streets [104], along sea-breeze fronts [105], or in updrafts along mountain ridges [77,106], which enable them to sustain altitude while gliding. The predominant type of soaring flight employed by Afro-Palearctic soaring migrants is thermal soaring. Thermal-soaring consists of two distinct, alternating stages: first a bird gains altitude by circle-soaring on rising warm air in a thermal, after which a bird makes progress in its intended direction by gliding on stretched wings toward another thermal [99,107]. Many species are facultative soaring migrants, i.e. they may alternate soaring with flapping flight under adverse soaring conditions. However, soaring is always the way to go for birds that need to conserve as much energy as possible during flight, and the larger and heavier a species, the more it tends to rely on soaring flight to subsidize its own energy reserves [97,99,101].
1.3.2 Barriers and bottlenecks

Geographical features such as mountain ranges and seas are formidable barriers for any migrant, but soaring birds are especially keen to circumvent large water bodies during migration. This is because thermals generally do not develop over water bodies in temperate regions, which means soaring birds cannot avoid flapping flight during sea-crossings [17,107–109]. Soaring birds migrating between Europe and Africa circumvent the continent’s main water bodies, causing enormous aggregations of soaring birds in geographical convergence zones [36,110–116]. A minority of central European soaring birds adopt an island-hopping strategy, crossing the Mediterranean via the Italian and Greek peninsula [117–119].

Fig. 1.2 A Honey Buzzard soars upward after crossing the Strait of Gibraltar on May 4th 2013. She was part of a flock of 6, including a female who’s migratory movements I have studied in this dissertation. She carried a GPS-logger and was seen by photographer Helge Sørensen near the beach of Bolonia, Spain, at 7:30 PM (see also: http://www.uva-bits.nl/news/back-in-europe-uva-bits-honey-buzzard-photographed-at-the-strait-of-gibraltar/).
Most of the birds which pass through geographical convergence zones are adult birds, and thus relatively experienced individuals [112,113,120], while many juveniles cross the Mediterranean, and presumably also other water bodies, directly [14,121,122]. In species where migration timing is not age-dependent, juveniles may learn a strategic migration route by following adults, perhaps even their parents, on their first outbound migration [123–125]. However, it is more common for juveniles of large soaring species to migrate up to several weeks later than their parents during their first outbound migration [14,120,126,127], and mortality tends to be very high among juvenile soaring migrants [109,128–130].

In addition to geographical barriers, soaring birds may also encounter ecological barriers during migration. One such barrier for African-Eurasian migrants is the world’s greatest desert: the Sahara [33,129,131,132]. The majority of migrants moving out of Europe cross this perilous environment twice a year, risking dehydration and fatigue with hardly any opportunity to land for shelter, water or food. How exactly (soaring) birds are able to overcome this barrier, and what strategies they use with regard to weather is still not fully understood [33,129,132,133].

1.3.3 Flight behaviour of soaring migrants in relation to weather conditions
In site-specific studies the flight behaviour of soaring migrants in relation to weather has mainly been studied along leading lines or geographical convergence zones for soaring migrants [45,93,103,107]. These studies involved visual observations, ringing surveys, radar work and some researchers even tracked flocks of soaring birds using a motorized glider. However, the bias toward site-specific observations may have important consequences for our current understanding of flight behaviour of soaring migrants as the weather conditions in geographical convergence zones are unlikely to be representative of the broad range of weather conditions that birds encounter elsewhere along the flyway. Moreover, site-specific studies have yielded much contrasting evidence about the influence of sidewinds on soaring migrants, especially near coastlines [38,134–136]. Nevertheless, we can
identify some general patterns in the flight behaviour of soaring birds with regard to weather on the basis site-specific research:

1. Soaring birds migrate when thermals form during daylight. Facultative soaring birds start travelling earlier in the day, mainly relying on flapping flight at first and using soaring flight later in the day. Heavier birds wait until several hours after sunrise before they can depart, relying almost exclusively on soaring flight [89,90,137].

2. The ground speed and altitude of migration increases from the daily start of migration until mid-afternoon and decreases sharply towards the end of the day, in accordance with the diel rhythm of thermal development [45,89,93,103,138]

3. Wind conditions have a big impact on the ground speed of soaring migrants [44,89,91,96,139], and large soaring species prefer tailwinds to cross the Mediterranean [30,118,140,141].

4. Several species increase their gliding airspeed, i.e. the speed at which they glide between thermals with respect to the air, depending on their climb rate in thermals [44,93,139]

5. Soaring migrants also achieve higher ground speeds and fly at greater altitude as the strength of thermals increases. This is because birds are able to complete longer climbs in a shorter amount of time in stronger thermals, enabling longer and faster glides, resulting in higher overall migration speeds. [44,45,89,91–93,103,138]

6. Soaring birds have also been reported to adjust their flight mode and flight path in response to the availability of thermal convection [51,105,110,137].

1.3.4 Seasonal and regional patterns in soaring migration

In addition to fine-scale flight responses to weather, the timing of peak migration of soaring birds at convergence zones is known to be related to annual variation in weather conditions at departure sites and ‘upstream’ the migration route [48,142]. Tracking studies on migrating birds have confirmed that birds readily adjust their
flight behaviour in response to conditions they encounter along the way [143] and most of the aforementioned effects of wind and climb rates on local flight behaviour of soaring birds can be extended to entire migratory journeys [72,83–85,144]. Nevertheless, tracking studies have also revealed a number of other aspects of long-distance soaring migration which were previously underappreciated in migration research. Most importantly, tracking studies have revealed a high degree of flexibility in daily time budgets, flight speeds and orientation strategies within and between species, and between individuals, seasons and different geographical regions and flyways [11,83,87,145]. However, in many cases it is not clear which of these patterns may be attributed to weather, other environmental factors or changes in the internal state of a migrant along the flyway.

1.3.5 Soaring migration theory
Besides the empiric research on soaring migration ecology, there have been several important theoretical contributions concerning soaring migration. First and foremost, Collin Pennycuick developed one of the most widely used biomechanical model of flying birds in the 1960’s – 1990’s. Using aerodynamic theory, Pennycuick’s model can be used to calculate the optimal flight speed for a bird depending on its morphology (size, shape and mass), its energy reserves (i.e. fat stores), flight mode and properties of the surrounding air [98,99,146]. The theory can be applied to determine optimal gliding airspeeds for soaring as well as optimal flight speeds for flapping birds. The underlying idea is that a bird should fly at different speeds depending on whether it aims to minimize travel time or energy consumption. The model enables us to calculate these benchmark speeds against which we can evaluate the flight behaviour of free-flying birds [6,97,102,147].

In extension, the optimality framework has been used in order to predict many other aspects of migratory flight behaviour, ranging from flight times, over flight altitude to orientation in response to wind [6,148]. A key concept within this optimality framework is that of ‘adaptive drift’ [6, 151]. Adaptive drift entails that birds may tolerate drift at the start of their journeys, and increase the degree at which they compensate while approaching their goal, if they encounter variable winds. They
may adjust the time, altitude and direction of flight in order to make optimal use of wind assistance along their journey. Using an optimality framework we can then derive expectations about the optimal orientation strategies for migrant birds depending on the properties of the wind fields they encounter along the flyway [6,148–152].

Since the advent of tracking it has become possible to define the individual destinations of birds, which is of great importance to quantify orientation behaviour in relation to wind [38,153–155]. Consequently, several empirical investigations of orientation behaviour have been conducted for soaring birds [11,82,156]. These studies generally seem to support the idea that birds travel faster by engaging in ‘adaptive drift’ along the way. However, while some of the expectations derived from the models of Pennycuick and Alerstam have broadly been confirmed by field observations and tracking studies, there is still a lot of scope for tracking research to contribute to the development of bird migration theory. For example, a recent study has revealed that most soaring migrants fly at suboptimal speeds to maximize migration speed while migrating over Israel [157], while the influence of wind on fine-scale flight behaviour of soaring migrants has yet to be accounted for in optimal soaring migration models [44]. One important missing link in soaring bird migration theory is a model which unifies the optimisation of flight speed and travel direction for soaring birds. However, this is hard to achieve without prior knowledge about the scale at which birds have adapted different aspects of their flight behaviour in order to complete migration under variable weather conditions.

1.4 THE EUROPEAN HONEY BUZZARD *Pernis apivorus*: AN ADEPT SOARING MIGRANT

In order to gain a deeper understanding of how weather shapes soaring migration at multiple scales I will focus on one of the world’s most numerous soaring migrants: the European Honey Buzzard *Pernis apivorus*. This enigmatic bird of prey is a common summer visitor throughout temperate and northern Europe and the westernmost regions of Russia [158]. They are the most numerous migratory bird of
prey at nearly every geographical convergence zone between Europe and Africa [112–114,126,159]. They travel 6,000 – 10,000 km’s into sub-Saharan Africa, mainly wintering in tropical rainforest, but reaching far into the savannahs of eastern and southern Africa [158]. Honey Buzzards regularly adopt flapping flight when passing through geographical convergence zones in morning hours and they are known to be less selective for tailwinds in order to engage in sea-crossings compared to other soaring birds [30,93,141,160]. Nevertheless, the fact that Honey Buzzards have almost never been reported to feed during migration [161] suggests they ought to be highly motivated to conserve as much energy as possible by soaring. In order to uncover how they do this, I investigate the relation between soaring flight and weather at various scales:

- In chapter two, I aim to gain a deeper understanding of how Honey Buzzards adjust their gliding airspeed between thermals depending on the climb rate they achieve in thermals and local wind conditions. I will compare their behaviour with theoretical benchmarks for time-optimal and risk-averse migration according to Pennycuick’s aerodynamic models for soaring flight, and determine to what extent soaring conditions and wind conditions affect the manner in which they compromise between either theoretical optimum.

- In chapter three, I will investigate how Honey Buzzards and ten other species of soaring migrants adjust their local flight paths in relation to local wind conditions and cloud cover dynamics while travelling along the eastern Black Sea coast near Batumi, Georgia [112]. This study is based on field observations conducted by over 100 volunteer observers during the pilot surveys of the Batumi Raptor Count project in 2008 and 2009.

- In chapter four, I study a few dozen migratory journeys of Honey Buzzards and Montagu’s Harriers *Circus pygargus* in order to compare the relative influence of soaring conditions, tailwinds, sidewinds and precipitation on the hourly and daily travel speed of two species which use soaring flight to a varying degree. I intend to corroborate whether the influences of wind and soaring conditions on flight behaviour at geographical convergence zones
apply across entire journeys. Moreover, I will determine if weather conditions can help explain commonly observed geographical and seasonal differences in the migration speed of soaring birds.

- In chapter five, I will investigate how Honey Buzzards adjust their seasonal migration routes and hourly orientation behaviour throughout the east-Atlantic flyway in the context of local wind conditions and seasonal wind regimes. In so doing, I aim to identify the scale at which birds optimize their travel routines in response to large-scale atmospheric circulation patterns.

In the final chapter I will summarize the general characteristics of European Honey Buzzard migration strategies in relation to weather from thermal to flyway. I will then discuss how weather may affect flight behaviour and migration patterns in other soaring migrants, taking into account differences in body size, flight mode and life-history traits that may affect the objectives, motion capacity and navigational abilities of any given species [5,6,10]. I hope this research may inspire ecologists working with many other animals which move through flows, ranging from birds, bats and insects in the air to mammals, fish, crustaceans and other invertebrates in the water.
Chapter 2

Soaring across continents: high-resolution GPS-tracking of Honey Buzzards *Pernis apivorus* reveals the importance of climb rates and wind for optimal soaring migration theory

Vansteelant W.M.G., J. Shamoun-Baranes, J. McLaren, J. van Diermen & W. Bouten

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2.1. **ABSTRACT**

Soaring birds reduce energetic costs of flight by exploiting vertical updrafts to gain altitude and gliding to approach their destination. Both vertical and horizontal flows influence flight speeds of soaring migrants. In order to understand how soaring migrants adjust their flight behaviour at the fine scale to the changing atmospheric conditions across entire migration routes we combine high-resolution GPS tracking data of migrating Honey Buzzards *Pernis apivorus* with optimal soaring migration theory.

We compared measurements of gliding airspeeds to predictions based on two distinct behavioural strategies for thermal soaring flight. The first strategy assumes birds alter their gliding airspeeds as a function of their climb rates in thermals to maximize cross-country airspeed over a full climbing-gliding cycle ($V_{\text{opt}}$). The second strategy assumes that birds alter their gliding airspeed in response to following or opposing winds to maximize the distance covered relative to the ground during each glide phase ($V_{\text{bgw}}$).

Honey Buzzards were gliding on average $2.05 \text{ ms}^{-1}$ slower than $V_{\text{opt}}$ and $3.42 \text{ ms}^{-1}$ faster than $V_{\text{bgw}}$. They increased airspeeds with climb rates, reduced airspeeds in tailwinds, and markedly reduced airspeeds when leaving thermals under 800 m above ground. Furthermore, measured airspeeds increasingly deviated from both models with increasing sidewinds. Our results suggest that Honey Buzzards adopt a risk-averse strategy which compromises between optimal exploitation of each thermal and slow glides to increase the likelihood of reaching thermals ahead. Orientation strategies should be included in future models to unravel how risk-averse soaring migrants trade-off wind drift and gliding range, particularly under poor soaring conditions.
2.2. **LIST OF SYMBOLS AND ABBREVIATIONS**

- $\beta$: Angle between heading and track direction over full climbing-gliding cycle
- $V_a$: Gliding airspeed
- $V_{ac}$: Horizontal airspeed during the climb phase
- $V_{bg}$: Best-gliding airspeed in still air, theoretical optimum for maximizing gliding range relative to the air
- $V_{bgw}$: Best-gliding airspeed in wind, theoretical optimum for maximizing gliding range relative to the ground
- $V_c$: Climb rate
- $V_{cc}$: Cross-country speed relative to the air
- $V_g$: Gliding ground speed
- $V_h$: Horizontal ground speed during the climb phase
- $V_{ms}$: Theoretical minimum-sink speed
- $V_{opt}$: Theoretical optimal airspeed for maximizing $V_{cc}$
- $V_s$: Sink rate
- $V_{xc}$: Cross-country speed relative to the ground
- $T_c$: Time spent climbing
- $T_{cc}$: Time spent in complete climbing-gliding cycle
- $T_g$: Time spent gliding
- $W_{Sg}$: Sidewind component along glide direction
- $W_{Sxc}$: Sidewind component along track direction over full bout
- $W_{fg}$: Tailwind component along glide direction
- $W_{Txc}$: Tailwind component along track direction over full bout
2.3. Introduction

Migrant landbirds face highly variable weather conditions during their seasonal journeys between Europe and Africa. These birds have developed various strategies to reduce the energetic cost and the time needed to complete their migration [6,148]. Soaring birds generally avoid flapping flight by gaining altitude in thermals and gliding across the landscape on stretched wings, thus reducing the amount of energy they need to reach distant locations [45,98,99,107]. While fine-scale updrafts are essential to soaring migrants, their hourly travel speeds and daily travel distances are largely determined by synoptic and regional wind conditions which they encounter along their route [72,82,83,144,162]. In order to understand how soaring birds control the time and energy they spend on the move, one needs to study their behavioural response to weather conditions at the fine scale [163]. Only recently with improvements in tracking technology is this feasible along entire migration routes [7,8,62].

2.3.1. Optimal soaring migration theory

Optimal soaring migration theory is a particularly useful and frequently used theoretical framework within which to study flight behaviour of soaring migrants [44,99,101,102]. A soaring bird gains potential energy by circling upward on stretched wings in a thermal, and converts this potential energy into kinetic energy to make fast progress across the ground by gliding between thermals (Fig 2.1.A). The rate at which a bird loses altitude during a glide, the sink rate ($V_s$), increases progressively with the gliding airspeed ($V_a$) and can be calculated from drag and lift forces acting on a bird [99,100,164,165]. These forces can in turn be calculated as a function of the mass of a bird and its change in size and shape through wing adjustments for increasing airspeed [98,99,165–167]. The relationship between sink rate and gliding airspeed is solved graphically as the ‘glide polar’ (Fig 2.1.B, C) and is central to the derivation of optimal soaring strategies.
Fig 2.1. Optimal soaring migration models. (A) During an idealized soaring trajectory in windless conditions a bird glides down to the same altitude as where it started climbing. (B) The minimum sink speed is the lowest airspeed a bird should achieve in gliding flight. The graphical solutions for finding optimal airspeeds for any objective is to draw a tangent to the glide polar from a point on the ordinates which define the constraints on its performance. The point where the tangent crosses the x-ordinate is the corresponding $V_{cc}$. To find the optimal airspeed $V_{opt}$ to maximize $V_{cc}$ as a function of $V_c$ the tangent is drawn from the observed climb rate in a thermal on the y-axis $(0,V_c)$. (C) To find the best-gliding airspeed $V_{bg}$ which maximizes gliding range in windless conditions we draw the tangent from the origin of the coordinate system $(0,0)$. We extended this solution to account for tailwinds by drawing a tangent to the glide polar from $(-W_{Tg}, 0)$. 
To model soaring flight, we can imagine a simplified soaring trajectory in which a bird glides down to the same altitude at which it started gliding in windless conditions (Fig 2.1.A). The most commonly modelled behavioural strategy for soaring migrants is a time-minimizing strategy, i.e. to maximize cross-country speed ($V_{cc}$), the average speed relative to the air over a full climbing-gliding cycle [99,101,102]. The gliding airspeed at which $V_{cc}$ is maximal is known as $V_{opt}$. Assuming windless conditions, $V_{cc}$ can be calculated in terms of the time spent climbing ($T_c$) and gliding ($T_g$) as follows:

$$V_{cc} = V_a * \frac{T_g}{T_g + T_c}$$  \hspace{1cm} (1)

If we assume that the altitude over which a bird sinks during the glide ($\Delta h$) is the same as the altitude over which it climbed in the preceding thermal (Fig 2.1.A), then $T_g$ and $T_c$ can be solved in terms of $\Delta h$ and the vertical speed in the glide ($V_s$) and climb phase ($V_c$) respectively:

$$\Delta h = T_g * V_s = T_c * V_c$$  \hspace{1cm} (2)

Thus we can substitute $T_g$ and $T_c$ in Eq. 1 to predict $V_{opt}$ (the gliding airspeed at which a bird reaches maximal $V_{cc}$) for a given $V_c$ (graphical solution in Fig 2.1.B.):

$$V_{cc} = V_a * \frac{V_c}{V_s + V_c}$$  \hspace{1cm} (3)

It can be shown that $V_{opt}$ is independent of wind conditions and orientation as long as updrafts are ubiquitously available (see Appendix).

2.3.2. The risk-avoidance hypothesis

Numerous studies have shown that soaring migrants do indeed increase their gliding airspeeds and cross-country airspeeds with improving soaring conditions, as expected for $V_{opt}$ [91]. However, some soaring birds don’t increase airspeed with climb rates at all, e.g. White Storks [96], and field measurements suggest soaring migrants usually do not reach $V_{opt}$ in a glide [44,139].

An alternative soaring strategy is to achieve maximal range relative to the air during the glide phase, which may well be optimal when thermals are far apart and difficult
to reach during a single glide [99]. To reach maximal range between thermals in windless conditions, a bird must glide at its best-gliding airspeed ($V_{bg}$), the airspeed to minimize its glide ratio (GR, graphical solution Fig 2.1B):

$$GR = \frac{v_s}{v_a}$$

In fact, out of 12 species of soaring migrants tracked by radar while migrating over Israel, none were gliding as fast as $V_{opt}$, and gradually reduced airs speeds toward $V_{bg}$ under deteriorating soaring conditions, probably to avoid the risk of not reaching another thermal before reaching the ground [157]. The most risk-averse species were those with the highest wing loadings, i.e. those for which energetic costs of flapping flight are highest [157]. Nevertheless, even if soaring migrants avoid the risk of being grounded between thermals, it is surprising that they glide so slow while migrating over Israel, where thermals tend to be strong and abundant [69,94,168].

### 2.3.3. The importance of wind

It is easy to see why soaring migrants that seek to maximize their glide range should also respond to head- and tailwinds. In a strong headwind along the glide direction of, say, 10 ms$^{-1}$ which is equal and opposite to the best glide airs speeds $V_{bg}$ of a given soaring bird, the bird would not make any headway with respect to the ground during its glide phase, and it may even be drifted back along its intended travel direction during the climb phase. Therefore, a bird must increase its gliding airspeed to overcome a headwind and to reach another thermal. Conversely, when flying in a tailwind, birds may reduce their own airspeed to reduce the energy, or altitude, invested in each glide.

Interestingly, when glider pilots aim to maximize their gliding range relative to the ground, for example to reach a thermal hot-spot, they commonly increase their airspeed in a headwind, and decrease it in a tailwind, by about half of the tail-/headwind component [169]. Birds may adopt a risk-averse flight strategy, adjusting their airspeed to maximize gliding range relative to the ground, to account for heterogeneity in soaring and wind conditions experienced along their migration.
route. This hypothesis is supported by the fact that soaring migrants do tend to reduce their gliding airspeeds in tailwinds [44,139,170]. In order to determine whether birds alter their gliding airspeeds in response to wind conditions we developed an extension of the model for risk averse soaring flight.

2.3.4. Integrating head- and tailwinds in optimal soaring migration models

To account for wind along a chosen heading we define the best-gliding airspeed ($V_{bgw}$) as the gliding airspeed that minimizes the ratio of sink to ground speed along its chosen heading (Fig 2.1.C):

$$f(V_a) = \frac{V_s}{V_a + W_{Tg}}$$

(5)

where $W_{Tg}$ is the tailwind relative to the bird’s heading. In choosing this approach we assume that the bird is either fully drifting with the wind (i.e. ignoring sidewinds) or that it is only interested in maximizing its progress along its heading.

In contrast to the risk-averse strategy the optimal gliding airspeeds based on the time-minimizing strategy ($V_{opt}$) does not change due to wind influences under different orientation strategies. By gliding at $V_{opt}$ a bird will maximize cross-country airspeed ($V_{cc}$) as well as cross-country ground speed ($V_{xc}$) in any wind conditions (see Appendix).

2.3.5. Combining optimality theory with high-resolution GPS tracking

To measure flight behaviour of soaring migrants across an entire migration cycle we remotely programmed GPS-loggers on five European Honey Buzzards *Pernis apivorus* to record the birds’ 3D positions at a 10 second resolution during two half-hour intervals each day a bird was travelling between the Netherlands and western Africa. We then combined tracking data with global weather models [85] to calculate flight parameters. To better understand flight strategies, we compared gliding airspeeds with predictions for two behavioural strategies derived from optimal flight models:
(1) a proposed time-minimizing strategy for cross-country soaring, in which birds adjust their gliding airspeed to climb rates in thermals optimizing their gliding airspeed \( V_{\text{opt}} \) in order to maximize cross-country airspeed and ground speed

(2) a risk-averse strategy for gliding, in which birds adjust their gliding airspeed to head- and tailwinds, gliding at airs speeds \( V_{\text{bgw}} \) that maximize their gliding range relative to the ground.

We expect the Honey Buzzards to glide at airs speeds in between \( V_{\text{opt}} \) and \( V_{\text{bgw}} \), i.e. that they simultaneously increase gliding airs speeds with climb rates according to \( V_{\text{opt}} \) and adjust their gliding airs speeds to head-and tailwinds according to \( V_{\text{bgw}} \). We also expect that Honey Buzzards fly closer to \( V_{\text{bgw}} \) than to \( V_{\text{opt}} \) in poor soaring conditions, which would indicate flexibility in risk-averse behaviour.

To determine whether either of the two models are better suited to specific weather conditions, we compare the model mismatch to the deviation between track direction and heading during the glide phase, to represent a potential effect of sidewind influence, and compare the model mismatch to the thermal exit altitude which represents the riskiness of each glide. We further compare predicted cross-country airs speeds and ground speeds with measured cross-country speeds in order to understand how behaviours which are not accounted for in the idealized soaring trajectory for optimal migration modelling may influence overall progress during migration. Finally, we discuss how wind can be integrated more fully into optimal soaring migration theory by accounting for risk-averse or time-minimizing orientation strategies in the context of long-distance migration.

**2.4. RESULTS**

Within each of the high-resolution GPS segments (Fig 2.2.A), we identified consecutive climbing-gliding cycles from the Honey Buzzards’ vertical speeds (Fig 2.2.B, see Materials & Methods). The number of climbing-gliding cycles which we used for analyses, the weather variables derived from the global weather model and
the flight parameters which were calculated by vector trigonometry (Fig 2.2.C, see Methods) are summarized for each individual in the supplementary materials (Supplementary materials Table S2.1, Fig S2.1, see also ‘List of symbols and abbreviations’).

Our calculations of the birds’ airspeeds are affected by the fact that wind data have a limited spatiotemporal resolution compared to real tracking data, and model predictions are affected by uncertainties in the parameterization of optimal soaring migration models. Nevertheless, we can infer meaningful conclusions about migratory soaring flight strategies from comparing realized and predicted flight behaviour in response to weather conditions, and we address data quality constraints and model assumptions in more detail (see Materials & Methods, Supplementary materials Fig S2.2).

As found in previous soaring migration studies [69,93,139] thermal exit altitudes increased strongly with climb rates in thermals (thermal exit altitude = 247.81 + 304.55*Vc; P < 2e⁻¹⁶ , R² = 27.64 %). It is known that thermals tend to lose vertical velocity in strong winds [171], which may cause some correlation between the predictor variables used to predict \( V_{\text{opt}} \) and \( V_{\text{bgw}} \), respectively. While we found some significant effects of horizontal wind components on climb rates in thermals and thermal exit altitudes, these correlations were usually very weak and therefore unlikely to bias our further analyses (Supplementary materials Table S2.2).

### 2.4.1. Observed vs. predicted airspeeds and the role of climb rates and tailwinds

Assuming a Honey Buzzard has a mass of 1 kg, a wing span of 1.3 m and a wing surface area of 0.26m\(^2\), the predicted minimum sink speed (\( V_{\text{ms}} \)) was 6.50 ms\(^{-1}\) and the best-gliding airspeed in windless conditions (\( V_{\text{bg}} \), i.e. \( V_{\text{bgw}} \) at \( W_{\text{Tg}} = 0 \) ms\(^{-1}\)) was 10.02 ms\(^{-1}\) (Fig 2.1.A). Measured airspeeds (\( V_a \)) varied between 1.68 ms\(^{-1}\) and 27.07 ms\(^{-1}\). \( V_a \) was lower than \( V_{\text{ms}} \) on 20 out of 1006 occasions, which is theoretically improbable. These underestimated airspeeds are likely to be caused by overestimating wind speeds with the global weather model. However, we also
Fig 2.2. Capturing soaring behavior with high-resolution GPS loggers. (A) For each day one of five Honey Buzzards (colour code) travelled between 52N and 10N during autumn 2012 (triangles) and spring 2013 (circles) we recorded two half-hour segments of soaring flight data. (B) One example of a half-hour segment of GPS-observations at 10 second intervals with automatically annotated climbs (red) and glides (green). This half hour segment yielded two uninterrupted climbing-gliding cycles for our analyses. (C) Horizontal winds (blue) and the birds’ displacements relative to the air (solid lines) and relative to the ground (dashed lines) during the climb phase (red), the glide phase (green) and over the full climbing-gliding cycle (grey), respectively. See glossary for other terms. Estimated airspeeds were derived from measured ground speeds and annotated wind vectors using vector trigonometry.
Fig 2.3. Comparison of measured and predicted optimal gliding airspeeds of Honey Buzzards under variable conditions. (A) The average measured $V_a$ and predicted $V_{opt}$ as a function of climb rates ($V_c$) according to a 2nd order loess regression model. The distance between measured $V_a$ (points) and $V_{opt}$ seems correlated with head-/tailwinds (colour scale). (B) A bilinearly interpolated surface of model fit ($V_a$-$V_{opt}$) as a function of climb rates $V_c$ and head-/tailwinds ($W_{Tg}$) confirms that Honey Buzzards flew most near $V_{opt}$ in windless conditions. However, they flew faster than $V_{opt}$ in headwinds and slower than $V_{opt}$ in tailwinds, or when reaching climb rates over 5 m/s. (C) The average measured $V_a$ predicted $V_{bgw}$ as a function of $W_{Tg}$ according to a 2nd order loess regression. There appears a weak gradient in climb rate (colour scale) according to the distance between measured $V_a$ (points) and predicted $V_{bgw}$. (D) A bilinearly interpolated surface of model fit ($V_a$-$V_{bgw}$) shows model fit varied according to $V_c$ and not $W_{Tg}$. 
expect speeds to be underestimated on other occasions, but we cannot determine a theoretical maximum speed, thus we did not reject extreme speeds for further analyses.

The optimal gliding airspeeds for maximizing cross-country airspeed (\(V_{\text{opt}}\)) varied between 10.12 ms\(^{-1}\) and 21.61 ms\(^{-1}\) and explained 20.23% of variation in observed gliding airspeeds (Fig 2.3.A). Birds were gliding on average 2.05 ms\(^{-1}\) slower than at \(V_{\text{opt}}\) (Fig 2.3.A, Welch t-test: \(\bar{V}_a = 13.60 \text{ ms}^{-1} < \bar{V}_{\text{opt}} = 15.61 \text{ ms}^{-1}, P < 2.2e^{-16}\)). However, the parallel regression curves of measured \(V_a\) and predicted \(V_{\text{opt}}\) as a function of climb rates (Fig 2.3.A) show that Honey Buzzards responded to \(V_c\) by increasing \(V_a\) at the same rate as \(V_{\text{opt}}\), and two-dimensional model-fit analysis confirmed that the difference between \(V_a\) and \(V_{\text{opt}}\) was smallest in weak tailwinds (\(W_{\text{Tg}} < 1.5 \text{ ms}^{-1}\), Fig 2.3.B).

The predicted best gliding airspeed for maximizing gliding range in head- and tailwinds (\(V_{\text{bgw}}\)) varied from 7.90 to 21.70 ms\(^{-1}\) and explained 37.50% of variation in gliding airspeeds (Fig 2.3.C). Birds were gliding on average 3.42 ms\(^{-1}\) faster than at \(V_{\text{bgw}}\) (Fig 2.3.C, Welch t-test: \(\bar{V}_a = 13.60 \text{ ms}^{-1} > \bar{V}_{\text{bgw}} = 10.19 \text{ ms}^{-1}, P < 2.2e^{-16}\)). \(V_{\text{bgw}}\) explained a large amount of variation in gliding airspeeds, although measured \(V_a\) decreased linearly with \(W_{\text{Tg}}\), and not asymptotically as predicted (Fig 2.3.C).

2.4.2. The influence of risk-aversion for grounding and orientation relative to wind

Visual inspection of model fit based on a loess regression reveals that Honey Buzzards were not gliding markedly slower than \(V_{\text{opt}}\) when leaving thermals at low altitude (Fig 2.4.A). However, we already noted that thermal exit altitudes are strongly correlated with low climb rates so that even \(V_{\text{opt}}\) will be relatively low when exiting thermals at low altitude. Moreover, the birds were gliding at airspeeds progressively closer to \(V_{\text{bgw}}\) when leaving thermals below 700 – 800 m (Fig 2.4.B), which is not likely to be due to a confounding effect head- and tailwinds as thermal exit altitudes were only weakly affected by wind conditions (Supplementary materials Table S2.2).
When the birds’ heading and track direction, and thus wind, were aligned (i.e. pure head or tailwinds, $\beta \approx 0$), the birds flew closer to $V_{opt}$, but still slower than predicted (Fig 2.4.C). Gliding airspeeds gradually approached $V_{bgw}$ as the deviation between heading and track direction increased, especially when $\beta \geq 50^\circ$ (Fig 2.4.D), i.e. when there was a strong influence of sidewinds.

Fig 2.4. Loess regression models reveal flexibility in behavior indicative of risk-avoidance for grounding between thermals and influence of orientation relative to wind. (A) When Honey Buzzards exited thermals at low altitude their gliding airspeed did not change much with respect to $V_{opt}$. (B) The birds did glide gradually closer to $V_{bgw}$ when leaving thermals at 800 m or lower. (C) When the deviation between heading and track direction ($\beta$, bottom) increased, $V_a$ decreased progressively further below $V_{opt}$. (D) The birds were gliding increasingly closer to $V_{bgw}$ when the deviation between heading and track direction was large.
2.4.3. Measured vs. predicted gliding airspeeds (\(V_a\)), cross-country airspeeds (\(V_{cc}\)) and ground speeds (\(V_{xc}\))

Frequency distributions reveal the intermediate position of measured \(V_a\) between predicted \(V_{opt}\) and \(V_{bgw}\) (Fig 2.5.A), as we described previously in more detail. Interestingly, the gap between the predicted and measured speeds becomes smaller when we “scale up” from gliding airspeeds \(V_a\) to cross-country airspeeds \(V_{cc}\) (Fig 2.5.B). Welch t-tests showed that the expected \(V_{cc}\) was on average 1.24 m s\(^{-1}\) lower at \(V_{bgw}\) than at \(V_{opt}\) (mean \(V_{cc}\) at \(V_{bgw}\) = 6.18 m s\(^{-1}\) < mean \(V_{cc}\) at \(V_{opt}\) = 7.41 m s\(^{-1}\), \(P < 2.2e^{-16}\)). The observed \(V_{cc}\) (mean = 9.16 m s\(^{-1}\)) was 2.99 m s\(^{-1}\) higher than the \(V_{cc}\) predicted at \(V_{bgw}\) (\(P < 2.2e^{-16}\)) and 1.75 m s\(^{-1}\) higher than the \(V_{cc}\) at \(V_{opt}\) (\(P < 2.2e^{-16}\)). However, the variation in measured \(V_{cc}\) explained by \(V_{bgw}\) was only 4.06% and by \(V_{opt}\) only 1.55%.

The gap between measurements and predictions, as well as between both models, is further reduced when looking at cross-country speed relative to the ground, \(V_{xc}\) (Fig 2.5.C). Welch t-tests showed that predicted \(V_{xc}\) was on average 1.24 m s\(^{-1}\) lower at \(V_{bgw}\) than at \(V_{opt}\) (Fig 2.4.B, mean \(V_{xc}\) at \(V_{bgw}\) = 6.98 m s\(^{-1}\) < mean \(V_{xc}\) at \(V_{opt}\) = 8.22 m s\(^{-1}\), \(P = 1.01e^{-14}\)). Observed \(V_{xc}\) (mean = 8.70 m s\(^{-1}\)) was 1.72 m s\(^{-1}\) higher than predicted at \(V_{bgw}\) (\(P < 2.2e^{-16}\)) and only 0.48 m s\(^{-1}\) lower than predicted at \(V_{opt}\) (\(P = 0.01\)). By accounting for tailwinds along the overall track direction (\(W_{Tx}\)) 19.09% and 19.73% of variation in cross-country speeds relative to the ground (\(V_{xc}\)) was predicted at \(V_{bgw}\) and \(V_{opt}\), respectively.

2.5. DISCUSSION

Consistent with optimal soaring migration theory and previous radar-tracking studies of soaring migrants [44,45,89,93], we found that Honey Buzzards adjusted their gliding airspeeds to climb rates in thermals. However, the birds also reacted to head-tailwinds as expected from a risk-averse migration strategy which maximizes range relative to the ground between thermals (\(V_{bgw}\)). Several radar-tracking studies
Fig 2.5. Frequency distributions of measured and predicted speeds at three different scales: (A) Gliding airspeeds, $V_a$, (B) cross-country speeds relative to the air, $V_{cc}$, and (C) cross-country speeds across the ground, $V_{xc}$. Measured speeds are plotted in grey, predictions according to $V_{opt}$ in red, and predictions according to $V_{bgw}$ in blue.

in Israel have reported wind-dependent gliding airspeeds in soaring migrants [44,93]. These wind effects were previously interpreted as a confounding effect of thermal-dependent gliding airspeeds, because wind conditions and climb rates happen to be negatively correlated in Israel [44]. However, when we consider soaring flight behaviour across the wide range of atmospheric conditions that birds encounter across an entire migration route soaring migrants do appear to adjust their gliding airspeeds in response to wind conditions, as well as to climb rates in thermals. This provides a behavioural mechanism that helps explain why wind is
the dominant factor explaining hourly ground speeds and daily travel distances of several North-American [72,77] and Eurasian soaring migrants [82–84,144], including the Honey Buzzards which we studied here [162].

The Honey Buzzards were more prone to adopt a risk-averse strategy when leaving thermals at low altitude, indicating some flexibility in behavioural strategies depending on local atmospheric conditions (Fig 2.4.A, Horvitz et al., 2014). However, our risk-averse soaring migration model does not yet account for the influence of sidewinds on gliding airspeeds (Fig 2.4.B). The birds achieved higher cross-country airspeeds than predicted by either model (Fig 2.5.B), possibly due to the influence of sidewinds during the climb phase. Moreover, the fact that measured and predicted cross-country ground speeds converged (Fig 2.5.C) regardless of the notable differences in measured and predicted cross-country airspeeds further stresses the importance fully integrating wind influences in (risk-averse) optimal soaring migration models.

2.5.1. The role of orientation

To fully incorporate wind in optimal soaring migration models we must take into account orientation behaviour in addition to gliding airspeeds [153,155,172,173]. The importance of orientation and wind becomes apparent when we consider that Honey Buzzards migrate between 6,000 and 8,000 km in a little under one month, which is substantially farther than the theoretical range of a soaring raptor with an average amount of fat [174]. Therefore, wind assistance is probably essential to enable long-distance migration in this species, and we expect Honey Buzzards to adjust their orientation strategies in order to make optimal use of supportive winds [47,151,173]. However, it is unknown at what scale soaring migrants adjust their orientation to wind, and the extent to which soaring birds tolerate drift during migration can vary widely across geographic regions and season [6,11].

While gliding, a bird which seeks to maintain some preferred travel direction should ideally account for the horizontal displacement it accumulated due to wind during the climb phase as well as the displacement it accumulates during the glide.
Although the optimal strategy to maximize cross-country airspeed or ground speed should be independent of wind, we found that the risk-averse strategy was most relevant when birds compensated for sidewinds (Fig 2.4.D). This suggests risk-aversion also plays a role for orientation decisions, in which case we expect a trade-off between wind drift from the preferred travel direction and maximizing gliding distance by travelling downwind. Therefore, integrating sidewinds in our risk-averse soaring migration model may help to unravel the navigational decisions of soaring migrants. Climb rates in thermals also may also need to be integrated in such a model, since the efficiency with which birds can overcome a headwind may constrain their potential to compensate for sidewinds.

2.5.2. The role of thermal selectivity during flight

We found substantial variation in the relative proportion of time spent gliding and climbing across each cycle (Supplementary materials Fig S2.1) which may explain why our models did not account for most of the observed variation in cross-country airspeeds (Fig 2.5.B). Soaring birds tend to leave weak thermal at lower altitude than strong thermals, indicating that the time spent climbing in thermals is affected by thermal strength and depth [69,175]. Selectivity for thermals may also affect the relative proportion of time spent gliding because a bird could interrupt a glide when it encounters an unexpected strong thermal, or extend a glide to reach a strong thermal which it can spot ahead. Although it is not known at what distance soaring birds can detect thermals using different kinds of information (e.g. social information, land-marks and cumulus clouds), it is known that they can select flight paths that support stronger updrafts than the surrounding landscape [77,176,177]. Unfortunately, we could not integrate selectivity for thermals in our models because resolving fine-scale thermal availability and strength requires high-resolution weather models [5,69,70], which have not been implemented across entire migration routes.
2.5.3. To soar, or not to soar

Soaring greatly improves the efficiency of flight from an energetic point of view, but most soaring migrants can periodically switch to flapping flight when soaring conditions are poor [44,70]. Apart from adjusting their flight behaviour to prevailing weather conditions while they are on the wing, soaring birds can opt to avoid flight altogether under particularly adverse conditions, for example in the absence of thermals, or when encountering strong adverse winds [76,86]. As climb rates constrain the ability of a soaring bird to overcome headwinds, we expect that selectivity for wind may be exacerbated under poor soaring conditions. We expect that optimal soaring migration models incorporating gliding airspeeds and orientation will help determine species-specific thresholds in weather conditions for soaring flight during migration.

2.5.4. Trade-offs in travel efficiency and risk-aversion across multiple species

Ultimately, a soaring migrant will compromise between efficient travel and risk-averse flight depending on its energetic requirements (i.e. morphology and physiology) and the frequency with which it can restore energy reserves during migration (i.e. flyway-specific soaring conditions and stop-over availability). For example, Golden Eagles *Aquila chrystaetos* breeding in North-America have been found to be less selective to soaring conditions in spring, compared to autumn, probably to minimize travel time during spring migration [86]. However, the reason Golden Eagles and other Nearctic soaring migrants can travel in the absence of thermals is largely because they can subsidize soaring flight with orographic updrafts [51,77,178], while Honey Buzzards and other Palearctic migrants do not encounter such updrafts along the eastern Atlantic flyway. It is desirable for researchers to integrate theory in tracking studies more frequently in order to interpret behaviours in an evolutionary context and to make comparisons of behavioural strategies across species and populations using different flyways.
2.5.5. Analogies between soaring and flapping migration

We took a first step towards incorporating wind in optimal migration models for soaring birds, reminiscent of how wind influences were first integrated in optimal migration models to calculate maximum range airspeeds of birds using flapping flight (i.e. accounting for variable head- and tailwinds, but ignoring orientation) [98,179]. Birds using flapping flight power their flight by using energy stored in the form of fat and protein, whereas soaring birds accumulate potential energy in thermals and convert this to kinetic energy to power migration [99,180]. However, the principles of energy and time conservation remain the same regardless of whether energy is accumulated by feeding or by using atmospheric currents [175,176,180], and we found that soaring birds reacted similarly to head- and tailwinds between thermals as migrants using flapping flight react to wind in order to minimize the energetic costs of flight between stop-over sites [97,102]. We also discussed how thermal soaring conditions may constrain the potential of soaring migrants to compensate for head- and sidewinds, reminiscent of how energy considerations determine the orientation strategies of birds using flapping flight [151,173,181]. In addition, we considered that soaring birds can adjust the amount of time spent in thermals as a function of thermal availability and thermal strength to minimize travel time, much like flapping birds optimize the time they spend on stop-over sites as a function of stop-over availability and quality [182–184]. The appearance of analogous weather-dependent migration strategies across species using different flight modes strengthens the notion that simple behavioural mechanisms can account for intra- and interspecific variability in flight strategies of migrant birds [6].

2.6. MATERIALS AND METHODS

2.6.1. Study species

The European Honey Buzzard *Pernis apivorus* is a common and widespread summer visitor in European woodlands [158]. They travel from their wintering
grounds in tropical Africa starting early April to arrive at their breeding grounds around early May [14,158]. Honey Buzzards usually do not feed during migration [161]. Consequently, they depend strongly on soaring flight to conserve their energy reserves during migration.

Because Honey Buzzards have a relatively low wing loading compared to many other soaring migrants they can soar in relatively weak thermals shortly after sunrise, until late in the evening [91,168,177]. As they keep soaring under a wide range of weather conditions, they are an excellent species with which to study the role of wind and soaring conditions for optimal soaring migration.

It is important to note that Honey Buzzards have been reported to spend up to 20% of their time flapping while thermals are still weak in early morning [93,168]. However, our tracking data shows that Honey Buzzards spend at least 93% of the time by soaring across entire migratory journeys (Bouten W., unpubl. accelerometer data).

### 2.6.2. The GPS experiment

We developed an experiment for five Honey Buzzards which we fitted with highly flexible and remotely programmable GPS-loggers (www.UvA-BiTS.nl; [62]). The birds were caught and handled according to the approach described in a previous publication concerning the influence of weather on the hourly and daily travel speeds of these birds [162]. Before Honey Buzzards departed from the breeding grounds in August 2012, we uploaded a measurement scheme for recording 3D GPS locations at 10 second resolution between 10:00-10:30 UTC and again between 12:00-12:30 UTC for each day a bird spent between latitude 52N and 10N, which covers the general migration range of this population. From previous studies, we expected that 10 seconds resolution would be adequate to resolve climbs and glides while not overloading logger memory, nor the download capacity of the data retrieving system. Data were downloaded through a relay network with a remotely accessible base station in the breeding territories. We retrieved 360 half hour segments of high-resolution data (Fig 2.2.A).
Assuming that birds use discrete thermals [99,104] then cross-country flight can be broken down into a series of climb-glide cycles. Birds will sometimes make a short climb while gliding through a thermal or make a short glide to adjust their position in the thermal column while climbing [185]. We first calculated the distance, altitude difference and duration between consecutive GPS locations to determine ground speed and vertical speeds. We then calculated the running average of a bird’s vertical speed from 2 fixes before (ca. 20 sec) until 2 fixes after (ca. 20 sec) any location. Locations where birds switched from a positive running average vertical speed to a negative running average vertical speed were taken to be the starting point of a new gliding bout, and vice versa for starting points of climbs (Fig 2.2.B). We paired each climbing phase with its consecutive gliding phase to obtain 1282 full climbing-gliding cycle of which 1178 cycles were recorded completely (Fig 2.5.A).

We removed 21 climbing-gliding cycles during which birds progressed less than 2000m due to highly tortuous movements in complex terrain. In addition, visual inspection of altitudinal profiles revealed that some of the high-resolution segments we recorded likely included flapping flight instead of soaring flight. These segments mainly occurred in strong headwinds above tropical rainforest in western Africa and the birds usually did not exceed 250 m above the ground during these flights. Because we are only interested in true thermal soaring flight, we removed all cycles where birds did not exceed 250 m (151 of 1157 cycles) for all calculations in this paper.

We finally recalculated the climb rate \( (V_c) \) between the first and the last location of each climb phase, and analogously we calculated, track direction, sink rate \( (V_s) \) and ground speed \( (V_g) \) during each glide. For complete climb-gliding cycles we calculated cross-country speeds relative to the ground \( (V_{xc}) \) between the start of the climb phase and the end of a glide (Fig 2.5.B).
2.6.3. Interpolating wind conditions and calculating airspeeds

We used vector trigonometry to determine the airspeeds of the birds while gliding ($V_a$) and across full climbing-gliding cycles ($V_{cc}$) from the corresponding ground speeds and track directions together with local wind vectors (Fig 2.5.B).

Wind vectors were linearly interpolated in space and time from a mesoscale deterministic atmospheric forecast model [71] to the starting point of each gliding phase and to the starting point of each full climbing-gliding cycle. Wind vectors were taken from the 925hPa pressure level in the ECMWF model, corresponding to an average flight altitude of ca. 700m above mean sea level (Supplementary materials S2.1). ECMWF forecasts provide wind vectors at a resolution of three hours and 0.25 degrees and thus only resolve mesoscale atmospheric processes, while ignoring effects of local terrain on fine-scale wind dynamics. Consequently, we can expect considerable error in fine-scale airspeeds due to inaccuracies in ECMWF wind data. However, as we are considering the broad range of landscapes and weather conditions that birds encounter during their entire migratory journeys we do not expect the mismatch between the resolution of the weather model and the resolution of the GPS-data to cause a structural bias with actual wind conditions experienced by the birds across their entire migratory journeys. Moreover, at the average altitude of flight, Honey Buzzards experience winds which are mostly driven by mesoscale and large scale atmospheric processes, such as the movement of high- and low-pressure systems [171], that are resolved well by ECMWF [71].

2.6.4. Modelling airspeeds under different optimality paradigms

MacCready Theory forms the basis of optimal gliding airspeed calculations, and has long been in use among glider pilots looking for optimal solutions for flight contests [186,187]. The theory was adapted for birds by describing how a bird changes it wing shape and size at varying airspeeds by various authors [164,166,188]. Optimal airspeeds for various objectives can be found graphically by drawing a tangent from the ordinates to the bird’s theoretical glide polar (Fig 2.1.B) [99].
We calculated the glide polar by implementing aerodynamic equations [99] in R (version 2.15.0; R Core Development Team, 2013) for a theoretical Honey Buzzard with a mass of 1 kg, a wing span of 1.3 m, a wing surface area of 0.26 m² (measurements from www.sempach.ch) and a body drag coefficient of 0.25 [-] flying at an average altitude of 700m (Supplementary materials Fig S2.1), corresponding to an air density of 1.15 kg/m³. As explained in the introduction, we first predicted $V_{opt}$ to minimize travel time. We compared our results with those from the program ‘Flight’ for the same model parameterization (version 1.23) and found no differences [99]. We then also implemented a new version of best-gliding airspeed, accounting for head-and tailwinds to maximize gliding range over the ground, $V_{bgw}$ (Fig 2.1.C).

### 2.6.5. Sensitivity analysis

It is important to consider that the body drag coefficient and some other dimensionless coefficients for describing theoretical relationships between airspeed and drag forces in flight mechanical theory are estimated with considerable uncertainty. These coefficients could be highly influential for predictions of gliding performance [99]. For example, the body mass of Honey Buzzards is likely to change substantially throughout the year as they fatten up before the onset of migration and progressively deplete their fat stores during travel. Consequently, we conducted a sensitivity analysis for the most influential and poorly calibrated variables in our reference model, i.e.: body mass, wing span, wing area, body drag and combinations of mass and body drag. We used exaggerated values of body size and mass compared to real Honey Buzzards (www.vogelwarte.ch) for our sensitivity analysis. As such we get an impression for how large or heavy a Honey Buzzard should be in order to fly at the observed airspeeds. We did not use body mass measurements of the specific individuals we tracked because they were measured during the breeding season only.

There is growing consensus that body drag coefficients of a large bird like the Honey Buzzard are likely around a value of 0.10 [99,189,190]. However, some studies have shown that an external device can increase the body drag by up to
50%, and the presence of an antenna can even double total body drag [191,192]. We assumed that loggers doubled the most recently updated body drag coefficient for large birds of about 0.10 - 0.12 to a coefficient of about 0.25 for our reference model. The lower limit of body drag coefficient was taken to be 0.10, assuming no increase in drag due to loggers. UvA-BiTS loggers are not cubic in shape, but rather rounded, and have a relatively short antenna which should result in less added drag than suggested in earlier studies [191,192]. The upper limit for body drag coefficient was taken at 0.40, which is slightly higher than the value of 0.30 which was used in optimal soaring studies from the ‘70’s through the ‘90’s [44,190].

The results of the sensitivity analysis are reported in Supplementary materials Fig S2.2. A body drag coefficient of 0.40 would nearly account for the relationship between measured gliding airspeeds and climb rates (Fig S2.2.D). However, it is unlikely that Honey Buzzards would actually have a body drag coefficient this high for reasons stated above, and because such high body drag coefficients have only been reported in wind tunnel studies using dead, mounted birds, which create significantly higher drag than live birds would (because live birds can maintain their streamlinedness in turbulence by retracting their body feathers) [147,190]. Additional sensitivity analysis for variation in mass, wing length, wing area and air density yielded no indications that the mismatch between observed and predicted gliding airspeeds can be accounted for by any other model uncertainties (Supplementary materials Fig S2.2). The average relation between climb rates and gliding airspeeds could only be simulated if birds had a mass below 0.6 kg (and then simulation only worked in the lower range of observed climb rates because light-weight birds could not overcome high drag at medium to high airspeeds).

Given the extremely low body mass and high body drag coefficient that would be required to simulate measured airspeeds we feel confident that Honey Buzzards glide slower than predicted from optimal theory.

**2.6.6. Comparing measured and predicted speeds**

We used loess regression models to visualize the response in predicted and measured airspeeds as a function of the main explanatory variable for each model.
respectively (Fig 2.3.A,C). Second, for each model we interpolated contour plots of model fit (observed – predicted airspeeds) as a function of $W_{Tg}$ and $V_c$. We produced contour plots through bilinear interpolation of model fit over 40 steps along each axis (Fig 2.3.B,D).

To test the risk-aversion hypothesis we applied loess regression models to investigate whether model fit changed as a function of the altitude at which Honey Buzzards exited a thermal. We also used loess regression models to check if birds used different strategies under the influence of sidewinds, which we quantified as $\beta[^\circ]$: the angle between the birds’ overall heading and overall track direction (Fig 2.3.B).

### 2.7. ACKNOWLEDGEMENTS

We are deeply indebted to all who were involved in locating, catching, handling and monitoring the five Honey Buzzards which we followed in this study. We explicitly mention Willem van Manen, Gerard Müskens and Peter van Geneijgen in this respect.

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We also thank one anonymous reviewer and Felix Liechti for providing helpful comments to an earlier version of this manuscript.
2.8. APPENDIX

Here we show that, regardless of orientation, if we assume ubiquitous availability of updrafts, wind will not affect optimal gliding airspeeds for maximizing cross-country airspeed/ground speed. We consider three scenarios: (1) where the bird is intended to maximize its forward ground speed component along the direction of its chosen heading, (2) where it intends to maximize its ground speed component along some preferred direction, and (3) where it intends to maximize its ground speed given its chosen track direction. The first scenario is consistent with a naïve strategy, for example following an endogenous heading, and the other scenarios accommodate some preferred direction (whether local or remote) but with different trade-offs between orientation and migration speed (which we further do not explore here). For simplicity we also assume zero airspeed during the climb phase and an idealized soaring trajectory (Fig 1), whereby a bird ends a glide at the same altitude as it started climbing.

The component of the ground speed $V_{g\delta}$ along its chosen heading $\delta$ is

$$V_{x\delta} = W \cos(\gamma - \delta) + \frac{V_c}{V_c + V_s} \cdot V_a$$  \hspace{1cm} (A.1)

The term $\frac{V_c}{V_c + V_s}$ represents the fraction of time during the glide and the angle $(\gamma - \delta)$ is the projection of the wind in the direction of heading. Since wind and the chosen heading are known in this scenario, the first term is a constant factor. Therefore, the gliding airspeed which maximizes Equation A.1 is, as we solved earlier in Equation 3, $V_a = V_{opt}$.

The other two scenarios can be treated simultaneously. We first define the angles of heading $\delta$ and wind $\gamma$ relative to the preferred direction. The forward and lateral ground speed component, $V_{xp}$ and $V_{xl}$ respectively are then

$$V_{xp} = W \cos \gamma + \frac{V_c}{V_c + V_s} \cdot V_a \cos \delta,$$  \hspace{1cm} (A.2)

$$V_{xl} = W \sin \gamma + \frac{V_c}{V_c + V_s} \cdot V_a \sin \delta$$  \hspace{1cm} (A.3)
It is most revealing to consider the proportion $f$ of the resultant lateral drift for which the migrant chooses to compensate, i.e.

$$V_{xt} = (1 - f) \cdot W \sin \gamma \quad (A.4)$$

This can accommodate any orientation strategy, with $f<0$ representing overdrift (heading partly into the wind), $f=0$ full drift and $f>0$ partial compensation to some maximal proportion (including if possible, full compensation $f=1$ and overcompensation $f>1$).

We can relate the airspeed and wind components of lateral movement using Equations A.3 and A.4:

$$\frac{V_c}{V_c + V_s} \cdot V_a \sin \delta = -fW \sin \gamma \quad (A.5)$$

If we make the reasonable assumption that the migrant does not intentionally fly away from its preferred direction (i.e. $V_{xp} > 0$), then from Equations A.2 and A.5, the forward components of movement becomes

$$V_{xp} = W \cos \gamma + \sqrt{\left(\frac{V_c}{V_c + V_s}\right)^2 V_a^2 - f^2W^2 \sin^2 \gamma} \quad (A.6)$$

Here we see that, for a given fractional compensation $f$ (and therefore lateral component of movement $V_{xt}$), the forward motion depends on airspeed in the same way as in the windless case and is maximized by gliding at an airspeed $V_a = V_{opt}$.

Furthermore, since the ground speed along the resultant track direction is

$$V_{xc}^2 = V_{xp}^2 + V_{xt}^2 \quad (A.7)$$

the overall ground speed $V_{xc}$ will also be maximized at $V_a = V_{opt}$.
### Table S2.1.
Summary statistics of flight parameters and indicators of soaring conditions. Bird speed variables were calculated from GPS observations and wind speeds were interpolated from a mesoscale atmospheric model.

<table>
<thead>
<tr>
<th>Bird</th>
<th>n</th>
<th>Mean [m/s]</th>
<th>SD</th>
<th>Mean [m/s]</th>
<th>SD</th>
<th>Mean [m/s]</th>
<th>SD</th>
<th>Mean [m/s]</th>
<th>SD</th>
<th>Mean [m/s]</th>
<th>SD</th>
<th>Mean [m/s]</th>
<th>SD</th>
<th>Mean [m/s]</th>
<th>SD</th>
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<th>SD</th>
<th>Mean [m/s]</th>
<th>SD</th>
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<td>3.20</td>
<td>9.11</td>
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<td>0.79</td>
<td>837.66</td>
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<td>48.53</td>
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<td>4.52</td>
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<td>0.14</td>
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<td>6.27</td>
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<tr>
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<td>3.35</td>
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### Table S2.2.
Correlations between thermal soaring conditions and wind conditions. We built linear regression models to investigate the direct relationship between each thermal climb variable (rows) and each wind variable (columns). Estimates and p-values for intercepts and coefficient sizes are given for each model respectively. \( R^2 \) [%] values indicate the variance in each of the soaring variables explained by each respective wind variable is very low.

<table>
<thead>
<tr>
<th>Variable</th>
<th>[TWg] [m/s]</th>
<th>[CWg] [m/s]</th>
<th>[TWx] [m/s]</th>
<th>[CWx] [m/s]</th>
<th>w [m/s]</th>
</tr>
</thead>
<tbody>
<tr>
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<td>Coeff. value</td>
<td>R²</td>
<td>Intercept value</td>
<td>Coeff. value</td>
<td>R²</td>
</tr>
<tr>
<td>Vc [m/s]</td>
<td>-1.82 &lt;2E-16</td>
<td>-0.04 1E-04</td>
<td>1.48</td>
<td>1.87 &lt;2E-16</td>
<td>0.01 0.33</td>
</tr>
<tr>
<td>Thermal Exit Alt [m]</td>
<td>-1.00 &lt;2E-16</td>
<td>-0.00 1E-03</td>
<td>0.81</td>
<td>0.03 &lt;2E-16</td>
<td>12.06 0.03</td>
</tr>
</tbody>
</table>
Fig S2.1. Frequency distributions of flight statistics derived from GPS-tracking and wind data from a mesoscale global weather model.
Fig S2.2. Model sensitivity analysis. Plots show predicted $V_{opt}$ and observed airspeeds (grey curve and s.e.- interval) in function of climb rates for different combinations of morphological parameters in an aerodynamic model for a theoretical Honey Buzzard. Model sensitivity was tested in function of (A) body mass, (B) wing length, (C) wing surface area, (D) body drag coefficient, (E) combined body mass and drag coefficients and (F) combined wing length and body drag coefficient.
Chapter 2 - Optimal soaring strategies
Chapter 3

Effect of wind, thermal convection, and variation in flight strategies on the daily rhythm and flight paths of migrating raptors at Georgia’s Black Sea coast


Publication:
3.1. ABSTRACT.
Every autumn, large numbers of raptors migrate through geographical convergence zones to avoid crossing large bodies of water. At coastal convergence zones, raptors may aggregate along coastlines because of convective or wind conditions. However, the effect of wind and thermal convection on migrating raptors may vary depending on local landscapes and weather, and on the flight strategies of different raptors. From 20 August to 14 October 2008 and 2009, we studied the effect of cloud development and crosswinds on the flight paths of raptors migrating through the eastern Black Sea convergence zone, where coastal lowlands at the foothills of the Pontic Mountains forms a geographical bottleneck 5 km wide near Batumi, the capital of the Autonomous Republic of Ajaria in southwestern Georgia. To identify key correlates of local aggregation, we examined diurnal variation in migration intensity and coastal aggregation of 11 species of raptors categorized based on size and flight strategies. As at other convergence zones, migration intensity of large obligate-soaring species peaked at mid-day, the core period of thermal activity. When clouds developed over interior mountains and limited thermal convection, these large obligate-soaring species aggregated near the coast. However, medium-sized soaring migrants that occasionally use flapping flight did not aggregate at the coast when clouds over the mountains weakened thermal convection. Numbers of alternate soaring-flapping harriers (Circus spp.) peaked during early morning, with these raptors depending more on flapping flight during a time of day with poor thermal convection. Small sparrowhawks (Accipiter spp.) aggregated at the coast during periods when winds blew offshore, suggesting aggregation caused by wind drift. Thus, weather conditions, including cloud cover and wind speed and direction, can influence the daily rhythm and flight paths of migrating raptors and, therefore, should be accounted for before inferring population trends from migration counts.

3.2. INTRODUCTION
During long-distance migration, many species of raptors travel almost exclusively by soaring in updrafts [45,107,109], using thermal convection [69,93,168] or
orographic updrafts [77,106]. Because thermal convection generally does not develop over large bodies of water outside the Trade-Wind Zones and Gulf Stream [171,193], soaring raptors typically make detours around large bodies of water [108,140,194,195]. Raptors that simultaneously migrate between continents while avoiding geographical barriers reach high seasonal concentrations at geographical convergence zones [107,112–114,196]. Hundreds of thousands of raptors may be involved, often representing significant proportions of the regional or even global species populations [110,112,113,116,197].

Migratory movements of raptors depend on weather conditions, such as wind speed and direction and thermal convection, and their reaction to weather differs across morphologically distinct groups, ranging from obligate-soaring migrants (e.g., large eagles) and facultative-soaring migrants (e.g., harriers) to actively flapping migrants (e.g., small falcons) [5,44,45,93,107,137]. Generally, soaring species fly faster with better soaring conditions [69,89,110,168] and many have distinct diurnal and seasonal rhythms in migration activity, preferred modes of flight, and route choice that result from thermal convective dynamics at multiple scales [44,51,90,126,142]. Wind speed and direction can also influence travel speeds [44,91,107], flight altitudes [45,89,90,198,199], preferred flight modes [50,51], and flight paths of raptors [51,140,199,200].

Understanding the effects of weather on flight paths and the spatial distribution of migrating raptors is particularly important where birds converge in space and time [107,201], e.g. to assess the potential impact of wind farm construction in a convergence zone [202,203] or to account for weather-induced variation in monitoring the population trends of migrants [197,204]. However, the effects of atmospheric conditions, such as wind and thermal convection, on spatial migration dynamics at convergence zones may be highly site-specific because of differences in local land use, topography, weather conditions, and the objectives of migrating raptors [5,107,126,168]. For example, Honey Buzzards (*Pernis apivorus*) migrating through Israel using soaring flight shift their flight paths during the day [205], taking advantage of differential development of thermal convection across a
heterogeneous landscape [69] and convergence lines associated with sea-breeze fronts [105]. In contrast, Honey Buzzards migrating through an isthmus in Italy compensate for wind drift by mixing gliding with flapping flight and so do not shift their flight path, possibly because they need to compensate for drift as they approach a sea-crossing [50]. Furthermore, some species use different migration routes at different times. For example, Red-tailed Hawks (Buteo jamaicensis) migrating along the Appalachian mountains in the eastern United States can travel by soaring and gliding between broadly spaced thermals during early autumn, but later migrants use orographic updrafts along mountain ridges [51]. Ultimately, local conditions must be considered in the context of raptor migration strategies when trying to understand how weather conditions affect migration.

Our objective was to examine the role of wind and thermal convection in shaping diurnal dynamics in the spatial distribution of raptor flight paths at a migration convergence zone along the eastern Black Sea coast in the Republic of Georgia [112]. The convergence zone is a geographical funnel for migrants bordered by the Black Sea coast to the west and the Pontic Mountains to the east. Raptors regularly shift flight paths between the mountain range and the coast when travelling through this convergence zone, leading to aggregations of raptors near the coast [206]. Cloud cover develops regularly over the Pontic Mountains during autumn migration [207] and anecdotal evidence suggests that soaring migrants may aggregate at the Black Sea coast to avoid the cloud cover [206] where thermal convection [171] and the flight altitudes of soaring migrants may be limited [89]. We quantified diurnal patterns in migration intensity and coastal aggregation along the eastern Black Sea for 11 species of raptors, determined if and how wind and convective conditions accounted for coastal aggregations, and examined the effects of different raptor morphologies and flight strategies. We expected that large soaring species dependent on thermal convection would exhibit strong mid-day peaks in migration intensity [45,126,168]. We also expected obligate-soaring species to aggregate more at the coast when clouds developed over the interior mountains in our study area [207–209].
3.3. METHODS

3.3.1. Study area.
Raptors migrating to Africa from eastern European, Russian, and western Siberian breeding grounds circumvent the Caspian and Black seas by traveling through and around the Caucasus mountains. Many raptors track a westerly course, travelling in high numbers via lowlands along the Black Sea coast [112,210], whereas fewer are seen along the Caspian coast of Azerbaijan [211]. A strip of coastal lowlands forms a geographical bottleneck 5 km wide near Batumi, the capital of Ajaria in southwestern Georgia, situated at the foothills of the Pontic Mountains (Fig 3.1). 800,000 – 1,000,000 migrating raptors of up to 35 are observed each autumn in the area [112].

The region has a warm, humid climate and is covered by broad-leaved forests with an evergreen understory, generally described as subtropical vegetation [207]. Average maximum daily temperatures range from 20°C – 30°C from August through September and the area receives a large amount of annual precipitation (~2800 mm), much of which falls between mid-August and mid-September [212]. Evapotranspiration over the forest canopy that covers the Pontic mountains leads to the development of dense, cloud cover [207]. Because thermal convection does not easily develop after precipitation (excess water must first evaporate before air is warmed [171]) or when cloud cover shields the earth from incoming solar radiation [89,171], we expected stronger thermal convection over the coastal zone (first 2 km) than the interior Pontic mountains. This cloud cover contrast between mountains and coastline is stronger in the early half of the migratory season due to the higher average temperatures (> 24°C; [207]). Between 10 and 19 September, temperatures decline sharply and average ~18°C until the end of the migration season [212].

Winds are generally weak in the area, ranging from 0 – 10 m/s [47], and so usually do not disrupt thermal convection [171]. Winds average ~3 m/s and are mainly from the southeast [212] during the autumn. Until mid-September, onshore winds can be generated by sea-breeze circulation [213] that strengthens thermal convection in the
Fig 3.1. Topography of the Batumi convergence zone (source: GMTED2010 at http://earthexplorer.usgs.gov/). Top: Regional topography of the Caucasus showing seas and mountains that constitute the convergence zone. Inset at the bottom indicates the location of our study area. Bottom: Topography of our study area at the foothills of the Pontic Mountains, near the city of Batumi (bulls-eye). All raptors that crossed a transect between survey stations 1 and 2 (stars, 2 and 6 km inland, respectively) were counted. Small gray insets around stations show areas from which sample counts were taken to calculate the coastal proportion of migrants (CPM). Weather conditions were estimated at Station 1. Large gray insets show approximate position of the sections of sky where cloud cover was visually estimated to calculate cloud contrast between coast and mountains.

coastal strip by transporting cold sea-air over land where it rapidly warms, forming a thermal front [208,209,213]. Further, onshore winds may weaken thermals above the interior mountains by bringing in moist air that enhances cloud development
[207]. Sea-breezes in early autumn may also, therefore, contribute to the seasonal difference in cloud cover between the mountains and the coastal strip [208,209].

3.3.2. **Raptor migration data.**
The Batumi Raptor Count is a standardized raptor-migration survey (www.batumi-raptorcount.org). Data from the 2008 and 2009 surveys were used for this study. From 20 August to 14 October each year, the survey took place simultaneously from two stations located 2 and 6 km east of the Black Sea coast, respectively (41°41'05" N 41°43'51" E and 41°41'08" N 41°46'43" E, Fig 3.1) [112]. At least three observers per station per day recorded all individuals and flocks that crossed an east-west transect running through these stations (bottom, Fig 3.1). For each record, we noted time of passage and categorized the location of birds relative to the survey station as overhead (between 50 m west and 50 m east from the station) or in one of six categories for raptors and flocks located 50 – 200 m, 200 – 2000 m, or > 2000 m to either the east or west of the stations. Distance codes were estimated in the field by using landmarks at known distances and were used together with recorded times of passage to eliminate double counts of simultaneously observed flocks [112]. We assumed no bias in counts by observers.

3.3.3. **Quantifying migration dynamics.**
Because weather data were available every 2 h (see section entitled Weather data below), count data were pooled in blocks from 1 h before until 1 h after each weather observation. We then calculated the total migration intensity (TMI) as the total number of individuals observed within 200 m on either side of both stations (Fig 3.1) during 2-h intervals. Solar noon shifted only 25 min throughout our study (from 20 August to 14 October) and we did not expect this shift to lead to an observable shift in the timing of daily peak migration.

Coastal aggregation was calculated as the proportion of raptors observed within 200 m around station 1 (Fig 3.1) relative to the total number of birds observed within 200 m of the two stations combined. We restricted data to a range of 200 m around each survey station (Fig 3.1, grey insets) to reduce count bias during periods where low visibility (e.g., during extensive and low cloud cover) prevented detection of
distant birds. When calculating coastal proportion of raptors, we only included 2-h intervals for a given species if more than one individual was observed during that period.

3.3.4. Missing data.
No counts took place during 12 days with stormy weather. Due to bad weather and other interruptions, several 2-h observation periods were missed at either one or both survey stations (191 missed out of 735 2-h periods). In our analyses, we only included observation periods if both survey stations were staffed simultaneously at the latest within 15 min of the intended start time and until at least 15 min before the intended end time of that observation period (258 of 544 periods). As a result, periods at the start and end of days (07:00 – 09:00 and 17:00 – 19:00) were poorly represented in our dataset. Additional missing entries in the dataset were random and not related to a specific time of day or weather condition.

3.3.5. Focal species.
In our analyses, we included only those species with observations during at least 34 2-h intervals or where at least 700 individuals migrated through the area each year [112]. Our analyses included 11 species, including, in order of decreasing abundance, Western Honey Buzzards (*Pernis apivorus*), Steppe Buzzards (*Buteo buteo vulpinus*), Black Kites (*Milvus migrans*), Eurasian Sparrowhawks (*Accipiter nisus*), Marsh Harriers (*Circus aeruginosus*), Booted Eagles (*Aquila pennatus*), Levant Sparrowhawks (*Accipiter brevipes*), Lesser Spotted Eagles (*Aquila pomarina*), Montagu’s and Pallid harriers (*Circus pygargus* and *C. macrourus*), and Short-toed Eagles (*Circaetus gallicus*). We combined Montagu’s and Pallid harriers because it was difficult to separate young and female birds of these species [214] and, because of their similar morphology, we expected them to react similarly to environmental conditions in the convergence zone [137].

All species were categorized for comparison across functional groups, taking into account the average mass of each species and their preferred flight strategy (soaring or flapping flight). Based on mass [158,214], we distinguished between large (> 1 kg, large eagles), medium-sized (500 g – 1 kg), and small raptors (< 500 g, small
harriers and sparrowhawks). Next, eagles, buzzards, and Black Kites were considered obligate-soaring migrants [107,158,215]. Although Western Honey Buzzards and Black Kites occasionally use flapping flight, both species soar whenever possible [93]. The small sparrowhawks were considered flapping migrants. Levant Sparrowhawks do routinely soar in large flocks during the daytime period of thermal convection in Israel [95], but, at the Black Sea coast, large flocks of soaring Levant Sparrowhawks are rare and many are seen migrating in low flapping flight (W. Vansteelant, pers. obs.). Harriers were categorized as alternate soaring-flapping migrants [137].

3.3.6. **Weather data.**
Weather conditions were estimated at the coastal station every two hours. For this analysis, we used visual estimates of cloud cover (0-8 scale) at two locations to determine the homogeneity of cloud cover along an east-west gradient in our study area. Raptors can soar under convective cloud types [216], but we did not classify cloud types because we were mainly interested in how fine-scale cloud cover differences across the convergence zone affected local raptor aggregation dynamics. Cloud cover was estimated for a segment of sky above the coastal survey station and for a segment above the Pontic Mountains (large insets, Fig 3.1). The latter segment was located above the highest mountain peak in our study area (~5 km from the coastal station) to facilitate a repeatable estimation of cloud cover in a fixed field of view with reference to clear landmark. Alternative datasets such as cloud cover imagery from satellites and regional weather forecast did not provide a sufficiently high spatial resolution to quantify spatial differences in cloud types within the convergence zone.

Observers also estimated wind direction at cardinal and inter-cardinal compass points and estimated wind strength using the Beaufort scale [217] which we assumed to be a sufficiently accurate measure of average wind conditions at a resolution of two hours. Analogous to the bird data, we assumed no observer bias in the weather data.
3.3.7. **Processing weather data.**
Cloud contrast was calculated as the difference between the cloud-cover estimate (0-8) for the mountains versus the coast, whereby negative values indicate more cloudy conditions over the coast and positive values indicate relatively high cloud cover over the mountains. Cardinal wind directions were translated to degrees. The Beaufort (Bft) scale and exact wind speed (m/s) were linearly proportional to each other within the range of our observations (0-5 Bft). Thus, wind strength was multiplied with the sine of wind direction to calculate the crosswind strength (Bft) perpendicular to the principal southbound direction of migration. The sign of crosswinds was positive for winds blowing from east to west (easterly winds) which would have a positive effect on the proportion of raptors observed near the coast due to wind drift. Aggregation was expected to decrease with birds drifting to the east with winds from the west (westerly winds, negative crosswind component). Both crosswind strength and cloud contrast were treated as continuous (rather than ordinal) variables with an interval measurement level in our analysis.

3.3.8. **Modeling approach.**
We first explored whether total migration intensity and the coastal proportion of migrants varied significantly over the course of a day. Next, we explored whether cloud contrast and crosswinds showed distinct diurnal patterns. We initially fit a full model including cloud contrast and crosswinds as predictive variables per species. However, because only single effects were significant (Supplemental Table S3.1), we eventually implemented single effect models to test whether cloud contrast or cross-winds explained the coastal proportion of migrants.

3.3.9. **Diurnal migration dynamics vs. flight strategy.**
To detect the occurrence of diurnal migration dynamics, we fitted first- and second-order generalized linear regression models \( \alpha = 0.05, \text{GLM, [218]} \) for total migration intensity (TMI) and the coastal proportion of migrants (CPM) of every species separately, assuming, respectively, a Poisson and a quasi-binomial error distribution with hour of day \( \text{hr and hr}^2 \) as predictor variable(s). Second-order
effects are only shown for those species where these were significant and explained more variation than linear models.

3.3.10. Diurnal patterns in cloud contrast and crosswinds. We also fitted 1st and 2nd order generalized linear regression models with hour of day as a predictor variable and cloud contrast and crosswind as response variables. We investigated the correlation between cloud contrast and crosswind with Kendall Tau Ranked $r$ [219], a non-parametric alternative to Spearman’s $r$.

3.3.11. Weather effects vs. flight strategy. We tested the effect of cloud contrast and crosswinds (single effects) on coastal raptor aggregation using a GLM with a quasi-binomial error distribution, a logit link function, and giving weights to the observations by the log10 of total migration intensity ($P = 0.05$, GLM, [218]). Weights were used to account for variation in bird numbers during the collection period and were aimed at making the resulting models representative for most migrating birds (rather than representative for every observation-moment). Observations of coastal aggregation at moments with higher migration intensity are given more weight than observations with low intensity. Shapiro-Wilkinson’s test of normality ($W$) was used to evaluate the distribution of the residual error in the GLMs [218]. Finally, we selected the most adequate model for each species on the basis of QAIC [220].

3.3.12. Seasonality in weather and aggregation. Because of the seasonality in weather conditions noted previously, we defined an early and a late migration period (before and after 15 September, respectively) corresponding with a transition from warmer to cooler temperatures in our study area [212]. Between early and late migration, we compared model results for two species with protracted migration seasons spanning the early and late autumn periods (Black Kites and Booted Eagles) [112]. We also tested for seasonality in the weather experienced by the birds by comparing mean cloud contrast and crosswinds between periods for each species (one-sided two-sample Student’s $t$-tests). All statistical modeling was conducted in program R 2.14.0 [221], using the ggplot2 package [222] for graphical representation of results.
3.4. RESULTS

<table>
<thead>
<tr>
<th>Type</th>
<th>Species</th>
<th>Model</th>
<th>Intercept</th>
<th>$\beta_{CC}$</th>
<th>$\beta_{CW}$</th>
<th>QAIC</th>
</tr>
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<tbody>
<tr>
<td>Large</td>
<td>Short-toed Eagle (34)</td>
<td>CC</td>
<td>-0.744*</td>
<td>0.247*</td>
<td>-</td>
<td>55.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CW</td>
<td>-0.551†</td>
<td>-</td>
<td>-0.187</td>
<td>59.5</td>
</tr>
<tr>
<td></td>
<td>Lesse Spotted Eagle (45)</td>
<td>CC</td>
<td>-1.294**</td>
<td>0.236*</td>
<td>-</td>
<td>18.1</td>
</tr>
<tr>
<td></td>
<td>Booted Eagle (116)</td>
<td>CC</td>
<td>0.074</td>
<td>0.251**</td>
<td>-0.41</td>
<td>39.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CW</td>
<td>0.382*</td>
<td>-</td>
<td>-0.125</td>
<td>43.4</td>
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<tr>
<td>Medium</td>
<td>Black Kite (121)</td>
<td>CC</td>
<td>-0.739**</td>
<td>0.04</td>
<td>-</td>
<td>54.6</td>
</tr>
<tr>
<td></td>
<td>Honey-buzzard (136)</td>
<td>CC</td>
<td>-0.876**</td>
<td>0.044</td>
<td>-</td>
<td>82.9</td>
</tr>
<tr>
<td></td>
<td>Steppe Buzzard (82)</td>
<td>CC</td>
<td>-1.379**</td>
<td>-0.023</td>
<td>-</td>
<td>28.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CW</td>
<td>-1.386**</td>
<td>-</td>
<td>0.127</td>
<td>28.6</td>
</tr>
<tr>
<td>Med. Alter.</td>
<td>Marsh Harrier (125)</td>
<td>CC</td>
<td>-0.308*</td>
<td>-0.024</td>
<td>-</td>
<td>104.7</td>
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<tr>
<td></td>
<td></td>
<td>CW</td>
<td>-0.334*</td>
<td>-</td>
<td>0.012</td>
<td>104.8</td>
</tr>
<tr>
<td>Small Alt.</td>
<td>Montagu’s/Pallid Harrier (120)</td>
<td>CC</td>
<td>-0.103</td>
<td>-0.009</td>
<td>-</td>
<td>55.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CW</td>
<td>-0.1</td>
<td>-</td>
<td>0.032</td>
<td>55.2</td>
</tr>
<tr>
<td>Small Flap.</td>
<td>Levant Sparrowhawk (98)</td>
<td>CC</td>
<td>-0.711**</td>
<td>-0.002</td>
<td>-</td>
<td>41.5</td>
</tr>
<tr>
<td></td>
<td>Eurasian Sparrowhawk (98)</td>
<td>CW</td>
<td>-0.506*</td>
<td>-</td>
<td>0.359*</td>
<td>39.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CC</td>
<td>-0.412*</td>
<td>0.04</td>
<td>-</td>
<td>57.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CW</td>
<td>-0.282*</td>
<td>-</td>
<td>0.281*</td>
<td>55.8</td>
</tr>
</tbody>
</table>

Table 3.1. Weather effects on coastal aggregation of each raptor species determined by linear logistic regression. Sample sizes (in parentheses) indicate the number of 2-hr periods during which observations were made. Results are for single effect models of cloud contrast (CC) and crosswinds (CW), respectively. Superscripts with estimates of intercept and effect size indicate significance levels, with marginally significant results at $P < 0.10$ (+) and significant results at $P < 0.05$ (*) and $P < 0.001$(**). Best models for each species are those with the lowest QAIC.
Fig 3.2. Diurnal dynamics of migration in our study area for our 11 focal species (see legend). The diurnal trend in total migration intensity (TMI, top: a–e) and the coastal proportion of migrants (CPM, bottom: f–j) is shown (average trend = solid lines; shaded area = ± SE) as function of time of day [hr]. Regression models assumed a Poisson or a quasi-binomial error structure for modeling TMI and CPM, respectively, and, for each graph, we modeled a second-order polynomial unless a linear regression model was more significant. Each subplot represents one of five functional groups of species that share similar size (large, medium, or small) and flight modes (obligate soaring, mixed, or flapping). TMI (top) was plotted on a logarithmic scale to avoid trends for the least abundant species that would be compressed when plotted with the most abundant species in the same plot. Note that the trends for CPM of Honey Buzzards and Black Kites overlap almost exactly.
Total migration intensity (TMI) and the coastal proportion of migrants (CPM) observed within 200 m of both count stations for all 2-hr time blocks are reported in Supplemental Tables S3.2 and S3.3. A summary of total seasonal counts and the phenology of raptors in our study area has been made available in a previous study (Verhelst et al. 2011).

3.4.1. Diurnal migration dynamics vs. flight strategy.
Obligate-soaring species and Eurasian Sparrowhawks had mid-day peaks in total migration intensity (TMI) (Fig 3.2, Table S3.2). Migration intensity of obligate-soaring migrants like Lesser Spotted Eagles (Fig 3.2.A) was up to 10 times higher at noon than during the morning or evening hours (note the logarithmic scale in Fig 3.2). Short-toed and Booted eagles, both soaring migrants, tended to increase in numbers during the day (Figs. 3.2.A, B). Harriers were most abundant in the morning and showed a marginal, but significant, decrease in migration intensity during the day, as was also true for Levant Sparrowhawks (Fig 3.2.E). Diurnal trends migration intensity were significant ($P < 0.001$) for all species, including the seemingly weak trend lines for harriers (Figs. 3.2.C, D). The flat trend line in the migration intensity of harriers is a plotting artifact due to the lower upward spread in the counts of harriers compared to the spread in counts of buzzards and kites.

Coastal aggregation often followed diurnal trends in total migration intensity (Fig 3.2). Obligate soaring migrants mostly aggregated at the coast around mid-day (e.g., Short-toed Eagles, Black Kites, and Honey Buzzards; Figs. 3.2.F, G, Table S3.3) or increasingly aggregated at the coast throughout the day (e.g., Booted Eagles, Fig 3.2.G). Diurnal trends of coastal aggregation were significant for all obligate-soaring species ($P < 0.001$), with the exceptions of Lesser Spotted Eagles ($P_{hr} = 0.1$) and Steppe Buzzards ($P_{hr} = 0.6$; Fig 3.2.F, G). In general, obligate-soaring species exhibited less coastal aggregation than other raptors. Average coastal aggregation was always high for Booted Eagles (> 40%) compared to that of other medium-sized soaring migrants (Fig 3.2.G).
Fig 3.3. Diurnal weather patterns at Batumi during migration surveys between 20 August and 14 October 2008 and 2009. Top: second-order diurnal evolution of cloud contrast \( (CC = -1.49 + 17.48 \times h - 9.46 \times h^2; \ P < 0.001) \) as a function of time of day. Bottom: second-order diurnal evolution of crosswind \( (CW = -0.54 - 5.99 \times h + 5.14 \times h^2; \ P < 0.001) \), with wind speed estimated using the Beaufort scale (Bft). Shaded areas around average trends represent ± SE.

For each environmental variable, we calculated kernel densities of total observation frequency at each 2-h interval between 08:00 and 18:00 for every interval value of the variable. Positive cloud contrast indicates conditions with greater cloud cover over the interior mountains than over the coastal lowlands. Positive crosswinds were winds blowing from the east (toward the coast).

Harriers adopting a mixed soaring-flapping flight strategy and the flapping Eurasian Sparrowhawks aggregated most strongly at the coast during the morning (Fig 3.2.H-J, Table S3.3). The diurnal trends of coastal aggregation were significant for all alternate soaring-flapping and flapping species \( (P < 0.001) \), with the exception of a non-significant increase in coastal aggregation during the day by Levant Sparrowhawks \( (P_{hr} = 0.3, \ Fig \ 3.2.J) \).

3.4.2. Diurnal dynamics of cloud contrast and crosswinds.
Over the course of an average autumn day at Batumi, an increasingly strong local cloud contrast develops due to cloud cover forming over the Pontic Mountains (Fig 3.3). Strong cloud contrast in the afternoon coincides with the afternoon prevalence of westerly winds (Fig 3.3), although the weak rank correlation between cloud contrast and crosswinds (Kendall Tau Ranked \( r = -0.1; \ P < 0.001 \)) suggests cloud development also takes place with easterly winds.
3.4.3. Effect of cloud contrast and crosswinds on coastal aggregation of raptors.

The response to local weather was consistent across species of the same functional group (i.e., with similar body mass and flight strategy; Fig 3.4, Table 3.1). Short-toed, Lesser Spotted, and Booted eagles aggregated significantly more at the coast with increasing cloud contrast (Figs. 3.4.A, B, Table 3.1). Large and medium-sized obligate soaring species exhibited an increase of 10 – 70% in coastal aggregation in response to increasingly positive cloud contrast (Figs. 3.2.A, B). The effect of cloud contrast was, however, not significant for Steppe Buzzards, Honey Buzzards, and Black Kites (Fig 3.4.B, Table 3.1). Alternate soaring-flapping harriers (Figs. 3.4.C, D) and flapping sparrowhawks (Fig 3.4.E) had weaker, non-significant responses to cloud cover (Table 3.1).

Crosswinds did not affect the coastal aggregation of either large and medium-sized soaring migrants (Figs. 3.4.F, G; Table 3.1) or alternate soaring-flapping harriers (Fig 3.4.H, Table 3.1). Wind did significantly affect the two smallest species (i.e., sparrowhawks; Table 3.1), with both observed at the coast more frequently with stronger easterly crosswinds (Fig 3.4.J, Table 3.1).

3.4.4. Seasonality in weather effects.

Atmospheric conditions were more homogenous across the convergence zone during the late migration period (after 15 September) than during the early migration period, with generally weak crosswinds (Avg. $CW_{\text{early}} = -0.84 < \text{Avg. } CW_{\text{late}} = -0.04$; 1-sided $t_{(1041.41)} = -11.3$, $P < 0.001$) and, more importantly, low levels of cloud contrast (Avg. $CC_{\text{early}} = 2.0 > \text{Avg. } CC_{\text{late}} = 0.7$; 1-sided $t_{(1560.48)} = 9.3$, $P < 0.001$). We found a significant positive effect of cloud contrast on coastal aggregation during the early part of the season for Booted Eagles, but not during the last half of the season ($\beta_{\text{early}} = 0.3$, $P < 0.01$; $\beta_{\text{late}} = 0.2$, $P = 0.1$). Black Kites did not respond to cloud cover during either period ($\beta_{\text{early}} = 0.1$, $P = 0.4$; $\beta_{\text{late}} = 0.2$, $P = 0.3$). Coastal aggregation increased with easterly crosswinds during the late migration period for Booted Eagles ($\beta_{\text{early}} = -0.2$, $P = 0.5$; $\beta_{\text{late}} = 0.4$, $P = 0.04$) and Black Kites ($\beta_{\text{early}} = -0.02$, $P = 0.7$; $\beta_{\text{late}} = 0.4$, $P = 0.04$).
Fig 3.4. Species-specific coastal aggregation (CPM) at the eastern Black Sea shore in response to local weather conditions. The effect of cloud contrast (top, a–e) and crosswinds (bottom, f–j) on coastal aggregation of raptors (solid lines ± SE) as determined by linear logistic regression is shown for each of the 11 focal species (see legend). Each subplot represents one of five functional groups of species that share similar size (large, medium, or small) and flight styles (obligate-soaring, mixed, or flapping). Note that graphs are curved despite linear model structure as a consequence of the (back-) transformation of data by the logit link function during logistic regression. Positive cloud contrast indicates greater cloud cover over the interior mountains than over the coastal lowlands. Positive crosswinds are offshore winds blowing from east to west, with wind speed estimated using the Beaufort scale (Bft).
3.5. DISCUSSION

3.5.1. Dynamics of diurnal migration intensity in relation to flight strategy. 
We observed a mid-day peak in abundance of most obligate-soaring raptors, as also observed at other convergence zones along the eastern Palearctic flyway [215] and for other species [45,107]. The largest species in our study, Short-toed, Lesser-spotted, and Booted eagles, restricted their daily periods of flight compared to smaller migrants, consistent with previous reports that large obligate-soaring migrants restrict their activity to the core period of thermal activity [45,107,126]. The migration intensity of Short-toed Eagles in our study increased linearly during the day, contrasting with the typical mid-day peaks in abundance of this species at other locations [93,95,215]. However, this unexpected trend was likely an artifact of the low number of 2-hr observation periods (N = 34) for this species and the concomitant lack of evening observations (after the 2-hr period from 15:00 – 17:00) that could be retained to detect the expected evening decrease in abundance of this species.

Alternate soaring-flapping harriers were most abundant in the morning in our study as also reported in Israel [137]. This morning peak in abundance suggests that harriers readily migrate using flapping flight at times with poor thermal convection [137]. This ability to fly during periods of poor convection should allow harriers to migrate over a broad geographical front rather than converging in a small geographical area. Nevertheless, the numbers of harriers observed in our convergence zone [112] far exceed the numbers seen elsewhere along the eastern Europe-Africa flyway [215,223,224]. As such, environmental factors such as habitat availability for feeding during migration [136] likely drive the regional convergence of harriers toward our study area.

3.5.2. Diurnal dynamics of coastal aggregation in relation to weather and flight strategies.
Obligate-soaring migrants responded to cloud development over the interior mountains by flying closer to the Black Sea coast. Short-toed, Lesser Spotted, and Booted eagles responded the strongest, likely because they are more dependent on
convection to sustain high ground-speeds during travel than smaller soaring raptors [93,215]. Apart from Booted Eagles, three other medium-sized soaring migrants (Honey Buzzards, Steppe Buzzards, and Black Kites) showed no increase in coastal aggregation in response to cloud contrast. Honey Buzzards and Black Kites do occasionally use flapping flight, allowing them to fly further and longer than larger eagles when there is weaker convection[93,107]. The stronger flight capacity of these medium-sized species also allowed them to travel earlier in the morning and later in the evening than large eagles in our study area and elsewhere [45,93].

Finally, Steppe Buzzards rarely approached the coast and thereby behaved differently than other soaring migrants in our study. This is surprising because Steppe Buzzards typically depend on soaring flight [44] (see the ‘Exceptional cases’ section for further discussion of this seemingly aberrant behavior).

Aggregation of small and flapping sparrowhawks at the coast increased with easterly winds (i.e., blowing offshore), suggesting that wind drift caused this aggregation. Along the east coast of the United States, accipiters are also observed in higher numbers when winds are blowing offshore [225] However, others have shown that these higher counts occurred because accipiters were flying lower to reduce the effect of drift, making them easier to detect by observers [89,198,199]. Further study is needed to determine if the coastal aggregation of accipiters we observed is also an artifact of higher coastal detection rates, i.e., if they fly lower near the coast with offshore winds or if aggregations are due to drift by wind.

Interestingly, easterly crosswinds, and not cloud development, were the main correlate of coastal aggregations of two medium-sized soaring species (Booted Eagles and Black Kites) during the last half of the autumn season. We expected this would be the case based on the increasing homogeneity of cloud cover, and thus the increasing homogeneity of thermal convective conditions across our study area in late autumn [207,213]. Nevertheless, to infer drift due to wind from the significant effect of crosswinds on Black Kites and Booted Eagles, we must first consider whether the observed aggregations were not due to a bias in detection rates due to birds flying lower with offshore (i.e., easterly) winds [90,198,199]. We suspect such
a bias is unlikely for medium-sized to large soaring species because nearly all birds flying within 200 m of our observatory were detected by observers with the naked eye and repeated efforts to find otherwise undetected high-flying raptors with binoculars have rarely proved successful (W. Vansteelant, pers. obs.). We, therefore, tentatively conclude that Booted Eagles and Black Kites drifted with offshore winds to aggregate at the coast during the last half of the migration season, and only did so during that period because of the strong seasonality in convective and wind conditions in our study area. Similar observations of shifting flight paths in response to seasonal variation in atmospheric conditions have been reported for Red-tailed Hawks migrating along the Appalachian Mountains in North America [51] and for other soaring raptors migrating through Israel [110]. Furthermore, juvenile raptors are generally more prone to drift [121] and juvenile Black Kites and Booted Eagles also migrate up to two weeks later than adult birds [158]. Consequently, drift-prone juveniles likely made up the bulk of the Booted Eagles and Black Kites observed in late autumn in our study.

In contrast to the strong effect of wind drift on raptor movements at more windy locations such as the Gibraltar Strait or other sea-crossings [140,226], the effect of drift in our study was likely small for most raptors because they could easily compensate for the weak winds in our study area (> 80% observations were 0 – 2 Bft). Similarly, others have suggested that drift only had an effect when winds were sufficiently strong (e.g., >5 m/s for actively flapping Sharp-shinned Hawks [199].

3.5.3. Influence of landscape on coastal aggregation dynamics.
The weak and non-significant response to cloud development and wind conditions by harriers and sparrowhawks in our study may be best explained by the fact that these species select their routes mainly to fuel their flights by feeding, in contrast to obligate-soaring raptors that do not regularly feed during migration [107,136,227,228]. The importance of habitat preferences in the choice of migration routes of fly-forage migrants is evidenced by the use of traditional stopover sites for resting and refueling by harriers during migration [122,227,229]
The eastern Black Sea convergence zone likely provides foraging and stopover opportunities for fly-forage migrants because numerous day-active passerines (e.g., swallows, pipits, wagtails, and bee-eaters) migrate near the coast and some food-rich wetlands can be found along the coast [230]. The high morning abundance and coastal aggregation of harriers (with large flocks > 2000 Montagu’s Harriers before 10:00, 4 September 2008, [112]) and sparrowhawks in our study area support this hypothesis. This coastal food supply is a likely reason why non-obligate soaring raptors such as harriers and Eurasian Sparrowhawks converge in such high numbers along the Black Sea coast, whereas they are considered broad-front migrants elsewhere along the eastern Europe-Africa flyway [113,114,215].

Soaring migrants may also shift their flight paths in response to factors other than weather conditions. For example, in Israel, Honey Buzzards migrating over the Negev shift their flight paths toward the Central Mountains in the evening to find roost sites [105,231]. It is likely, therefore, that species like Honey Buzzards, Black Kites, eagles, and Steppe Buzzards leave from, and return to, the interior mountains in our study area during mornings and evenings (despite regular persistence of cloud cover over the interior mountains during evenings) because they roost inland. This may be because (large) raptors are sensitive to human disturbance [232] and so avoid human settlements in the coastal zone for roosting (W. Vansteelant, pers. obs.).

3.5.4. Exceptional cases.
We found that Booted Eagles aggregated at the coast in high numbers at all times of the day compared to other soaring species, and similar observations have been reported elsewhere around the Black Sea [206] and Mediterranean basin [233]. Although coastlines can provide an important visual leading line for orientation during migration [107], it is not clear why Booted Eagles follow coastlines so strongly compared to other obligate-soaring migrants.

Steppe Buzzards and Levant Sparrowhawks in our study rarely responded to cloud development by aggregating at the coast, contrasting with their active response to convective conditions elsewhere, e.g., Israel [95,107,126]. However, during at least
three of 10 exploratory single-day counts 6 km east of our study area (from 24 August to 8 September and 12 to 30 September), up to 20,000 Steppe Buzzards and a maximum of 1000 Levant Sparrowhawks were recorded flying over the interior mountains under clear skies while migration intensity of these two species was low at our survey sites. These anecdotal observations suggest that the migratory corridor of Steppe Buzzards and Levant Sparrowhawks is broader than that of other species in our study and that this corridor was insufficiently covered during our study, making it difficult to detect relative displacements in the flight paths for these species in response to weather. In Israel, the main migration corridor of these species is also broader than that of other raptors [205]. This broad migration front appears in Israel, and probably also in our study area, because Steppe Buzzards and Levant Sparrowhawks migrate into Africa predominantly via an easterly route over the Bab-el-Mandeb Strait at the southern end of the Red Sea in Yemen [223] rather than over the westerly route of our other focal species that cross into Africa at the Suez Strait [110,195,215,224].

3.6. Conclusions.
Our results suggest that weather conditions should be accounted for before inferring population trends from migration counts [204] and more work is needed to elucidate the effect of weather on the ability of observers to detect migrating raptors. Given the anecdotal observation of coastal raptor aggregations in northeast Turkey [206], the weather effects observed in our study likely apply to the entire southeastern Black Sea coastline. If so, our results may have implications concerning the planned construction of power lines 20 km south of our study area [234]. Because such structures pose collision and electrocution risk for migrating raptors [201,235], developers should assess the potential impact of these power lines on migrating raptors, identifying high-risk zones, especially near the coast, and evaluating possible mitigation measures.
3.7. ACKNOWLEDGMENTS
We thank J. Jansen for his support in organizing Batumi Raptor Count 2008 and our ongoing partnership in coordinating BRC ever since. We are very grateful to all the volunteers who participated in the counts and all sponsors who made the field work possible. W. V. expresses special thanks to Hawk Mountain Sanctuary for supporting this study as a Conservation Leadership Internee and staff members L. Goodrich and D. Barber for useful comments and practical support during the start of this study. Further, we thank three anonymous reviewers and CGE-colleagues M. Kemp, N. Anders, J. McLaren, J. Spaaks, I. Soenario, and L. Veen for critical feedback on preliminary versions of this manuscript.
### 3.8. Supplementary Materials

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**Table S3.1.** Weather effects on coastal aggregation of each species (N = sample size) determined by linear logistic regression model with *cloud contrast* (CC), *crosswinds* (CW) and their interaction as added effects. Superscripts with estimates of intercept and effect size indicate significance level of all significant results at $P < 0.10$ (*); $P < 0.05$ (*); $P < 0.001$(**). No model was fully significant and therefore single-effect models are reported in results section.
Chapter 3 – Flight paths of soaring raptors in relation to wind and thermal convection

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Table S3.2. Total migration intensity (TMI) per 2-h interval (h) and per day of year (DOY) for 11 species of raptors observed within 200 m range of two survey stations situated 2 and 6 km from the Black Sea coast. Species columns give TMI as calculated in 2008 and 2009, respectively. Day of year (DOY) 233 is 21 August and DOY 284 is 11 October.
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## Chapter 3 – Flight paths of soaring raptors in relation to wind and thermal convection

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Table S3.3. Coastal proportion of migrants (CPM) per 2-h interval and per day of year (DOY) for 11 species of raptors observed within 200 m of two survey stations located 2 and 6 km from the Black Sea coast, respectively. Species columns give CPM’s as calculated in 2008 and 2009, respectively. Day of year (DOY) 233 is 21 August and DOY 284 is 11 October.
Chapter 3 – Flight paths of soaring raptors in relation to wind and thermal convection
Chapter 3 – Flight paths of soaring raptors in relation to wind and thermal convection
Chapter 4

Regional and seasonal flight speeds of soaring migrants and the role of weather conditions at hourly and daily scales


Publication:
4.1. ABSTRACT

Given that soaring birds travel faster with supportive winds or in good thermal soaring conditions, we expect weather conditions en route of migration to explain commonly observed regional and seasonal patterns in the performance of soaring migrants. We used GPS-loggers to track 13 Honey Buzzards and four Montagu’s Harriers for two to six migrations each. We determined how tailwinds, crosswinds, boundary layer height (a proxy for thermal convection) and precipitation affected hourly speeds, daily distances and daily mean speeds with linear regression models. Honey Buzzards mostly travel by soaring while Montagu’s Harriers supplement soaring with flapping. Therefore, we expect that performance of harriers will be less affected by weather than for buzzards. Weather conditions explained between 30% and 50% of variation in migration performance of both species. Tailwind had the largest effect on hourly speeds, daily mean speeds and daily travel distances. Honey Buzzards travelled significantly faster and farther, and Montagu’s Harriers non-significantly faster, under better convective conditions. Honey Buzzards travelled at slower speeds and shorter distances in crosswinds, whereas harriers maintained high speeds in crosswinds. Weather conditions varied between regions and seasons, and this variation accounted for nearly all regional and seasonal variation in flight performance. Hourly performance was higher than predicted at times when we suspect birds had switched to intermittent or continuous flapping flight, for example during sea-crossings. The daily travel distance of Montagu’s Harriers was determined to a significant extent by their daily travel time, which differed between regions, possibly also due to weather conditions. We conclude with the implications of our work for studies on migration phenology and we suggest an important role for high-resolution telemetry in understanding migratory behavior across entire migratory journeys.
4.2. **INTRODUCTION**

Migrating birds encounter widely varying weather conditions throughout their seasonal journeys. Weather conditions may affect the timing of migration onset [142], stop-over schedules [236–239], the route followed by migrants [77], and their speed during travel [5,240]. If adverse weather conditions are met during migration, birds risk delayed arrival and poor body condition, which in turn may affect their competitiveness or reproductive success. Thus, weather influences during migration may carry over to later stages of the annual cycle [5,130,241–243]. Unfortunately, despite that the travel speeds of many migratory organisms clearly depend on the environmental conditions through which they travel [143,244–246], it is not clear yet if weather affects migrating birds differently between different stages of their migration cycle [5, 247]. For large birds, we are now able to record flight behavior as well as the weather conditions which they encounter over entire migratory journeys, due to recent advances in animal tracking and meteorological modeling.

The way weather affects migration depends on the flight mode of a bird, which is largely determined by its body size and morphology [5,17,99,101,180]. Storks, pelicans and raptors tend to soar on thermals and orographic updrafts to avoid the high energetic cost of flapping flight [101]. Consequently, the migratory itineraries of obligate soaring migrants are limited by the availability of suitable soaring conditions en route [5]. For example, strict soaring migrants do not usually travel at night when thermal updrafts are absent and tend to circumvent large bodies of water where such updrafts are too weak to support soaring [45,107]. Soaring birds may also interrupt their travel under adverse weather conditions [76] which may cause delays in their annual schedules [48,126,142]. Moreover, soaring birds achieve higher ground speeds under stronger updraft conditions [44,139,248], and they choose local flight paths along landscape features that support strong updrafts [51,103,105,106,126]. The ground speed of soaring migrants is strongly affected also by wind conditions. Local radar and visual studies have shown that soaring migrants travel significantly faster when flying with tailwinds, while they travel slower when winds have an increasingly strong crosswind component [44,45,139].
Chapter 4 – Flight speeds and weather influences at hourly and daily scales

Tracking studies have shown similar effects of wind persist along the entire migratory journey of soaring migrants [72,83,84,144]. Some raptors have more slender wings, such as harriers and falcons, and they are potentially less affected by weather conditions in comparison to obligate soaring migrants as they more frequently alternate soaring with flapping flight (facultative soaring migrants) [137]. Consequently, they are able to continue migration during the night [249], and to some extent under adverse weather conditions [76,95]. Furthermore, birds travelling by flapping are supported by tailwinds to the same extent as soaring birds, but are less affected by crosswinds as they lack the passive soaring flight phase during which birds may get fully drifted by crosswinds [45].

Even though aforementioned studies have revealed strong influences of wind and weather on the ground speeds of soaring migrants, these influences are rarely quantified simultaneously and for entire migration routes in autumn and spring [72]. Satellite and GPS tracking studies on individual soaring migrants have revealed surprisingly similar patterns in hourly and daily speeds and daily travel distances achieved by different species of obligate as well as facultative soaring migrants [72,83,84,250]. For example, Palearctic soaring migrants typically achieve relatively high hourly speeds and longer daily travel distances over the Sahara [84,145,251,252] and it is often suggested that this is because birds may adjust their flight behavior over the hostile environment of this ecological barrier. Furthermore, several soaring migrants travel faster during spring migration compared to autumn [83], possibly resulting from a seasonal urge to arrive early at their breeding sites [253,254]. However, too little is known about the extent to which regional and seasonal performance relates to variation in the weather conditions encountered during travel [143]. Recently, non-soaring, nocturnal migrants were shown to migrate faster over Europe in spring, compared to autumn, because tailwinds are more common in spring [73]. Furthermore, soaring birds like White Storks *Ciconia ciconia* have been suggested to achieve higher speeds over the Sahara desert because relatively strong thermal convective conditions enable faster flights in this region [144]. Also, more than half of the variation in travel performance of soaring
Turkey Vultures *Cathartes aura* can be explained from atmospheric conditions they encounter en route [72]. Overall, we expect the effects of weather conditions along entire migratory journeys may explain some of the seasonal or regional patterns in travel performance of (soaring) migrants.

We studied travel performance of two long-distance soaring migrants travelling along the East Atlantic flyway between Europe and Africa [255], using UvA-BiTS GPS-loggers [62]. Both species migrate at roughly the same time of the year, and thus encounter similar large-scale weather conditions during their travel, but use distinct migration strategies: the preferably soaring European Honey Buzzard *Pernis apivorus* [107,158] and the facultative soaring Montagu’s Harrier *Circus pygargus* [137]. We first describe general patterns in measured hourly speeds, mean daily speeds and daily travel distances, as well as in the weather conditions encountered for each species between different seasons and regions. Subsequently, we predict hourly speeds, daily speeds and daily distances from key weather conditions for soaring flight: boundary layer height (as a proxy for thermal convective conditions), precipitation, and wind conditions relative to the realized travel direction. We expected that boundary layer height should have a stronger positive effect on the hourly and daily performance of Honey Buzzards compared to Montagu’s Harrier, due to the aforementioned differences in their migration strategies. Finally, we add regional and seasonal factors to our weather models to explore whether any spatiotemporal behavioral patterns are not accounted for by weather conditions encountered en route.

### 4.3. METHODS

#### 4.3.1. Study species and GPS-tracking

Honey Buzzards and Montagu’s Harriers are long-distance migratory birds breeding in temperate regions and wintering in sub-Saharan Africa [158]. Previous tracking studies using satellite transmitters revealed that autumn routes of adult Honey Buzzards breeding in Sweden converged in Southern Spain to minimize the crossing of the Mediterranean Sea en route to tropical rainforests in western Africa
Tracking a large number of individual Montagu’s Harriers throughout Europe revealed western birds are using routes via Spain and Italy to their western Sahelian wintering quarters [256]. Both species migrate almost exclusively during daylight hours [137,248]. Montagu’s Harriers, however, may extend their travel into the night [137], especially during sea crossings [227,228].

We used UvA-BiTS GPS-loggers [62] to track adult breeding birds, and thus experienced migrants. The Honey Buzzard was studied in two conifer-dominated (80% coniferous wood of which 74% Pinus sylvestris) areas in the center of the Netherlands (52.37˚N, 5.82˚E, van Manen et al. 2011). We trapped 13 individuals (Table S4.1) at their nests with a mist net using a live or stuffed Eagle Owl Bubo bubo as a lure. Montagu’s Harriers were studied in their core breeding area in the Netherlands situated in the vast and open arable landscape of Eastern Groningen (53.14˚N, 07.03˚E; Trierweiler 2010). We trapped four breeding birds near their nest with a pole trap or a mist net using a stuffed raptor decoy. GPS-loggers were fitted using Teflon or Tygontube harnesses [258,259]. Maximum mass of the harness and device amounted to maximum 5% of the bird’s body mass. Birds were handled for less than 20-60 minutes after capture and so far we never observed nest desertion or failure related to our manipulations. GPS-locations were sampled at a resolution of 10 seconds to 1 hour over the whole annual cycle. Data were downloaded in the breeding area through a combined fixed- and mobile relay-antennae system [62].

4.3.2. Defining migration
For the full dataset spanning the entire annual cycle (> 500,000 GPS-locations) we first calculated ground speeds from every location to the next and to the previous point and then averaged these two speeds to calculate ground speed for each location. Based on the frequency distribution of ground speeds we identified and removed erroneous GPS-locations (ground speeds > 30 m/s).

In order to distinguish migration from other parts of the annual cycle we calculated daily travel distances as loxodrome distances between consecutive night roosts (first and last location obtained between 00:00 and 23:59 for each day). Based on
histograms of daily distance we defined travel days as those days when more than 25 km was covered between roosts [11]. We only included travel days in our analyses, i.e. stopover days (days with daily distance < 25 km) were omitted.

Part of our study population of Honey Buzzards is known to exploit multiple wintering sites making itinerary movements [33] between them (UvA-BiTS, unpublished data). Montagu’s Harriers also show within-year itinerancy [260]. In order to distinguish between travel days and itinerary movements we defined the onset and end of migration as the first and last set of travel days with a three-day running average daily travel distance of at least 65 km. Finally, we also left out pre- and post-migratory movements as these seem to differ from genuine migratory movements [80,261]. We defined these as movements preceding or following stopovers lasting at least three consecutive days within the breeding range (north of latitude 52N) or near the wintering stages (south of latitude 25N).

Our dataset contained 27 spring journeys and 22 autumn journeys for 13 Honey Buzzards and four spring and five autumn journeys for four Montagu’s Harriers. Some travel days were not covered completely due to small gaps in the GPS data which in a few cases lead to an incorrect classification as stop-over day. In a few cases this misclassification was propagated when defining the core migration period based on the three-day running average of daily travel distance, in particular for Honey Buzzard #56 and Montagu’s Harrier #187 (Supplementary material Table S4.1). We have chosen to leave the migratory travel days with some missing hourly values out of the analysis rather than to make assumptions to estimate these missing values. Less than 5% of the total data set was not used because part of the hourly values within a day was missing. The number of migratory trips obtained per individual, species and season with the average number of travel days and travel distances that were retained are summarized in Table S4.1.

### 4.3.3. Hourly speeds and daily distances

Instantaneous speed measurements are most useful for studying animal movement ecology [78]. However, it is not ideal to use instantaneous speeds for quantifying performance of soaring migrants as soaring flight consists of stages of circle-
soaring in thermals alternated with glides between thermals [45] and instantaneous speeds during soaring and gliding do not accurately reflect cross-country performance [45]. Instead, we defined hourly travel segments (described in more detail below) which are a good measure of short term ground speed because these segments include at least 5 – 10 complete soaring-gliding bouts [45,93,103]. Furthermore, we expect that daily travel distance is a biologically meaningful scale of movement because soaring migrants are restricted to the daylight period for travel.

For every travel day, we used a minimum ground speed of 1.5 m/s between two consecutive measurements to determine the start and end of the daily travel period. Subsequently, we resampled the whole dataset, creating 1 hour segments, by retaining consecutive locations with a time difference as close to one hour as possible (minimum and maximum segment duration was 50 and 70 minutes, respectively). Hourly speeds (m/s) were recalculated after resampling, and hourly speeds lower than 1.5 m/s were classified as resting events, which were omitted from the hourly travel performance analyses. 7583 and 1376 hourly travel segments were obtained for Honey Buzzards and Montagu’s Harriers, respectively.

After resampling, we also recalculated daily distances, as the loxodrome distance between the first and last hourly location of the daily travel period. The final dataset contained 1223 and 205 daily distances for Honey Buzzards and Montagu’s Harriers, respectively.

4.3.4. Daily mean speeds and the role of travel time
Daily travel distance is the sum of hourly speeds over the daily travel time, thus daily travel time has a profound effect on daily distance [145]. The length of the daylight period, and thus the length of the period with favorable soaring conditions, varies considerably across the migration period, particularly in spring [81,83]. Furthermore, migrants may interrupt flights (e.g. for foraging or to avoid rain or strong headwinds) [76] or may extend their daily travel period through dusk and dawn [137,227,228]. As our aim is to quantify the effect of weather on performance while travelling, we predict daily distance based on those conditions encountered
during travel hours only. In order to adjust for variation in daily travel times we also calculated daily mean travel speeds. Comparing daily mean speeds with daily distances allows for a better understanding of the role of travel time in shaping daily travel performance.

4.3.5. Regional and seasonal patterns in weather conditions and performance
In order to evaluate regional and seasonal patterns in migration performance and weather conditions encountered by the birds we used an ANOVA and a Tukey’s HSD. A t-test was used to compare the two seasons. In both cases differences with a p-value of 0.05 or lower were considered significant.

We used the borders of global biomes [263] to distinguish six regions in terms of their geographical position and their characteristic vegetation: temperate forests (broad-leaf and coniferous forest in Europe), Mediterranean (including subtropical grasslands north of 25˚N), sea, desert, tropical grasslands (including flooded savannas), and tropical rainforest (rainforest and mangroves).

If birds change their behavior above different regions we want to ignore those segments during which birds crossed from one region into another. We, therefore, subset our data to hourly speeds determined over segments where a bird was continuously travelling over the same region (i.e. start and end location fell within the same region), and for days during which at least 60% of the hourly segments was spent over the same region.

4.3.6. Modeling weather effects
The response variables in our study are hourly speed, daily mean speed and daily distance. We adopted a backward model selection procedure including four predictor variables (boundary layer height, tailwind, absolute crosswind and precipitation) in our initial linear regression model for hourly speeds and three predictor variables (mean daily boundary layer height, tailwind and absolute crosswind) in our initial regression model for daily distance and daily mean speed. During variable selection, predictor variables with a p-value lower than 0.05 were removed starting with the least significant variable until all remaining variables were significant. In order to compare the relative importance of between predictor
variables (i.e. relative effect sizes) we additionally fitted the final models based on normalized response and predictor variables, i.e. for each model we standardized all variables to units of standard deviation after which linear regression coefficients yielded effect sizes showing the change of the response variable in units of S.D., for every unit of S.D. change in one of the predictor variables.

We obtained boundary layer height (m), u- and v-wind components (i.e. latitudinal and longitudinal wind velocities, m/s) and the accumulated rainfall (mm) from the ECMWF (European Center for Medium-Range Weather Forecasts) regional atmospheric model at a resolution of 0.25° and 3 hours [71]. Data were linearly interpolated in space and time for each hourly location. Boundary layer height is a good approximation of convection at hourly to daily scales as a higher boundary layer is associated with stronger thermals (allowing faster and higher climbs during soaring), as well as with more dense thermal fields [171], both of which are likely to affect the performance of soaring migrants [67,69,94,144].

Wind strength and direction may vary strongly with altitude above the ground [171] and the ECMWF regional atmospheric model grid provides conditions at different barometric pressure levels relative to sea level (i.e.: at 10 m above the sea, and at pressure levels 925, 850 and 700 mB). Therefore, we first calculated hourly flight direction to determine hourly tailwind and crosswind components (cf. Chevallier et al. 2010) at each pressure level, and then linearly interpolated tailwind and crosswind components from the two pressure levels nearest to the bird’s effective flight altitude. The two closest pressure levels were determined based on the vertical distance between the geopotential heights of the pressure levels (available in ECMWF) and the bird’s altitude above the sea. ECMWF precipitation data represent accumulated rainfall over three-hour periods, hence we used an estimate for hourly rainfall by dividing the ECMWF-scores by three.

We determined mean daily values for each predictor variable across all hourly travel segments between 00:00 and 23:59, and so excluding all resting hours. In order to obtain daily tailwind and crosswind components we calculated the tailwind and absolute crosswind component at each hourly location relative to the daily
mean axis of movement before we averaged each component across each day. We then predicted daily distance in function of daily mean boundary layer height, mean tailwind and mean absolute crosswind. We did not analyze the effect of precipitation at the daily scale because the strongest effect of precipitation on daily distance likely comes from birds interrupting travel altogether under rainy conditions [45,76].

4.3.7. Regional and seasonal differences in response to weather
In order to identify potential differences in response to weather between different regions and seasons we describe and compare regional and seasonal patterns in predicted and observed performance. Furthermore, we test whether any significant additional variation in performance can be explained by regional or seasonal effects that are not accounted for by weather conditions. To do so, we compare three extended versions of the final weather models for each response variable for each species, by including region, season or both factors together as additional predictor variables. We then use Aikaike’s Information Criterion (AIC) to compare model fit, and Pearsons R to compare the amount of variation explained between models.

All statistical modeling was conducted in the program R 2.15.0 [221], using the ggplot2 package [222] for graphical representation of results.

4.4. Results
Honey Buzzards on average spent 25 days to migrate between their breeding grounds in the center of the Netherlands and their individual wintering grounds across tropical West to Central Africa (Supplementary material Table S4.1). They usually crossed the Mediterranean Sea in one to two hours at its narrowest point at the Strait of Gibraltar (Fig 4.1.A I). Two birds flew parallel to the eastern Spanish coast for 3 and 6.5 hours, respectively, in spring 2010. However, these birds also continued to travel over land on those days such that Honey Buzzards never spent an entire day only over the sea (Supplementary material Table S4.1). These events were not plotted in Fig 4.1.A since we only plotted hourly locations when at least 60% of daily travel time was spent over the same biome. When crossing the desert,
Figure 4.1. Migration routes (I), hourly travel speeds (II), daily travel distance (III), daily mean travel speed (IV) and daily travel times (V) of honey buzzards (A) and Montagu’s harriers (B) for autumn (top panels) and spring (bottom panels) migrations respectively. Migration routes are plotted as the hourly locations (semi-transparent points) from all travel days. Box-plots show mean (bold line) and spread of values (box bounds = inter-quartile range of values from the 25th to the 75th percentile, whiskers = 1.5*inter-quartile range) with outliers (dots). Full box-plots show distributions of observed values and dashed box-plots show predicted values for each variable. Colours of box-plots and in background of migration routes indicate different regions (Table 4.1).
some Honey Buzzards made notable detours deviating east (both autumn and spring) or west (spring) from their initial heading (Fig 1.A I., Supplementary material Table S4.1). One occasion involving two birds suggests the birds detoured in avoidance of a dust storm [264]. Honey Buzzards travelled short distances over the rain forests so relatively few travel segments were obtained there (Fig 4.1.A I, Table 4.1). Montagu’s Harriers travelled about 28 days to reach their wintering grounds in the Sahel in Senegal and Niger. Two used a westerly route via Spain and two others flew over the Central Mediterranean (Fig 4.1.B I, note one spring journey was removed during data processing due to frequent gaps in data). They travelled only short distances over the Sahel, so we have a relatively small sample over tropical grasslands (Fig 4.1.B I). On two occasions Montagu’s Harriers made long autumn sea-crossings lasting up to 19 hours. In spring the harriers used islands as stepping-stones between North-Africa and the Italian peninsula (Fig 4.1.B I).

4.4.1. Seasonal and regional patterns in encountered weather conditions
Weather conditions differed between regions and in some regions also between seasons (Supplementary material, Figs S4.2.A, S4.2.B and Table S4.3). However, Montagu’s Harriers only encountered seasonally different hourly tailwinds, while all hourly and daily conditions encountered by Honey Buzzards differed between seasons. Largest differences in mean conditions were usually tenfold the size of the variance in mean conditions per region and season. For example, Honey Buzzards encountered significantly more crosswinds over the desert and more frequent tailwinds over Europe in spring than in autumn (Supplementary material Figs S4.2.A, S4.2.B, Table S4.3). Crossing the Sahara, Honey Buzzards experienced hourly and daily mean boundary layer heights reaching 700 m lower in spring compared to autumn. Moreover, the boundary layer heights were much lower over the tropical grasslands and forests in autumn compared to spring, likely because of frequent autumn rains (Supplementary material Fig S4.2.A, Table S4.3).

4.4.2. Seasonal and regional patterns in performance and travel time
Honey Buzzards showed a significant difference in migratory performance between regions and seasons (Fig 4.1.A II-IV, Tables 4.1. 4.2) at both the hourly and the
daily scale. Honey Buzzards travelled consistently faster and further during spring than during autumn migration. Within seasons, the highest regional hourly and daily speeds and daily distances were achieved above the Sahara (Fig 4.1.A II-IV, Table 4.1). In autumn, Honey Buzzards achieved higher hourly speeds above sea compared to the average over terrestrial regions (Fig 4.1.A II). In both seasons, shortest daily distances were reached above rainforest (Fig 4.1.A III) because they achieved moderately lower daily mean travel speeds (Fig 4.1.A IV) and because they travelled for about 1-3 hours less per day, compared to elsewhere in Africa and the Mediterranean.

Overall, performance of Montagu’s Harriers did not differ significantly between seasons (Table 4.2), but hourly speeds and daily distances were lowest on arrival in the Sahel, and highest among the terrestrial habitats on departure from the Sahel (Fig 4.1.B II-III). Daily mean speeds were more or less consistent across terrestrial regions (Fig 4.1.B IV, Table 4.1). In autumn, Montagu’s Harriers achieved the lowest daily distance and travel times above tropical grasslands of the Sahel. In spring, daily mean speeds and travel times were lowest in the temperate region. Furthermore, they achieved far greater daily distance and travel time over open sea than over any other area (Fig 4.1.B III/V; Table 4.1).

4.4.3. Weather effects on performance
The final models are given for Honey Buzzards in Table 4.3.A and for Montagu’s Harriers in Table 4.3.B. The full models before backward model selection are shown in Supplementary material Table S4.4, including the significance and normalized regression coefficients for each weather variable. Variation in weather conditions predicted 48% of the variability in hourly speeds, 41% of variation in daily distances and 32% of variation in daily mean speeds achieved by honey buzzards. For Montagu’s harriers, our final weather models predicted 42% of the variation in hourly speeds, 33% of variation in daily distances and 32% of variation in daily mean speeds.

The effects of weather on hourly speed were similar for both species, with a dominant positive influence of tailwinds, an additional positive effect of boundary
Chapter 4 – Flight speeds and weather influences at hourly and daily scales

Honey Buzzards travelled significantly slower at the hourly scale with increasing rainfall, although they travelled in weak to moderate rains (Table 4.3.A) which only had a small influence on hourly travel speeds compared to other weather variables (Table 4.3.A). Precipitation had no effect on the hourly performance of Montagu’s Harriers (Table 4.3.A).

Table 4.1: Regional patterns in hourly speed, daily distance and daily mean speed as observed from GPS-tracking and as predicted from weather conditions encountered en route of migration (see Table 2 for models), during autumn and spring migration of Honey Buzzards and Montagu’s Harriers respectively. Class identifiers (a – f) were determined by a Tukey-HDS test for each variable in both species to identify those biomes over which speeds or distances were significantly similar.
The daily distance and daily speed of Honey Buzzards was determined by daily tailwind and added effects of daily mean boundary layer height and crosswinds, whereas the performance of Montagu’s Harriers was affected only by tailwind at the daily scale (Tables 4.3.A, 4.3.B). For Honey Buzzards the normalized effect of tailwinds on hourly speed, daily distance and daily mean speed was almost two times as large as the normalized effect of boundary layer height, whereas the performance of Montagu’s Harriers was affected only by tailwind at the daily scale (Tables 4.3.A, 4.3.B). For Honey Buzzards the normalized effect of tailwinds on hourly speed, daily distance and daily mean speed was almost two times as large as the normalized effect of boundary layer height, whereas the performance of Montagu’s Harriers was affected only by tailwind at the daily scale (Tables 4.3.A, 4.3.B). For Honey Buzzards the normalized effect of tailwinds on hourly speed, daily distance and daily mean speed was almost two times as large as the normalized effect of boundary layer height, whereas the performance of Montagu’s Harriers was affected only by tailwind at the daily scale (Tables 4.3.A, 4.3.B). For Honey Buzzards the normalized effect of tailwinds on hourly speed, daily distance and daily mean speed was almost two times as large as the normalized effect of boundary layer height, whereas the performance of Montagu’s Harriers was affected only by tailwind at the daily scale (Tables 4.3.A, 4.3.B). For Honey Buzzards the normalized effect of tailwinds on hourly speed, daily distance and daily mean speed was almost two times as large as the normalized effect of boundary layer height, whereas the performance of Montagu’s Harriers was affected only by tailwind at the daily scale (Tables 4.3.A, 4.3.B). For Honey Buzzards the normalized effect of tailwinds on hourly speed, daily distance and daily mean speed was almost two times as large as the normalized effect of boundary layer height, whereas the performance of Montagu’s Harriers was affected only by tailwind at the daily scale (Tables 4.3.A, 4.3.B).

Table 4.2: Seasonal averages, and differences therein (student’s t-test), of hourly speed, daily distance and daily mean speed as observed from GPS-tracking and of hourly and mean daily weather conditions encountered by Honey Buzzards and Montagu’s Harriers respectively. P-values of significant seasonal differences (P<0.05) are highlighted in bold.
Table 4.3.A: Final linear regression models for hourly speed, daily mean speed and daily distance of Honey Buzzards in function of significant weather variables and three extended models testing for additional regional or seasonal effects not accounted for by weather conditions. Regional and seasonal factors do not improve model fit (AIC) nor the amount of variation explained (R²), except for daily distance models where regional effects account for up to 6% more of total variation than can be explained by weather conditions.
### Table 4.3.B.: Final linear regression models for hourly speed, daily mean speed and daily distance of Montagu’s Harriers in function of significant weather variables and three extended models testing for additional regional or seasonal effects not accounted for by weather conditions. Regional and seasonal factors to not improve model fit (AIC) nor the amount of variation explained (R²), except for daily distance models where regional effects account for up to 13% more of total variation than can be explained by weather conditions.
and almost 5 times larger than the normalized effect of absolute crosswinds (Supplementary material Table S4.4), showing that tailwinds have a much stronger influence on migration performance than other weather variables. For Montagu’s Harriers the normalized effect of tailwinds on hourly speeds was three times the normalized effect of boundary layer height (Supplementary material Table S4.4).

4.4.4. Regional and seasonal differences in the influence of weather

The predicted seasonal and regional patterns in hourly speed, daily distance and daily speed overall closely matched the patterns we observed for both species (Fig 4.1.A II-IV; Table 4.1). Region and season accounted for less than 1% of the variation in hourly and daily speeds of either species when weather effects were accounted for (Tables 4.3.A, 4.3.B). These small regional effects do not improve the overall predictive ability of our hourly and daily speed models because the influence of weather is much greater (Tables 4.3.A, 4.3.B). Regional effects did explain ca. 7% and 13% additional variation in daily distances which was not accounted for by weather conditions encountered by Honey Buzzards and Montagu’s Harriers respectively. Seasonal differences, however, only accounted for about 2% of all variation in daily travel distance.

Honey Buzzards reached consistently higher speeds than predicted over the sea (Fig 4.1.A II, Table 4.1). Furthermore, daily distances travelled by Honey Buzzards are consistently lower than predicted above the tropical forests, whereas this is not the case for daily speeds (Fig 4.1.A III-IV), indicating that they seem to make frequent short stops there. For Montagu’s Harriers, daily distances achieved over the sea were much higher than predicted due to extremely long travel times (Fig 4.1.B-II-III; Table 4.1). Furthermore, daily distances achieved by Montagu’s Harriers which frequently interrupted travel over the tropical grasslands were lower than predicted by tailwinds (Fig 4.1.B-III; Table 4.1). In contrast, predicted daily mean travel speeds were accurate over the grasslands of the Sahel as well as over the sea (Fig 4.1.B- IV; Table 4.1).
4.4.5. Diurnal patterns in hourly speeds

We observed a striking diurnal pattern in the accuracy of prediction of hourly speeds with a tendency for both species to migrate slower than predicted at sunrise and sunset, most notably so for Honey Buzzards which wait for thermal convection to develop after sunrise (Fig 4.2).

**Figure 4.2.** The diurnal pattern of the difference between predicted and observed hourly speeds for honey buzzards (top panels) and Montagu's harriers (bottom panels) during autumn (left panels) and spring (right panels) respectively. For each season we calculated minimum and maximum dawn, sunrise, sunset and dusk times encountered by all birds. The daytime period is shown in yellow, between the latest sunrise and earliest dawn encountered throughout either season for each species. Orange indicates range between earliest and latest sunrise and sunset times, while red zones indicate earliest and latest twilight periods in each season. Night time is shown in grey, between the latest dusk and the earliest dawn experienced during migration.
4.5. DISCUSSION

4.5.1. Species-specific weather effects
Our results show that weather explains between 40% and 50% of the variation in hourly speeds and between 30% and 40% of variability in daily distances and daily mean speeds achieved by soaring migrants. We show that wind conditions as well as boundary layer height, which reflects the depth of the atmospheric boundary layer in which thermal convection develops and how high birds can climb while soaring [69,94], are important determinants of hourly travel performance for Honey Buzzards and Montagu’s Harriers along their entire migratory journey. Previously the influence of both wind and convective conditions on soaring flight was observed for our study species only from single-site studies [44,69,93,137,248]. Some authors have compared the travel speed of Broad-winged Hawks in the Americas and Honey Buzzards in Europe between a northern and southern location along their respective migration flyways and also found that travel performance was higher at southern latitudes where thermal soaring conditions were better [248,265]. Moreover, Black Storks *Ciconia nigra* migrating between Europe and Africa, and Swainson’s Hawks *Buteo swainsoni* migrating over the Americas, like our study species, also achieved higher hourly ground speeds at southern latitudes, most likely due to better thermal convective conditions [84,266]. Turkey Vultures *Cathartes aura*, breeding in North-America, were shown to be affected strongly by ‘turbulent kinetic energy’ (a proxy for vertical atmospheric energy, including thermal convection) and wind strength for migration [72] along their entire journeys. Unlike most of these studies, however, we explicitly quantified the relative effects of different weather variables on performance, showing that tailwind is the highly dominant factor affecting daily travel distance of both an obligate and a facultative soaring migrant along the entire flyway (cf. Mellone et al. 2012). Honey Buzzards were more sensitive to variation in boundary layer height than Montagu’s Harriers, which we expected because harriers may modulate their flight time substantially for reasons other than optimizing travel performance as a function of convective conditions [137,228]. Our results also show that the hourly speeds of facultative
soaring Montagu’s Harriers are less affected by variation in crosswind than Honey Buzzards. We expected this because harriers could overcome crosswinds rather efficiently by switching to flapping flight [156] compared to Honey Buzzards which we expect to refrain from such energetically costly flapping, even if they then must accept some drift from their intended travel direction.

Moreover, we provide evidence that a preferably soaring species travels faster and further with stronger average daily thermal convection [72,84,94,144]. Harriers, however, extended their daily travel time in the absence of suitable soaring conditions, during early morning and after dusk, thereby reducing their reliance on daily boundary layer conditions [145,228]. The absence of a crosswind effect on daily speeds and travel distances of harriers is consistent with our expectation that facultative soaring migrants would more readily use flapping flight to compensate for drift and thus fly at higher ground speeds than possible during soaring flight.

4.5.2. Regional and seasonal patterns in migration performance and weather conditions
When accounting for weather conditions on the way, no more large differences were found in the performance of soaring migrants, neither among terrestrial regions nor between seasons. Thus we show that seasonal flight speeds of soaring migrants are not primarily due to a seasonal change in behavior as often suggested for higher migration speeds noted in spring compared to autumn [252–254], but are rather predominantly the effect of weather conditions encountered during flight [73,143]. The small regional differences in migration speeds which we could not explain from weather conditions could arise from regional variation in flight orientation, foraging strategies, airspeeds or a combination of changes in flight behavior. A recent study showed that soaring migrants passing over Israel adjust their gliding airspeeds to thermal soaring conditions, but that they glide more slowly than expected in order to stay in the air longer during the gliding phase, thereby increasing the chance of reaching the next thermal without the need to resort to flapping [157]. Such a risk-averse strategy may be more important in regions or seasons with relatively poor soaring conditions, and thus soaring
migrants may adjust their airspeeds to soaring conditions differently between different regions or seasons. However, we expect the effect would be small in comparison to the strong influence of weather. Given this strong dependence on weather, soaring migrants may most efficiently influence their performance by choosing the best available atmospheric flows for travel. To do so, they could interrupt their travel under disadvantageous conditions [76], or orient themselves in the best possible angle relative to the wind in order to maximize the progress they make toward their destinations [11].

While both species reduced their travel time and speeds when approaching seasonal destinations (e.g. when reaching the Sahel in autumn, and when reaching the temperate forest in spring), these patterns are accounted for by weather conditions, and so we suspect the birds were not flying slower because they were relaxing while approaching their destinations [266,267]. Only above sea we consistently underestimated the hourly and daily performance for both species. The general absence of thermals over large water bodies in the temperate zones prohibits stationary circle-soaring there and requires soaring migrants to cross water bodies using flapping flight [45,107,108]. We actually would expect that a transition to flapping flight to lead to higher ground speeds than predicted from our model, given the model was parameterized on predominantly continental soaring migration data. Behavioral information from accelerometers integrated in tracking devices can help to distinguish flapping from soaring flight events to generate a more complete understanding of how weather influences these migrants [62,268].

4.5.3. The role of travel time
Remaining differences in daily travel distance between regions (7%-13% of total variation for Honey Buzzard and Montagu’s Harrier respectively) show that daily performance is affected by how soaring migrants modulate their travel time. Honey Buzzards, for example, travelled much shorter distances than predicted above tropical forests (Fig 4.1, Table 4.1), probably because they frequently interrupted their travels there due to precipitation [76]. Montagu’s Harriers reduced their daily travel time, hourly speeds and daily distances over the Sahel in autumn and over the
Mediterranean region in spring, likely because they were foraging to replenish their energy reserves there [250,261]. Other fly-forage migrants such as Ospreys *Pandion haliaetus* also vary their travel and feeding schedules depending on regional and seasonal energy requirements [145]. In addition, the birds may have reduced their daily travel time because they arrived close to their seasonal destinations [266,267]. Montagu’s Harriers travelled much further per day over the sea than predicted by weather conditions, because Montagu’s Harriers did not interrupt travel during sea-crossings in the central Mediterranean even when stepping stones were available as in spring (Fig 4.1.B-I/V) and continued to fly even when soaring conditions were not available. Interestingly, winds experienced by Montagu’s Harriers during sea-crossing were significantly weaker in spring than in autumn, with a lower proportion of strong crosswinds (Supplementary material Figs S4.2.A, 2.A). This suggests that, similar to Marsh Harriers [269], some Montagu’s Harrier may have evolved a seasonal loop migration, whereby they avoid a detour in spring by crossing the Mediterranean directly, as winds are more favorable for sea-crossings in that season. Montagu’s Harriers that do make sea-crossings in autumn tend to select specific wind conditions to do so [140].

Overall, the take-off and stop-over decisions of soaring migrants, which determine their daily travel times, seem more influential for overall daily performance than modulations in flight speed [254]. This finding stresses the need for further research on how precipitation and other weather factors may affect the daily time budgets of soaring migrants [76,145].

**4.5.4. The role of orientation and wind**

There are only small regional patterns remaining in hourly speeds that are not accounted for by weather, nor by travel time. Honey Buzzards, for example, achieved consistently higher hourly speeds than predicted in spring, and migrated consistently slower than predicted in autumn (Fig 1.A II/IV, Table 4.1). The fast Sahara-crossing in spring is clearly related to stronger winds over the desert during spring (Supplementary material Table S4.3.A, Fig. S4.2.A) which enabled Honey Buzzards to reach higher ground speeds than they were able to reach under the
strong convective conditions over the Sahara in autumn (Supplementary material Table S4.3.A, Fig. S4.2.A). However, the Honey Buzzards should also compensate relatively more for winds during (the last stage of) the desert crossing in spring while they navigate towards the Gibraltar Strait [11] whereas they seem to drift with prevailing winds over the Sahara in autumn. If Honey Buzzards are held back more by side winds when compensating, than otherwise, we should expect our model, which was parameterized from a dataset combining drift and compensation events, to predict, on average, slightly higher speeds than achieved during compensation. Honey Buzzards did experience relatively strong absolute crosswinds in spring, suggesting they regularly compensated for wind drift when travelling toward Gibraltar. This example shows it is important to consider that we calculated tail- and crosswind components relative to the realized hourly and daily travel directions, rather than the intended travel direction [10,11,153,172]. We thus studied the influence of wind on flight after they decided how to compensate for side winds and, therefore, wind compensation decisions may account for small seasonal differences in regional behavior [10,11,153,172].

4.5.5. Daily patterns of hourly behavior
We showed that weather predicted travel performance much less accurately during morning and evening hours compared to mid-day flights, especially for Honey Buzzards. During the course of a day, the internal motivation and navigational decisions of a soaring migrant may change for reasons other than weather conditions. For example, birds are likely to begin searching for a suitable roosting site in the evening [105,231]. However, we suspect Honey Buzzards also react differently to weather in the morning because they are not able to compensate for wind as efficiently as compared to mid-day. This is because, at mid-day, Honey Buzzards should climb faster in stronger or closely spaced thermals allowing them to exit thermals at higher altitudes [44,45,138,248] and to glide more steeply between thermals which are likely to be available along the best possible travel direction to compensate for drift [180]. Montagu’s Harriers do not alter their behavior so strongly at specific times of the day, because their superior flapping
abilities allow them to move independently of diurnal cycles in the atmosphere [137].

4.5.6. Negotiating dust-storms
Several Honey Buzzards made obvious detours over the Sahara and these occurred most frequently in spring. We know some of these detours were caused by dust-storms [264], and given the prevalence of detours is higher in spring when dust-storms are most frequent [270], we suspect more detours to be associated to such storms [131]. Our models did not predict flight performance any worse during detours than when keeping course, probably because they were drifting with the wind ahead of a storm, although detours did cause an estimated delay of arrival in Gibraltar of two to six days [264]. Our tracking data suggests that Honey Buzzards prefer making a detour, potentially increasing their migration route by several hundred kilometers, rather than to sit and wait through a dust-storm or try and fly through one, a behavior more often observed in Ospreys, Marsh and Montagu’s Harriers (personal observation Roine Strandberg (Lund University, Sweden), RHGK & BJK). The latter strategies may pose an increased risk of running severe delays, or death by starvation or dehydration [129,131], especially during dust-storms that last several days. Considering that we only study migrations that were successfully completed by adult birds returning to the breeding grounds, we should expect these individuals to be well adapted to cope with disadvantageous or dangerous weather.

4.5.7. Implications for migration phenology
While the general timing of migration may in part be endogenously controlled in response to day length [271,272], general climatic conditions also influence timing of migration [5]. For example, long-distance migrating raptors, including both our study species, have advanced their autumn migration passage dates in southern France by 5-10 days over the past 40 years, probably due to climate change [115]. On an even finer time scale, the onset of migration can be triggered by weather conditions at the region of departure [142,273]. Our results suggest that soaring
migrants may also have advanced arrival dates if gradually ameliorating flight conditions have improved migration performance [240].

For example, an increase of 1 m/s in average tailwind components experienced by a soaring migrant would lead to an increase of 15 -20 km travel distance per day. Honey Buzzards, which normally travel approx. 160 km per travel day, would then be able to complete their whole journey 2-3 days faster than they do now. Furthermore, higher temperatures would also lead to stronger convection, increased boundary layer height, and thus a higher travel performance [144,247]. Interestingly, conditions for soaring raptors have ameliorated in recent decades over Europe in spring (i.e. higher temperatures and increasing frequency of tailwinds, Hüppop and Hüppop 2003, Pirazzoli and Tomasin 2003, Tøttrup et al. 2008, Kemp et al. 2010) but may, for example, have deteriorated over the Sahara by an increase in the frequency and intensity of dust-storms or crosswinds.

Understanding the impact of migration events within the annual cycle, and subsequent fitness consequences, will require researchers to unravel trends in adverse and supportive weather conditions along entire flyways [5,247]. We also need to separate the effects of weather on migration performance (including time-consuming detours) from the effects of weather on departure and stop-over decisions in relation to precipitation, wind conditions and foraging opportunities [76,140,145]. We expect interspecific comparisons of behavior such as the analysis presented here will be helpful to further our understanding of the role of weather in shaping the evolution of bird migration [5,240,247,273].

4.6. CONCLUSIONS

Soaring migrants use atmospheric currents to travel across the landscape, and their performance is dictated by weather conditions encountered on their way. Our results demonstrate that two soaring migrants were affected similarly by weather conditions across their entire migratory ranges, indicating their flight behavior remained consistent across the full journey. In effect, regional and seasonal weather
conditions dictated performance patterns for each species [73,143]. After accounting for effects of weather, a small but significant effect of regions and seasons on flight performance remained, indicating that soaring migrants do change their flight behavior between regions and seasons. However, the effect on migratory performance is notably small compared to the dominating effects of regional and seasonal variation in weather. More work is needed to determine the effects of weather on other aspects of soaring migration, such as foraging and take-off decisions [76,145] and strategies for dealing with crosswinds [11,77], which ultimately also affect migration performance and timing [5,10,240].

The future analysis of high-resolution migration tracks and behavior inferred from accelerometer data, such as can be obtained with the remotely reprogrammable GPS-loggers we used in this study [62], will allow researchers to further resolve the influence of environmental cues on movement by distinguishing between distinct behavioral responses to the environment (e.g. drift vs. compensation, foraging vs. resting, flapping vs. soaring flight) that are important to interpret performance at multiple scales [5,10].

4.7. ACKNOWLEDGEMENTS

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Supplementary Materials

Table S4.1: Metadata for all individuals tracked in this study. Devices 56 – 58 were deployed in the summer of 2008 but their 2008 autumn migrations were excluded due to the low sampling resolution in that season. We retained relatively short tracks for some individuals compared to their conspecifics (e.g. Montagu’s Harrier #187, Honey Buzzard #56 & #58) because of occasional gaps in the tracks of these individuals, which sometimes caused erroneous classification of travel days as non-travel days. Bird #123 spent the summer of 2010 in Africa due to which only one autumn and one spring journey could be tracked.
Fig. S4.2.A.: Regional and seasonal frequency distributions of boundary layer height (I), tailwind (II), crosswinds (III) and precipitation (IV) encountered per hour and per day by Honey Buzzards. Seasons are indicated by color (legend) and are plotted per region (vertical facets).
Fig. S4.2.B.: Regional and seasonal frequency distributions of boundary layer height (I), tailwind (II), crosswinds (III) and precipitation (IV) encountered per hour and per day by Montagu’s Harriers. Seasons are indicated by color (legend) and are plotted per region (vertical facets).
### Table S4.3.A: Regional and seasonal differences in hourly boundary layer height, tailwind, absolute crosswinds and precipitation encountered by Honey Buzzard (top) and Montagu’s Harrier (bottom). Class identifiers (a – f) were determined by a Tukey-HDS test for each variable in both species to identify those biomes over which daily weather conditions were significantly similar.

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### Table S4.3.B: Regional and seasonal patterns in daily mean boundary layer height, tailwind and absolute crosswinds encountered by Honey Buzzard (top) and Montagu’s Harrier (bottom). Class identifiers (a – f) were determined by a Tukey-HDS test for each variable in both species to identify those biomes over which daily weather conditions were significantly similar.

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Table S4.4: Initial linear regression models for hourly speed, daily mean speed and daily distance in function of key weather conditions, before backward selection of significant predictor variables. Effect sizes are calculated from original values as well as from values normalized by their grand-means (i.e. means of each variable over the entire dataset for that species). Exact P-values are given for each of the individual factors in the full models.
Chapter 4 – Flight speeds and weather influences at hourly and daily scales
Chapter 5

Catching the wind: how wind regimes shape orientation strategies and migration routes of European Honey Buzzards *Pernis apivorus* along the east-Atlantic flyway

Vansteelant W.M.G., J. Shamoun-Baranes, W. van Manen, J. van Diermen & W. Bouten

*Publication:*
*Manuscript submitted*
5.1. ABSTRACT
Numerous avian migrants travel substantial detours between their seasonal destinations. For some species, it is likely they do this to exploit atmospheric circulation patterns that are conducive for migration. By tracking individuals over entire migratory journeys we can determine at what scale birds develop orientation strategies in response to wind regimes within their flyway.

We tracked 62 migratory journeys of 12 adult European Honey Buzzards *Pernis apivorus* with high-resolution GPS-loggers and determined geographical and seasonal patterns in orientation behaviour. We found that Honey Buzzards frequently (over)drifted with sidewinds, and that they adjusted their orientation strategy depending on the prevailing wind direction. The response to wind direction was clearly related to long-term wind regimes, and the fact Honey Buzzards overcompensated at the onset of spring migration suggests they can anticipate on wind regimes, thus travelling along detours to catch favourable winds further *en route*.

Although Honey Buzzards detour consistently over western Africa, they use different routes between different years. We discuss how complex detours in relation to transient atmospheric circulation patterns could be learnt through experience and social information. Future studies are likely to reveal that many other animals are capable of anticipating flow regimes along their seasonal journeys.

5.2. INTRODUCTION
Animals which move through air or water must compensate for prevailing flows in order to reach specific destinations during foraging or migration [276,15,277]. When moving short distances it is relatively easy for goal-navigating animals to correct for lateral flow with respect to the shortest possible travel route [278]. However, animals travelling long distances, such as migrant taxa, are likely to encounter multiple flows during a single journey and tend to follow complex routes between their destinations [194,12]. For example, the migration patterns of sea-
turtles are determined during early-life, when hatchlings are drifted to distant shores by the ocean currents until they arrived at a suitable nesting-site to which they will return for the rest of their life, once they have grown to sufficient size in order to negotiate the ocean current along the way [279]. Migrating birds also follow complex migration patterns, often involving substantial detours from their shortest possible migration route [194], and several species encounter or select for supportive winds along most of their migratory journey [156,162,11,82]. The excellent navigational abilities of migrating birds suggest they may be making such detours to make use of predictable, favourable wind fields along the migratory flyway [15,47,150,6,280]. For example a seasonal detour along a low-level jet enables fast migration during spring in North-American migrants [12,281]. However, we know very little about the extent to which birds may anticipate wind regimes throughout their journeys, and at what scale detours are adaptive for migrants [15,6,173,134].

The orientation strategies of animals on the move can be categorized into several distinct categories ranging from (over)drift to (over) compensation with respect to prevailing flow [276]. The rise of animal-tracking technology has paved the way to in-depth studies of orientation behaviour of migrating birds across entire migration flyways [11]. Such research has mainly been conducted on soaring migrants using the East-Atlantic flyway, and has revealed substantial geographical and temporal variability in orientation behaviour of soaring migrants at daily scales [156,11,82]. Soaring migrants using this flyway generally fly over the Strait of Gibraltar to cross the Mediterranean at its narrowest point [108,140,14,282], and the extent to which these birds tolerate drift from their shortest possible route towards Gibraltar is usually greatest at the onset of a journey, whereas birds tended to (over)compensate for sidewinds as they approached their seasonal destinations. Species such as Marsh Harriers *Circus aeruginosus*, Montagu’s Harrier *Circus pygargus*, Lesser Kestrels *Falco naumanii*, Booted Eagles *Aquila pennatus* and Egyptian Vultures *Neophron percnopterus* compensated or overcompensated for wind drift the most when approaching the Strait of Gibraltar [156,11,82] and birds which ended up at a coastline often ended up (over)compensating to avoid being blown out to sea [11].
Allowing drift at the onset of migration and compensating for wind close to the destination is suggestive of ‘adaptive drift’ [150,148], a strategy for dealing with variable winds en route which serves as a useful benchmark for explaining detours in animal migration. However, the flexibility in the orientation behaviour of soaring migrants in the East-Atlantic flyway, which we also expect to occur in other migrants elsewhere, is not fully understood.

By adapting a strategy of adaptive drift birds flying through variable winds allow different degrees of drift en route, altering their orientation in relation to wind in order to minimize travel time. If winds vary randomly en route, birds should tolerate wind drift at the onset of a journey and (over)compensate for wind drift when approaching a goal [150]. In other words, whether or not it is adaptive for a bird to drift or to compensate for wind in any particular location ultimately depends on the wind conditions along the entire flyway, the distance to the destination and the risks associated with flight [47,6,134]. Planning truly time-optimal travel itineraries through dynamic wind fields in order to minimize migration time requires omniscience about wind fields and can include a range of strategies including overdrift or overcompensation along the way [173]. While long-distance migrants encounter multiple wind regimes throughout a single journey, we expect these birds will have evolved mechanisms to anticipate and exploit favourable winds along the flyway [150,281,134], even if they cannot exactly predict wind conditions en route.

Birds which have adapted orientation strategies in response to wind regimes should adjust their response to wind depending on the wind direction they encounter in different parts of the flyway. Marsh Harriers react differently to wind depending on the prevailing wind direction when they are near the Strait of Gibraltar or near the breeding areas in spring [11], as do Montagu’s Harriers throughout most of their journey [156]. However, wind-dependent orientation strategies have not been reported for any other species and so it remains unclear to what extent migrants use wind regimes along their respective flyways [47,6,134,143].
In this study, we aim to increase our insight into capabilities of long-distance migrants for using regional and seasonal wind regimes by studying orientation behaviour of European Honey Buzzards *Pernis apivorus*. More specifically, we describe the hourly orientation behaviour of 12 adult individuals travelling along the east-Atlantic flyway over 34 spring and 28 autumn migrations between spring 2010 and autumn 2014. We defined five orientation behaviours in response to prevailing sidewinds with respect to the shortest possible travel route, ranging from overcompensation, full compensation and partial compensation/partial drift, to full drift and overdrift [276]. We then discuss latitudinal and seasonal patterns in orientation behaviour in the context of the local wind conditions encountered by the birds and the regional and seasonal wind regimes along the flyway. By doing so, we want to help solve the complex evolutionary puzzle of long-distance navigation in European Honey Buzzards [14] and the evolution of migratory detours in general.

5.3. MATERIALS AND METHODS

5.3.1. Tracking Honey Buzzards
We tracked 12 adult Honey Buzzards which breed in mixed forests of the Veluwe in the center of the Netherlands, and which were faithful to specific sites in western Africa in winter. These birds were tracked with high-resolution GPS-trackers [62] at time intervals from 3 seconds to 1 hour during daylight hours across 2-5 complete migration cycles each. Even though the Honey Buzzards travelled through the Strait of Gibraltar in both autumn and spring we noted great inter-annual variation in the route choice of individual Honey Buzzards (Fig 5.1.A). Moreover, we observed striking intra-annual similarities in the route choice of different individuals, in particular for birds flying over the Sahara around the same date, indicating wind fields shape annual migration routes to a great extent (Supplementary materials, Fig S5.1).

5.3.2. Data processing
We extracted migratory movements from the Honey Buzzard tracking data by calculating distance travelled between the first and last location of each day. Travel
days were defined as those days where birds travelled more than 25km. We then partitioned the annual cycle in stationary periods and travel periods. We excluded all travel days preceding pre-migratory stop-overs or following post-migratory stop-overs in order to obtain all travel days spent on active migration. Pre- and post-migratory stop-overs were defined as stationary periods which lasted three days or longer in the breeding range (north of 51°N) but outside the core breeding area before autumn migration or in the wintering range (south of 10°N) but outside the core wintering range before spring migration. We also removed all incomplete travel days (<4 hourly segments recorded).

In order to compare orientation behaviour across the entire dataset we subsampled each travel day to hourly segments (deviation max. 10 min.) between the first and the last location at which a bird achieved a trajectory speed ≥ 1.5 ms\(^{-1}\) on that day according to data before resampling. The total number of journeys and the average number of hourly travel segments and travel days recorded on each journey are summarized per individual in Supplementary materials (table S5.1).

5.3.3. Goal destinations and quantifying detours

Birds were assumed to intend to travel along the shortest possible route towards their breeding sites in spring and towards their wintering sites in autumn, using the Strait of Gibraltar as an intermediate goal destination in both seasons. Because Honey Buzzards were highly site faithful to breeding and wintering sites we calculated individual goal destinations as the average position of each bird during the core breeding period (July) and early wintering period (November), respectively. We also assumed that the birds intended to travel towards the western Pyrenees in autumn before heading towards Gibraltar (Fig 5.1.A., black squares). The birds switched goal-destinations when crossing latitude 36 at Gibraltar or when crossing latitude 44 in the Pyrenees in autumn. To quantify detours in relation to wind conditions we calculated the tortuosity of the birds realized migration routes compared to the shortest possible migration paths with respect to Gibraltar, i.e. between Europe and Africa respectively (Fig 5.1.A.). We did not calculate detours with respect to the Pyrenees in autumn because the western Pyrenees are situated on
the great-circle route from Gibraltar to the Honey Buzzard’s breeding area Netherlands (Fig 5.1.A.).

While we can quantify orientation behaviour *en route* with respect to individual destinations, we could not compare great-circle distances between these destinations with the cumulative travel distances in between these exact locations because some early migration days were lost during data processing and subsampling procedures. We therefore calculated the great-circle routes and the cumulative distance travelled across Europe and Africa to or from Gibraltar between the first and last hourly segment which we recorded for each journey separately. We then averaged the great-circle distances and cumulative travel distances per season for each bird before calculating track tortuosity across each continent.

5.3.4. Determining hourly wind conditions and orientation strategies

We linearly interpolated zonal (U-) and meridional (V-) wind components from the surface to the 700mb pressure level in space and time to the starting point of each hourly segment from the ECMWF reanalysis II dataset [71]. We then linearly interpolated wind data between pressure levels to the flight altitude of the bird above ground level. The flight altitude above the ground was calculated by combining flight altitude data relative to sea-level provided by the GPS-trackers and the ETOPO30 global elevation model in the UvA-BiTS Virtual Lab [62].

We calculated the intended travel direction of a bird at the start of each hourly segment as the great-circle direction to its next goal destination (Fig 5.1.A.) and calculated the forward and sideward trajectory speed of the bird, as well as the tailwind and sideward speed, with respect to the intended travel direction. Orientation behaviours were classified based on the amount of sideward movement with respect to sideward (Fig 5.1.B., 5.1.C.). In contrast to previous studies we defined five rather than three types of orientation behaviour with respect to flow by distinguishing ‘overdrift’, ‘full drift’ and ‘partial compensation/drift’ as separate types of ‘drift’ strategies [156,11,82]. To do this, we quantified the ‘drift ratio’ (DR) as the ratio between sideward speed of the bird and the sideward it experienced across each hourly travel segment (Fig 5.1.C), which we then used to
Chapter 5 – Wind regimes shape migration routes and orientation behaviour

(A) AUTUMN

(B) Overdrift  Full Drift  Partial Compensation  Full Compensation  Overcompensation

(C) 

Sideward ground speed [ms⁻¹] vs Sidewind [ms⁻¹]
Goal-directed migrations of adult Honey Buzzards between summer 2010 and summer 2014 and the classification of their orientation strategies. (A) We tracked 62 migratory journeys of 12 adult Honey Buzzards which travelled between individually fixed breeding and wintering sites (colour code) via the western Pyrenees in autumn, and over the Strait of Gibraltar in both seasons. (B) Birds may use any of five orientation strategies with respect to local wind conditions at any point. (C) We categorized these strategies for each hourly travel segment, based on the sideward speed of a bird and the sidewind it encountered relative to its shortest possible travel direction, except when sidewind speed < 0.5 ms\(^{-1}\) (black).

classify overdrift (DR $\geq$ 1.2), full drift (0.8 < DR < 1.2), partial compensation (0.2 < DR <= 0.8), full compensation (-0.2 <= DR <= 0.2) and overcompensation (DR < -0.2) throughout the flyway, ignoring those cases where birds experienced no sidewinds (< 0.5ms\(^{-1}\), Fig 5.1.C.). Overdrift implies that a bird was heading away from its intended travel direction into the direction where the wind was blowing towards, while overcompensation implies that a bird was heading away from its intended travel direction into the direction where the wind was coming from.

5.3.5. Geographical and temporal variability in orientation behaviour

In order to gain insight into orientation strategies we mainly focus on geographical and temporal patterns in orientation behaviour. Moreover, to obtain a statistical measure of orientation with respect to flow we performed linear regressions to calculate the effect of sideward wind speed on sideward ground speed and the effect of tailwind on forward ground speed [analogous to 8,10,11]. The ratio between these two effects is a measure of the drift tolerance (T). T > 1 indicates overdrift, T =1 indicates full drift, 0 < T < 1 indicates partial compensation/partial drift, T = 0 indicates full compensation and T <0 indicates over-compensation. We calculated drift tolerance using linear regression models across five latitudinal bands of 10° latitude in each season.
5.3.6. Wind-dependent orientation strategies and wind regimes

We looked for wind-dependent migration strategies in each of the five latitudinal bands by calculating drift tolerances for those cases where birds experienced a wind with a westward component separate from those cases where the wind had an eastward component. We then mapped orientation strategies across the flyway depending on whether birds experienced winds with a westward or eastward component respectively.

NCEP reanalysis-II data were used to calculate the average proportion of days during the Honey Buzzard migration season (defined as the period between the earliest and the latest recorded travel date in our dataset) on which winds had a westward or eastward component at 12:00 UTC in order to quantify diurnal wind regimes. We used wind data at the 925mB pressure level only, which corresponds to an average flight altitude of ca. 750m for migrating Honey Buzzards [162]. Calculations were made at the spatial resolution of the NCEP data (2.5°x2.5°) and we visualized wind regimes from 2010-2014 by linearly interpolating the average seasonal proportion of westward and eastward winds between grid points.

In order to explore whether birds were selective for winds in time and space we visually compared the winds which birds encountered along their migratory routes with the average winds across the longitudinal range utilized by the birds and between the earliest and latest day of the year on which birds were recorded travelling through each latitudinal band.

All analysis were conducted using the R Language for Statistical Programming (R.3.0.2) [221] and all figures were prepared using the ggplot2-package [222]. NCEP reanalysis-II data were obtained and processed using the RNCEP-package [78].

5.4. RESULTS

We used a total of 5501 and 6308 hourly travel segments for mapping and analysing the orientation behaviour of Honey Buzzards in autumn and spring respectively (Supplementary materials, table S5.1).
5.4.1. Detours during autumn and spring in Europe and Africa
The Honey Buzzards stayed within a rather narrow migration corridor along the great-circle route between the Netherlands and Gibraltar in Europe, whereas they were making detours of 10% - 30% additional distance to the great-circle route between Gibraltar and the wintering areas in Africa (Fig 5.1.A, table S5.2). The detours across Africa were also slightly larger in spring, compared to autumn (Fig 5.1.A, table S5.2). However, seasonal differences in the extent of detours within Europe and Africa were less pronounced than regional differences in the extent of detours. Interestingly, the birds required fewer travel days to travel longer distances in spring than in autumn (Supplementary materials, table S5.2).

5.4.2. Geographical flexibility in orientation behaviour
Fig 2 shows the geographic distributions of orientation strategies, whereby a high proportion of blue segments indicates areas with a higher proportion of drift and overdrift, whereas reds indicate segments during which birds are overcompensating for wind drift. In general, the Honey Buzzards exhibited highly flexible orientation behaviour and were overdrifting and overcompensating more than half of the time throughout the entire flyway (Fig 5.2, maps). Seasonal drift tolerance (T) reached 0.75 in autumn compared to 0.95 in spring (Supplementary materials, table S5.3, in bold).

While full compensation (Fig 5.2, orange) was a rare strategy the birds overcompensated over half of the time in certain parts of the flyway, mainly when arriving at a geographical bottleneck such as the Strait of Gibraltar and the Pyrenees (Fig 5.2; Supplementary Materials, table S5.3). In addition, Honey Buzzards avoided being blown out to sea by overcompensating for sidewinds whenever they ended up near a coastline (Fig 5.2, maps) and they (over)compensated more than half of the time when approaching a goal-destination (Fig 5.2). This effect was especially clear at the end of spring migration because all birds only had a short distance left to travel before reaching the same general breeding area north of 50°N (Fig 5.2, graphs). Finally, we found that Honey Buzzards frequently overcompensated at the onset of spring in western Africa (Fig 5.2), although on
Chapter 5 – Wind regimes shape migration routes and orientation behaviour
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Fig. 5.2. Geographical flexibility in hourly orientation strategies during autumn (top) and spring (bottom) migration. (A) We mapped hourly travel segments using the unique colour code for each orientation strategy and (B) concomitantly determined the relative frequency of each orientation strategy and cases with negligible sidewind across geographical bands of 2 degrees latitude.

Average they overdrifted between 5°N and 15°N (Fig 5.2, Supplementary Materials, table S5.3, latitudinal band 10).

5.4.3. Wind-dependent orientation strategies in relation to regional and seasonal wind regimes
Honey Buzzards have some distinct regional and seasonal patterns in orientation behaviour (Fig 5.3, maps) and encounter widely varying wind conditions along their migration route (Fig 5.3, circular histograms). The average drift tolerance (T) differed more between latitudinal bands than it did depending on the zonal wind direction within each latitudinal band (Supplementary materials, tables S5.2 and S5.3). However, in autumn birds tolerated more drift when winds were blowing eastward than when winds were blowing westward, while in spring they tolerated more drift in winds blowing westward throughout most of the flyway (Supplementary Materials, table S5.4).

While the birds clearly overcompensated in eastward winds and overdrifted in westward winds at the onset of spring migration (Fig 5.3, maps spring, lat 10°N), this difference in orientation behaviour was not well resolved in our numerical analysis (Supplementary Materials, table S5.4), probably because winds tended to be very weak in this region (Fig 5.3, first column circular histograms). Also in spring, we note a sharp change in travel direction at latitude 20°N which was accompanied by a sharp change in wind. In general, the travel direction of the Honey Buzzards tended to be biased in the direction toward which the winds en route were blowing, which also tended to be the dominant winds within their longitudinal migration corridor (Fig 5.3, circular histograms). However, during spring, Honey Buzzards encountered substantially more eastward winds than we would expect on the basis of the average wind conditions in the flyway between
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**Fig. 5.3.** We mapped starting points of all hourly travel segments, colour-coded per orientation strategy, between cases in which a bird experienced a wind with a westward component (left map) and cases in which a bird experienced a wind with an eastward component (right map) for autumn (top) and spring (bottom). Colour maps represent the seasonal wind regimes across western Europe and Africa between 2010-2014, showing the seasonal proportion of days during which winds had a westward component (U < 0, left map) or eastward component (U >0, right map). The winds experienced *en route* are summarized per geographical band (first column of circular histograms). For comparison, we summarized wind conditions within the longitudinal range and time periods utilized by the birds within each geographical band (second column of circular histograms). Histograms show the frequency of winds depending on speed (colour legend) and the direction in which winds were blowing.

5°N and 35°N (Fig 5.3). Moreover, in autumn they experienced substantially more westward winds in latitudinal band 30°N than would be expected from the average seasonal conditions within their usual migration corridor (Fig 5.3, circular histograms). When birds encountered winds that deviated strongly from the average seasonal pattern, they were likely altering their route to select winds which were more favourable for migration than the average seasonal conditions. This can be seen on the maps (Fig 5.3) as most birds are crossing the desert through a corridor where winds were aligned with their dominant travel direction more frequently than elsewhere in the seasonal wind regime (Fig 5.3, colour scale on maps). Winds almost always have a strong westward component across the desert. However, when entering the desert near 20°N, Honey Buzzards tend to catch tailwind support by flying (north)eastward in winds with an eastward component (Fig 5.3, colour scale maps).

In Europe, drift tolerance (T) rarely exceeded 0.5 (Supplementary Materials, table S5.3) and the birds tolerated most drift between 35°N – 45°N, over the Iberian peninsula (Fig 2), with T = 0.56 when winds had an eastward component in autumn and T = 0.55 when winds had a westward component in spring (Supplementary...
materials, table S5.4). The birds generally experienced moderate headwinds at the onset of autumn migration, while winds became more conducive to migration over the Iberian peninsula (Fig 5.3, circular histograms). In spring, the Honey Buzzards encountered adverse winds over western Africa, while they experienced favourable winds blowing to the east or northeast most of the time over Europe (Fig 5.3, circular histograms).

5.4.4. Additional observations
Three Honey Buzzards (B0178/B6053, B0184 and B0387) wintered east of 5°E in central Africa and were the only individuals to travel over the central sahara in respectively 3 out of 5, 2 out of 4 and 1 out of 2 consecutive spring migrations (Fig S5.1). Nevertheless, these birds used the same general migration corridor as other individuals in autumn and also spent most of their time (over)drifting over Sahara in spring (Fig 5.2, map).

5.5. DISCUSSION
Twelve adult Honey Buzzards revealed remarkably flexible orientation strategies across the East-Atlantic Flyway that seem to be adaptive in the context of the wind regimes above western Europe and Africa during autumn and spring migration. As expected under the classic assumptions for ‘adaptive drift’ the Honey Buzzards tolerated a high degree of drift in between consecutive goals, and more so in Africa, while they increasingly compensated as they approached goal destinations and while crossing geographical barriers [11,150,6]. This partly explains the seasonal detours of these Honey Buzzards, and probably many more species using the same flyway [156,162,11,82], but ‘adaptive drift’ does not explain the high degree of flexibility in orientation behaviour throughout most of the flyway.

Moreover, we found that Honey Buzzards overdrifted or overcompensated most of the time they were on the move. When birds ‘overdrift’ they effectively adjust their heading downwind, which could also be interpreted as an adjustment in their preferred direction away from the great-circle route to the next goal [173]. While overdrift has not previously been applied in the context of bird migration, the
strategy is also known as compass-biased downstream orientation for migrant insects, which are usually too small to compensate for wind as birds do [276,283,284]. Nevertheless, a large bird like a Honey Buzzard could clearly benefit from catching the wind along a detour if winds are favourable there, and especially if drifting in opposing winds balances for the accumulated drift later in the journey [6,173].

Most importantly, while the high degree of overcompensation near goals and barriers was expected, we did not expect that birds would predominantly overcompensate for wind at the onset of spring migration. When a bird is consistently overcompensating away from a known goal or a barrier it indicates that the bird intends to move elsewhere than we assumed [173]. Over western Africa the birds clearly intended to maintain more westerly travel direction in spring, even in weak opposing winds, until they encountered a window of opportunity with strong eastward wind which could facilitate the Sahara-crossing. Given that birds are most likely to find a tailwind for crossing the Sahara along the western detour (Fig 3, maps) we may conclude that the birds intend to make the westward detour over the Sahel because it is adaptive in the context of the seasonal wind regimes over western Africa.

5.5.1. The advantages of detours in the context of seasonal and regional wind regimes

Throughout most of the year, the wind regime over the Sahara is dominated by winds blowing (south)westward, forming a formidable barrier for spring migrants. These trade winds are known regionally as the ‘Harmattan’ [132,285,33], and they dominate the climate to the north of the Inter-Tropical Convergence Zone (ITCZ). The ITCZ is the zone where the Harmattan trade winds from over the Sahara collide with cooler air that is drawn in from the Gulf of Guinea [285,286]. The ITCZ migrates northward in spring (March – July) and southward in autumn (Sep – Nov) and is situated at approximately 20°N during the peak Honey Buzzard migration over western Africa in late April through early May. As winds from the north and the south converge at the ITCZ they are deflected toward the west, and the Honey
Buzzards seem to travel west along the ITCZ until they can catch a tailwind to cross the Sahara, which is most likely to occur in westernmost Africa, near the Atlantic ocean [285]. When Honey Buzzards enter western Africa in autumn they tend to circumvent the Atlas mountains toward the east. Once they reach the desert, the same wind regime which counteracts migrants during spring actually facilitates a fast desert-crossing in autumn, when Honey Buzzards catch a ride on the Harmattan winds toward the southwest. They start (over)compensating toward their goal destinations only after leaving the desert. The extreme temperatures and aridity of the Sahara are probably an additional incentive for birds not to battle the winds in this region during both seasons [33,131,129]. In addition, western Africa contains the globe’s two most important sources of atmospheric dust [287] and powerful dust-storms occur most frequently in spring, April being the high season [287]. The occurrence of dust storms in the central Sahara in spring may therefore be another potent selective force favouring the evolution of a relatively westerly migration corridor in spring [162,131,129],

In Europe, it may be that Honey Buzzards aim to circumvent the high Pyrenees along the Atlantic side in autumn because they encounter disadvantageous winds over western Europe until they have crossed the Pyrenees. In contrast, increased activity of the North-Atlantic oscillation is known to establish favourable tailwinds for migrating birds over Europe in spring [73], which may enable Honey Buzzards to cross the Pyrenees over a wider front.

5.5.2. ‘Adaptive drift’ in long-distance migration
Understanding complex orientation strategies in response to wind has been hampered by our knowledge and expectations about destinations of migrant birds. The frequency with which Honey Buzzards overdrifted and overcompensated for wind at an hourly resolution suggests that orientation strategies and navigational abilities of migrant birds are likely to be more sophisticated than assumed in most previous studies. As discussed above, we found the strategy of ‘overdrift’ to resemble the strategy of ‘compass-biased downstream orientation’ in some migratory insects [276,288], i.e.: the birds do not seem to navigate toward any
specific geographical location during this detour, but rather to travel toward a broad area in western Africa where they stand a good chance of finding a favourable wind to start the desert-crossing. Moreover, in contrast to passerines which mainly adjust their time-schedules or flight altitude in relation to the occurrence of favourable winds [47,6,289,75], Honey Buzzards seem to select for wind by making a detour where winds are more forgiving for spring migration over the desert, and flying westward until they encounter a window of opportunity with supportive winds to cross the desert. This requires that large, soaring birds have the ability to gauge wind fields at a scale in between the local perception of wind under the classical formulation of ‘adaptive drift’ in variable winds [150] and the ‘optimal orientation’ benchmark for birds that perfectly anticipate flows across entire migrations [173]. It is reasonable to expect such abilities given that many migrants have adjusted their migration routes and timing to the occurrence of atmospheric conditions that are conducive to migration [47,6,283]. Moreover, the strategy to travel toward a broad target area rather than a specific goal or along a fixed heading also resembles that of hatchling-sea turtles [277,244], emphasizing we may expect convergent patterns in the evolution of orientation strategies across taxa travelling through water, as well as through air [276,283].

5.5.3. Implications for other species using the East-Atlantic flyway
All Honey Buzzards which we studied returned to Europe via the Strait of Gibraltar, even if they wintered far to the east, emphasizing a strong selection for Honey Buzzards to avoid a direct sea-crossing in spring. In contrast, Montagu’s Harriers which breed and winter at comparable longitudes as Honey Buzzards tend to migrate directly over the central Sahara and central Mediterranean in spring [256]. The seasonal wind field over the western Sahara may contribute to the convergence of soaring birds at this geographical bottleneck, since the ground speed of birds using soaring flight is affected more strongly by wind conditions than that of birds using flapping flight [156,162]. Adult Honey Buzzards from other populations do migrate over the central Mediterranean in spring, but less so than in autumn, possible because they avoid flying into the Harmattan winds over the Sahara, or because they seek to avoid headwinds over the Mediterranean [33,160,118,117].
Honey Buzzards migrate late in spring and early in autumn compared to most other Palearctic migrants, and wind conditions may change relatively fast over western Africa as the ITCZ migrates northward in spring and southward in autumn. In late April, the ITCZ is positioned further to the north compared to when most other soaring birds leave western Africa around mid-March, which may explain why some migrants make even sharper detours through western Africa in spring [269], and why some do not seem to detour at all [82,256].

Short-toed Eagles and Booted Eagles are known to travel over the central Sahara in spring, even though they are highly reliant on soaring flight, possibly more so than Honey Buzzards [82]. However, while these species may feed in northern Africa or in the Sahel, just before the Sahara-crossing, Honey Buzzards usually fast all of the way [161], which makes it extra advantageous for them to profit from supportive atmospheric conditions during migration. Ultimately, we must evaluate the internal drivers, motion capacity and navigational capabilities of different migrants in order to compare their respective orientation strategies [276,6,290].

5.5.4. Mechanisms for the evolution of detours in response to wind regimes
It is worth noting that the Honey Buzzards adjusted their travel direction upon entering or leaving the Sahara near the conspicuous cliffs that demarcate that Adrar and Tagant plateau in Mauretania. These clear landmarks do not appear on most global elevation maps but may greatly aid birds to remember a complex migration route across this region. However, regardless of the presence of such landmarks, how could Honey Buzzards learn a large scale detour in the first place, especially when they do not seem to visit the westernmost limits of their spring migration corridor during autumn?

To help answer this question, it is especially useful to consider the individuals which wintered furthest east of all the Honey Buzzards (B0178/B6053, B0184 and B0387). The fact that these birds were the only individuals that travelled over the central Sahara in spring indicates that there is a limit to the distance that a bird is willing accumulate in order to profit from wind support [6,173]. Moreover, it indicates that experience and learning play an important role in the development of
individual migration routes and concomitant patterns of migratory connectivity within and between the African-Eurasian flyways [13,291,292].

Long-lived soaring migrants are known to adopt more efficient migration strategies as they age [293] and Honey Buzzards start travelling via geographical bottlenecks once they return to Europe as adults [14]. It is likely that social information plays an important role in the cultural inheritance of complex migration routes in long-lived, long-distance migrants [124,125,128,123]. Honey Buzzards are among the most numerous migrants using the East-Atlantic flyway, and they travel within a very brief migration period compared to other trans-Saharan migrants [113], which could enable unexperienced birds learn to detour over western Africa from their elders [294]. Moreover, social information has been proposed to guide unexperienced soaring birds of other species around other barriers such as the Mediterranean [124,125,128].

Tracking juvenile birds into adulthood will help to better elucidate the relative contributions of genetically imprinted migration strategies, environmental factors and experiential and social learning in the development of individual migration routes [292]. However, regardless of the cues and mechanisms used for navigation, the context of geographical and seasonal wind dynamics is particularly important to understand the evolution of bird migration flyways [47,6,281,295]. As tracking devices are elucidating the migration strategies of migrant birds at an accelerating pace [7,8] and opportunities for integrating meteorology into bird migration are increasing [5], we expect that interspecific comparisons of orientation behaviour will soon yield greater insight into the capabilities of migrant birds and other animals moving through flows to anticipate predictable flows and to adjust their orientation strategies accordingly [6,134,4].

5.6. ACKNOWLEDGEMENTS
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facilitated by infrastructures for e-Science, developed with support of the NLeSC and LifeWatch, carried out on the Dutch national e-infrastructure with support of SURF Foundation. ECMWF data were provided by KNMI and the ESA FlySafe initiative within the framework of the Integrated Applications Promotion (IAP) Programme. NCEP reanalysis data were provided by the NOAA-ESRL Physical Sciences Division, Boulder Colorado from their Web site at http://www.esrl.noaa.gov/psd/. Our special thanks goes to Edwin Baaij for excellent technical assistance and device development. We also thank James D. McLaren for insightful discussions on the subject of this paper.
### 5.7. Supplementary Materials

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*Table S5.1*. Metadata of our tracking dataset after subsampling the migratory journeys of 14 individuals to hourly segments and filtering out incomplete travel days (i.e. < 4 segments per day) and migratory journeys (i.e. < 15 complete travel days).
### Table S5.2. Quantifying detours across Europe and Africa for each individual Honey Buzzard.

We first calculated distances between the Strait to Gibraltar to the first or last point of each migratory journey, then averaged distances per season, and finally calculated track tortuosity to quantify detours over each continent. Detours were larger over Africa than over Europe for all birds and the birds wintering most to the east (B0178.6053, B0184, B0387) made relatively longer detours than other birds.

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### Table S5.3. Results obtained from linear regression models of forward speed vs. tailwind speed and sideward speed vs. sideward wind for each geographical band of 10° latitude, and across the entire flyway (in bold), for each season respectively. Drift tolerance (DT) was calculated as the ratio between the effect size (β) of forward wind on forward movement and the effect size of sideward wind on sideward movement to quantify drift tolerance (T) under each of the different scenario’s.
### Table S5.4. Results obtained from linear regression models of forward speed vs. tailwind speed and sideward speed vs. sidewind speed separated between cases where birds experienced winds blowing eastward and cases where winds were blowing westward for each geographical band of 10° latitude, and for each season respectively. Models with one or more non-significant terms are indicated in italics. We calculated Drift Tolerance (T) analogous to Table S5.3.
Fig. S5.1. Seasonal timing and routes of Honey Buzzards during autumn (top) and spring migrations (bottom) over five consecutive years of tracking (left – right). This visualization shows a striking similarity in the geometry of flight paths of birds that are passing the same region around the same time (especially in Africa), indicating that different birds have a high degree of consistency in their response to synoptic wind fields and regional topography.
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Chapter 6
General discussion
Throughout this dissertation I have characterized the flight behaviour of European Honey Buzzards in relation to atmospheric processes at multiple scales, ranging from their inter-thermal gliding behaviour (chapter 2), over the routes they choose through a geographical convergence zone (chapter 3) to their flight behaviour at hourly and daily scales along an entire flyway (chapters 4 and 5). The main overarching conclusion from my work is that Honey Buzzards seem to avoid high energy expenditure while flying through variable weather conditions, looking for as much atmospheric support as they can find in the thermal fields and wind regimes they encounter between their strategic destinations. They do so by gliding at moderate airspeeds, enabling them to glide relatively long distances toward the best available thermals (chapter 2) and therefore to adjust their migration routes through any given landscape in function of thermal availability (chapter 3). Honey Buzzards are especially likely to glide slowly between thermals when leaving weak thermals at low altitude, which is when the risk that they require flapping flight to stay aloft is greatest (chapter 2). Under more favourable conditions, fine-scale adjustments of gliding airspeed in relation to tailwinds and headwinds probably aid birds to reach specific target thermals (chapter 2). When birds compromise their airspeed they do have less potential to counteract drift in variable winds. I have shown that Honey Buzzards overcompensate for sidewinds mostly when they encounter a barrier, for example when they track the Mediterranean coastline toward Gibraltar, or when they cross the Pyrenees (chapter 5). This confirms my assumption at the start of this research that soaring birds behave differently at geographical convergence zones than elsewhere along the migration route.

Since Honey Buzzards were gliding slower than they could it is not surprising they mainly overcompensated in weak winds over tropical western Africa, while (over)drifting in regions with stronger winds (chapter 5). Moreover, while Honey Buzzards do not achieve the highest possible cross-country airsrequencies across consecutive climbing-gliding cycles, they still reach high ground speeds because they can select stronger thermals (chapter 2 and 3) and because they benefit from tailwind assistance along most of the way (chapter 4 and 5). Indeed, tailwinds are the dominant factor explaining variability in the hourly and daily ground speeds of
Honey Buzzards throughout the east-Atlantic flyway (chapter 4). Contrary to common expectations, Honey Buzzards don’t try to travel faster by increasing their ownairspeed during spring, nor during barrier crossings (chapter four and five). It may seem like a risky strategy for a migrant to rely on the weather to such a great extent, especially during barrier-crossings. However, many migrants perish in headwinds over the Sahara, and severe conditions over the desert may repel soaring birds from subsidizing flight by flapping [33,129,131]. It makes sense then, that Honey Buzzards not only anticipate on thermal soaring conditions at local and continental scales, but that they also anticipate on seasonal wind regimes, developing complex migration routines whereby they detour through areas with more supportive, or less adverse, winds in order to complete migration (chapter 5).

I should emphasize that I studied the behaviour of adult Honey Buzzards which survived the entire journey to Africa and back again. Whatever happened to migrants which perished or relocated to other breeding areas is unknown due to the fact that tracking data is obtained from the GPS-loggers through a range-limited ground-based receiver system [62]. However, among the adults I studied, I found no indication that the flight behaviour of individual birds differed substantially between sexes nor between individuals, other than their individual destinations in Africa and the timing of migration (see below). Consequently, I expect my results are representative of the flight behaviour of most adult Honey Buzzards, which appear to make prudent decisions with regard to weather. In order to fully understand the implications of atmospheric circulation patterns for the evolution of migratory behaviour in Honey Buzzards and other migrants, however, it is necessary to understand how weather during migration affects migration timing and individual fitness in my study species.

6.1. INDIVIDUALITY AND WEATHER-DEPENDENT VARIABILITY IN MIGRATION TIMING

Timing within the annual cycle is one of the key factors determining whether or not weather conditions during migration affect individual fitness and concomitant
behavioural adaptations. Although I have no information about the body condition of individual birds upon arrival in the Netherlands, the annual variability in their individual migration timing (Fig 6.1) can shed more light on the extent to which weather conditions affect migration timing of Honey Buzzards. Below I provide a preliminary overview of the timing of migratory journeys which I used in chapters 2, 4 and 5, on the basis of which I will discuss the role of weather in unusual events.

Migration timing is under strong endogenous control in most migrants [271,296] and this is also the case for the Honey Buzzard. Spring departure dates were highly consistent between years in most individuals. Exceptionally early departures were followed by pre-migratory stop-overs in west-Africa before initiating the main journey around the same date as when they departed from the main wintering grounds in other years (Fig 6.1, symbols). The onset of autumn migration did vary between years for each bird (Fig 6.1). Autumn migration was initiated 6-8 days earlier in birds which broods failed at an early stage, as compared to birds which successfully raised offspring (van Manen et al. in prep., pers. obs.). Females seemed to depart earlier than males, suggesting that intrinsic factors such as breeding status and sex may influence autumn migration timing [120,297]. However, more research is needed to separate endogenous mechanisms from external influences, such as the timing of external departure cues [142].

Weather conditions may play a vital role in stop-over decisions of soaring migrants [76]. However, Honey Buzzards hardly ever stopped-over during autumn, at least not until they had left the desert behind them (Fig 6.1), and birds only accumulated serious delays when they engaged in prolonged stop-overs or when they travelled slowly (<100 km d⁻¹) in west Africa. During spring, stop-overs were generally not correlated to any particular stage of the migration, although females which ran into severe delays usually interrupted travel for several days to the north of the Pyrenees (Fig 6.1, purple). It is relevant to note that females which made stop-overs in Europe during spring were also those that had travelled the furthest, coming from Cameroon and Angola (B184, B178.6053, see chapter 5), suggesting they might have depleted their energy reserves en route and consequently interrupted migration
to forage [75]. The possibility that Honey Buzzards engage in emergency stop-overs could explain why some researchers have observed low numbers of migrating individuals with full crops, indicative of recent feeding, during spring migration [161].

I cannot say if weather influences, either in the Sahel or earlier along the migration route, affected the decision to engage in post-migratory stop-overs in autumn. On the other hand, birds which stopped in Europe during spring usually encountered precipitation on the first day of the stop-over (pers. obs.), suggesting that harsh weather can trigger longer stop-over events. In addition, it is worth mentioning here that at least one bird was delayed for two weeks after it had encountered a dust-storm during spring migration [264], and I suspect that delays accumulated during the spring desert-crossing by B182 in 2012, B56.600 in 2012 and 2015, B183.599 in 2012 and B178.6053 in 2012 and 2015 could be related to similar events (chapters 4 and 5). Extreme delays in the arrival of Honey Buzzards at the breeding site usually resulted in reduced breeding success (van Manen et al. in prep.). I hope tracking studies of Honey Buzzards can be sustained for long enough time in order to determine the threshold conditions that lead to emergency stop-overs [75] and other extreme events which are difficult to observe through other techniques.

However, all in all, severe delays which caused breeding failure occurred only rarely throughout the course of this research (van Manen et al. in prep., Fig 6.1, asterisks). The number of travel days (i.e. > 25 km travelled per day) remained relatively consistent across years in both seasons, yet hourly and daily travel distances vary greatly in relation to wind conditions en route (chapter 4). This suggests that the detours birds take enable them to catch tailwind assistance along the way (chapter 5) without extending their overall travel time. Moreover, while Honey Buzzards rely on thermals to stay aloft, they do not stand to gain much ground speed by maximizing their cross-country airspeed as a function of climb rates due to the dominant influence of wind on ground speed (chapter 2 and 4). This emphasizes why the birds are better off catching the wind, rather than fighting it, while on migration.
Even if bad luck stops a Honey Buzzard from breeding successfully due to delayed spring arrivals in some years, such a long-lived bird is likely to succeed in other years, which is sufficient to be successful in evolutionary terms. This explains why Honey Buzzards can afford a risk-averse flight strategy in which they tolerate a strong influence of weather conditions along the way, instead of ‘racing against the clock’ during migration. Of course, long-lived birds will only be able to reach maximal reproductive output for part of their entire life-cycle and capital breeders produce only one small brood per year, such that they may require multiple attempts in order to pass their genes to the next generation. Nevertheless, the window of opportunity for reproduction during the lifespan of a Honey Buzzard seems to be considerably wider than for many small and relatively short-lived species. Short-lived migrants may lay multiple broods in one year, but the first brood of the season is usually most successful and many such migrants will not live much longer than one year such that their reproductive fate is strongly entwined with a timely arrival on the breeding grounds [298]. Consequently, many such small, short-lived migrants do tend to adjust their airspeed depending on seasonal and regional motivations [254].

6.2. THE INFLUENCE OF WEATHER ON OTHER SOARING MIGRANTS

In order to compare the flight behaviour of Honey Buzzards with other migrants it is important to consider that migration strategies may differ greatly depending on the phylogenetic lineage of a bird [280,299]. This is because different types of birds are adapted to different types of flight in light of their feeding and nesting habits,
and because their anatomical and physiological constitution depends on evolutionary heritage. Therefore, it is most straightforward to compare Honey Buzzards with other Accipitridae, which are all obligate or facultative soaring migrants.

6.2.1. Other obligate soaring Accipitridae

My research into European Honey Buzzards broadly confirms the general patterns in the fine-scale flight behaviour of soaring Accipitridae which were previously observed visually and by tracking radar at geographical convergence zones (chapter 1). However, I was also able to demonstrate for the first time that wind-dependent flight behaviour is likely to be ubiquitous among soaring birds (chapter 2, chapter 5). This is especially important because soaring birds are likely to respond differently to sidewinds while passing through a geographical convergence zones or when migrating along leading lines depending on strategic goals within a regional context. Moreover, wind effects could not be separated from confounding influences of soaring conditions in previous site-specific studies [44,139]. Clearly wind conditions are hugely important in shaping migratory journeys at larger scales, while soaring conditions mainly regulate the time which a bird can spend aloft, and this is likely to be the case for most soaring Accipitridae [82–84]. Moreover, while medium-sized and large soaring birds can only travel 4,000 – 5,000 km’s relative to the air by thermal-soaring before exhausting their energy reserves [102,174], catching tailwinds along detours seems to enable birds to travel even farther and faster than they could by thermal-soaring straight toward their goal [97,150,151,155]

My comparison across multiple raptor species in chapter three suggests that larger soaring migrants tend more towards risk-averse flight behaviour than smaller soaring birds. This fits with recent findings that Honey Buzzards are among the least risk-averse soaring migrants in Israel [157]. Indeed, large birds tend to glide relatively more slowly with respect to their potential maximum speed, because it is more important for large birds to avoid energetically costly flapping flight [157]. For any given climb rate in a thermal, large birds can reach relatively high speeds
due their size difference with respect to smaller birds, which should enable them to overcome stronger winds. There is, however, a trade-off between the glidingairspeed of a bird and the climb rate it can achieve in a thermal which depends on body size. For example, large birds will be more risk-averse by being more selective for weather conditions, simply because they require stronger thermals to sustain soaring flight. Ultimately, soaring birds of different sizes are likely to reach similar migration speeds due to these negative trade-offs between climbing and gliding flight.

While the daily timing of migration of large soaring birds is known to be heavily affected by the availability of thermals [93,103,138], we still know very little about the selectivity of soaring birds for wind and soaring conditions across an entire flyway [76]. As I discussed for the case of Honey Buzzard migration, spring stop-overs mainly seem to take place when birds were likely to have depleted their energy reserves before running into adverse weather over Europe, suggesting that other obligate soaring migrants may also use stop-over sites in case of emergencies. However, regardless of whether birds fatten-up at stop-overs or on staging sites, accumulating energy reserves for travel is a key component of the migration cycle, if not the main component determining overall migration speeds [15,16]. Unfortunately, we still know very little about the physiological adaptions of soaring birds for migration, which includes their fatten-up strategies [174,300]. Tracking studies stand to deliver many new insights into this important component of the migration cycle, which may involve pre- and post-migratory stop-overs (see also below).

All soaring raptors which have been tracked for multiple years display great interannual variability in migration routes in combination with highly repeatable individual (spring) migration timing, much as we found for European Honey Buzzards (chapters 4-5), suggesting that weather conditions shape the routes of all soaring birds to a great extent [11,13,83,228,256,301,302]. Several North-American soaring Accipitridae have been shown to select migration routes which provide better soaring conditions at local to regional scales, mainly in the form of
orographic updrafts [51,77]. Considering the African-Eurasian flyways, orographic updrafts are only likely to play a role for birds travelling along the Great Rift Valley. Most soaring birds which migrate between Eurasia and Africa probably depend on thermals to stay aloft, and while availability of thermal convection may affect local flight paths in a geographical convergence zone (chapter 3), I suspect that thermals are usually sufficiently plentiful not to cause large-scale inter-annual variations in the migration routes of birds along the east-Atlantic flyway (with the exception of detours around water bodies and other barriers). Instead, large-scale circulation patterns such as synoptic wind fields appear to be the main force shaping migration routes in between strategic destinations (chapter 5). Other obligate soaring Accipitridae which migrate along detours over the Sahara are therefore likely to do so in response to large-scale wind regimes. However, while Honey Buzzards initiate detours in anticipation of wind regimes further ahead (chapter 5), it remains unclear whether they learn wind dynamics directly through experience, or whether they learn traditional routes through peer pressure instead. Longitudinal tracking studies of soaring birds which differ in the extent to which they socialize during migration will reveal more details about the process of route-learning.

**6.2.2. Facultative soaring Accipitridae**

In addition to obligate soaring migrants there are a range of facultative soaring Accipitridae such as harriers (Circus) and hawks (Accipiter). These birds primarily adopt flapping flight to forage on their staging sites, and it is therefore appropriate to say they supplement flapping with soaring, rather than saying they supplement soaring by flapping during migration [101,137]. These species spend a big part of their journey in active flight, extending their daily travels into the night on many occasions [93,145]. As I have shown in chapters 3 and 4, facultative soaring migrants are generally less influenced by weather conditions (especially not by sidewinds and soaring conditions), and many are able to cross the Mediterranean sea and other geographic obstacles with great ease compared to other obligate soaring birds [118,122,140]. Due to all these reasons, facultative soaring migrants fly considerably faster than obligate soaring migrants. However, such species
require regular feeding in order to maintain flapping flight for such a long distance. They may feed opportunistically, sometimes even hunting while they are travelling (known as a fly-forage strategy) [303]. On the other hand, species such as Montagu’s Harriers visit traditional stop-over sites [228,256,304], and aggregations of such migrants in a geographical convergence zone may even be driven by food availability rather than weather patterns (chapter 3). Consequently, frequent stop-overs reduce the overall migration speed of fly-forage migrants, even though they are able to fly fast. The net result will be that they migrate at similar speeds as obligate soaring migrants.

Interestingly, ospreys are known to have a wide range of individual stop-over strategies, whereby some birds using stop/overs for several weeks while others do not stop-over at all, seemingly stocking all the fat reserves they need before departure [302,303]. Some authors have also classified Honey Buzzards (*Pernis*) and Kites (*Milvus*) as facultative soaring migrants due to their superior sea-crossing abilities, and Oriental Honey Buzzards *Pernis ptilorhyncus* do engage in long stop-overs during spring migration, in contrast to their European conspecifics which only engage in emergency stop-overs. It remains unclear whether Oriental Honey Buzzards stop-over during spring to profit from exceptionally good feeding opportunities along the way, or to compensate for inadequate feeding opportunities on the wintering sites or breeding sites [305]. In any case, we should expect different species to adjust stop-over schedules and flight strategies in tandem depending on the seasonal distribution of their energy resources (i.e. atmospheric energy and food). This conclusion emphasizes once more that the fatten-up period prior to the main migratory flight, which may involve extensive pre- and post-migratory movements in many soaring migrants, should be considered as a key component of the migration cycle in order to compare migration strategies between species [80,304].

### 6.2.3. Other soaring migrants

The migrations strategies of soaring Accipitridae are often compared with the strategies of raptors and other soaring birds that have a different phylogenetic
origin. This mainly concerns falcons (which mainly use flapping flight during migration) and storks and pelicans (which are obligate-soaring migrants). Birds which belong to different phylogenetic clades but which adopt a similar flight mode will certainly reveal some convergent behaviour in response to soaring conditions and wind. Storks do suffer much more drag during flight than other soaring birds due to their long neck and legs while pelicans soar less efficiently due to their big bill, forcing these species to glide near maximum-range air speeds [96,99]. Storks also feed opportunistically during morning and evening hours when thermals are absent [18], although stop-overs are less well defined and time-consuming than for facultative soaring raptors, which suggests that storks are likely to adjust migration routes in relation to large-scale wind regimes in similar ways to soaring Accipitridae, especially given the fact they are able to complete migration within a few weeks [84,144,247], which is comparable to the migration performance of many raptors.

Falcons, on the other end of the spectrum, are agile flyers, fully adapted to life in the air, and they can afford to fly considerably faster by flapping flight than Accipitridae with similar size and wing loading [299]. Such efficient flyers can move under almost all weather conditions, and can readily be seen flying through pouring rain at geographical convergence zones (pers. obs.). The travel schedules of these birds are thus likely to be determined by the availability of food along the flyway in addition to atmospheric constraints. Large Peregrine Falcons *Falco peregrinus* may migrate along relatively straight lines in between their goal destinations, apparently compensating for wind as they go along [266]. However, many migrant falcons are much smaller than the powerful Peregrine, and will follow different migration routes depending on the season [156,301,306], probably in response to large-scale wind regimes. Moreover, weather conditions have a big impact on flight behaviour of migratory falcons during sea-crossings and above other barriers. For example, Eleonora’s Falcons *Falco eleonorae* and Sooty Falcons *Falco concolor* select for tailwinds in order to cross the Indian Ocean between eastern Africa and Madagascar [81,307,308], while Amur Falcons *Falco amurensis* depend on monsoon-winds to make their trans-oceanic flights between India and
eastern Africa [309]. Finally, Hobbies *Falco subbuteo* cross the western African rainforest at high speed and along a relatively narrow corridor as this area seems to be a substantial ecological barrier for this species [306,310]. It is not known how important tailwinds are for Hobbies to cross this barrier, but overall, most long-distance migrants that have been tracked so far seem to use regional and global atmospheric circulations to their advantage, especially in the face of barrier-crossings.

### 6.3. IMPLICATIONS FOR BIRD MIGRATION RESEARCH

While flight mode clearly has a big impact on the motion capacity of birds, the subject of soaring migration has naturally been treated separately from that of flapping migration in most of ornithological literature. Nevertheless, from a physiological perspective, if we properly knew the rate of energy accumulation and energy expenditure in soaring and flapping birds, we should be able to compare their flight behaviour in the context of their total energy budget. The concept of ‘energy height’, which measures the total energy that a migrant can spend - regardless of whether that energy is provided through the consumption of food and the metabolisation of fat and protein or through the accumulation of potential energy in thermals - therefore has great potential for unifying migration research across birds using distinct modes of flight [180]. Using advanced animal telemetry, integrating physiological and movement sensors, we will soon be able to empirically investigate the energy maintenance of a wide spectrum of migrating birds at multiple scales [6,59,163,180,311].

Body size is responsible for important universal scaling effects in animal locomotion and explains much of the interspecific variability in the flight speeds of migrating birds [100,280,299]. Consequently, body size mediates the potential of a migrating bird to correct for flow. I therefore expect that body size will be an important factor in scaling the selectivity of migrants for wind as well as their orientation strategies during migration, at least within monophyletic lineages of migrants which usually adopt a similar flight mode [299]. Moreover, when
quantifying flight strategies through the concept of ‘energy height’, body size may serve as a unifying concept in the study of weather and migration across species using distinct flight modes, whether they be raptors, passerines or waterfowl.

However, while body size mediates the motion capacity of a migrant, we must remain aware of the internal motivation and navigational abilities which drive a migrants movement decisions in relation to weather conditions and other environmental factors at local to global scales [10,72]. An additional challenge in comparing the strategies of different migratory species is therefore the variation in the spatial distribution of resources which migrants use to fuel migration. While soaring birds mainly depend upon ephemeral but ubiquitous thermals, many flapping birds, especially large species, may spend a large amount of time feeding in rare stop-over habitats. Wetland species are less likely to encounter suitable resting and feeding sites and have to make long non-stop flight in between stop-overs, while passerine migrants interrupt migration by day regardless of where they end up during travel. The scale across which birds optimize their flight behaviour in relation to weather conditions is therefore radically different depending on their energy maintenance strategies which are partly dependent on flight mode and body size, but also on phylogenetically constrained habitat preferences.

In addition to the motion capacity and resource distributions which drive seasonal migrations, there are various other life-history-traits, which may or may not be mediated by body size, which greatly differ between phylogenetic lineages and which will further affect the development of migratory behaviour [16,280,312,313]. All migrant birds are thought to have far more advanced long-term spatial memory and cognitive abilities than non-migrant species [16,314]. Moreover, migration timing is under strong endogenous control in the vast majority of migrants [271,315]. However, the extent to which birds rely on endogenous mechanisms for navigation and orientation depends upon species-specific traits such as longevity and sociality during migration [123,293]. My finding that Honey Buzzards learn a complex migration route in anticipation of seasonal wind regimes lead me to the conclusion that experience and social learning are likely to play a role in their
migratory learning process [14,128]. However, soaring birds live longer than many other migrants, especially compared to small, flapping passerines. Moreover, diurnal migration facilitates social interactions between soaring migrants, even if they do not rely on parental guidance like many large, flapping migrants [107,123,265,294]. The learning abilities of long-lived soaring migrant should therefore not readily be extrapolated to short-lived species, neither to solitary travellers nor to species which stay within the same flock during an entire journey. Social interactions offer many benefits for migrants ranging from energy conservation to the avoidance of predation across a wide range of taxa [316–319], which might also homogenize migration strategies in relation to weather across individuals within a species. However, longevity is probably a key trait for the emergence of cultural inheritance of risk-averse migration routes in opportunistically social birds such as Honey Buzzards, especially when those routes are transient atmospheric corridors instead of directed flights between fixed locations.

6.4. CONCLUSIONS

Time-optimal strategies are usually considered to be characteristic of bird migration [280,312,313], though my research contributes to a fuller appreciation of the importance and drivers of risk-avoidance in bird migration [6,184], and for soaring birds in particular. In order to be successful, all migrants must complete migration in sufficiently good conditions and within a sufficient time-frame to ensure successful completion of the annual cycle. While travelling through a highly dynamic atmosphere, it makes sense for migrants to compromise speed in order to avoid excessive risk.

To understand the evolution of bird migration, it is most informative to identify converging patterns in flight behaviour, and I have argued how, for example, weather-related energy maintenance strategies of birds using different flight modes may be compared in future tracking studies. There is much work to be done for researchers in order to unravel how genetic information, environmental variability,
social interactions and life-long experience contribute to the development of migratory behaviour across multiple scales depending on body size, flight mode and life-history traits [4,5,7,10]. Tracking entire flocks of birds and the internal state of individuals, combined with experiments such as displacement studies [320–322] and modelling approaches [5,7,173,289], will greatly advance our ability to identify the endogenous and exogenous mechanisms which shape the world’s great migrations across multiple scales.
Summary
Naturalists have investigated the mysteries surrounding bird migration since the writings of Aristotle. However, the human eye can only see so far, such that scientific understanding of bird migration has long been constrained by knowledge collected at sites where migrants can easily be detected from the ground. This is problematic because the behaviour of migrants in any specific site does not necessarily reflect their behaviour elsewhere along their migration routes. Moreover, as migrants flap, bound and soar their way through the atmosphere, weather conditions may shape migration across multiple scales. Local wind conditions affect the instantaneous flight speeds and directions of migrant birds, and such effects may accumulate *en route*, affecting the distribution of migration routes, the speed and timing of migration and the body conditions of migrants upon arrival at their destinations. Local weather conditions are also driven by large-scale circulation patterns, and birds may encounter various weather systems throughout a single journey, such that we can only fully understand their reaction to local weather conditions within this broader context. Bird migration research has yielded much contrasting evidence about the flight behaviour of migrants in relation to weather due to a historical bias toward site-specific observations. Fortunately, new technologies, and animal telemetry in particular, are vastly expanding the scale at which researchers can monitor and observe bird migration and their environment across space and time, enabling researchers to address some long outstanding questions about the ecology of bird migration. In this dissertation, I combine visual observations of raptor migration and GPS-tracking studies to investigate the influence of weather on the soaring migration of the European Honey Buzzard *Pernis apivorus*, a common, widespread migrant in the African-Eurasian flyways.

Soaring birds are a fascinating group of migrants because solar-powered thermal soaring is an exceptionally energy-efficient flight mode which enables large birds to travel much farther than they could by flapping flight. However, as soaring migrants depend on the availability of thermals, and while they are drifted by the wind when climbing in thermals, they are much at the mercy of the weather conditions they encounter along the way. In chapter 1, I present a brief overview of the historic developments in the study of weather and bird migration before introducing current
knowledge on the role of weather for soaring migrants. Most research on weather and soaring migration has been conducted at geographical convergence zones, i.e. areas through which large numbers of birds circumvent migration barriers such as the Mediterranean. Visual observations and radar tracking have shown that soaring migrants usually travel faster when they fly in tailwinds and when they can climb fast in strong thermals. However, it is unclear why some soaring migrants adjust gliding airspeeds between thermals in relation to wind, and the effects of sidewind on local flight behaviour often differ between sites. Moreover, it is unknown how weather effects accumulate to shape regional and seasonal migration patterns.

In chapter 2, I used a high-resolution GPS-tracking experiment to study the fine-scale flight behaviour of Honey Buzzards as they glide between thermals throughout the flyway. The climb rates of Honey Buzzards were highly variable, and the birds increased their inter-thermal gliding airspeed, i.e. the speed at which they glide relative to the air, when they encountered stronger thermals. Such an adjustment in airspeed is expected if birds aim to minimize travel time by maximizing their cross-country speed across each climbing-gliding cycle. However, Honey Buzzards were gliding on average 2 ms\(^{-1}\) slower than expected on the basis of aerodynamic theory, and they also increased gliding airspeed in headwinds while decreasing their airspeed in tailwinds. The latter response is expected if birds aim to minimize the rate at which they lose altitude, or in other words, when they aim to maximize their gliding range. Such a strategy is beneficial because it reduces the likelihood that birds must switch to flapping flight in order stay aloft under poor soaring conditions. Under favourable soaring conditions, birds gain time to make decisions when they glide longer distances, which may be beneficial for navigation, or to select for the best thermals that are available ahead. My results show that Honey Buzzards compromise between both strategies, and soaring migration models could be improved further by the dual optimisation of flight speed and travel direction, also taking into account the influence of sidewinds.

Given that Honey Buzzards compromise their gliding airspeed in order to increase the efficiency of thermal-soaring flight we can expect them to follow routes which
sustain relatively good soaring conditions compared to the surrounding landscape. Given that thermal availability often depends upon landscape features, and presuming that soaring birds can detect thermals by looking for other soaring migrants further ahead, we can expect common adjustments in the flight paths of different individuals in relation to thermal availability and prevailing winds. In chapter 3 I studied how 100,000’s of Honey Buzzards and a range of other obligate and facultative soaring migrants shifted their flight paths in relation to weather dynamics along the eastern Black Sea coast in the eastern African-Eurasian flyway. Diurnal and seasonal dynamics in cloud cover generated corresponding dynamics in the spatial distribution of soaring raptors. I demonstrate that large, obligate soaring migrants shift their flight paths towards the shore in order to avoid poor thermal soaring conditions under dense cloud cover which forms over the mountains inland. In contrast, facultative soaring migrants which supplement soaring with flapping flight (e.g. harriers) were not constrained by cloud cover dynamics and mainly seemed to aggregate in the area due to feeding opportunities along the coast. This emphasized how different environmental factors contribute to the formation of migration patterns between different types of soaring migrants.

Given that soaring birds are capable of selecting flight paths in function of thermal availability in a local context, wind and soaring conditions are likely to explain much of the frequently observed regional and seasonal discrepancies in the travel speed of soaring migrants. This is an important consideration for migration ecologists because adjustments in migration speed are often assumed to indicate changes in the internal state and objectives of long-distance migrants. In chapter 4, I investigated to what extent variability in the travel speed of Honey Buzzards and Montagu’s Harriers *Circus pygargus* was determined by the soaring conditions as well as tailwinds and crosswinds along the birds travel direction at hourly and daily scales. I showed that Honey Buzzards travelled significantly faster in tailwinds, and to a lesser extent when they were exposed to better soaring conditions or weak sidewinds. Montagu’s Harriers flew significantly faster in tailwinds but were not dependent on soaring conditions and sidewinds. Nevertheless, variability in weather conditions accounted for most regional and seasonal variability in the flight speeds.
of both species, suggesting that large-scale wind dynamics must play a major role in shaping the journeys of soaring birds.

Honey Buzzards usually made big detours over western Africa during both autumn and spring migration, and the high inter-annual variability of individual migration routes suggests that large-scale weather systems play an important role in shaping these detours. Moreover, the fact that Honey Buzzards and other soaring birds enjoy tailwinds along during most of their migration, including western Africa, suggests that detours may be due to ‘adaptive drift’ in the context of time-optimal migration. Interestingly, if birds are able to anticipate wind conditions ahead, then they might not aim to travel along a straight line at all, and migration routes may be fine-tuned by transient wind fields. In order to find out at what scale Honey Buzzards anticipate on wind conditions with respect to their seasonal destinations, I studied their orientation behaviour at an hourly resolution in chapter 5. I found that 11 out of 12 adult Honey Buzzards deliberately engage in a westward detour regardless of wind conditions over tropical western Africa, which is adaptive in the context of the dominant wind regimes further along the way. By moving westward before they arrive at the desert, the birds are least likely to get stuck in headwinds during the desert-crossing. Every year, one or two unfortunate birds run into delays over the Sahara. Fortunately, wind regimes are more forgiving for birds throughout the rest of the flyway, and while the Saharan wind regime counteracts migration in spring, it facilitates fast desert-crossings (also along a detour) in autumn.

Honey Buzzards mostly (over)compensated for wind when approaching the Mediterranean and while crossing the Pyrenees. This confirms my prerogative at the start of this dissertation that the flight behaviour of soaring birds at geographical convergence zones is likely to differ substantially from the behaviour of birds elsewhere along the flyway. Nevertheless, I argue in chapter 6 that the migration behaviour of Honey Buzzards is characterized by the avoidance of risk in the face of variable weather conditions across all scales of migratory movement, ranging from inter-thermal glides (chapter 2), over route adjustments within a geographical convergence zone (chapter 3) to regional and seasonal journeys (chapter 4 and 5).
While Honey Buzzards glide slower than they could along tortuous routes (chapter 2 and 4), they completed their journeys within 3-4 weeks every year. Some birds ran into delays of a week or more, which they usually accumulated while crossing the Sahara in adverse winds, and when they interrupted migration for one or more days in western Europe (chapter 6). While delays usually result in breeding failure, these long-lived birds arrive on time and in sufficiently good condition to initiate breeding in most of the years they return to Europe. As a result, there is no particularly strong selection in favour of fast migrants which ‘race against the clock’ for time-optimal migration. In fact, individuals which ignore atmospheric currents are likely to end up along more risky migration routes, for example by crossing the desert along a straight line (chapter 4 and 5).

My finding that risk-aversion shapes the soaring migration of Honey Buzzards from thermal to flyway is of immediate relevance for other soaring birds. Obligate soaring species are even more likely to optimize the efficiency with which they can use thermals and to reduce the need for flapping flight during migration. On the other hand, facultative soaring migrants must factor in the time they need for refuelling at stop-overs, and weather conditions will affect their refuelling schedules, such that they might take more risks with regard to weather during flight (chapter 3 and 4). Nevertheless, soaring birds demonstrate a range of intermediate strategies, relying on soaring flight and weather to a variable degree, even within species. While soaring migrants and flapping migrants have long been treated separately in ornithological literature, they should be seen as extremes within a continuum of analogous energy maintenance strategies which are driven by the seasonality in the distribution of their energy resources. Whether birds accumulate energy in thermals or at stop-overs, migration comes down to the efficient allocation of energy for long directed movement within a sufficient, rather than optimal, timeframe. Risk-aversion seems to be a characteristic and adaptive feature of migratory bird behaviour in the face of changing conditions throughout their annual cycle.
Samenvatting
Natuurvorser onderzoeken de mysteries van de vogeltrek reeds sinds het werk van Aristoteles. Onderzoek aan trekvogelgedrag bleef echter gedurende lange tijd beperkt tot de kennis die we konden verzamelen op basis van visuele waarnemingen van trekvogels. Dit is problematisch omdat trekvogels in het wild zich slechts op een beperkt aantal locaties goed laten observeren, en omdat zij zich op die locaties niet noodzakelijk op dezelfde manier gedragen als op andere locaties langs hun trekroute. Bovendien worden trekvogels tijdens hun flappende, golvende of zwevende vlucht sterk beïnvloed door de weersomstandigheden die ze tegenkomen onderweg. Weersinvloeden vormen het trekgedrag van vogels op verschillende schalen in tijd en ruimte. Lokale windomstandigheden bepalen de vliegsnelheid en vliegrichting van trekvogels, en dit heeft uiteindelijk een weerslag op de verspreiding van hun trekroutes, de snelheid en de timing van hun migratie, en de hun lichaamsconditie bij aankomst op hun bestemming. Lokale weersomstandigheden worden bovendien gestuurd door grootschalige luchtstromen en weersystemen, en lange-afstandstrekkers zullen gedurende een enkele reis verschillende weersystemen doorkruisen. Om de reactie van trekvogels ten aanzien van lokale weersomstandigheden ten volle te begrijpen moeten we hun vlieggedrag dan ook binnen de bredere context van dergelijke grootschalige weerspatronen kunnen onderzoeken. Dit is echter geen makkelijke opgave, en onderzoek aan weersinvloeden op trekvogels heeft in het verleden dan ook veel tegenstrijdige resultaten opgeleverd. Gelukkig bieden nieuwe technologieën, en met name de ontwikkeling van loggers en zenders, de mogelijkheid om het gedrag van vogels over steeds langere tijdspannes en afstanden te volgen. Zo is het nu haalbaar om belangrijke uitstaande vragen rond trekvogelecologie beter te gaan onderzoeken. In dit proefschrift combineer ik traditionele veldwaarnemingen van trekkende roofvogels met onderzoek op basis van GPS-loggers teneinde meer inzicht te krijgen in de invloed van weersomstandigheden op de zwevende trek van de Wespendief *Pernis apivorus*, een algemene en veel voorkomende trekvogel binnen de Afrikaans-Europese trekvogelroutes.

Zwevende vogels zijn een fascinerende groep onder de trekvogels. Door gebruik te maken van zonne-energie in de vorm van thermiekbellen zijn deze grote
vogelsoorten in staat om op energiezuinige wijze grotere afstanden af te leggen dan wat zij op eigen kracht zouden kunnen presteren. Dit maakt zwevende trekvogels echter ook afhankelijk van thermiek om überhaupt te kunnen reizen. Bovendien worden zij van hun vliegrichting afgedreven door de wind telkens zij in een thermiekbel cirkelen, waardoor ze in grote mate zijn overgeleverd aan de weersomstandigheden die ze tegenkomen onderweg. In hoofdstuk 1 geef ik een overzicht van de historische ontwikkelingen in het onderzoek naar de relatie tussen weersomstandigheden en vogeltrek alvorens de casus van zwevende trekvogels verder toe te lichten. De hoofdmoot van het onderzoek naar de invloed van weer op zwevende trekvogels werd in het verleden verricht in geografische ‘bottlenecks’: plaatsen zoals de Straat van Gibraltar waarlangs zwevende trekvogels in grote getale barrières zoals de Middellandse Zee omzeilen. Onderzoek op basis van visuele waarnemingen en radarmetingen in dergelijke ‘bottlenecks’ heeft aangetoond dat zwevende trekvogels vooral sneller reizen met rugwind en wanneer zij snel hoogte kunnen winnen in krachtige thermiekbellen. Het is vooralsnog echter onduidelijk waarom sommige zwevende trekvogels hun luchtsnelheid (m.a.w. hun vliegsnelheid ten opzichte van de lucht) aanpassen ten opzichte van de windomstandigheden wanneer zij van de ene naar de andere thermiekbel glijden. Zijwind heeft daarenboven een tegenstrijdige invloed op het lokale vlieggedrag van zwevende trekvogels tussen verschillende ‘bottlenecks’ en het blijft onduidelijk in welke mate regionale en seizoenale migratiepatronen tot stand komen onder invloed van atmosferische processen.

Om het fijnschalig vlieggedrag van Wespendieven langs hun volledige trekroute te kunnen onderzoeken maakte ik in hoofdstuk 2 gebruik van GPS-loggers met een experimenteel meetprogramma op hoge resolutie. Hieruit bleek dat de stijgsnelheid van Wespendieven in thermiekbellen zeer variabel is, en dat de vogels hun luchtsnelheid tijdens hun glijvlucht tussen thermiekbellen aanpassen in functie van de klimsnelheid die ze bereiken in een thermiekbel. Hoe sneller ze kunnen stijgen, des te sneller ze glijden. Dit is het gedrag wat men zou verwachten indien een vogel de totale duur van de migratie zoveel mogelijk tracht te beperken. In dat geval moet een vogel namelijk proberen om haar ‘zweefsnelheid’ (de gemiddelde luchtsnelheid
van aan het begin van één thermiekbel tot de volgende) te maximaliseren. De luchtsnelheid van Wespendieven tijdens het glijden was gemiddeld echter 2\text{ms}^{-1} trager dan wat volgens aerodynamische modellen optimaal zou zijn om de zweefsnellheid te maximaliseren. Bovendien verhoogden zij hun luchtsnelheid tijdens het glijden wanneer zij in tegenwind vlogen, en verlaagden zij die luchtsnelheid in een rugwind. Dit gedrag zou men verwachten indien een vogel de snelheid waarmee zij hoogte verliest probeert te minimaliseren, of in andere woorden, wanneer zij de lengte van haar glijvlucht tracht te maximaliseren. Een dergelijke strategie is vooral voordelig bij zwakke thermiek, met name wanneer thermiekbellen schaars zijn, omdat ze dan zelfs zonder actieve vlucht over grote afstanden in de lucht kunnen blijven. Een langere glijvlucht geeft echter ook voordelen bij goede thermiek, omdat de vogel zo tijd wint om beslissingen te nemen, wat nuttig kan zijn om te navigeren, of om de best mogelijke thermiekbellen in het omliggende landschap uit te zoeken. Mijn onderzoek toont aan dat Wespendieven tussen beide strategieën schipperen. Om nog beter te bepalen in welke mate de vogels hun zweefsnellheid dan wel de afstand die ze afleggen per glijvlucht proberen te maximaliseren zouden simulatiemodellen naast luchtsnelheid ook vliegrichting moeten optimaliseren, om zo ook rekening te houden met de invloed van oriëntatiegedrag en zijwind.

Omdat Wespendieven hun luchtsnelheid tijdens de glijvlucht compromitteren om de efficiëntie waarmee ze zweven te verhogen kunnen we verwachten dat zij ook hun route zullen verleggen op basis van waar de best mogelijke thermiek zich bevindt. De beschikbaarheid van thermiek wordt onder meer bepaald door het onderliggende landschap. Als zwevende vogels thermiekbellen kunnen vinden door soortgenoten en andere zwevende vogels te volgen dan zouden verschillende individuen een gegeven landschap op gelijkaardige wijze moeten doorkruisen. In hoofdstuk 3 heb ik geanalyseerd hoe honderdduizenden Wespendieven en andere strikt zwevende en facultatief zwevende trekvogels hun vliegroutes verleggen in functie van weersomstandigheden langs de oostelijke kustlijn van de Zwarte Zee, een belangrijke 'bottleneck' langs de oostelijke Afrikaans-Europese trekroute. De vliegroutes van zwevende trekvogels vertonen er dagelijkse en seizoenale
verschuivingen die samenhangen met verschuivingen in de lokale bewolkingsgraad. Grote, strikt zwevende trekvogels vlogen dichter bij de kust wanneer zij daardoor een dik wolkendek boven het landinwaartse bergmassief konden vermijden. Trekvogels die zwevende vlucht aanvullen met actieve trek werden daarentegen niet beperkt door bewolking en leken er vooral te aggregeren om gebruik te maken van de hoge voedselbeschikbaarheid langs de kust. Deze resultaten benadrukken dat de trekpatronen van verschillende types zwevende vogels door diverse omgevingsomstandigheden kunnen worden bestierd.

Gezien zwevende vogels in staat zijn om gunstige routes te kiezen in functie van beschikbaarheid van thermiek op lokale schaal lijkt het waarschijnlijk dat regionale en seizoenaire verschillen in de vliegsnelheid van trekvogels (m.a.w. hun snelheid ten opzichte van de grond) ook door weersomstandigheden bepaald worden. Dit is een belangrijke overweging voor trekvogelecologen omdat dergelijke grootschalige verschillen in de vliegsnelheid van trekvogels vaak worden toegewijkt aan regionale en seizoenaire veranderingen in de motivatie en conditie van vogels. In hoofdstuk 4 onderzocht ik in welke mate de vliegsnelheid van Wespendieven, alsook Grauwe Kiekendieven *Circus pygargus*, wordt bepaald door thermiek, rugwind en zijwind ten opzichte van hun vliegrichting, en dit van uur tot uur en van dag tot dag. Wespendieven vlogen significant sneller met een rugwind, en in mindere mate onder invloed van gunstige thermiek en zwakke zijwind. Grauwe Kiekendieven vlogen eveneens sneller met rugwind maar werden daarentegen niet beïnvloed door thermiek, noch door zijwind. Desalniettemin verklaren variabele weersomstandigheden zowat alle regionale en seizoenaire verschillen in de uurlijkse en dagelijkse vliegsnelheid van beide soorten, wat aangeeft dat migratiepatronen van zwevende vogels door grootschalige weerssystemen gevormd kunnen worden.

Zowel in het voorjaar als het najaar trekken Wespendieven langs een grote omweg over westelijk Afrika, maar ze kiezen een meer westelijke omweg in het voorjaar. De routes van individuen die gedurende meerdere jaren gevolgd werden met GPS-loggers bleken zeer variabel te zijn, wat suggereert dat hun omweg over Afrika in grote mate door grootschalige weersystemen tot stand komt. Gezien Wespendieven
en andere zwevende trekvogels gedurende het grootste deel van hun reis met een rugwind vliegen lijkt het erop dat zij langs hun omweg zo goed mogelijk gebruik proberen te maken van regionale en seizoenale wind regimes. Bovendien zou het kunnen dat zij anticiperen op voorspelbare windomstandigheden, in welk geval ze helemaal misschien helemaal niet in een rechte lijn over Afrika willen vliegen. Teneinde te bepalen in welke mate Wespandieven anticiperen op windomstandigheden keek ik in hoofdstuk 5 naar hun uurlijkse oriëntatiegedrag langs de volledige oost-Atlantische ‘flyway’. Van de 12 Wespandieven die ik onderzocht waren er 11 die tijdens het voorjaar opzettelijk langs een westelijke omweg naar Gibraltar trokken, ongeacht de windomstandigheden bij vertrek uit tropisch Afrika. Dit blijkt een gunstige aanpassing te zijn in de context van de dominante windregimes boven de Sahel en de Sahara. Door westwaarts te reizen lopen de vogels immers minder risico om boven de Sahara in een tegenwind terecht te komen, ook al waren er elk jaar wel één of twee vogels die boven de woestijn vertraging opliepen door tegenwind. Gelukkig zijn de windregimes elders in de ‘flyway’ over het algemeen relatief gunstig voor trekvogels. Zo is de windrichting gedurende het hele jaar vrij consistent boven de Sahara, waardoor Wespandieven in het najaar de woestijn meestal snel kunnen doorkruisen.

Wespandieven compenseerden vooral voor zijwind terwijl ze de Middellandse Zee naderden en tijdens de oversteek van de Pyreneeën. Dit bevestigt mijn oorspronkelijke aanname bij de aanvang van dit proefschrift dat het vlieggedrag van Wespandieven in ‘bottlenecks’ afwijkt van hun vlieggedrag daarbuiten. Desalniettemin beargumenteer ik in hoofdstuk 6 dat Wespandieven zich op elke schaal die ik onderzocht risicomijdend gedragen, gaande van hun gedrag tussen thermiekbellen (hoofdstuk 2) en hun routekeuze binnen een ‘bottleneck’ (hoofdstuk 3) tot regionale en seizoenale etappes van hun migratie (hoofdstukken 4 en 5).

Niettegenstaande Wespandieven trager vliegen dan wat mogelijk is tijdens hun lange omwegen (hoofdstukken 2 en 4) vervolledigen ze hun volledige migratie meestal binnen 3 tot 4 weken. Sommige vogels liepen een vertraging op van een week, soms zelfs langer, en dit gebeurde meestal wanneer ze vertraging opliepen.
tijdens de oversteek van de Sahara, of wanneer ze hun reis voor een of meerdere dagen hadden onderbroken in West-Europa (hoofdstuk 6). Hoewel vogels met een dergelijke vertraging gewoonlijk niet succesvol konden broeden arriveerden deze langlevende vogels in de meeste jaren wel op tijd, en in voldoende goede conditie om te broeden. Het lijkt er dus op dat er geen sterke selectie bestaat voor individuen die tijdens de trek ‘racen tegen de klok’. Vogels die geen rekening houden met atmosferische processen nemen immers onnodige risico’s, bijvoorbeeld doordat ze vast komen te zitten in een tegenwind boven de woestijn (hoofdstukken 4 en 5).

Mijn conclusie dat Wespendieven van thermiekbel tot ‘flyway’ risicomijdend gedrag vertonen heeft onmiddellijke gevolgen voor onderzoek naar andere zwevende trekvogels. Grotere, strikt zwevende soorten hebben nog meer baat bij het optimaliseren van de efficiëntie waarmee ze thermiekbellen gebruiken en bij het vermijden van actieve vlucht. Aan de andere kant moeten facultatief zwevende soorten ook rekening houden met de tijd die ze nodig hebben om op te vetten waardoor ze mogelijk meer risico’s nemen met betrekking tot het weer wanneer ze zich verplaatsen tijdens de migratie. Zwevende vogels vertonen dus een brede waaier aan trekstrategieën waarbij ze in verschillende mate afhankelijk zijn van zwevende vlucht en weersomstandigheden, maar dergelijke variatie zien we ook terug tussen individuen van dezelfde soort. Zwevende en actief trekkende vogels zijn in het verleden dan wel apart behandeld in de trekvogelliteratuur. Toch moeten we deze trekstrategieën begrijpen als extremen op een continuüm van analoge energiehuishoudingsstrategieën die tot stand komen in functie van de seizoenaal beschikbaarheid van energiebronnen. Ongeacht of vogels hun energie uit thermiek of uit voedsel putten, migratie is een proces waarbij een vogel de voor haar beschikbare energie zo efficiënt mogelijk moet aanwenden om een lange reis binnen een voldoende, en niet per se optimale, tijdspanne te vervolledigen. Risicomijdend gedrag is daarbij hoogstwaarschijnlijk een belangrijk aspect in het vlieggedrag van trekvogels, wat hen in staat stelt om te overleven onder voortdurend veranderende omstandigheden.
Samenvatting

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Author contributions

Chapter 2: The study was conceived by W. Vansteelant. W. Bouten and J. Shamoun-Baranes conceived the design of the flexible GPS system used for the study. JvD coordinated the catching and tagging of the Honey Buzzards and A. Schlaich, R. Klaassen and B. Koks coordinated catching and tagging of the Montagu’s Harriers. WV wrote the paper and performed the analyses in close deliberation with all co-authors. E. van Loon advised on statistical approaches in particular and all co-authors made significant contributions to the development of the manuscript.

Chapter 3: W. Vansteelandt conceived this study while monitoring raptor migration in Georgia with B. Verhelst and many other volunteers during Batumi Raptor Count 2008 and 2009. K. Bildstein advised WV at the start of this study during an internship at Hawk Mountain Sanctuary (PA, USA). W. Bouten and J. Shamoun-Baranes advised WV while completing this the study at IBED (UvA). E. van Loon consulted on analytical methods. WV wrote the paper with feedback from all co-authors.

Chapter 4: The approach to compare fine-scale flight behaviour with optimal soaring migration models was conceived by WMGV. WB and JS conceived the design of the flexible GPS system used for the experiment and WB and WMGV designed the measurement scheme. JvD coordinated the field work including catching and tagging of the birds and (with WMGV) performing manual downloads of the data. WMGV performed the analyses in close deliberation with all co-authors. JM derived equations for calculating optimal migration speeds, and assisted in model formulation and interpretation. Each co-author delivered valuable input to WV while writing the manuscript.
Chapter 5: W. Vansteelant conceived the study and conducted all analyses in discussion with W. Bouten and J. Shamoun-Baranes. The field work was coordinated by J. van Diermen and W. van Manen who also commented on interpretation of the analyses. WV wrote the paper with input from all co-authors.
Author affiliations (in order of appearance)

Wouter M.G. Vansteelant
Email address: vansteelant.wouter@gmail.com
Computational Geo-ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, the Netherlands

Judy Shamoun-Baranes
Computational Geo-ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, the Netherlands

James D. McLaren
Computational Geo-ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, the Netherlands

Jan van Diermen
Treetop Foundation/www.boomtop.org, Talmastraat 112 9406 KN Assen, the Netherlands

Willem Bouten
Computational Geo-ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, the Netherlands

Brecht Verhelst
Edward Grey Institute of Field Ornithology, Oxford University, Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom

E. Emiel van Loon
Computational Geo-ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, the Netherlands
Author affiliations

Keith L. Bildstein  
Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, 410 Summer Valley Road, Orwigsburg, Pennsylvania 17961, USA

Raymond H.G. Klaassen  
Dutch Montagu’s Harrier Foundation, P.O. Box 46, 9679 ZG, Scheemda, The Netherlands and Animal Ecology Group, Centre for Ecological and Evolutionary Studies, Groningen University, P.O. Box 11103, 9700 CC Groningen, The Netherlands

Ben J. Koks  
Dutch Montagu’s Harrier Foundation, P.O. Box 46, 9679 ZG, Scheemda, The Netherlands

Almut E. Schlaich  
Dutch Montagu’s Harrier Foundation, P.O. Box 46, 9679 ZG, Scheemda, The Netherlands and Animal Ecology Group, Centre for Ecological and Evolutionary Studies, Groningen University, P.O. Box 11103, 9700 CC Groningen, The Netherlands

Willem van Manen  
Treetop Foundation/www.boomtop.org, Tamastraat 112 9406 KN Assen, the Netherlands
Wouter M.G. Vansteelant was born June 29\textsuperscript{th} 1987 in Roeselare, Belgium. He fell in love with nature as a child and started birding in his teens. In 2008 he joined Batumi Raptor Count to help monitor and conserve migrant raptors along the eastern Black Sea coast in the Republic of Georgia. He has continued to work in raptor conservation at Batumi ever since and currently coordinates research activities in the Batumi bottleneck.

In spring 2011 Wouter worked as a Conservation Leadership Intern at Hawk Mountain Sanctuary (PA,USA) to study the influence of weather on raptor migration in Georgia. Later that year, he moved to the Computational Geo-Ecology group at the University of Amsterdam to start his Ph.D. research under supervision of Willem Bouten and Judy Shamoun-Baranes. In 2013 he was part of ‘Vogel het Uit!’, an award-winning project by the Computational Geo-Ecology research unit for integrating citizen science and bird tracking research using social media and a mobile app.

Wouter has a deep-rooted passion for nature conservation and science communication and he has frequently lectured about his research and conservation work at public events, ranging from international birdfairs to Lowlands University. He also sits as secretary in the Migrant Landbird Study Group.
List of publications:

Peer-reviewed


Popular scientific


Book chapters

Billions of birds migrate across entire continents each year. Yet we know very little about how weather conditions shape their epic journeys. In this dissertation, Wouter Vansteelant combines classic field observations and cutting-edge animal tracking technology in order to unravel how European Honey Buzzards *Pernis apivorus* negotiate the weather from thermal to flyway. Migrating birds are often thought to maximize their migration speed by adjusting flight behaviour to variable weather conditions. However, Honey Buzzards seem to compromise between time-optimal and risk-averse strategies across multiple scales of migratory movement, ranging from the speed at which they glide between thermals to the migration routes they choose during each season. The birds effectively allow themselves to be pushed by the weather during most of their journeys, travelling along detours in anticipation of large-scale wind regimes between Europe and Africa. Weather conditions thus greatly affect the routes and timing of individual migrants. Nevertheless, by going-with-the-flow Honey Buzzards avoid the risk of exhausting their energy reserves along the way while they manage to arrive on time to breed almost every year.