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

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Summary

The life cycle of many bird species involves the twice-annual movement between a breeding ground and a wintering ground that we refer to as ‘migration’. To complete these journeys, birds must successfully navigate many obstacles including a dynamic atmosphere. To make optimal use of this ever-fluctuating milieu requires not only an uncanny sense of timing but an intuitive sense of the environment and its proclivities.

The subject of this thesis is the relationship between bird migration and the atmosphere, though we perhaps give the most consideration to the role of wind. Often the concepts addressed lean toward migrants engaged in flapping flight, however, many of the theoretical discussions apply to birds in general; where appropriate, we distinguish between weather effects on different flight strategies. All measurements of bird migration dynamics were made in the Netherlands using either Medium-Power Military Surveillance Radar (MPR) or Doppler weather radar. Atmospheric data were obtained almost exclusively from gridded datasets derived from analysis/forecast models in combination with data assimilation systems.

The thesis is roughly divided into three parts: tools and methods, biological analyses, and applications.

Tools and methods

There are many ways in which the atmosphere can influence migration. Components of the atmosphere (e.g. wind condition, temperature, humidity) can each exert independent influence on migratory efficiency, yet the specific influence of each component must often be considered in the context of the others.

A significant obstacle in these types of analyses is therefore the efficient management of (often large amounts of) data. A wide range of variables must be collected from often disparate data sources stored in various formats and often at different spatio-temporal resolution. These data must be appropriately merged, and, in order to be useful, tools must be in place to visualize and analyze these data. Having these tools and systems in place is often the first step toward conducting efficient and productive analyses. We therefore began by introducing in Chapter 2 the RNCEP package containing functions to obtain atmospheric data from two high-quality, and freely-available, gridded global data sets, potentially process those data into various longer-term climatic indices, and visualize the data on a map. In order to benefit a diverse research community, the package was written in the open-source R language.

Wind is a particularly challenging variable to consider in bird migration studies. Whereas variables such as temperature and humidity can be described with a single value, two values (often speed and direction or zonal and meridional components) are generally necessary to properly quantify wind condition. The fact that wind is composed of two interdependent components complicates quantitative comparisons of wind condition in relation to migration, for example in linear models. It is possible to reduce the two components of the wind to a single value, which is often termed ‘wind profit’ in bird migration studies, but doing so requires making specific assumptions about a bird’s goals (and perhaps abilities). In Chapter 3, we described methods that have been previously applied to determine wind profit and developed some new methods as well. We determined the sensitivity of these various methods to uncertainty in their assumptions, and we quantified differences between the methods for specific wind conditions. To illustrate the cumulative effects of these methods, we simulated bird flight according to the different assumed behaviors using real wind conditions. We identified differences in ground- and airspeed, route, and arrival probability that arose when selecting one method or another. Because of the differences we identified, and because the magnitude of these differences depended heavily on the specific wind conditions encountered, researchers should consider the assumptions that are made in the application of a particular wind profit equation in the context of their specific migratory system. To facilitate these considerations, we have incorporated into the RNCEP package a dynamic flight-simulation model in which the specific assumptions of a wind profit equation can be applied to a particular migratory system to determine the real-world consequences of the assumptions that are made.

Biological analyses

With tools and methods in place, it was possible to derive biological insight by analyzing bird migration dynamics in relation to atmospheric conditions. In Chapter 4, we considered seasonal differences in avian migration speed. The speed and direction of the wind can have a dramatic impact on the groundspeed of a migrating bird, which in turn affects a migrant's overall migration speed. Wind conditions, while variable, also exhibit persistent dynamics described by the general circulation of the atmosphere. We hypothesized that wind conditions in Western Europe were more supportive of northeasterly-directed spring migration than southwesterly-directed autumn migration. We further proposed that these seasonal differences in wind support may lead to seasonal differences in the groundspeed of migrants, resulting in equivalent differences in overall migration speed. Using a simple wind profit equation, we first quantified any differences in the frequency of supportive winds between spring and autumn throughout Europe. We found that winds in the Netherlands were much more supportive of spring migration than autumn migration. Similarly, we found that migrants in the Netherlands had a significantly higher groundspeed in spring compared to autumn. Since these seasonal differences in groundspeed were not caused by seasonal differences in airspeed, our results suggested significantly higher migration speeds through the Netherlands in spring compared to autumn due to prevailing winds. The frequency of beneficial winds may also affect migration speed by impacting the time birds must remain at a stopover site waiting for wind conditions in which they can make acceptable progress. We proposed that areas with frequently prohibitive winds may be considered as a kind of ecological barrier and that birds may be able to optimize time and energy expenditure by circumventing some of these areas.

Birds have the opportunity to select often quite different atmospheric conditions simply by adjusting their altitude. By considering the altitudes birds select during migration, we may derive a better understanding of the influence of different atmospheric components on migration and also determine the priority birds place on different atmospheric properties. The majority of quantitative empirical research has suggested that birds select migratory altitudes based primarily on considerations of wind condition. In Chapter 5, following the approaches presented in several previous studies, we considered whether and to what degree wind could explain altitude distributions of nocturnally migrating birds in the Netherlands. We then performed forward stepwise variable selection using Generalized Additive Models to determine the specific influence of various atmospheric variables on, and the precedence these variables take in determining, altitude distributions of avian migrants. Overall,

we found weak correlations between altitude distributions of wind support and altitude distributions of migrating birds; however, we did find wind to be influential: increasing tailwind support with height increased the probability of birds climbing to higher altitude; birds sought out supportive winds at higher altitude when winds near the surface were prohibitive; and birds seemed to assess wind support at a given altitude in relation to conditions at the surface rather than in relation to best wind conditions available. We also found that birds avoided lower temperatures. Nonetheless, altitude itself explained the largest amount of variability in avian altitude distributions and suggested that migrants generally preferred lower altitudes. While birds can minimize the time and energy spent on migration by selecting altitudes with more profitable wind conditions, high altitude flight may entail risks that birds deem unnecessary when they can make acceptable progress at lower altitude. This suggested that birds balanced trade-offs between multiple objectives and optimized their travel based on multiple criteria.

Applications

As our understanding of migratory dynamics in relation to atmospheric conditions improves, we can move toward developing applications that benefit both birds and society. In this context, we developed an ensemble prediction system in Chapter 6 to forecast migration intensity at two locations in the Netherlands using measurements obtained from Doppler weather radar. This ensemble system can be applied, for example, in flight safety to help prevent collisions between birds and aircraft. Natural systems tend to be chaotic in that subtle variations in any of a number of initial conditions can accumulate and propagate through the system to produce dramatically different outcomes. Ensembles tend to dampen chaotic influences on predictions by averaging the outcomes suggested by many different models, making ensemble predictions generally more robust. Also, the agreement among the individual models in an ensemble implicitly indicates the probability of a particular outcome. Our use of an ensemble also enabled us to account for the effects of many different atmospheric variables on bird migration despite the complicated correlations that often exist between these variables. We determined the performance of our ensemble system in reference to some benchmarks, and we determined how well models developed for each location predicted conditions at the other location. The ensemble development procedure we implemented was robust and exportable such that it could be used to quickly develop predictive models of migration intensity in new locations. Since networks of weather radar already exist, the procedure we outlined can potentially be used to develop

standardized predictive models over vast geographical areas.