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

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Publication date
2012

[Link to publication](#)

Citation for published version (APA):

Kemp, M. U. (2012). *How birds weather the weather: avian migration in the mid-latitudes*. [Thesis, fully internal, Universiteit van Amsterdam].

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General discussion and synthesis

7.1 Weather or climate?

Tinbergen (1963) posited that, for a complete understanding of any animal behavior, four fundamental questions concerning said behavior should be addressed: mechanism (called ‘causation’ by Tinbergen), adaptation (called ‘survival value’ by Tinbergen), ontogeny, and phylogeny (called ‘evolution’ by Tinbergen).

Mechanistic questions concern the behavior itself: what exactly is the behavior, what processes are involved, and how is the behavior carried out? Questions of adaptation are concerned with why a particular behavior is advantageous to the animal in terms of its survival (or, perhaps ultimately, the survival of its offspring). Ontogenic questions deal with the developmental stages in an animal’s life-cycle that have resulted in a particular behavior; questions of ontogeny often attempt to distinguish between innate and environmentally-induced behavior. Phylogenetic questions concern the progression of ancestry, selected by nature, that has resulted in a particular animal exhibiting a particular behavior. Mechanistic and ontogenic questions are generally concerned with ‘how’ a behavior occurs, whereas adaptive and phylogenetic questions are concerned with ‘why’. Questions of ontogeny and phylogeny are considered ‘dynamic’ in that they address a sequence of events that has resulted in a particular behavior, whereas questions of mechanism and adaptation are considered ‘static’ in that they are concerned with the behavior itself.

The analyses herein have been devoted primarily to understanding bird behavior in response to atmospheric conditions. Atmospheric dynamics can have an impact on the answers to each of Tinbergen’s four questions; however

some questions are better addressed through considerations of ‘weather’ while others are best addressed with considerations of ‘climate’. Weather describes short-term atmospheric conditions and fluctuations, while climate describes long-term averages and trends of atmospheric conditions. Perhaps more succinctly, “climate is what you expect, weather is what you get”. Thus, questions regarding the influence of atmospheric processes on avian behavior in terms of phylogeny and (perhaps to a slightly lesser degree) ontogeny correspond with climatic conditions. Conversely, questions regarding the influence of atmospheric processes on avian behavior in terms of causation and function (i.e. mechanism and adaptation) correspond with weather conditions.

In Chapter 3, we considered different behaviors that birds can adopt to deal with various wind conditions. These behaviors differed largely with respect to the bird’s degree of compensation for side-wind displacement. We then illustrated how these behaviors can impact travel speeds, routes, and the probability of successful arrival. Thus, we examined the mechanism of compensation and the potential adaptive or survival value of the different behaviors. In that context, we considered behavioral responses to instantaneous wind conditions (i.e. weather); however in Chapter 4, we examined persistent wind patterns over 30 years to determine if these persistent (i.e. climatic) dynamics could affect differences in avian migration speed between spring and autumn. These wind patterns may not only influence an individual bird’s migration duration over a particular season, persistence in these conditions may influence many aspects of avian behavior. Birds may learn to anticipate particular wind conditions at different times and locations and adapt their wind selection and compensation and navigation strategies in response (i.e. ontogeny see e.g. Klaassen et al., 2011; Thorup et al., 2003; GagHardo et al., 2001). As well, these persistent wind patterns have shaped ancestral dispersal, influencing current migration routes (i.e. phylogeny Alerstam, 2001). On an evolutionary scale, adaptation to persistent patterns in wind conditions is a potential explanation for some ‘loop’ migrations (cf. Berthold, 2001; Alerstam et al., 2003) in which a bird’s outbound and return journeys follow different paths.

Because atmospheric conditions, expressed as both weather and climate, can influence many aspects of avian behavior, we introduced the RNCEP package of functions in Chapter 2 that can be used to quickly retrieve weather data for any location on Earth and subsequently calculate climatic variables from those data. Similarly, the flight simulator function in the RNCEP package can be used to consider individual migratory flights at particular times and locations, or it can be used to consider the same migratory flight over a sequence of many days, months, or years. Thus, this suite of functions is useful

when addressing questions of a mechanistic, adaptive, ontogenic, or phylogenetic nature.

7.2 Optimal migration

Optimal migration theory defines a framework around which questions concerning the adaptive or survival value of behaviors may be examined (Alerstam, 2011); however, the application of optimal migration concepts depends on our having a correct understanding of what criteria determine optimality, particularly when multiple objectives are being optimized simultaneously. The ultimate measure of the optimality of a particular behavior is its effect on an animal's fitness (i.e. the animal's ability to produce viable offspring). We often consider, as proxies for fitness, more immediate optimality criteria including energy consumption, time expenditure, predation risk, and survival probability, and we often assume that for a behavior to persist it should be optimal. This is probably a good assumption in practice, since nature does not indefinitely tolerate inefficiency; however, behaviors can be optimal only in relation to the particulars of the environment, which are constantly changing. Thus, it is probably unavoidable that suboptimal behaviors exist as environments are dynamic and heterogeneous. An optimal behavior today in one location may be suboptimal tomorrow in a different location. As well, behavior that is globally optimal (i.e. optimal in the widest range of circumstances) may appear decidedly suboptimal for any one time and location. Furthermore, what is optimal behavior for a particular species may not be optimal for all individuals of the species, though individual variability by the members of a species likely makes the species as a whole more robust against the uncertainties of a dynamic environment. Regardless, no species or individual can exhibit optimal behavior in all regards, since to optimize one criterion often necessitates a sacrifice of another. This situation, thankfully, leads to conditions in which no single species dominates all niches and multiple species can coexist.

While natural systems are deterministic, i.e. they are determined explicitly by prior events, they are also chaotic. Small variations in any of an infinite number of determining factors can accumulate through the system and produce wildly different outcomes. Weather is a prototypical chaotic system described metaphorically by the 'butterfly effect' (Abraham and Ueda, 2000), which has become synonymous with chaos theory. Owing to this chaos, an 'optimal' behavior in some cases may be to remain flexible in response to particular stimuli. For instance, it is often beneficial for a bird to delay migration until wind conditions are supportive; however, it is probably not beneficial for this behavior to be hard-coded such that a bird will not migrate

without supportive winds, particularly if supportive winds are very infrequent (Weber and Hedenström, 2000). Unsurprisingly, research suggests that birds often do migrate without tailwind assistance, particularly in locations where tailwind support is infrequent, but that the birds still preferentially select less-prohibitive wind conditions from those available (see e.g. Karlsson et al., 2011; Erni et al., 2002*b*). We found complimentary results in Chapter 5 in which birds showed a preference for altitudes with better wind conditions, but were not blindly driven to seek out the most supportive winds available. Rather, birds were balancing trade-offs between different immediate optimization criteria in order to maximize the most important optimization criterion: successfully passing their genes onto the next generation. It seems that in altitude selection as in the timing of migration, bird's behavioral responses to wind (at least) are flexible and somewhat opportunistic.

7.3 Robust decision-making

Behavioral responses should probably be based on multiple stimuli rather than on a single factor whenever possible. The Three Mile Island nuclear disaster in the United States in 1979 illustrates this point, as the meltdown was due in large part to operators relying on a single sensor. Unbeknownst to the operators who had come to rely on the sensor, it was only indirectly related to the state of the system (Rogovin and Frampton Jr., 1980). Consulting other sensors would have indicated the true situation, or at least suggested a disagreement between sensors. When multiple cues are consulted, decision making is more robust against potential errors between a particular cue and the outcome it suggests. Unsurprisingly, we find that birds do utilize multiple sources of input to make decisions. In navigation, for example, birds consult the sun and stars, as well as geomagnetic references, landmarks, and perhaps even scent to determine their location in relation to their goal (Able, 2001; Wallraff, 2004; Åkesson and Hedenström, 2007; Wiltschko and Wiltschko, 2003). Debate remains regarding how birds prioritize between these cues and codify them into a single indication of direction, but Liu and Chernetsov (2012) reviewed studies with conflicting results on this point and have suggested that the conflicts may be due to genuine differences between species.

In navigation, issues such as the sizes and locations of ecological barriers can affect the optimality of a bird selecting a particular route; however, navigational cues (e.g. celestial, geomagnetic, and landmark indicators) should all theoretically agree on a bird's location in relation to its goal. If there is disagreement, one or more of the cues are incorrect and the bird must decide which to believe. Atmospheric variables, on the other hand, may often

give conflicting cues that are each correct (e.g. wind conditions are supportive, indicating to the bird that it should migrate, but at the same time a change in atmospheric pressure is indicating an approaching storm). When different atmospheric cues give conflicting signals, birds should consider the impacts suggested by each cue individually because of the independent influences of the different atmospheric components. Certain atmospheric variables may take precedence in particular situations, but only when other variables are determined to be within acceptable limits. The dynamics and thresholds of acceptability and optimality remain in flux because the optimal decision with regard to one variable is determined by the states of all other variables.

Naturally, optimal decision-making depends as well on an individual's tolerances and capabilities with respect to different atmospheric conditions. The influence of decreasing air pressure with altitude, for instance, affects the flight dynamics of birds differently depending on their morphology (Penny-cuick, 2008). Differences in flight capacity can determine in which wind conditions birds can make forward progress or in which wind conditions a bird can fully compensate for sidewind displacement. Swanson and Liknes (2006) showed that bird species exhibit differences in their ability to tolerate cold temperatures. Although that study considered birds at rest, differences in the thermoregulative capacities of birds likely persist in flight. Thus, different bird species may prioritize atmospheric variables differently and therefore base their decisions more heavily on particular atmospheric cues, similar to the intra-specific differences in the prioritization of navigational stimuli suggested by Liu and Chernetsov (2012).

7.4 Assessing wind drift

What is made clear throughout these analyses is that weather has a strong impact on the decisions made by migrating birds. We have examined what birds do in response to particular atmospheric conditions, and we have postulated as to why birds might react in the ways we observe. Thus, we have primarily focused on the 'why' questions of phylogeny and adaptation. We have not considered in great detail, however, how birds are capable of reacting in the ways we observe. For instance, we have seen that birds adjust their timing and altitude selection during migration at least partly in response to weather conditions. In particular, birds seem to avoid wind conditions that prohibit their movement in seasonally appropriate directions. In order to choose between wind conditions, particularly with regard to altitude selection, a bird must have some way to determine the influence of different wind conditions.

Being primarily Earth-bound, it may be difficult for humans to compre-

hend a bird not being able to perceive the influence of wind. When we ride a bike, for instance, we can see the progress we are making, and we can feel the wind pushing us in a particular direction. The reason we are able to judge the influence of the wind while cycling is because we are bound to the “stationary” Earth and can use it as a frame of reference. We know that we want to proceed along a particular direction relative to the Earth and by visually assessing our speed in that direction (and accounting for the effort we are exerting), we get an indication of how much the wind is assisting or prohibiting our movement. As well, we are able to feel the speed and direction of the wind because we are not generally moving along with the wind and are instead, for all intents and purposes, bound to the Earth. We therefore feel pressure in the direction from which the wind is blowing, and the intensity of this pressure indicates the wind’s speed.

A bird in flight should also be able to utilize the fixed Earth as a visual point of reference and determine how the wind is effecting its progress; however, there are complicating factors to consider. Many species, particularly passerines which were the focus of much of this thesis, migrate at night; so on moonless nights, particularly in areas with sparse human populations, Earth-bound objects may be difficult to see. Cloud, haze, or fog may obscure a bird’s view of the Earth as well. Even under the best atmospheric conditions, the higher a bird flies, the shallower the angles become between it and its ground-based points of reference. The shallower these angles become, the more difficult it is to visually assess movement in relation to the reference object, which is why the stars (while helpful in determining direction) are useless in assessing wind drift – they are simply too far away.

We may be tempted to evaluate a bird’s perception of its environment in terms of our own senses. After all, ours are the only senses we have to experience the world. Even things that we can “sense” using instrumentation, we must translate to a medium that we can sense unaided in order for us to process the information; consider, for example, our use of “false color” to view parts of the electromagnetic spectrum outside of our visible range or high-speed photography to view actions that are too fast for our eyes to perceive. Because we view the world through our own senses, it is difficult for us to imagine, for example, what it means to “sense” the Earth’s magnetic field as birds do. We understand, however, that this is a sense quite different from any of our own and therefore requires scrutinization. We may be less discerning of senses that we share with birds (such as vision), expecting that these senses function similarly to our own, but we would be remiss in doing so. Birds are much more visually acute than humans and have significantly larger eyes relative to their body size than other vertebrates. Consider that approximately

50% of the volume of a bird's cranium is dedicated to housing its eyes, while human eyes occupy only about 5% of the volume of their skull (Waldvogel, 1990). The relatively large size of bird's eyes is not only indicative of the importance of vision in the life of birds, larger eyes allow for larger images to be projected onto the retina increasing visual acuity (Jones et al., 2007). Bird's large lateral viewing area (Martin, 2011) allows them to simultaneously consider their movement relative to several reference objects on both sides of their head, which should aid in their ability to quickly and accurately assess wind drift by visual means Liechti (2006). Another important aspect of avian vision is their 'flicker-fusion frequency' or the frequency at which they can visually resolve images. Humans perceive continuous motion in images flickering at rates above 50 to 60 Hz, and images flickering at even higher rates become blurred, unstable, and erratic in human vision. Birds have a much higher flicker-fusion frequency than humans and can resolve individual flickers at rates upwards of 100 Hz (Jones et al., 2007). As well as helping birds to avoid obstacles by allowing them to resolve the very fast movements associated with high-speed flight, this high flicker-fusion frequency also enables birds to better detect very slow movement. For instance, unlike humans, birds are able to visually detect the movement of the sun and stars (Jones et al., 2007). It is reasonable to suspect, therefore, that birds are more capable of assessing wind drift by considering the relative motion of reference objects on Earth than humans would be at equivalent altitude. So with a visual point of reference, birds are well-adapted to assess the influence of different wind conditions on their movement.

Research has suggested that some migrants can assess wind conditions even without having a visual point of reference on the Earth (see Richardson, 1990*b*, and references therein); however, a cogent theory to describe how birds can assess wind drift without a visual point of reference has been elusive. Nonetheless, birds have been observed with radar maintaining constant flight trajectories even when their view of the Earth was totally obscured. Without evidence suggesting otherwise, we may assume that a bird in flight is unable to feel the wind the way we do on Earth. Pressure, which we said is what we feel from the wind on Earth, describes a force defined as mass \times acceleration. The wind exerts a force on us and we exert an equal and opposite force so as to maintain our position. It is the acceleration of the wind that we feel, not the movement. A bird in the air, without a visual point of reference, will be moved along with the wind and, therefore, will not feel any acceleration. Consider that when cycling at the same speed and in the same direction as the wind, we are unable to feel the wind directly; however, because we are on the Earth, we are able to determine that we are moving faster than we should

be for the effort we are exerting. Thus, a bird moving along with the wind without a visual point of reference would likely be unable to feel the wind itself; nonetheless, the bird may be able to feel changes in wind condition, because changes denote an acceleration. The problem, however, is that while the bird may be able to feel the way in which the wind is changing, it won't know the state from which the wind is changing. In other words, a bird without a visual point of reference can feel the fluctuations around the mean wind conditions but never knows what those mean conditions actually are. That is, unless there is anisotropy in these fluctuations that provides information on the mean airflow. Reynolds et al. (2010) have suggested that there is in fact asymmetry in these fluctuations and have theorized that insects can use this information to orient in relation to the wind. The ability to detect these fine-scale fluctuations has not been convincingly demonstrated in birds, though the potential for birds to utilize this information has been theorized for some time (Larkin, 1980).

Birds may also be able to assess wind drift without a visual point of reference by calibrating an alternative reference system while visual points of reference are available. For example, a bird could determine the pressure field it experiences when it is compensating for displacement using visual points of reference. Once the visual points of reference are unavailable (e.g. after the sun has set or when the bird has climbed to higher altitude or flown over a dense cloud layer), the bird may be able to maintain its degree of compensation by maintaining the pressure field it determined was appropriate. A bird that assessed drift in this way would continue to compensate for the wind conditions it experienced when it calibrated the reference pressure field and would not be able to account for changes in wind condition that occurred thereafter. Liechti (1993) found that birds at high altitude appeared to compensate for displacement according to the wind conditions at lower altitude, which is in accordance with birds assessing drift in the manner just described.

Many of the theories developed concerning avian migration inherently assume that birds are able to assess the effect of the wind on their progress. For instance, those of the flow-assistance models we introduced in Chapter 3 that assume compensation implicitly assume that birds can assess the effect of the wind in order to compensate for it. The accompanying trajectory simulator (i.e. the FLAT model) then applies these assumptions to move a simulated bird through space, even in locations where the means by which birds determine the effects of wind are uncertain (such as at sea). We observe birds behaving in ways that suggest they are able to determine the effects of wind. For instance in Chapter 5, we found that wind was important in altitude selection, implying that birds are able to distinguish between the effects of wind at dif-

ferent altitudes. Nonetheless, we should consider when and where this ability to assess the influence of wind is feasible (and at what level of accuracy). Also in Chapter 5, we found that wind support relative to support at the surface was better able to describe altitude distributions than wind support relative to all altitudes. Perhaps birds consider wind conditions with respect to conditions at the surface because conditions assessed near the surface are easier to determine and more reliable.

Clearly, gaps remain in our knowledge of the sensory abilities of birds to judge the atmosphere, particularly when they are in motion. Future research utilizing high-resolution GPS tracking data, perhaps in combination with simulation models such as the FLAT model described in Chapter 3, may indicate when and where birds are (un)able to assess the influence of wind, potentially providing insight into the mechanisms involved.

7.5 Quantifying model performance

Many of the analyses in this thesis rely on models of one sort or another to either capture relationships contained in data (e.g. Chapters 5 and 6) or conceptually reduce a system to some manageable core components (e.g. Chapter 3). Models can be quite useful tools both for increasing our understanding of a system and for generating predictions of future conditions; however, the measure according to which a particular model's performance should be assessed is not always so clear.

In theory, the measure used to assess a model's performance should depend only on the goals one hopes to achieve with the model. In reality, however, there are limitations on what is quantifiable, and researchers must often aggregate (i.e. summarize) measurements and/or predictions and describe model performance based on those aggregates. In studies of altitude selection by avian migrants, for instance, researchers have often extracted a single attribute of an altitude distribution of migrants for examination – for example, the altitude with the greatest number of birds (e.g. Gauthreaux, 1991) or the altitude above or below which some proportion of the birds occurred (e.g. Shamoun-Baranes et al., 2003*b*). Particularly if the aim of the research is to better understand variability in these specific attributes, using these aggregated descriptors is beneficial (or at least not limiting). We began examining altitude distributions by applying just such a method in Chapter 5; however, the decision to use these aggregates may also be based on the fact that it is more difficult (both technically and conceptually) to consider altitude profiles in their entirety. In particular, there is a statistical challenge to quantitatively compare modeled and predicted distributions of any kind.

We applied several measures in Chapter 5 to compare predicted and measured altitude distributions of avian migrants. We compared these distributions by ranking the altitude bins and determining the correlation between the ranks. This measure, called Spearman's ρ , is an ordinal-level measure of association that has been applied in several previous studies for the purpose of comparing predicted and measured altitude distributions of avian migrants (e.g. Liechti et al., 2000; Schmaljohann et al., 2009) and has the benefit of being easy to apply and interpret. As well, Spearman's ρ can be used to compare measurements and predictions that are on different scales. For instance, measured altitude distributions of avian migrants can be compared directly with altitude distributions of wind support or estimates of flight range. This method has its weaknesses as well: e.g. absolute comparisons are not possible, and the influence of each altitude bin is equivalent regardless of how many birds are or are not present. Consider a situation in which 90% of birds are observed in only one altitude bin and the other 10% of birds are scattered throughout the remaining altitudes. A model then predicts that 90% of birds will occur in the correct altitude bin and the other 10% of birds are scattered throughout the remaining altitudes. Even though 90% of birds were correctly predicted in the one altitude bin, the Spearman's ρ correlation between the predicted and measured distributions will be dominated by the influence of the 10% of birds scattered throughout the remaining altitude bins of the measured and predicted distributions. Consider another situation in which predicted and measured distributions over 20 altitude bins are compared. Suppose that birds are only ever present in the lowest 10 altitude bins. A model that predicts all birds occurring in the lowest 10 altitude bins, but predicts the distribution of those birds in the lowest 10 bins completely at random, will on average have a Spearman's ρ correlation of 0.86 with the measured distribution. This suggests quite a strong correlation, but all that is truly known about the system is that birds always fly in the lowest 10 altitude bins. Therefore, another weakness of Spearman's ρ is its dependence on particular features of a dataset (e.g. the number of altitude bins), often disallowing meaningful comparisons between the results of different studies.

In an effort to arrive at more quantitative comparisons between predicted and measured altitude distributions of birds, we applied two other measures: root-mean-squared-error ($RMSE$) and the proportion of variance explained (Var_{exp}). $RMSE$ is defined as

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (x_i - y_i)^2}{n}}, \quad (7.1)$$

and we calculate Var_{exp} following Bruderer et al. (1995b) as

$$Var_{exp} = 1 - \frac{\sum_{i=1}^n |x_i - y_i|}{\sum_{i=1}^n x_i + y_i}. \quad (7.2)$$

In both cases, x_i are measured values and y_i are predicted. These two measures require predictions to be on the same scale as measurements, so comparing altitude distributions of wind support and altitude distributions of proportional bird density are not possible. These are both ratio-level measures of the accuracy of predictions, which can be used to quantify error per altitude bin; Spearman's ρ , on the other hand, summarizes all altitude bins in a profile with one value. There is one potential aspect to consider, however, when comparing predicted and measured altitude distributions, that *RMSE* and *Var_{exp}* cannot capture. These altitude distributions are determined over space, vertically, but neither *RMSE* nor *Var_{exp}* considers how close the predictions were to the measurements in terms of distance over vertical space. As a simple example, suppose that all birds were measured in one altitude bin centered on 0.3 km. According to either *RMSE* or *Var_{exp}*, predictions are considered equally incorrect if all birds are predicted in one altitude bin centered on 4 km or one altitude bin centered on 0.5 km. Clearly, a prediction that places birds in a bin 3700 m away from the proper bin is less correct than a prediction that places birds in a bin 200 m away, but *RMSE* and *Var_{exp}* do not reflect this.

For examining avian altitude distributions in future research, and developing models to predict avian altitude distributions, we suggest that another measure of model performance be considered, perhaps alongside those previously mentioned. This measure, called the earth movers' distance (*EMD*; Haibin and Okada, 2007; Urbanek and Rubner, 2011), is commonly used in image analysis and retrieval to quantify differences between images. Informally, *EMD* determines the minimum amount of work required to turn one distribution into another, thereby reducing the comparison of two distributions to a transport problem. Because the distance between altitude bins is a true distance (in the case of our altitude analyses in Chapter 5, the distance between the centers of the bins was 200 m), *EMD* can describe the conversion of one distribution to another in units of distance (e.g. meters). The resulting metric indicates the average distance that the birds in the predicted distribution would need to be moved (vertically) in order to reproduce the measured distribution. Thus, altitude bins in one study being of different resolution than altitude bins in another study does not prevent explicit comparisons between the results of the two studies. While *EMD* can be calculated on absolute distributions (e.g. using the actual number of migrants per altitude bin), there will be variability in the *EMD* measurements that is due only to differences in these absolute numbers disallowing meaningful comparisons between *EMD*

from one time or location to the next. By considering proportional distributions, the results of all comparisons will be equivalent.

The earth movers' distance, which is most often utilized in fields as seemingly-unrelated to bird migration as computer science and image retrieval, can help us better understand variability in avian altitude selection and highlights the benefit to be gained from incorporating concepts, methods, and tools from other disciplines into ecological and biological research.

7.6 Migration research

As with many ecological topics, exploring the patterns and dynamics involved in bird migration is benefited by the efficient integration of data from multiple fields. Not only must we integrate data, we must combine entire systems, procedures, methods, and the expertise necessary to fully utilize each. In fact, much of this thesis is predicated on integrating tools and methods from different disciplines to better understand migratory dynamics. The radars we have used, for example, provide incredible information on bird movements but were developed (and, indeed, continue) to serve entirely different purposes. To effectively handle, process, and utilize data from numerical weather models, which we used extensively in these analyses, requires knowledge of the underlying atmospheric systems they describe and the often unique formats in which they are stored. Many of the methods we employed require knowledge of statistical analysis and programming and can be computationally demanding. As well, the large amounts of data involved necessitate effective data management, storage, and access techniques. In short, being open to and receptive of technologies and techniques used in other fields will continue to benefit biological and ecological research, which necessarily considers interactions between many different systems.

Tools and workflows that facilitate the integration of information from different systems are therefore of the utmost importance, and they will become increasingly so as data sets become larger and more complex. As mentioned elsewhere in this thesis, the recently-developed capacity to automatically extract bird migration information from Doppler weather radar is an exciting and potentially revolutionary step. The spatial and temporal coverage of these radar systems is unprecedented in ornithology, allowing for research on a scale that has been hitherto impossible. Nonetheless, efficiently processing, organizing, and maintaining these data will be a substantial task. An individual radar can generate gigabytes of data per hour, and associated environmental data sets can be similarly cumbersome. In Europe, each radar is maintained by the country in which it resides, which can lead to issues regarding data

conversion, transmission, and consistency between sites.

Utilization of these radar systems in meteorology is not immune to these challenges, and the meteorological offices of many European countries have taken steps toward addressing these issues through the organization of the The Operational Programme for the Exchange of weather RAdar information (OPERA). The OPERA network is intended to provide a platform wherein “expertise on operationally-oriented weather radar issues is exchanged and holistic management procedures are optimized... [with the intent to] harmonize data and product exchange at the European level.” Utilizing these data for bird migration studies will require a similar level of organization. An optimal situation may be to have data relevant to bird migration studies organized under the umbrella of the OPERA network such that bird migration information becomes a typical product of OPERA output. Opportunities to similarly utilize the NEXRAD radar network in the United States are also being explored (Chilson et al., 2012). Occasionally, partnerships of this sort can be confounded by a divergent set of goals; however, this specific partnership has the potential to be mutually beneficial for both the biological and meteorological communities. Since each group often considers radar echos relevant to the other as “clutter”, improvements in identification advance the research potential of both groups. Furthermore, the timing and spatial distribution of migrating birds have shown strong relationships with climatic variability (see e.g. Sinelschikova et al., 2007; Jonzén et al., 2006; Jenni and Kéry, 2003; Hüppop and Hüppop, 2003; Crick, 2004) such that knowledge of one system may provide insight into the other.

The potential benefits of a network of radar sensors such as OPERA or NEXRAD in bird migration studies far outweigh the challenges associated with developing and implementing the required systems and workflows to obtain and organize the relevant data. Simply being able to quantitatively map the seasonal flow of avian biomass over such a large area will represent a considerable leap forward and result in data sets that benefit conservation and management efforts. Beyond that, with coverage over large geographical areas and measurements made from standardized systems, there is enormous potential to conduct comparative analyses. Behavioral differences due to the time of the year, the altitude of flight, and the type of underlying landscape can be examined at a scale and resolution previously unattainable. We may determine which behaviors are unchanged over time and space and which behaviors are dependent on environmental conditions and in what ways. For instance, in Chapter 4, we examined the effect of persistent wind patterns on migration speed. With an extensive and contiguous radar network, we can determine whether these patterns persist outside of our study area and con-

sider the cumulative effects of these persistent patterns over entire migration routes. As well, we can determine if the atmospheric influences on avian altitude selection we uncovered in Chapter 5 persist in other areas with different atmospheric conditions and landscapes. Predictive models of migration intensity such as those we developed in Chapter 6, and indeed flight safety in general, will surely benefit from a unified network of sensors that will allow us to implement geostatistics in our analyses, incorporate the element of space in our models, and make predictions that account for upstream and downstream flows of birds between sensors. These types of models will likely utilize not only the measurements from the individual radar systems in the network, they will incorporate simulation models such as the FLAT model described in Chapter 3 to propagate birds measured at a particular radar site through space and time. In all these cases, tools such as those contained in the RNCEP package from Chapter 2 will be useful as they facilitate the handling and integration of environmental data in bird migration studies, specifically allowing for the rapid adjustment of the spatial and temporal domains considered. Utilizing radar measurements across large geographic areas and integrating knowledge from multiple disciplines, we may more fully address all four of Tinbergen's questions when considering how birds weather the weather.