Optimality in Bird Migration (BIRD)

An ESF scientific programme

The European Science Foundation acts as a catalyst for the development of science by bringing together leading scientists and funding agencies to debate, plan and implement pan-European initiatives.

Bird migration is one of the most fascinating of all life-history traits in wildlife. Migration is not, however, of a unitary character. Migration varies among species, populations, age groups and sexes, and may even vary within an individual. Differences occur with respect to distances migrant birds travel, the routes they follow, the timing of departure and arrival, and the behaviour during the move. The causes, adaptive significance and consequences of this variation are, however, largely unexplored.

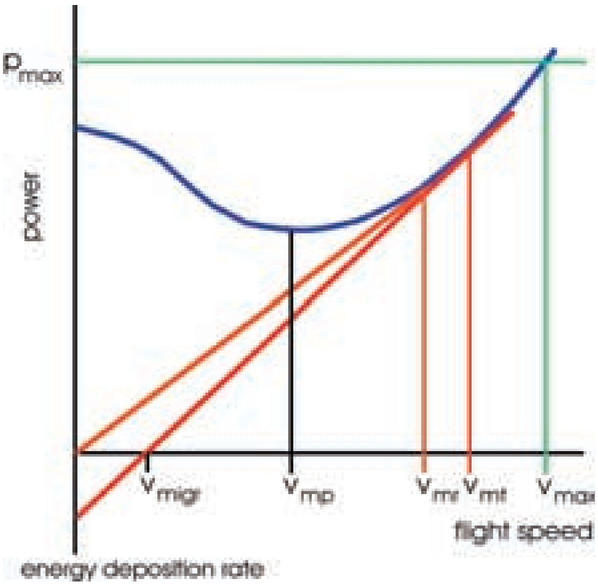
More detailed knowledge of the variation of migration and its mechanisms and regulatory processes is crucial for understanding the role of migration within the complete life cycle of a migrating species and for understanding how natural selection is acting to mould migratory life-histories, and for elucidating the evolution of those life-histories.

Future studies on bird migration have to take much greater advantage of comparative and integrated studies, combining theory, field observations, and laboratory studies, and linking physics, physiology, ecology and behaviour. The characterisation of migration must consider the physiological mechanisms underlying migratory behaviour, the ecological consequences of that behaviour, and how those consequences affect evolution.

The programme aims to integrate the various sub-disciplines and to unify different perspectives.

The dynamic interplay between theoretical development and empirical work on physics, physiology and ecology, is a fine example of highly successful use of the optimality approach in biology, and it will shed light on our understanding of the evolutionary consequences of bird migration, and of the adaptive significance of migratory habits as well as the migrants' flexibility to respond to human alterations of ecological systems.

Power required for horizontal flapping flight in relation to airspeed. Maximum power available from the flight muscles (P_{max}) is assumed to be independent of speed. Hypothetical rate of energy accumulation at stopvers is represented along the ordinate extending downwards from the origin. Characteristic flight speeds indicated are associated with minimum power (V_{mp}), maximum range (V_{mr}), minimum time of migration (V_{mt}) and maximum sustained power (V_{max}). V_{mr} is graphically constructed by drawing a tangent from the origin to the power curve; V_{mt} is constructed analogously by drawing a tangent from the downwards extending ordinate, representing the rate of energy accumulation. The point where this tangent intersects the speed axis defines the overall rate of migration (V_{migr}). (Alerstam & Hedenström, J. Avian Biol. 29: 343-369, 1998).

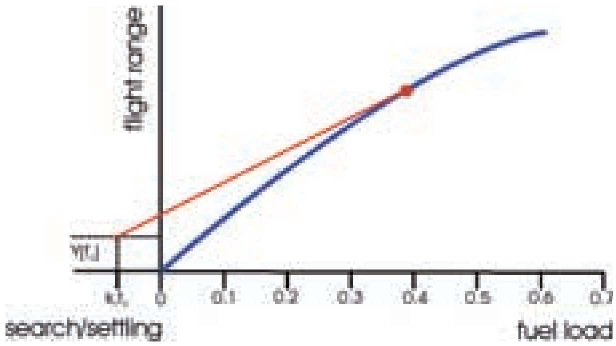


Scientific background

The last century saw immense advances in the study of bird migration, not least as a consequence of the systematic application of new study techniques such as ringing, radar and satellite telemetry. However, it was only in the 1960s that investigation of bird flight and decision making reached the quantitative level to be incorporated in general theoretical frameworks. In parallel the understanding of physiological and orientation mechanisms in birds were much improved. During the last decade a more coherent theory, combining optimality reasoning with aerodynamics and physiology, grew into what can be termed "Optimal Migration Theory". Bird migration research is now an interdisciplinary field that draws from developments in biomechanics, sensory biology, eco-physiology, behavioural ecology and population ecology.

A fundamental theory is that of animal flight mechanics which yields a U-shaped function between power and speed. To generate the mechanical power output (the rate of work to overcome the aerodynamic drag components) a bird must flap its wings, which costs muscle power. It is generally believed that also the metabolic power function follows a U-shape, but whether the conversion of fuel consumption to power output is constant or variable remains open.

Another crucial question is how far a bird can fly given a certain amount of fuel. Aerodynamics theory assumes that this should be a function of diminishing return, because progressively heavier birds will experience increasing flight costs. This function forms the basis for the theory of optimal stopover and departure decisions. In addition we combine these basic observations with different optimality rules (minimising time, energy or predation risk of migration) and physiological constraints (fuel deposition rate, load-carrying capacity) to understand patterns and strategies of migration as observed in nature.



Gain in potential flight distance in relation to relative fuel load. For a given search/settling time (t_0) and initial energy loss (f_0, converted into potential flight distance Y (f_0)), the optimal departure fuel load and the associated flight distance can be found by constructing a tangent to the gain curve from a point (kt_0, Y (f_0)) in the second quadrant, identifying the optima (filled dot). (Alerstam & Hedenström, J. Avian Biol. 29: 343-369, 1998).

A new generation of models combine life-history theory and migration in an optimal annual routine context. Here timing and effort of reproduction, moult and migration are chosen so that fitness is maximised over an entire life-cycle of the bird. This approach may prove to be a valuable tool for predicting responses to long-term global changes of climate. Population dynamical modelling of migratory populations is of great concern when tackling conservation issues in an increasingly threatened environment.

Migration varies among species, among populations, among age groups and among sexes, and may even vary within an individual. Differences occur with respect to distances migrant birds travel, the routes they follow, the timing of departure and arrival, and the behaviour during the move.

The strategies to cover long migratory distances differ among species. Some move in many short steps, others negotiate the same distance in one or two jumps with very long flights. Consequently, the physiological requirements, and the ecological and time constraints are rather different. Moving by a series of short flights requires smaller fat reserves on board, thus lower carrying costs, but it requires many different suitable stopover sites en route. The disappearance of one site is less dramatic, as these 'hoppers' can easily move to the next site. Migrating long hauls, by contrast, is expensive due to the costs of carrying the extra fat, and is risky because the disappearance of one particular stopover site may impair further migration. However, birds may counterbalance these disadvantages, either by gaining time because they do not need to find themselves good feeding grounds at many successive stopover sites, or because they may be less exposed to predation at their 'familiar' feeding sites than the 'hoppers' at their many different 'unknown' staging sites.

A more detailed knowledge of the variation in migration and its mechanisms and regulatory processes is crucial for understanding the role of migration within the complete life cycle of a migrating species and for understanding how natural selection is acting to mould migratory life-histories, and for elucidating the evolution of those life-histories.

Migratory behaviour and migratory life-histories constitute prime examples for the study of the interactions of organisms and their environment. Migration is an adaptation to cope with seasonally and/or spatially fluctuating environments and resources. Not only has a migrant to deal with its direct environment, it also must anticipate dramatically changing environmental conditions on its journey.

Conservation issues

Migratory birds are potentially faced with long-term population declines and, thus, need special attention.

Like many other European migrant birds, the redstart suffered from environmental changes at its African wintering grounds.
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Understanding the processes which determine the size of animal populations is a central question in ecology because of its scientific importance and because it is essential for population-oriented conservation.

Ecological systems are currently undergoing major changes as natural resources are depleted by growing human populations, resulting in new problems. To find answers to new problems, the need for groundbreaking research is just as important as the application of already existing knowledge. This transfer of research knowledge to resource managers and conservationists is particularly critical for sustaining ecological systems. Because ecological systems can be irreversibly damaged by human activities, we have to act now to preserve options for the future. At the same time, we can develop a vigorous research programme to improve our scientific understanding and future approaches to conservation.

Migratory birds are particularly appropriate for addressing conservation issues. Birds are conspicuous, species differ vastly in ecological requirements and tolerances and they can serve as sensitive indicators of environmental conditions. Demographic parameters (e.g., breeding productivity, survival, dispersal movements) that relate to population health and habitat suitability are more easily monitored in birds than in any other group of organisms. In addition, birds are of wide public interest.

Migration is the key to the biology of several species that are becoming increasingly scarce or currently face the risk of extinction. To determine the specific migratory routes, to identify the important fuelling areas, and to elaborate the species-specific energetic and ecological

The ultimate prerequisite for successful migration in many migrant birds is fat as fuel for their long flights. Before departure on such flights, a large amount of fat is stored in thick subcutaneous deposits. The relative lean garden warbler (left) weighing about 18 grams would not be able to undertake long flights in contrast to the fat bird (right) weighing about 30 grams and well prepared for its trans-Saharan journey to Afrotropical wintering grounds. © F. Bairlein

conditions during stopover and at the wintering grounds are not only of fundamental scientific importance. They are also a prerequisite for conservation programmes.

In many migratory birds, there is a strong link between changes in the number of breeding birds and the ecological conditions during migration and on the wintering grounds in sub-Saharan Africa. Many trans-Saharan migrants, for instance, are suffering from low rainfall and consequently poor ecological conditions in the western Sahel.

For most birds we have only very fragmentary information on these relationships. Sound conservation of migrants is an international affair. Migrants breed in one country, transit several others, and spend the non-breeding season in yet another country. Migrants will be affected if breeding or crucial non-breeding habitats and resources are altered for human use. To generate sound conservation strategies in migratory organisms all the political, economic, and biological problems must be considered and brought into sharp focus.

The concept of optimal migration

Evolution by natural selection is a process of optimisation. In recent years, considerable theory has been built up to predict various aspects of bird migration using optimality models. Starting from flight mechanical theory several 'ecological' criteria have been added to the models to explain the temporal and spatial course of migration and the adaptations that enable birds to accomplish their migratory journey successfully. The theory of bird flight yields quite specific predictions about gliding and soaring performance of different species, and about the speed in flapping flight, and how this speed is expected to vary in relation to environmental cues, such as flight altitude, wind, or fuel burden.

The optimal policy for a migrating bird to reach its destination within the appropriate time differs depending on the demands that act on the bird. Time, energy, and safety from predators are of main current concern.

Selection may have favoured birds that minimise *energy* expenditure for migration so that they reach maximum distance with least power requirements. Such birds should carry only as much fat as needed to reach the next fuelling site, and to leave some spare fuel to settle in the new stopover site. Birds may also be selected to minimise the energy spent during migration if food is difficult to acquire.

However, birds could also be selected to minimise the *time* spent on migration, so as to reach their destination (wintering, breeding or moulting areas) as soon as possible to obtain good territories or to spend as little time as possible in unknown areas along the migration route. In this case, a high overall speed of migration, including both flight and stopover, would be favoured. Such birds should minimise time spent on stopover and carry maximum fat loads at departure to fly long distances without further interruptions for feeding.

A third possibility is that *predation* constitutes such a significant hazard to migrants that they are primarily adapted to minimise the associated mortality risk during migration. In this case, birds should be inclined to depart with smaller fat reserves than is optimal under time-selected migration.

Using dynamic programming models, the adaptive aspects of flight behaviour, fuel deposition, and responses to environmental cues can be evaluated, and patterns of stopover, fuel load at departure, responses to different fuel-deposition rates, and habitat selection in migrating birds can be predicted.

Migratory fuelling

The interplay between energy consumption during the flight and refuelling is crucial for understanding the temporal and spatial course of flight and stopover.

How birds prepare for the energetic demands of migration is central for the understanding of their life-histories. Flight is energetically expensive and in particular long-distance migrants, which travel thousands of kilometres one way from their summer breeding grounds to distant wintering areas, exhibit extraordinary feats of physiological endurance. To migrate these long distances and to cross vast distances over inhospitable terrain such as seas or deserts requires considerable amounts of energy.

To fuel flights between successive sites along the migratory route many migrants store fat and, to some extent, protein reserves before departure. The total amount of fuel accumulated varies between and within species. Birds migrating as 'energy minimisers' do not need much fat 'on board' whereas the 'time minimisers' usually rely on higher fuel stores. Those birds which have to cross huge inhospitable areas like deserts and the sea may even double their body mass before they commence migration. En route, the birds almost entirely rely on these reserves. How far a bird can fly depends on its reserves and its ability to maintain water balance.

Even orientation performance in migrating birds could be influenced by energy stores. Adequately fat birds oriented towards the seasonally appropriate directions whereas lean birds did not, they rather oriented in the opposite direction.

Concerning fattening and the energetics of migration two important questions have to be answered:

Which are the physiological, nutritional, ecological and behavioural needs and constraints for fuelling, and how does the rate of fuel accumulation influence stopover decisions of migrants?

How is the deposited fuel used during migration, and how do migrants keep flying for many hours?

To accumulate fuel, birds have to forage and eat. However, only little is known about the foraging ecology, and the energetic and nutritional demands of fattening migrants.

The energy content of food is traditionally assumed to be the main predictor for foraging decisions and their consequences. However, recent data revealed that dietary nutrient composition clearly influences the rate of daily body mass gain during migratory fattening. Consequently, the role of nutrient requirements and nutrient supplies for fuelling migrants need to be considered. Many migrating species change diet selection during fuelling periods, although the adaptive significance is poorly understood. There is, however, considerable recent evidence that seasonal shifts in diet selection in migrating birds maximise the rate of fattening. Timing of migratory fat deposition, daily fat deposition rates, and fat loads at departure are closely related to the conditions for appropriate diet selection.

Migratory physiology

Concerning physiology, migration involves the deposition of reserves, changes in muscles and in the digestive organs, the activation of hormones and enzyme systems for energy storage and utilisation, changes in blood oxygen transport properties, and development and synchronisation of migratory behaviour, including daily and seasonal patterns. The control of these processes is complex, and because of this complexity far from clear.

Gonadal hormones, for example, play an important role in the control of spring migration, but for autumn migration. Similarly, thyroid hormones seem to be involved in the regulation of spring migration, but not in autumn.

Recent studies have revealed that in addition to the storage and depletion of fat, the muscles and belly organs of migrating birds can also undergo considerable changes in size in the course of migration. In garden warblers, for instance, the digestive tract is reduced to 60 % in mass after crossing the Sahara desert, probably an effect of the

Many European migrant birds being 'trans-Sahara migrants', cover distances of thousands of kilometres on their annual flights to and from Africa passing the huge inhospitable area of the Sahara.
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extraordinary energy and nutrient demands of such flights. As a consequence, fat deposition rates at the beginning of a stopover phase are reduced compared to that of birds with a fully functional digestive system. The dynamics of reduction and rebuilding of the digestive tract seem to be very rapid, within a few days. These changes in stores and organ sizes seem to represent evolutionary compromises between their functions during storage, flight and post-arrival phases.

The physiological syndromes of migration are almost unknown. Moreover, the physiological requirements may be rather different for different species, in different seasons, and for birds using different migration strategies. Consequently, there is a series of major physiological questions which need to be addressed more intensively. So far, physiological and biochemical processes and constraints have not been accounted for in optimisation models.

To stop or to go – the decision between stopover and flight

Timely fattening for migration requires the availability of appropriate locations along the birds' migratory route for both feeding and shelter. During breeding, most birds are relatively sedentary for some weeks. During this period, habitat use can quite easily be monitored. During stopover, however, many migrants make temporary use of habitats, and these may be different from those of either their breeding or their wintering quarters. In addition, migrants have to find good feeding places for successful fattening at successive stopover sites. During stopover, most migrants do not occur in all available habitats, rather they seem to rely on particular habitats or even specific structures of the habitats where they apparently can fatten up most efficiently. There is strong evidence that the selection and use of particular habitat sections is genetically based, and that it reduces the effects of competition between and within species. This mechanism may also help migrants to locate suitable feeding sites at each successive stopover site during migration and to maximise the rate of fat deposition, as well as to cope with the novelty in resources encountered at successive stopover sites.

For most species, however, stopover ecology and the species-specific habitat requirements are poorly known. Comparative work at various stopover sites would shed light on the flexibility of habitat use in migrants, and would permit the identification of the major stopover habitats and resources for migrants.

This is of particular concern for conservation.

The ESF programme

Future studies on bird migration should involve comparative and integrated studies, combining theory, field observations, and laboratory studies, and linking physics, physiology, ecology and behaviour. Migration is a general biological phenomenon, not simply a trait characteristic of a particular taxon. The characterisation of migration must consider the physiological mechanisms underlying migratory behaviour, the ecological consequences of that behaviour, and how those consequences affect evolution.

The dynamic interplay between theoretical development and empirical work on physics, physiology and ecology, is a fine example of highly successful use of the optimality approach in biology. It will evaluate our understanding of the evolutionary possibilities and limitations in bird migration, and of the adaptive significance of migratory habits as well as the flexibility of migrants to respond to human alterations of ecological systems.

Since fuelling plays a crucial role for understanding migration strategies and the selective forces and constraints acting upon them, and for taking appropriate conservation measures, the programme particularly emphasises studies of the ecology and physiology of fuelling as the basis for the evaluation of the existing theory and models, and for practical applications in conservation.

There are a number of constraints on the optimal decision due to recurring local environmental (extrinsic) cues (e.g. food distribution, abundance and availability, feeding conditions, weather, intra- and interspecific competition, predation risk) and intrinsic cues (e.g. age, sex, physiological capabilities, digestive capacities, parasite load, endogenous migratory time programme).

Consequently, the birds' response to variability in resources is of particular interest to reveal the stopover decisions, and the trade-offs between time-, energy-, or predation-selected migration, and the adaptive significance of the various migratory habits.

To unravel these complex relationships, several basic questions need to be addressed.

Which are the conditions (body mass, fat score, biochemical status) of birds at arrival and at departure from stopover? Are there differences between age classes, or sexes? Which are the conditions (habitat, food, shelter, etc.) required for fuelling? Are these requirements variable in space and time? Which are the constraints (food, weather, predators, competitors, parasites) influencing the timing and the extent of migratory fuel accumulation at a stopover site? Which fuels (fat, protein) are accumulated and to what extent? How does the daily rate of fuelling affect the bird's decision to stay or fly?

The goals of the programme will be achieved by a combination of empirical and experimental studies in the field and in the laboratory and theoretical approaches.

To answer the questions addressed, comparative analyses of different groups of migrants are most efficient, including songbirds, shorebirds, geese or raptors. Evaluating the models could benefit from such a link between scientists studying different groups of migrants, using rather different migration habits and migratory performances.

Programme activities

The programme will focus on exchange of both junior and senior researchers and workshops.

The programme will strengthen interactions among groups from different countries with different skills, stimulate the development of new ideas, initiate collaborative research, facilitate the exchange of expertise and knowledge, and attract new researchers to the field.

Exchange visits

To support young scientists to get involved in research and data analyses is the most efficient way to make considerable novel contributions to the understanding of bird migration. Exchange visits are important to increase mobility between research centres in Europe. Travel grants are available for visits lasting from one week up to six (exceptionally 12) months by young or senior scientists visiting research centres outside their home country. Applicants must be currently working in a European institute. Preference will be given to doctoral students and young researchers.

The deadline for submitting grant proposals for visits beginning after 1 January is 30 September and 31 March for visits beginning after 1 July.

Workshops

The programme will fund workshops dealing with the scientific themes outlined above. Some workshops and conferences will be organised by the programme steering committee, but there will also be funding available for workshops proposed by individuals in the participating countries on topics with a clear connection to the programme's aims.

Workshops should be planned for 20-40 participants with a significant proportion of young researches and last from three to five days.

The deadline for submitting proposals for workshops to be held the next year is 30 September each year.

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For the latest information on this programme consult the *BIRD* home page: http://www.esf.org/bird

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