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How birds weather the weather: avian migration in the mid-latitudes

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1.1 Birds and migration

Historical evidence suggests that birds have captured the imagination of humans for a very long time. Perhaps the earliest evidence of this is a 30,000 year-old avian figurine carved from mammoth ivory that was found in the Hohle Fels cave of modern-day Germany (Conard, 2003). Since then, bird feathers have adorned religious and ceremonial artifacts and attire, and feathers, feet, blood, etc. often play a central role in ceremonial customs and rituals. From isolated island tribes to the raucous celebration of Brazil's carnival, these customs persist today. Bird-related imagery pervades our literature and art, from holy books to Shakespeare to political propaganda. In fact, specific birds have come to symbolize particular ideas: doves reflect peace; eagles suggest strength; owls invoke wisdom; swans denote beauty; storks are associated with birth and ravens with death.

It is really no wonder birds have captured our imagination so. They inhabit a realm of the earth that for most of our history was unavailable to us; they take to the air in flight. In so doing, they liberate themselves from the potential confines of geographical barriers that would otherwise restrict their habitat. They are thus able to travel often great distances to avail themselves of the most beneficial habitat for different life stage events: e.g. breeding, fledging, molting. During summer, migratory birds travel to higher latitudes in order to breed where long days produce bountiful food resources. Due to the often harsh winters associated with these latitudes, local competition for resources is reduced and can even be restricted to those organisms able to make the migratory trek each year. Their chicks having had the benefit of their first weeks spent in high latitude summer, these birds then make their way back

to the warmer climes of lower latitudes as summer days shorten and winter approaches. Clearly there are benefits of being so mobile; nonetheless, this lifestyle brings a set of unique hazards known only to migrants.

The migratory journey itself is fraught with potential dangers, and birds must successfully navigate through changing landscapes and environments. In the middle latitudes, through which migratory birds commonly pass, violent storms are often associated with the transition between summer and winter. Yet even during times of more serene weather, there is the potential for dehydration and/or emaciation. Birds may be blown off course, potentially over areas where rest and food are unavailable such as the open ocean. Presuming that a bird is able to complete its migratory journey, there is still the potential of arriving at the breeding location too early to find there is no food yet available or arriving too late and being unable to secure a mate or having too little time to fledge young. Nonetheless, an almost unfathomable number of migratory individuals of a dazzling array of species make these migratory journeys twice each year.

At times of peak migration intensity, airspace over large areas of Western Europe become saturated by a multitude of different bird species, at different elevations, leaving from different points of departure, and bound for different destinations. These birds are complex biological beings each making their own decisions in a dynamic world. Nonetheless, many of these decisions are markedly similar across quite large groups. Certain strategies, which are generally more successful than others, are perpetuated by natural selection. Thus, birds that make “good” decisions survive to migrate and produce offspring who are then more likely to make a similar decision when confronted with similar circumstances. It is due to this that we see the flight strategies of so many birds, even across species, converging at similar times and locations.

Research suggests that certain environmental cues trigger related responses among many bird species. The length of the day, in conjunction with an internal clock or biorhythm, has been suggested as a driver of migratory restlessness (Gwinner and Helm, 2003; Gwinner, 2003). While this circannual rhythm can explain seasonal variability in migratory activity, there can be large variation in the intensity of migration from day-to-day even during the peak of migration season (Richardson, 1978). This day-to-day variability is believed to be a result of birds choosing to migrate during times with preferential weather conditions, and the altitudes at which birds fly during migration is also believed to be influenced by meteorological conditions. Wind direction and speed, precipitation, humidity, cloud cover, surface pressure and the types and relative positions of frontal boundaries have all been suggested to influence migration to varying degrees (Richardson, 1978; Erni et al., 2002*b*; van Belle et al., 2007;

Yaukey and Powell, 2008). However, the specific weather variables that trigger particular responses in birds are difficult to pin down. For instance, we find statistical relationships between particular atmospheric properties and the intensity of migration, allowing us to model different aspects of migration; however, weather variables are known to be strongly correlated in time and space making causal effects rather difficult to discern even with advanced statistical techniques (Pyle et al., 1993). Richardson (1978) makes a distinction between ‘ultimate’ and ‘proximate’ factors influencing migration. He suggests that certain atmospheric variables have direct (i.e. ‘ultimate’) selective influence on the evolution of migration by way of their impact on survivability, whereas ‘proximate’ variables are those that birds use to make migratory decisions and can be ultimate factors as well or serve as proxies for (possibly difficult to detect) ultimate factors.

1.2 Navigation and orientation

In order to successfully and consistently complete migratory journeys, birds must have some mechanism(s) by which they orient (i.e. determine direction) and navigate (i.e. chart a course to a remote goal) (Able, 2001). While it has long been suggested that birds exhibit an endogenous migratory direction, guiding even inexperienced migrants in seasonally-appropriate directions, the mechanism by which birds discern this direction has been more elusive. Current theory suggests that birds may possess two magneto-detection senses used for orientation: one composed of magnetite in the beak and one composed of light-sensing cryptochromes in the eyes (Wiltschko and Wiltschko, 2005). A recent study has even identified a group of cells in pigeons’ brains that respond to the direction and strength of the Earth’s magnetic field (Wu and Dickman, 2012). Birds are also believed to use celestial visual cues to discern direction (Emlen, 1967), and some have suggested olfactory cues may be used in navigation as well (Wallraff, 2004).

In order to assess the amount of displacement from their preferred direction of movement, birds are believed to use visual cues to determine drift (Richardson, 1990*b*). Alerstam (1979) suggests that if birds do assess drift in this way, they may be able to fully compensate using fixed objects on the ground; however, if a bird attempts to fully compensate for displacement using objects that are themselves somewhat displaced by the wind (such as waves in the sea or clouds in the sky), the bird will actually incur drift equivalent to the speed at which the reference object is displaced. Sound has also been theorized as a potential supplementary indicator of drift for migrating birds (Griffin and Hopkins, 1974); however, no specific evidence of this has been

found.

It is unlikely that (particularly experienced) birds conduct migratory journeys using an endogenous direction alone. It is argued that along with various “compasses” to discern direction, birds develop a mental map of their environment through experience to assist in navigation (Able, 2001) and that they use visual landmarks and geomagnetic “signposts” to help discern their location (Åkesson and Hedenström, 2007; Wiltschko and Wiltschko, 2005).

1.3 Individual weather effects

A great deal of theoretical and empirical research has gone into understanding the influence of particular atmospheric components on different aspects of bird migration and physiology. Here we will outline the current state of knowledge with regard to these individual weather effects, particularly with regards to nocturnal migrants engaged in flapping flight but with some consideration of other types of migrants as well.

1.3.1 Wind

Wind condition is considered one of the more influential atmospheric components on bird migration (Alerstam, 1979; Liechti, 2006). Wind speeds are of the same order of magnitude as bird airspeeds, so it is easy to understand how the speed and direction of the wind can have a large impact on the efficiency of migration.

Wind is believed to be of primary influence on the departure decisions of migrants (Richardson, 1990*a*; Erni et al., 2002*b*). While some early research suggested contrariwise, it is rather well established that most birds prefer to initiate migration with tailwinds (i.e. winds supporting movement in seasonally appropriate directions) than headwinds (i.e. winds opposing movement in seasonally appropriate directions) (Richardson, 1978). Beyond this broad generalization, however, there remains some ambiguity. For instance, some research suggests that birds avoid initiating migration in high-speed winds (Schaub et al., 2004; Richardson, 1990*a*). This may be particularly true of diurnal soaring migrants that rely on thermal uplift to gain altitude and reduce the energetic costs of migration, since high wind speeds can disrupt thermal development; however, considering wind speed in isolation of wind direction ignores the fact that these two components are linked such that the influence of each on migration is dependent on the value of the other (see Chapter 3). Consider, as well, that if a bird has one preferred direction of movement, there are many more directions into which the wind could blow that are unsupportive than directions that are supportive, making increasing wind speed more

often undesirable. Nonetheless, it is possible that birds prefer lower speed winds regardless of direction, since a bird may be more quickly and dramatically blown off course by higher speed winds if the direction of those winds shifts. Regardless, some migration takes place in almost all wind conditions, and persistent wind patterns along particular migration routes – in combination with an individual’s fuel reserves and the refueling opportunities of a particular location – can affect the optimality of departing under particular wind conditions (Alerstam and Lindström, 1990; Weber et al., 1998; Weber and Hedenström, 2000; Erni et al., 2002*a*).

Once in flight, wind directly influences the groundspeed and track direction (i.e. direction of movement relative to the Earth) of individual migrants. Therefore, wind condition influences the optimality of a bird selecting a particular airspeed, route, and altitude (Alerstam, 1979; Liechti, 2006). To optimally utilize their fuel reserves, for example, birds are expected to reduce their airspeed in tailwinds and increase their airspeed in head- and side winds (Liechti, 1995). Radar observations of migrants in different wind conditions have tended to support these expectations; however, Shamoun-Baranes et al. (2007) have raised concerns over the legitimacy of the approach used in many of these studies. It is often assumed that birds should select flight altitudes that maximize wind support such that they minimize the time and energy required for migration. While many previous studies have suggested this to be the case (e.g. Schmaljohann et al., 2009; Liechti et al., 2000; Bruderer et al., 1995*b*), we have found that a more appropriate phrasing is that birds select altitudes to avoid prohibitive winds and that lower altitudes are generally preferred (see Chapter 5).

Coupled with inherent variability in individual preferences (e.g. differences in the preferred direction of migration) and priorities (e.g. soaring migrants needing to utilize thermal uplift), variation in flight behavior and individual responses to wind likely arise from variability in the navigational capacities of different species (or even different age groups of the same species), since a bird’s ability to identify its own location and the location of its goal has some bearing on the optimal strategy for dealing with winds (Alerstam, 1979). A bird that knows the explicit location of its final goal, for example, can continually reorient itself toward that final goal, always choosing the most direct route to its final destination. A bird following an endogenous direction, however, has to base all wind compensation decisions around the more immediate goal of maintaining that endogenous direction. Knowledge (or lack thereof) that birds may have of persistent wind patterns along the migration route can also affect the optimal strategy for dealing with winds (Alerstam, 1979). For instance, if a bird can assume that side winds will be evenly distributed from both sides

of its preferred direction over the course of the migration route, compensation for side wind displacement may not be beneficial. Similarly, the frequency of beneficial winds in an area affects optimal departure decisions (Weber and Hedenström, 2000), so knowledge of this frequency may influence a bird's tolerance for accepting suboptimal winds.

1.3.2 Temperature

Migrants are generally found to initiate migration during cooler temperatures in autumn and warmer temperatures in spring (Richardson, 1990*a*). Clearly, cooler temperatures in autumn and warmer temperatures in spring indicate the approach of winter and summer, respectively, and birds may have developed an increased urge to migrate in response to these conditions. In both cases, however, these variations in temperature are often associated with wind conditions that are supportive of migratory movement for the particular season: winds from lower latitudes support movement toward the poles and usher in warmer temperatures, while winds from higher latitudes support movement toward the equator and bring cooler temperatures. It is possible, therefore, that relationships observed between migration intensity and temperature could be a coincidental result of the more direct relationship between migration intensity and supportive wind conditions. During flight, both very high (see Schmaljohann, 2008, and references therein) and very low temperatures (Klaassen, 1996) likely hamper migratory efficiency (at least through their impacts on the rate at which a bird loses endogenous water), and there is potentially some optimal range of temperatures within which birds operate most efficiently. While very low temperatures are associated with higher rates of energy expenditure in birds at rest (Wikelski et al., 2003), it remains unclear if this persists in birds during flight – particularly since migrants employing flapping flight likely produce excess heat that is better dissipated in cooler temperatures.

1.3.3 Humidity

As with temperature, humidity is also correlated with other atmospheric variables and indicative of synoptic conditions. Thus, correlations found between migration intensity and (changes in) humidity may be coincidental. Alternatively, humidity may represent one of the 'proximate factors' suggested by Richardson (1978).

Several theoretical studies suggest that the flight range of migrating birds may be severely limited by dehydration (Carmi et al., 1992; Klaassen, 1995, 1996). Thus, birds should prefer conditions of higher humidity. Nonetheless,

Schmaljohann et al. (2009) specifically tested whether birds migrating through the Sahara Desert selected altitudes that minimized energy expenditure (i.e. selection based on wind condition) or altitudes that minimized the rate of water-loss (i.e. selection based on humidity) and found that birds primarily selected altitudes that minimized energy expenditure. Elkins (2004) suggests that high humidity may be troublesome in combination with freezing temperatures, which could lead to the accumulation of ice on plumage; however birds have been observed flying at altitudes with temperatures well below freezing even when the atmosphere was very humid such that the formation of ice crystals was to be expected (Bruderer, 1971).

1.3.4 Precipitation

It is generally accepted that birds prefer to avoid migrating during precipitation events (Erni et al., 2002*b*; Richardson, 1990*a*), and precipitation is suggested to depress migratory altitudes (Bruderer, 1971). Any precipitation is likely to inhibit visibility, making navigation and the avoidance of obstacles more difficult. Liquid precipitation has the potential to saturate a bird making it heavier (and thus less efficient in flight) and also making it more difficult for the bird to regulate its internal body temperature. Solid precipitation such as hail has the obvious potential to inflict bodily damage if a bird is struck, and there are reported cases of large numbers of birds being killed by hail (Gates, 1933; Smith and Webster, 1955; Stout and Cornwell, 1976). As well, precipitation (and the often associated cloud cover) tend to cool the surface of the Earth during the day, which suppresses the development of thermals supportive of soaring migration.

1.3.5 Atmospheric pressure

While a correlation between (changes in) atmospheric pressure at the surface of the Earth and migratory activity is found (particularly in autumn) in statistical analyses of the timing of bird migration in relation to weather (Richardson, 1990*a*), it seems unlikely that changes in surface pressure over time directly influence migratory efficiency to a significant degree. Rather, atmospheric pressure at the surface and its changes over time are determined by one's position relative to high and low pressure systems, which is indicative of synoptic level conditions and therefore the states of many atmospheric variables that likely do influence migratory efficiency such as wind speed and direction, temperature, and precipitation. Thus, atmospheric pressure at the surface may also represent one of the 'proximate factors' that birds use to determine the overall suitability of the atmosphere for migration.

Pressure varies much more dramatically with altitude than it does at the Earth's surface, however, and decreasing atmospheric pressure with altitude can have a significant impact on a bird's flight efficiency (Pennycuik, 2008). Changes in pressure affect the lift-to-drag ratio of a flying bird. As pressure decreases, it becomes easier for a bird to move forward because parasitic drag decreases, but at the same time it becomes more difficult for the bird to maintain altitude because induced drag decreases. The trade-off between the two is such that birds are generally able to make more efficient progress at higher altitude (i.e. lower pressure); however, the act of climbing requires energy (Hedenström and Ålerstam, 1992) that could otherwise be used to make forward progress, so a bird's flight must be sufficiently long to make up for the cost of climbing.

Atmospheric pressure is also directly related to oxygen partial pressure; as pressure decreases with altitude, so too does available oxygen. Birds have physiological adaptations resulting in a more efficient exchange of oxygen from the pulmonary to the circulatory system than mammals. For example, house sparrows (*Passer domesticus*) in a hypobaric chamber simulating atmospheric pressure at 6 km altitude were observed to be normally active, whereas white mice (*Mus musculus*) in equivalent conditions were described as 'moribund' and 'comatose' (Tucker, 1968). These sparrows even extracted a higher percentage of oxygen from the air entering their lungs at (simulated) 6 km than they did at sea level. It is argued, however, that because the birds have to increase pulmonary ventilation (i.e. take in more air) at higher altitude in order to extract sufficient amounts of oxygen, their rate of water-loss increases, which is expected to impose limitations on the bird's flight range (Carmi et al., 1992).

1.4 Atmospheric data

Atmospheric data of various types, obtained using a range of methods, are available in many different formats. The largest differences are perhaps between data that are measured using various instrumentation and data that are generated as output from models. Even this distinction, however, can be quite blurred. Atmospheric variables that are difficult to measure directly are often estimated using models describing their relationship with variables that are easier to measure. A variable as common as atmospheric humidity, for example, is rarely measured directly but rather estimated from calibrated relationships between it and variables easier to measure such as temperature, electrical resistance/capacitance, thermal conductivity, or absorption of particular bands of the electromagnetic spectrum (Foken and Nappo, 2008). As

well, measurements of various atmospheric variables are often used first to calibrate atmospheric models and then to validate (and even update) modeled output (see e.g. Kalnay et al., 1996). Conversely, modeling techniques are often used to fill gaps between and identify and correct errors in atmospheric measurements (see e.g. Hijmans et al., 2005).

In the following chapters, we make use of a variety of atmospheric variables obtained almost exclusively from gridded atmospheric models. Specifically, we utilize data from the National Centers for Environmental Prediction (NCEP) / National Centers for Atmospheric Research (NCAR) Reanalysis I data set (Kalnay et al., 1996), the NCEP / Department of Energy (DOE) Reanalysis II dataset (Kanamitsu et al., 2002), the analysis product of the European Centre for Medium-Range Weather Forecasts (ECMWF Persson, 2011) deterministic model, and the High-Resolution Limited Area Model (HIRLAM Cats and Wolters, 1996; Undén et al., 2002). The ECMWF and two NCEP data sets combine state-of-the-art analysis/forecast atmospheric models with data assimilation systems to produce high-quality gridded global datasets in a consistent manner over extensive time periods. They reflect a situation in which models and measurements are combined in order to maximize the full potential of each. The resolution of these global data sets can be somewhat coarse for some applications, however, which is why we have also utilized the HIRLAM data set. HIRLAM uses initial boundary conditions from a coarser-scale global model, such as ECMWF, and similarly combines analysis/forecast atmospheric models with a data assimilation system to downscale these atmospheric data to a higher spatiotemporal resolution over a reduced spatiotemporal extent.

While in-situ and remote-sensing based atmospheric products, i.e. data obtained from various measurement devices, were also available and appropriate for many of our analyses, our use of gridded-atmospheric data has specific advantages. In particular, use of these data sets ensures that the methods we apply are reproducible and exportable. Researchers in other locations are not dependent on the availability of measured data in their area to conduct our analyses, and the results of their analyses should be directly comparable to our own due to similar input data. As well, because the atmospheric models we use incorporate forecasting systems, the relationships we uncover between bird migration and atmospheric dynamics, and the models we develop to describe these relationships, can be applied toward the prediction of future migratory conditions.

1.5 Radar as a tool in bird migration studies

Radar utilizes radio waves, electromagnetic radiation with a range of wavelengths between 1 mm and 100 km, and radar measurements are obtained from a two-stage system composed of a transmitter or antenna to project electromagnetic energy and a receiver or dish to capture any of the electromagnetic energy that is reflected or scattered by a distant object. From the time delay between the transmission of the radar signal and the return of the radar echo, the distance of the remote object can be determined. As well, due to the Doppler effect, any shift in frequency between the transmitted and received radio waves indicates the motion of the object relative to the receiver; a shift toward higher frequencies indicates an object moving toward the receiver, while a shift toward lower frequencies indicates an object moving away from the receiver. Water containing some impurities (e.g. salt), scatters radar signals quite strongly, so biological targets such as birds, whose lean body mass is often composed of more than 50% water (Ellis and Jr., 1991) containing electrolytes, can produce quite strong radar echoes.

Eastwood (1967) recounts when birds were first regularly detected by radar in the 1940's, when higher-power S-band radars came into use. Initially unrecognized by radar operators as birds, these 'spurious' echoes were dubbed 'angels', and they understandably caused trouble for operators interested in monitoring aircraft. Realizing the potential of radar technology in ornithological study, researchers in England, Switzerland, and the United States during the post World War II era began independently to build a body of research confirming that birds could be measured with radar. Since that time, radar has become the primary tool to study the migratory flight behavior of birds in relation to the environment (Bruderer, 1997).

The application of radar methods in bird migration studies revolutionized the field through the middle of the 20th century and showed us, among other things, the sheer amount of migration that occurs outside of our range of vision, particularly during the night. Radar continues to be an invaluable tool in the study of avian migration, allowing us to accurately quantify what we would otherwise be unable to see. It provides a platform for making high-resolution, standardized measurements at different times and places of the location, speed, direction, and wing-beat frequency of migratory individuals as well as the size and altitude distribution of migratory populations.

Often radar systems are set up for a particular purpose, and this usually means that some feature of the radar is exploited at the expense of another feature. A radar system, for instance, that is meant to measure the speed, direction, and even wing beat frequency of individual migrants may only be able to sample a small portion of the migrants in a passing population. Al-

ternatively, a system that measures the speed and direction of all individuals in a passing population, and gives detailed information on the intensity of migration, may lack in altitude resolution, while a system with high altitude resolution may be unable to resolve the behavior of each individual migrant. Thus researchers must utilize the strengths of a particular radar system and also realize its limitations. Potentially, data from multiple radar systems can be combined in analyses such that the strengths of each system are exploited. Regardless, radar technologies continue to improve and we may ultimately be able to discern both individual and population level dynamics with high lateral, altitudinal, and temporal resolution in a single radar system. A particularly exciting potential exists through the use of Doppler weather radar. Recently, algorithms have been developed to automatically extract bird migration information from operational weather radar (Dokter et al., 2011), creating the potential to revolutionize the study of bird migration once again. One particularly beneficial aspect of this development is that large geographical areas are already covered by networks of existing weather radar. Networks such as these allow for continuous continental-scale analyses able to consider variation in migratory behavior between areas far-removed from one another.

In the analyses herein, we make use of data obtained from Medium-Power military tracking radar (MPR) and Doppler weather radar. The MPR is a 10 cm wavelength S-band radar used operationally by the Royal Netherlands Air Force (RNLAf) to monitor the airspace over the Netherlands and track aircraft for military purposes. The MPR was equipped with the ROBIN4 (Radar Observation of Bird Intensities) software, developed by TNO Defense, Security, and Safety, to discriminate birds from other objects like aircraft and precipitation. Speed and direction can be discerned and measured by the MPR for individual birds at distances greater than 50 km and for flocks of birds at distances greater than 100 km. The MPR also provides information on the intensity of migration; however, the altitude resolution of this radar system is rather poor. The weather radars used in these analyses are 5 cm wavelength C-band Doppler radar used operationally by the Royal Netherlands Meteorological Institute (KNMI) to monitor atmospheric phenomena such as precipitation and wind condition. The algorithm developed by Dokter et al. (2011) allowed for the automated extraction of bird movement data from these weather radars, which were validated in a field campaign using a 3 cm X-band dedicated bird-detection radar of the type ‘Superfledermaus’ (Bruderer et al., 1995a). Migration intensity, along with the speed and direction of passing populations, is measured by these weather radars and summarized over the entire radar volume at discrete altitude intervals of 200 m thickness. Tracks of individual migrants are not calculated from these weather-radar data, however,

and the geographical extent of these radar measurements is much smaller than that of the MPR. Neither of the radar systems used in these analyses provides information on species composition, and both suffer from the well-known shortcoming of the use of radar in ornithology which is that birds in the lowest altitude layers are often missed due to interference from ground clutter.

1.6 The importance of tools and methods for efficient analysis

There are a great many seasonal and environmental factors influencing migration, and the particular influence of many of these factors can depend on the state of other factors. As well, there are a great many methods by which to quantify migratory activity. While this thesis focuses on radar methods, data from counting and ringing campaigns as well as various tracking devices, which continue to become lighter, smaller, and more accurate and energy efficient, provide a wealth of information that can quickly overwhelm. Equivalently, environmental data sets exist at increasingly higher spatial and temporal resolution, and, particularly concerning tracking devices, the spatial domain that must be considered is not known a priori and can be quite extensive.

Because of this, large amounts of data must be managed and organized and the efficiency with which this is done determines the overall effectiveness of migration research. Consider a researcher interested in birds' reaction to wind. This researcher spends time to manually collect relevant wind data and merge them with his or her bird data only to discover that the wind data retrieved describes wind conditions at an undesired altitude. The researcher must then start over and manually retrieve the wind data once again, being sure (again) that each mouse-click and key-stroke is correct. This same researcher, after obtaining wind data for the correct altitude, finds some significant results and shares these results with some colleagues in other locations who have similar sets of bird data. Before these new researchers can perform the same analysis, they must each retrieve wind data yet again for their particular location – which buttons did the first researcher click again? Now consider an alternative. Instead of manually retrieving their wind data, the original researcher integrated the retrieval of wind data into their analysis, likely through the use of a scripting language (e.g. R, Python, or Perl). Further, the original researcher designed the data retrieval portion of their analysis in a robust and flexible way such that adjusting the altitude and/or location from which the wind data were obtained required only that a few parameters be modified. While the first iteration of data retrieval is likely to be more time consuming

using this approach, this extra time is regained in spades by significantly reducing the time needed to retrieve the data for modifications and extensions to the analysis.

Analyses performed in this way are also explicitly reproducible. Along with the manuscript describing their results, researchers can provide unambiguous descriptions of their analyses in the form of a ‘script’. In doing so, any issues arising from data handling and processing are captured and traceable. Research conducted following this paradigm has one further advantage in that these scripts are effectively tools that can be used by others. Rather than each researcher needing to develop an equivalent tool, tools that are effective can naturally propagate through the scientific community. Through the use of open-source scripting languages, extensions, modifications, and improvements can be continually incorporated. Because of the benefits of research carried out in this way, we have developed a tool in the open-source R language (described in Chapter 2) that allows researchers to quickly and easily incorporate weather and climate data in their analyses.

The efficiency and effectiveness of bird migration studies is also determined in large part by the flexibility of the tools and methods used to visualize data during the exploratory phase of analyses. Interactive research environments, which allow for the rapid merging and visualization of many types of data, can minimize potential bottlenecks associated with suboptimal visualization. In light of the benefits of such a research environment, we have developed the Virtual Lab for Bird Migration Modeling (VL-BMM) combining a high-performance computing environment, multiple high-resolution monitors with variable modes of input, and high-speed access to relevant databases. As well as maximizing individual research potential, the VL-BMM facilitates collaboration as experts with different backgrounds (e.g. ornithology, meteorology, statistics) can interactively explore and discuss data and formulate and test ideas quickly and efficiently. The VL-BMM is also portable, making it useful for demonstrations, community outreach programs, and discussions with members of industry (e.g. aviation, military, and wind-energy production) who can benefit from products (e.g. forecast models) arising from bird migration studies.

1.7 Synopsis

The chapters herein span a range of topics centering around the relationship between birds and weather. We begin with two chapters describing tools, concepts, and methods meant to facilitate and guide analyses of bird migration in relation to weather. In Chapter 2, we introduce the RNCEP package

of functions to assist with the incorporation of atmospheric data in ecological studies. In Chapter 3, we discuss different methods of quantifying wind support for animals moving in flows. These methods require making specific behavioral assumptions, which we have incorporated into a dynamic simulation model built on functions contained in the RNCEP package. We then move on to two chapters exploring some specific influences of weather on migratory dynamics. In Chapters 4, we consider how persistent wind patterns, in relation to the direction of migratory flight, can influence migration speed, specifically affecting differences in migration speed between spring and autumn. In Chapter 5, we consider atmospheric factors that may influence the altitudes birds choose during migration. We attempt to determine the specific influence of these factors and the priority birds give each. Lastly in Chapter 6, we consider a practical application of bird migration studies in the context of flight safety. This chapter is quite different from the rest, as it is not concerned specifically with which atmospheric factors influence migration and how. Rather, we outline a method in this chapter to develop predictive models of migration intensity with the aim of providing accurate predictions rather than biological insight.