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Optimal Bird Migration: Accumulating Fuel, Negotiating Wind and Trade-Offs in Fitness

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Summary

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Migratory birds have long fascinated the curious, inspired the spiritual and pleased the aesthetic, but also form an integral part of global biodiversity, connecting remote ecosystems and providing important ecosystem services. Migration evolves in populations as a response to seasonal differences in expected benefits to fitness between regions, typically arising from latitudinal gradients in climate and food availability. Dedicated research supported by advances in tracking technology have revealed remarkable control of the migratory process and adaptations to variable environments, e.g. through flexibility in accumulation of energy reserves (fuel deposition), reaction to wind and use of navigational abilities. Nonetheless, while our knowledge about how migrants negotiate unpredictable environments remains in some aspects tentative and rudimentary, populations of especially long-distance migrants are decreasing at alarming rates under anthropogenic environmental changes. Therefore, improved understanding of the underlying behaviour controlling the migratory process is both beneficial to humans and can make a vital difference in our efforts to maintain biodiversity.

This thesis addresses optimal migration behaviour which through facilitating reliable and efficient migration benefits individual and population fitness. We developed analytical and individual-based models (IBMs) incorporating dynamic wind and landcover data to assess optimal migration in a spatial context for several migratory populations according to survival, successful arrival, time and energy expenditures. Resultant optimal behaviour was compared with tracking and mark-recapture data. In reality, attainment of optimal migration strategies is constrained by selective pressures to maintain strategies and historic migratory routes, and by environmental limitations to effective adaptation. Nonetheless, modelling migration from an optimality perspective provides not only a means to compare with actual migratory behaviour, but also to assess the adaptive value of given abilities and behavioural strategies in variable environments.

Although many animal orientation strategies have been considered for movement in non-uniform flow, we still lack a benchmark of the absolute fastest strategy. In Chapter 2 we develop analytical and individual-based models of optimal time-minimizing orientation for non-stop movement to specific goals in horizontal flows. We then demonstrate how to use optimal orientation as a benchmark for any animal navigating in horizontal flow to a specific goal. Specifically, we assess the performance (efficiency) of three generic orientation strategies relative to the optimal benchmark in prevalent geophysical flow patterns and in two avian migration systems: massive movements of thrushes *Turdus* sp. crossing the North Sea to the Netherlands and 6000 km non-stop flights by Great Snipes (*Gallinago media*) from Scandinavia to Africa. We first demonstrate that in weak flow relative to self-propelled speeds (airspeeds), many orientation strategies are near-optimal. In strong predictable flow, e.g. the thrush movements, vector orientation (constant-heading movement) is near-optimal when adjusted to flow on departure. In strong unpredictable flow, e.g. the Great Snipe flights, goal navigation (following only a map sense) was surprisingly efficient over 33 seasons of variable winds. This research highlights the influence of flow speed and goal distance on time-optimal orientation, and the adaptive value of flow predictability and navigational capability.

The relation between wind selectivity and compensation for wind drift has not been assessed in spatiotemporally varying environments. In Chapter 3 we use an IBM incorporating 12 seasons of dynamic wind data and landcover data to estimate optimal wind selectivity and compensation for wind on departure among 10,000 modelled juvenile (vector-orienting) Willow Warblers (*Phylloscopus trochilus*) migrating from Scandinavia to the Iberian Peninsula. We compared resultant orientation based on optimal constraints to drift and transport cost on departure with radar measurements of migrating songbirds (passerines) departing after dusk. Modelled migrants arrived more reliably and faster when selecting up to moderately unsupportive winds (~4 $m \cdot s^{-1}$ headwinds) and partially compensating for wind on departure to enhance arrival and avoid the Atlantic Ocean barrier. Model results were highly consistent with the radar data as well as other radar studies along this flyway.

Many avian migrants intersperse nocturnal flights with extended stopover to 'refuel' for continued flight bouts. While optimal departure fuel loads have been studied extensively, risk-averse choice of stopover regarding when to stop and refuel (as well as depart) has not been quantified for nocturnal migrants. We accordingly extended the classic analytical model of optimal stopover in 'continuous' environments to assess risk-averse choice given initial stopover costs and the probability of encountering a low-quality stopover following each nightly flight. We show that risk-averse threshold fuel loads can enhance migration speeds by a factor of 1.5 to 2.8 among relevant modelled environments. Modelled fuel loads in environments with high and low encounter probabilities resembled observed fuel loads of migratory populations with ubiquitous and scarce food availability, respectively. By being risk-averse to future low-quality refuelling events, this new approach to modelling stopover scheduling emphasises the importance of premium stopover sites among nocturnally migrating birds.

Astounding barrier crossings by passerines have been confirmed or proposed, but the reliability of wind conditions to support such journeys given realistic fuel loads is uncertain. In Chapter 5 we use the IBM of Chapter 2 incorporating 33 seasons of wind data to demonstrate the feasibility of non-stop migration across the Atlantic Ocean by the 25 gram Northern Wheatear (*Oenanthe oenanthe leucorhoa*) from Canada to its African wintering grounds. We also assessed the effect of departure fuel load and flight altitude given their impact on optimal airspeed and energy expenditure. Arrival success considering 33 seasons of wind data was 62% when departing with high fuel loads (equalling their lean body mass) and flying at high altitudes (at the 700 mb pressure level, or approximately 3000 m above mean sea level). For these conditions, wheatears departing from Canada reached Africa non-stop within 31-68 hours. Moderate wind on departure enhanced arrival success to 75%. Interestingly both goal orientation and vector orientation were equally successful, i.e. where orientation was continually or never updated using a map sense, respectively. Whether natural selection might favour non-stop migration by *leucorhoa* wheatears is speculative, but the incredible time savings compared to the detoured route via Europe render it a viable possibility.

Birds are proposed to optimize energy expenditure in extended flight by adjusting their airspeed to experienced wind conditions. In Chapter 6 we extend the IBM framework and use GPS data to assess reaction to wind and energy expenditure by (non-breeding) gulls crossing the English Channel to their breeding colony. We show that these gulls adjusted their altitude and orientation to exploit vertical wind structure and adjusted their routes in conditions favourable to coastal soaring. They additionally demonstrated remarkable flexibility in adjusting their airspeed to wind conditions at sea, even at night. Nonetheless, despite the gulls' apparent awareness and ability to react to variable wind conditions en route, their airspeeds remained overall lower than predicted by an energy-minimizing strategy. We discuss physiological and performance constraints underlying this apparently sub-optimal reaction, but suggest that trip-related costs are not a primary concern to these flexible opportunists.

In the Synthesis, we discuss the relevance of optimal solutions in light of evolutionary and environmental constraints and discuss implications of model results for migration theory regarding orientation and navigation, reaction to wind and stopover behaviour. Specifically, we discuss the surprising reliability of simulated migration based on adjusting endogenous headings to wind on departure (Chapters 2, 3 and 5) and, contrastingly, the reliability of endurance flights based on goal orientation, i.e. following only a map sense (Chapters 2 and 5). Migration data of nocturnal passerine migrants regarding migratory orientation and fuel load data during stopover both match predicted behaviour based on time-minimization (Chapters 3, 4). Contrastingly, airspeeds and energy expenditure among the gulls during their commuting flights (Chapter 6) suggest that, unlike many long-distance migrants, these flexible and opportunistic birds have adapted to a currency of travel emphasizing both instantaneous as well as trip-related energy expenditure.

In conclusion, we recommend simulating migration using spatiotemporal environmental data as a means to interpret migratory behaviour and to estimate the costs associated with proposed strategies. Accurate estimation of these costs is crucial to assessing fitness consequences, facilitating appropriate management policies for migratory populations.