PROPOSAL

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SCIENTIFIC PROGRAMME

on

Optimality in Bird Migration

- towards an understanding of avian migration strategies -

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I. Scientific context

1 General introduction

Migration is one of the most fascinating of all life-history traits. The annual seasonal migration of billions of birds has always fascinated many people. Solely within the European-African Bird Migration System, each year approx. 3-5000 millions of birds belonging to some 200 species breeding in the Palaearctic region migrate to Afro-tropical wintering grounds (MOREAU 1972, CURRY-LINDAHL 1981). The principal migratory routes are identified, and the principal mechanisms of the endogenous control of avian migration and orientation are known (ALERSTAM 1990, BERTHOLD 1991, 1993, 1996, GWINNER 1990). Similarily, the mechanics of flight of birds has been studied comparatively well (PENNYCUICK 1989). The ecological and evolutionary bases of migration as well as the physiology of migration, however received least attention, although they are crucial for understanding.

Migration is not an unitary character rather there is much variation in migratory life-history traits and migratory performances. Migration varies among species, among populations, among age groups and among sexes, and may even vary intraindividually. 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 (ALERSTAM 1990, BERTHOLD 1993). The causes, adaptive significance and consequences of this variation are, however, largely unexplored.

For example, 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 fewer 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 and large numbers of migrants might die. 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 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 mold 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.

Migration consists of a syndrome comprising behavioural, physiological, morphological, and life-history traits (DINGLE 1996). Therefore, progress in the field of migration research and future studies of migration need a much broader interdisciplinary approach, which considers the interaction of behaviour, physiology, and morphology, and which rests on sound evolutionary theory.

Moreover, besides its principal contribution to basic science a better understanding of the various migratory strategies and life-styles is also a prerequisite for sound conservation strategies and action plans.

2 The concept of optimal migration

Evolution by natural selection is a process of optimization (MCNEIL ALEXANDER 1982, ALERSTAM & LINDSTRÖM 1990). In recent years, considerable theory has been built up to predict various aspects of bird migration with optimality models. Starting from flight mechanical theory (PENNYCUICK 1975) several 'ecological' criteria have been added to the model to explain the temporal and spatial course of migration and the adaptations that enable birds to accomplish their migratory journey successfully (ALERSTAM & LINDSTRÖM 1990, LINDSTRÖM & ALERSTAM 1992, HEDENSTRÖM & ALERSTAM 1997).

The theory of bird flights yie ld quite specific predictions about gliding and soaring preformance of different species, and about the speed in flapping flight, and how this speed is expected to vary optimally in relation to environmental cues, like flight altitude, wind, or fuel burden.

The optimal way for a migrating bird to reach its destination within the appropriate time difffers depending on the demands that act on the birds. Time, energy, and safety from predators are of main current concern (ALERSTAM & LINDSTRÖM 1990).

Selection may have favored birds that minimize **energy** expenditure for migration so that they reach maximum distance with least power requirements. Such birds should carry only as much fat as is 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 minimize the energy spent during migration if food is difficult to get.

However, birds could also be selected to minimize 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 favored. These birds should minimize time spent on stopover and to carry maximum fat loads at departure to fly long distances without further interruptions for feeding.

A third possibilty is that **predation** constitutes such a significant hazard to migrants that they are primarily adapted to minimize the associated mortality risk during migration. In such case, birds should be inclined to depart with smaller fat reserves than is optimal in 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 (ALERSTAM & LINDSTRÖM 1990, LINDSTRÖM & ALERSTAM 1992, HEDENSTRÖM & ALERSTAM

1997). However, there a significant differences between theoretical predictions and allometric equations based on empirical data. Thus, a critical evaluation of these discrepancies remains to be done. It will enable a more refined understanding of migration performances and the underlaying selection processes.

These three basic features of how to accomplish migratory journeys are neither mutually exlcusive nor do they include other possibly important factors which yet need to be identified.

Spring migrants are likely to be time-selected rather than energy selected whereas autumn migrants appear to be mainly energy-selected (e.g. SAFRIEL & LAVEE 1988). However, late autumn migrants show evidence for time-selection as they have much higher average body mass than earlier migrating conspecifics (e.g. BAIRLEIN 1997, BERTHOLD et al. 1991, LINDSTRÖM et al. 1996).

A yet almost unidentified subject is the role of parasites and diseases in migrants, and the adaptations of the birds to cope with (CLAYTON & MOORE 1997, LOYE & ZUK 1991). Migratory birds are exposed to different parasite faunas during their annual cycles, while resident birds only experience a single parasite fauna. Some studies reveal that migratory species indeed have more severe infections than residents (MØLLER & ERRITZØE 1998). This may have implications for the fitness of the birds and for our understanding of the susceptibility of migratory birds to environmental perturbations. Considerable evidence exists that immune defences are dependent on body condition. As migration is generally an energy expensive habit where migrants are often close to their energetic limits that they can sustain, even small changes of the energetic performances of migrants, e.g. due to habitat changes, may have dramatic consequences for the ability of migrants to mount an efficient immune defence when exposed to parasite challenges, and for survival, and hence decreases in population size of migratory birds (MØLLER & ERRITZØE 1998). The relationship between body condition, refuelling and immune defence in migratory and resident species has rarely been studied, and it deserves more attention.

An optimality approach also needs evaluation of the evolution of geographical migration patterns and partial migration, involving assumptions about frequency-dependent selection processes (ALERSTAM & LINDSTRÖM 1990).

3 Migratory fuelling - the energetics of migration

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 particular long-distance migrants, which go thousands of kilometers one way from their summer breeding grounds to distant African wintering sites, exhibit extraordinary feats of physiological endurance. To migrate these long distances and to cross thousands of kilometers of the inhospitable terrain of the Sahara or the open sea requires considerable amounts of energy. Migrant birds, therefore, must fuel before migratory flights.

The principal fuel for migratory flights is fat. Lipids are clearly the best fuel for migration. However, recent studies showed that in several species, namley shorebirds, the energetic demands of migration cannot be met entirely with lipids, and that protein is catabolized as well.

To fuel flights between successive sites along the migratory route many migrants store fat reserves before departure. In addition, birds may accumulate considerable amounts of proteins, however, we know little about the deposition of protein. The total amount of fuel accumulated varies between and within species. Birds migrating as 'energy minimizers' do not need much fat 'on board' whereas the 'time minimizers' usually rely on hihger fuel stores. Those birds which have to cross huge inhospital 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.

However, although the theory of bird flight offers a possibility of predicting optimal reserves of fuel, the adaptive significance of different fuel loads is poorly understood. More detailed field studies and experiments are needed to test and distinguish between the predictions based on the current optimization approach.

Even orientation performance in migrating birds could be influenced by the energy stores. Adequate fat robins and chaffinches oriented towards the seasonally appropriate directions whereas lean birds did not rather they oriented in the opposite directions (BÄCKMAN et al. 1997, SANDBERG 1994).

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

(1) 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;

(2) 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 on the foraging ecology, and the energetic and nutritional demands of fattening migrants.

There was common sense that energy of food is the main predictor for foraging decisions and consequences. However, recent data revealed that dietary nutrient composition clearly influences the rate of daily body mass gain during migratory fattening (BAIRLEIN 1998, BAIRLEIN & GWINNER 1994). 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 (BAIRLEIN 1990), although the adaptive significance is poorly understood. There is, however, considerable recent evidence that seasonal shifts in diet selection in migrating birds are to maximize the rate of fattening (BAIRLEIN & GWINNER 1994). Timing migratory fat deposition, daily fat deposition rates, and fat loads at departure are closely related to the conditions for appropriate diet selection.

4 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 utilization, changes in blood oxygen transport properties, and development and synchronization of migratory behaviour, including diel and seasonal patterns. The control of these processes is complex, and because of this complexity not clear in many details.

Gonadal hormones, for example, play a considerable role in the control of spring migration, but not so in fall migration. Similarily, tyroid hormones seem to be involved in the regulation of spring migration, but not in fall (WINGFIELD et al. 1990, TOTZKE et al. 1997).

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 (KARASOV 1996, PIERSMA ET AL. 1996, PIERSMA & GILL 1997). In garden warblers, for instance, the digestive tract is reduced to 60 % in mass after a Sahara desert, likely as an effect of the extraordinary energy and nutrient demands for such flights (HUME & BIEBACH 1996). As a consequence, fat deposition rates at the beginning of a stopover phase are reduced compared to birds with a fully functional digestive system. The dynamics of reduction and rebuild of the digestive tract seems to be very rapid, within one or two days. Comparative data on intraindividually and repeatedly reversed changes in stores and organ size seem to represent evolutionary compromizes between their functions during storage, flight and post-arrival phases (PIERSMA 1997). More detailed information about the time course, the cost of maintenance and cost of rebuilding organs would enable a cost-benefit approach in order to elucidate the functional significance of organ size flexibility in migrants, and to understand the temporal division into flight and stopover.

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:

- energy density from different fuels, and how these fuels are obtained and used;
- minimum mass and demands of lungs and heart to support mechanical power output;
- the extent and adaptive role of phenotypic flexibility in organ size;
- the extent to which protein from organs are consumed during flight;
- the requirements for basal metabolism in an active bird, and its relationship to basal metabolism of the inactive bird;
- muscle physiology.

So far, physiological and biochemical processes and constraints have not been accounted for in the optimization models based solely on aerodynamics (ALERSTAM & LINDSTRÖM 1990).

5 Stopover behaviour - the decision between stopover and flight

Although fattening/fuelling takes place at stopover sites, stopover ecology is among the least studied topics in the ecology of avian migration (WALSBERG 1990, LINDSTRÖM 1995).

Timely fattening for migration requires the availabilty of appropriate locations along the birds' migratory route for both feeding and shelter. During breeding, most birds are rather 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 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 (BAIRLEIN 1983, BERTHOLD 1996), and 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 novelity 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.

We know little about the distribution and ecology of migrants in their African wintering grounds. We do not know whether migrants use single specific wintering site or whether they roam between several sites, or whether some species undertake regular migrations within Africa (e.g. PEARSON & LACK 1992). Other important but yet unanswered questions include: (i) What kind of habitats do they use? (ii) Which resources are used? (iii) Share the habitats used in stopover sites, in the wintering area and in the breeding season certain characteristics? (iv) How do migrants cope with novel situations? (v) To what extent do migrants interact with species of the resident avifaunas during stopover and in winter? (vi) What are the ecological conditions and physiological adaptations in wintering migrants?

II. The proposed *Scientific Programme*

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. Migration is a general biological phenomenon, not simply a trait characteristic of a particular taxon (DINGLE 1996). The characterization of migration must consider the physiological mechanisms underlying migratory behaviour, the ecological consequences of that behaviour, and how those consequences guide 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, and 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 migrants flexibility to respond to human alterations of ecological systems.

The proposed Scientific Programme *aims at initiating the integration of various sub-disciplines, such as ecology, physiology, behaviour and genetics, thereby earning a much better understanding of the bird migration syndrome. It aims to form a forum for more trans-disciplinary studies in bird migration.*

1 The goals

To understand fuelling is crucial for understanding the migration strategies and the selective forces and constraints acting upon them and for taking appropraite conservation measures. Therefore, the programme aims to give particular emphasis to studies of the ecology and physiology of fuelling, as the basis for the evaluation of the existing theory and models, and practical application in conservation.

The proposed goals will be achieved by a combination of field and laboratory studies, and are based on existing models on optimal bird migration and their predictions (ALERSTAM & LINDSTRÖM 1990, WEBER & HOUSTON 1997).

The basic hypotheses

ALERSTAM & LINDSTRÖM (1990) formulated three basic hypotheses derived from the model of optimal migration:

- Birds trying to *minimize time (= maximize migration speed)* on migration should be sensitive to the rate of fuel deposition. The departure fuel load should correlate positively with the rate of fuel deposition. Birds which decide with respect to time-minimization should leave a stop-over site for further migration with maximum fuel loads.
  In such time-selected migrants, birds at northern sites should show higher fuel reserves than at more southern sites in autumn, and opposite in spring, and fuel mass of late migrating cohorts should be higher than of early migrants.
  In time-selected migration, a risk-prone foraging during fuel deposition is predicted with preference of variable food rewards, hence a wider spectrum of food.
- In birds *minimizing cost of transport (energy-minimization; energy economy)* the departure fuel load should be independent of the rate of fuel deposition. These birds should travel with as low extra weight as possible.
  In energy-selected migration, risk-proneness could be advantageous if the expected energy budget for the migratory journey is insufficient. Otherwise, risk aversion may increase the probability of avoiding shortfalls.
- Birds trying to *minimize mortality (predator-minimization)* should adjust their decisions to stay at or leave a stopover site with respect to predator-load (risk) of a particular site. To militate against mortality risks birds should be inclined to depart with smaller fuel reserves than is optimal in time-selected migrants. Birds in predation-selected migration should switch from stopover sites or habitats with a high rate of fuel deposition but also high predation risk to more protected sites with a smaller rate of fuelling according to which sites or habitats provide the minimium possible ratio between mortailty and the speed of migration.

Basic questions to be addressed

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 hazard) and intrinsic cues (e.g. age, sex, physiological capabilities, digestive capacities, parasite load, endogenuous migratory time program).

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, the follwoing 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 (e.g. along the migratory route; autumn vs spring)?
- 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 affects the bird's decision to stay or fly?

2 The methodology

The goals of the programme and the basic questions will be achieved by a combination of studies in the field and the laboratory.

Field studies

Body conditions and body composition of birds at arrival and at departure will be studied by

i measuring body mass, subcutaneous fat reserves, and muscle score (cf. BAIRLEIN 1995);

ii the use of diagnostic blood parameters which indicate fuel use and fasting (cf. BAIRLEIN & TOTZKE 1992, JENNI-EIERMANN & JENNI 1994);

iii assessment of parasite loads (including haematozoa, coccideans, helminths and ectoparasites) and diseases (for methods see, for instance, CLAYTON & MOORE 1997). Immunocompetence tests will be carried out in birds which will be kept in cages overnight. These immunocompetence tests reveal a generalized, integrative response to all different parasites (CLAYTON & MOORE 1997, A.P. MØLLER, pers. comm.).

iv culling small sub-samples of birds for a more detailed and more sophisticated biochemical analysis in order to evaluate the enzymatic and hormonal mechansisms of migratory fuelling and use of fuels, including the determination of body fat, body protein, and body carbohydrate composition, measurements of enzymes (for instance: adiposelipoprotein lipase, cytochrome-oxidase, β-hydroxyacyl-CoA-dehydrogenase, citrate synthase; cf. LUNDGREN & KIESSLING 1985, MARSH 1981, RAMENOFSKY 1990), and hormones related to migration behaviour (for instance: corticosterone, testosterone, thyriod hormones, pancreatic hormones; TOTZKE et al. 1997, WINGFIELD 1990), and size and structure of digestive organs (e.g. HUME & BIEBACH 1996, PIERSMA et al. 1996, PIERSMA & GILL 1998). In addition, a more detailed evaluation of the entire parasite load could be carried out in these culled birds (CLAYTON & MOORE 1997).

Trapping of migrants can and will be designed in a way that access to these particular groups of birds is facilitated.

Daily rates of fuelling and their environmental constraints will be studied

i in within-season retraps.
During stopover a fairly well number of birds can be caught after their first catch, so that the course of body mass change (fuel deposition) can be followed up.

ii in color-marked individuals by remote control monitoring of body mass changes by the use of automatic electronic balances (LINDSTRÖM & ALERSTAM 1992, FRANSSON 1998).
Electronic balances will be set up at repeatedly used feeding places (e.g. northern wheatear; V. DIERSCHKE & F. BAIRLEIN unpubl.), on repeatedly used perches, or they will be attached to artificial feeders (FRANSSON 1998) where supplementary feed will be provided to attract birds and also to enable increased intake rates.

iii by supplementary feeding.
It will enable to vary feeding conditions experimentally, so that direct links between feed availability and rates of fuelling and departure fuel load can be assessed (for example, CARPENTER et al. 1983, LINDSTRÖM & ALERSTAM 1992, FRANSSON 1998). This will particularly done in habitats with low food variability and availability, like on some small islands or at coastal sites, or in birds preferring more open habitats with rather easy access and visibility of the birds.

iv by experimentally manipulating predator abundance using predator skin mounts and recording the migrants behaviour and consequences for daily body mass gain and habitat use.

v by experimentally influencing the competitor relationships in order to assess the role of competition.
Apart from analysing the routine data of body condition and fuelling on days with low and high numbers of migrants staging at a particular site, there are several possibilities to influence the competitor structure. Newly arrived migrants can be removed from a site, or migrants can be released. These birds may come from a nearby site or the removed ones can be released following keeping in captivity after removal. Another recent tool is the use of tape lures to attract migrants. These can be alternately used on successive days so that various abundances of migrants can be obtained (S. RUMSEY, pers. comm.).

Food, energy and nutrient intake rates will be assessed by

i detailed field observations on time budgets, foraging substrates, foraging routines and foraging techniques in individually marked birds (using color bands and radiotransmitters) by focal techniques (MARTIN & BATESON 1986, EXO 1992).

ii fecal sampling and digestive flushing.

Both are well established methods to identify the food types of birds, and can be easily done in trapped birds (e.g. BRENSING 1977, RALPH et al. 1985, JENNI et al. 1990). The use of stable isotopes to determine diets of free-living birds (e.g. GANNES et al. 1997) is proposed to be evaluated.

iii measurements of field metabolic rates.

In birds with temporary territories on stopover (e.g. pied flycatcher) or in birds with high rates of retraps (e.g. northern wheatear, whinchat), measurements of field metabolic rate(FMR) will be conducted using the double labelled water (DLW) technique (cf. NAGY 1980, SPEAKMAN 1997), and remote heart rate recording by the use of radiotransmitters (e.g. LUND1989).

Habitat suitability will be assessed by

i recording the food supply, both arthropodes and fruits, by standard methods commonly used in ecological studies (e.g. SUTHERLAND 1996), in order to determine the conditions required for fuelling.

ii recording the presence/absence of predators and their interactions with the stopover migrants.

The field sites will be selected by their geographical locality (northern, central, southern Europe), habitat structures, and the expected numbers of focus species. To study migration at several sites along the migratory route is the most efficient way for a better understanding of the performance of migratory birds, and the selection processes operating on them (LINDSTRÖM et al. 1996).

An important aspect will be the comparison of sites distant from ecological barriers and at ecological barriers. Migrants confronted with wide ecological barriers devoid of suitable refuelling sites are forced to store extra large fuel reserves to accomplish the impending long flights (ALERSTAM & LINDSTRÖM 1990, BAIRLEIN 1991).

Ideal sites for the proposed field experiments on induced feeding, predator variation and competitor variation are in particular sites where there is a high variation in the daily number of catches and easy habitat structure allowing access to the birds. Good candidates are small islands and some coastal sites (F. BAIRLEIN unpubl.).

Concerning some of the targeted songbird migrants field sites will be selected from sites which operated within the ***ESF Scientific Network* on Songbird Migration** (BAIRLEIN 1993). The *ESF Scientific Network* on Songbird Migration set an excellent and outstanding framework which could now be used to develop bird migration research a significant step further. The creation of the *Network* has launched a new era for the study of bird migration in Europe.

Laboratory studies will be conducted to study

i basal metabolic rates of birds in resting conditions and in relation to fat load, and diet.

Metabolic rates will be determined by respirometry, as routinely used in many studies (e.g. CAREY 1996, KLAASSEN & BIEBACH 1994, PIERSMA et al. 1996).

These date are further necessary to calibrate heart rates and metabolic rate. Heart rate could be altered by forced behavioral traits of birds kept in metabolic containers, so that heart rate and metabolic rate could be recorded in parallel (e.g. HUEPPOP 1995).

ii maximum energy intake rate, and its relationship to food quality and metabolic rate.

Maximum energy intake can be assessed by feeding birds in captivity under controlled feeding conditions (e.g. BAIRLEIN 1985, 1998).

iii the relationship between migratory activity, feeding opportunities, photoperiod and fat status.

BIEBACH (1985) and GWINNER et al. (1985) demonstrated that migratory activity was governed by a combination of fat status and feeding possibilities. Moreover, there is recent evidence from studies of birds in captivity that, besides a basic endogenous control (GWINNER 1986, BERTHOLD 1996), migant birds are able to adjust the timing of autumnal fat depositon to time of season and/or food availability. Short-term food shortage of garden warblers and blackcaps during the period of autumnal migratory disposition (BAIRLEIN & TOTZKE in prep.) as well as shifting the the light:dark cycle further into autumn in bluethroats (Lindström et al. 1994) or in blackcaps (BAIRLEIN & TOTZKE in prep.) resulted in subsequent increase in the rate of fat accumulation. Interestingly, the data obtained are in accordance to field observation at autumn stopover sites with much heavier and fatter birds during later passage (e.g. BERTHOLD et al. 1991, BAIRLEIN 1997).

iv physics, energy conditions, and the use of fuels in birds in wind tunnel flights.

Wind tunnel experiments, making use of the excellent facilities at Lund University (PENNYCUICK 1995), will be conducted to get further insights in the metabolic, physiological and physical performance of migratory flights, which so far have mainly be obtained from theoretical considerations on flight aerodynamics. These studies are very likely to evaluate our current knowledge on bird flight performances.

Dynamic programming models

The data obtained in the empirical and experimental field and laboratory studies will continuously enter dynamic programming (e.g. HEDENSTRÖM & ALERSTAM 1997, WEBER & HUSTON 1997). So far, we have simple deterministic models based on time and energy. Discrepancies between such models and data have proved instructive. Some work has been done on state-dependent models. This approach needs to be extended to models that can take account of changes in various aspects, and that put migration into the context of a bird's annual cycle. The *Programme* aims to combine simple analytical models together with dynamic programming models of annual migration routines and decision making processes in the migrant bird.

3 The target species

To meet the questions addressed by the *Programme* comparative analyses of different groups of migrants are most efficient, including songbirds, shorebirds, and even raptors. In particular, evaluating the models could benefit from such a link between different groups of migrants, using rather different migration habits and migratory performances.

With respect to the proposed combination of field and laboratory studies, songbirds, however, are the most obvious candidates for the proposed subjects of interest.

Trapping of songbirds at stopover by the use of nets is comparatively easy and could be carried out in a standardized routine along the migratory route (BAIRLEIN 1995). Many migrant songbirds are quite numerous at stopover sites, so that appropriate numbers of birds can be obtained. Species of particular concern are Garden Warbler (*Sylvia borin*) and Blackcap (*Sylvia atricapilla*), Reed Warbler and Sedge Warbler (*Acrocephalus scirpaceus*, *A. schoenobaenus*), Pied Flycatcher (*Ficedula hypoleuca*), redstart (*Phoenicurus phoenicurus*), wheatear (*Oenanthe oenanthe*) and whinchat (*Saxicola rubetra*). These species and species groups are among the most numerous migrants in Europe (BAIRLEIN 1997), most are rather visible and easy to observe and to handle in the field, and they are rather easy to handle in captivity under controlled experimental condition. As consequence, considerable ecological, behavioral, and physiological data are already available which facilitate to design further studies.

Compared to shorebirds, maximum fat loads and maximum rates of fattening are higher in passerines (LINDSTRÖM 1991), and metabolic/mass relationship is higher in passerines than in larger species.

Compared to shorebirds, the probabilty of within-season retraps which are an ultimate prerequisite for studying fuelling rates during stopover is much higher for passerines, and experimental field work is almost unlikely to carry out with shorebirds due to the difficulties of routine trapping of shorebirds.

Compared to passerines, apart from few exceptions, shorebirds are difficult to handle in captivity under controlled indoor conditions. As a consequence much less on the internal control of migration is known of shorebirds.

Nevertheless, any study on shorebirds matching with the goals of the *Programme* will be incorporated.

4 The *Programme* concept

Basically, the *Scientific Programme* aims to support pre- and postdoctoral students, and to organize scientific conferences.

Grant scheme: To support young scientists to get involved in research and data analyses is the most efficient way to make considerable novel contribution to the understanding of bird migration. A grant scheme is to incorporate young scientists and to increase their mobility between research centres in Europe. The grant scheme will offer exchange visits for collaborative research in different countries in Europe, and to initiate trans-disciplinary studies. Such visits would bring together young scientists and enable the exchange of ideas and the promotion of the research. Students can apply for a grant. The applications will be reviewed with respect to their objectives and relationship to the goals of the *Programme*, and the quality of the proposal. Exchange visits will be normally awarded for stays of up to 12 months.

Workshops are to review the state-of-art in the framework set by the goals of the *Programme*, and to provide a forum for intensive discussions. Tentative subjects for five annual workshops are:

- 'Environmental control of migration',
- 'Cost-benefit relations in migratory birds',
- 'Causes and consequences of changes in migration resources',
- 'The concept of optimality in bird migration models'.
- 'Evolution of migration',

III. Significance of the *Programme* and the role of ESF

The proposed *Programme* would be an outstanding innovative initiative in the study of bird migration. No other such project ever attempted to integrate between different disciplines, and to cross traditional disciplinary boundaries. The work is very likely to benefit from the integration of international specialists and expertise.

The *Programme* emphasises the involvement of young scientists, and to combine the work of scientists and the data collection programmes carried out by skillful amateurs which play a particular role in the large-scale study of birds. The *Programme* would run in close link with the European Union for Bird Ringing (EURING), the network of all European Bird Ringing Centres, and representing hundreds of skillful amateurs all across Europe.

The *Programme* aims to act on a wide geographical scale, owing to the migratory birds habits. Apart from the ***European Science Foundation***, there are no sources for support for such a large-scale, multi-national and multivariate project. By its basic objectives, the ESF is the only organization which can provide the means for such an integrated large-scale collaborative project in Europe.

The *Programme* would foster the leading role of European scientists in the study of bird migration. Nowhere else such an approach would be able to be carried out because of the long tradition Europe has in the study of bird migration, and because of the extraordinary web of well trained amateur ornithologists all over Europe.

IV. Conservation issues

Migratory birds are particularly faced by long-term population declines and, thus, need special attention (e.g. MARCHANT et al. 1990, BAUER & BERTHOLD 1996).

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

Migratory birds are particularly appropriate for addressing conservation issues. Birds are conspicious, 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, movements) that relate to population health and habitat suitability are more easily monitored in birds than in any other vertebrate taxon. 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 (MARCHANT et al. 1990, BAUER & BERTHOLD 1996). To evaluate the specific migratory routes, to identify the important fueling areas, and to elaborate the species-specific energetic and ecological conditions during stopover and at the wintering grounds are not only of fundamental scientific importance. They are also a prerequisite for conservation programmes (BAIRLEIN 1994).

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 (MARCHANT 1992).

For most birds we have only very fragmentary information on these relationships. Some important questions therefore are:

- Which are the factors involved in populations changes of migrant species?
- How do migrants cope with the many anthropogenic environmental changes?
- How flexible do they respond to environmental changes?

Sound conservation of migrants is an international affair. Migrants breed in one country, transit several others, and spend the nonbreeding season in yet another country. Migrants will be affected if breeding or crucial nonbreeding 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.

V. Programme Elements

The principal elements of the *Programme* will be the following:

Programme student grants scheme

A basic aim of the *Programme* is to support pre- and postdoctoral students to get involved in field research and data analyses. This grant scheme is to incorporate young scientists and to increase their mobility between research centres in Europe. The scheme will offer exchange visits for collaborative research in different countries in Europe. Students can apply for a grant. The applications will be reviewed with respect to their objectives and relationship to the goals of the *Programme*. Exchange visits will be awarded for stays of up to 12 months. The proposed budget would enable to offer six to eight 12-months grants a year.

Organization of workshops

Five workshops are proposed to be organized within the *Programme*. The main goal of the workshops is to provide a forum for the exchange of expertise and research results, and to review scientific issues on a very high level.

Each workshop will be attended by about 40 scientists. The workshops will be open to researchers from all European countries, and even from other continents, who can apply to attend and who will be selected for participation on the basis of their experience and appropriateness of the workshop to their research interest.

Supporting the central Data Bank

The creation of a central Data Bank within the *Network* was a great success, and the *Programme* should continue to do so. The main goals of the Data Bank are to compile all standard data obtained within the *Programme*, to derive regular data reports and preliminary analyses, and to encourage rapid data analysis by participants. To achieve the goals of the Data Bank, some managerial tasks including some office expenses are needed.

Programme Newsletter

At least once per year, a *Programme* Newsletter will be circulated to advertise all *Programme* activities, to keep participants informed, to promote cooperation and integration, and to show preliminary results regularly derived from the project and the Data Bank.

VI. *Programme* organization

A *Programme Steering Committee* will be set which takes the overall responsibility of the *Scientific Programme*. The *Steering Committee* will tentatively have the following members:

Austria	Prof. Hans Winkler (Vienna)
Belgium	Dr. Erik Matthysen (Antwerp)
Finland	Prof. E. Lehikoinen (Turku)
France	Prof. Anders Pape Møller (Paris)
Germany	Prof. Franz Bairlein (Wilhelmshaven)
Italy	Dr. Fernando Spina (Bologna)
The Netherlands	Prof. Arie van Noordwijk (Heteren)
Norway	nn
Spain	Prof. Emilio Barba (Valencia)
Sweden	Dr. Anders Hedenström (Lund)
Switzerland	Dr. Lukas Jenni (Sempach)
UK	Prof. William Sutherland (Norwich)

VII. Potential professional participants and exchange destinations

The list includes some tentative participants, many of them already expressed their interest. However, this list is not closed. Rather it should stimulate to join the *Programme*.

Austria	Prof. J. Dittami	Vienna
	Prof. H. Winkler	Vienna
Belgium	Dr. E. Matthysen	Antwerp
Finland	Prof. E. Lehikoinen	Turku
France	Prof. A.P. Møller	Paris
Germany	Prof. F. Bairlein	Wilhelmshaven
	Prof. P. Berthold	Radolfzell
	Dr. H. Biebach	Andechs
	Prof. E. Gwinner	Andechs
	Dr. A. Helbig	Hiddensee
	Dr. M. Starck	Jena
Italy	Prof. E. Baldacinni	Pisa
	Dr. F. Spina	Bologna
Lithuania	Dr. G. Valkiunas	Vilnius
The Netherlands	Prof. R. Drent	Groningen
	Dr. M. Klaassen	Nieuwersluis
	Prof. A. van Noordwijk	Heteren
	Dr. T. Piersma	Den Burg
	Dr. H. Visser	Groningen
Poland	Prof. P. Busse	Gdansk
Spain	Prof. E. Barba	Valencia
	Prof. C. Herrera	Sevilla
Sweden	Prof. T. Alerstam	Lund
	Dr. A. Hedenström	Lund
	Dr. Å. Lindström	Lund
	Prof. U. Norberg	Göteborg
Switzerland	Prof. B. Bruderer	Sempach
	Dr. L. Jenni	Sempach
	Dr. F. Liechti	Sempach
U.K.	Prof. R. McNeill Alexander	Leeds
	Prof. P. Butler	Birmingham
	Prof. A. Houston	Bristol
	Prof. I. Newton	Monks Wood
	Prof. C. Pennycuick	Bristol
	Prof. W. Sutherland	Norwich

Appendix: **List of selected references**

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