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Optimal bird migration revisited

Thomas Alerstam

Department of Biology, Lund University
Ecology Building, SE-22362 Lund, Sweden
email: Thomas.Alerstam@zooekol.lu.se

Abstract Using optimality perspectives is now regarded as an essential way of analysing and understanding adaptations and behavioural strategies in bird migration. Optimization analyses in bird migration research have diversified greatly during the two recent decades with respect to methods used as well as to topics addressed. Methods range from simple analytical and geometric models to more complex modelling by stochastic dynamic programming, annual routine models and multiobjective optimization. Also game theory and simulation by selection algorithms have been used. A wide range of aspects of bird migration have been analysed including flight, fuel deposition, predation risk, stopover site use, transition to breeding, routes and detours, daily timing, fly-and-forage migration, wind selectivity and wind drift, phenotypic flexibility, arrival time and annual moult and migration schedules. Optimization analyses have proven to be particularly important for defining problems and specifying questions and predictions about the consequences of minimization of energy, time and predation risk in bird migration. Optimization analyses will probably be important also in the future, when predictions about bird migration strategies can be tested by much new data obtained by the modern tracking techniques and when the importance of new trade-offs, associated with e.g. digestive physiology, metabolism, immunocompetence and disease, need to be assessed in bird migration research.

Keywords Bird migration · Optimality · Migration strategy · Flight · Stopover · Predation · Wind · Routes · Timing

Introduction

Birds carry out their migratory journeys in a multitude of different ways. In some cases they deposit large fuel reserves and make long flights while in other cases they proceed by small fuel loads and short flights. They fly at different times during the night or the day, use flapping or soaring flight to variable degrees, fly at high or low altitudes, solitarily or in flocks, respond differently to weather and winds, show different moult schedules in relation to migration, and so on.

In order to understand the adaptive values associated with this fascinating variability in migratory behaviours between and within species, populations and individuals, optimization analysis is used. Suggesting critical constraints, costs and benefits for a certain type of behaviour and predicting the optimal solutions under different conditions in a way that permits testing by observations and experiments is the essence of this approach. By assuming different main optimization criteria, like time, energy and predation risk, it is also possible to test the shifting relative importance of these main criteria as selection forces (i.e. how important these criteria are in affecting fitness) under different situations in bird migration.

I am happy to have been contributing to generate interest in developing optimization analyses in the field of bird migration, mainly starting with an article co-authored with Åke Lindström (Alerstam and Lindström 1990) where we also coined the concept of “optimal migration”. The use of optimization methods was not new to bird migration research at that time, but such approaches were adopted mainly in evaluations of e.g. partial and differential migration at population levels (cf. review by Alerstam and Hedenström 1998) while, concerning birds’ behaviour on actual migration, there were rather few optimization analyses, notably the work of Pennycuick (1969, 1975) and Tucker (1974) on bird flight and a few attempts to analyse how migrating birds could exploit winds in an optimal way (Alerstam 1979a, b). At that time I was struck by our large ignorance about the adaptive values of the widely variable behaviours of migrating birds and particularly by the fact that we could not even tell if the birds were primarily behaving to save energy, speed up migration or avoid hazards like predation. The three most important influences on our ideas (Alerstam and Lindström 1990) were from flight theory (Pennycuick 1969, 1975, Tucker 1974), optimal foraging theory (e.g. Stephens and Krebs 1986) and the notion of resulting speed of migration as calculated from ringing recoveries by Hildén

and Saurola (1982). It became obvious that a theoretical framework incorporating both flight (when energy is consumed) and fuel deposition before departure and at stopover sites was necessary to predict migration strategies. The relationships (1) between flight power and speed, (2) between flight range and fuel, (3) between total migration speed (or total duration of migration) and flight speed, energy consumption during flight and energy deposition rate at stopover sites, as well as (4) the derivations of the marginal increase in range with increasing fuel and with increasing time, were fundamental components of this first approach. Further aspects of optimal bird migration were soon explored and developed in collaboration with Åke Lindström, Gudmundur Gudmundsson and Anders Hedenström.

Looking at the optimal bird migration field today, two decades later, it is reassuring to see the large interest that it has attracted and the great expansion and progress with respect to aspects analysed (Table 1) as well as to methods and approaches used (Table 2). The derivations and predictions about flight and fuelling behaviour based on the fundamental relationships mentioned above have been summarized by Alerstam and Hedenström (1998) and also in more recent reviews (Hedenström 2008, 2009) and will not be repeated again in this contribution. Rather, I will briefly review optimization analyses about the different aspects in Table 1, indicating how they have advanced understanding of adaptations and strategies in bird migration and paying attention to possibilities for the future.

In the early phase of the optimal migration field, simple analytical models (e.g. Pennycuik 1975; Alerstam and Lindström 1990; Weber et al. 1994) and simple vector models (e.g. Alerstam 1979a, b) were used (Table 2). Such models are still particularly useful for generating qualitative predictions and illustrating the main principles and effects of key trade-offs. However, migratory traits do not evolve deterministically in isolation in response to only a single optimization criterion, so more extensive and complex models based on the techniques of stochastic dynamic programming (e.g. Weber et al. 1998; Clark and Burton 1999; Bauer et al. 2008), annual routine analysis (McNamara et al. 1998; Hedenström et al. 2007; Barta et al. 2008) and multi-objective optimization (Vrugt et al. 2007) have been used to obtain more realistic predictions for different types of behavioural decisions during the whole migratory journey or annual cycle. Such complex models require an extensive set of assumptions about several constraints, trade-offs and stochastic effects. Being applied to specific cases where there is detailed knowledge to help specifying these

assumptions, these models have a great potential in predicting effects on migration of e.g. habitat loss at stopover sites (Weber et al. 1999) or climate change (Bauer et al. 2008), both immediate and long-term changes if the birds can eventually adapt in an optimal way to the changed conditions. In addition, these models are important for efficient conservation and management of migratory populations (Klaassen et al. 2008). Additional approaches such as game theory (e.g. Kokko 1999) and spatial simulation models with genetic algorithms (Erni et al. 2003, 2005) have also been adopted in very fruitful ways to take density-dependent and spatial effects into account. I think that both simplistic and complex models have proven their usefulness and are needed in a complementary way in optimization analyses of bird migration.

Flight (speed, mode, climbing).

Predictions about different optimal flight speeds (airspeeds) for minimizing energy over time, energy over distance or total duration of migration, respectively, based on the power curve for flapping flight (Pennycuik 1975, 2008) gave hopes that flight speed may serve as an important attribute to reveal the shifting importance of different optimization criteria in different ecological situations (Alerstam and Lindström 1990; Alerstam 1991; Hedenström and Alerstam 1995).

Uncertainties about the exact relationship between flight power and speed make comparative and qualitative predictions about differences in speed between different situations more robust than specific quantitative predictions. It has been argued that the flight power curve is in many cases not U-shaped at all and, consequently, that the birds' flight speeds must be determined, not by power requirements, but by other (unknown) factors (Chernetsov 2010). However, there are several convincing demonstrations of U-shaped power curves (e.g. Tobalske et al. 2003) and it is mostly a matter of how flat or well-defined the lower part of the power curve is (which may differ between species, individuals and test conditions), because high power requirements must be unavoidable at very slow and fast speeds (Engel et al. 2010).

Several studies have analysed and confirmed that migrating birds often tend to increase their airspeed in headwinds and reduce speed in tailwinds (e.g. Bloch and Bruderer 1982) showing that migrants generally do not fly at a fixed (wind-independent) minimum power speed. Other studies have confirmed and analysed the increase in true airspeed of migrating birds with increasing flight altitude (and

decreasing air density) and have also investigated the wingbeat pattern in relation to air density (e.g. Schmaljohann and Liechti 2009). However, there are few studies that have explored and tested the variation in flight speed between different types of ecological situations where different optimization criteria may apply. Skylarks were demonstrated to fly at much faster airspeeds on migration compared to their song flight speed, a difference that was in agreement with predictions (Hedenström and Ålerstam 1996). However, swifts increased their airspeed to a smaller degree than predicted when orienting into increasingly strong winds during nocturnal summer roosting flights (Bäckman and Ålerstam 2001). Swifts were flying at significantly faster airspeeds on spring migration compared to autumn migration and summer roosting, which may indicate a stronger element of time-selection for spring migration, but the differences in airspeeds between seasons were rather small (Henningsson et al. 2009). Still, during brief intervals of display flight swifts can fly more than twice as fast as their typical speeds in sustained cruising flight, and during these fast flights they probably reach their maximum flight speed performance (Henningsson et al. 2010).

It was recently demonstrated that nocturnal passerine migrants fly at consistently higher airspeeds in spring than in autumn, with spring speeds exceeding autumn speeds by on average 16 % (Karlsson et al. 2010). This result was based on large samples of speed measurements from tracking radar studies during several years at two different places in southern and northern Scandinavia, respectively. It is unlikely that this difference in speed was caused by seasonal differences in body mass or wing morphology and the most likely explanation is that the birds during spring fly at a higher optimal speed for minimizing total duration of migration (Karlsson et al. 2010). This is a very exciting finding that will stimulate the exploration of seasonal differences in migration strategies.

I think that further studies of the variation in flapping flight speeds in different situations, when applied within well-defined categories of migrants, within species or preferably even within individuals, may provide highly important insights into the selective factors affecting the birds in different situations (e.g. spring versus autumn, early departure versus final approach phase of migration, females versus males, juveniles versus adults, forward versus retreat migration) and also be helpful for elucidating the nature of the power curve. Comparisons of performances of birds

flying in wind tunnels with their free flight under natural conditions will be of particular importance in this latter respect.

Other issues about flight that have been addressed in optimal migration analyses are the use of flapping versus soaring flight, where the profitability of the latter mode is more restricted in time-selected compared to energy-selected migration (Hedenström 1993), and the wind-dependent trade-off between horizontal and vertical flight speed during the climbing phase when birds depart on migratory flights (Alerstam 1985; Hedenström and Alerstam 1994).

Fuel deposition

Fuel deposition at stopover sites has attracted a particularly great interest in the optimal migration field with much stimulating theoretical as well as empirical work during the two recent decades. The basis for the predictions about the birds' fuel deposition rules is the so-called range curve, i.e. the decelerating function of flight range in relation to fuel load (or to stopover time if a certain fuel deposition rate is assumed) where the marginal rate of increase in range will become reduced with successively heavier fuel burdens (Alerstam and Lindström 1990).

It has been objected (Chernetsov 2010) that recent studies in wind tunnels have indicated much smaller flight costs with increasing body mass than predicted from flight mechanical theory, suggesting that the range versus fuel relationship would approach linearity and thus offer little as a basis for analysing and understanding the birds' patterns of fuel deposition on migration. However, this conclusion seems premature since the mass-dependence in airspeed has been ignored in these measurements and arguments. It is the scaling of energy cost over distance (and not energy cost over time) with body mass that is given from flight mechanical theory and forms the basis for deriving a correct range curve. Testing this scaling relationship at a fixed airspeed (Chernetsov 2010) can be very misleading and biased towards both smaller and larger scaling exponents compared to the correct estimate. While I think that it is premature for these and other reasons (incompatibility between metabolic power measurements and mass reduction in the wind tunnel study by Kvist et al. 2001) to exclude the possibility that the extra cost of flying with heavy fuel burdens influences the fuel deposition of birds using flapping flight, this cost may be much less important and even non-existent in soaring flight for which range curves may be

quite different from those referring to flapping flight (Alerstam 2000). Empirical studies of fuel deposition habits among soaring migrants are eagerly awaited to reveal if indeed there exist profound differences in fuel economy related to flight mode.

Alerstam and Lindström (1990) used the range curve in combination with assumptions about settling costs (energy and time) at each new stopover site to predict optimal mean departure fuel loads for migrants travelling under different average conditions of settling costs and deposition rates. Departure fuel loads were predicted to vary with both settling cost and deposition rate in time-selected migration but only with settling cost in energy-selected (minimization of flight transport costs) migration. For time-selected individuals experiencing variable fuel deposition rates at different stopover sites it was expected that they depart when their marginal rate of gain in flight range (their instantaneous speed of migration) had decreased to the mean rate expected on the further journey, whereas energy-selected individuals were expected to depart at a threshold fuel load independently of their fuel deposition rate (Alerstam and Lindström 1990). These predictions were tested for migrants experiencing both experimentally induced (bluethroats *Luscinia svecica*) and natural variation (rufous hummingbirds *Selasphorus rufus*) in fuel deposition rate at a stopover site (Lindström and Alerstam 1992). The results showed a positive relationship between departure fuel load and deposition rate, thus rejecting energy minimization, but with a slope that was much shallower than predicted for time-selected migration. What was wrong?

Lindström and Alerstam (1992) suggested two possible explanations for the surprisingly shallow slope – that different individuals had consistently different expectations about future deposition rates or that the expected speed of migration increased along the route. Further possible explanations were suggested by Klaassen and Lindström (1996), that added fuel caused increased locomotion costs, and by Hedenström and Alerstam (1997), that the birds were minimizing total energy costs during migration, including not only costs of transport but also existence costs. A particularly influential suggestion put forward by Houston (1998) was that the birds adopted the experienced fuel deposition rate at each new stopover site as the expected rate also for the further journey – interpreting the changing experienced deposition rates as global variation in contrast to the interpretation that experienced deposition rates reflect local variation in relation to an expected fixed or changing deposition rate along the further journey.

237 This suggestion was also important to draw attention to the behavioural
238 mechanisms that the birds may use for their fuel deposition rules. What kind of
239 information about expected fuelling conditions can we expect to be preprogrammed in
240 the bird or acquired by experience during actual migration, respectively, and which
241 are the mechanisms (rules) for the birds' fuelling decisions?

242 With important random variation in fuel deposition rates between stopover
243 sites, the "global update rule" suggested by Houston (1998) will of course lead to a
244 slower migration speed compared to the expectation rule, because the birds will miss
245 opportunities to exploit the best sites to their full potential and by staying rather long
246 at the poor sites they will also miss opportunities to exploit better conditions at a new
247 site. However, Weber (1999) demonstrated that the global update rule may be more
248 advantageous (giving a faster migration speed) than the expectation rule in
249 environments with spatial autocorrelation between the quality of the stopover sites.
250 He also considered two additional rules for the birds' fuelling decisions that were
251 related to the global update rule, i.e. the distance rule (where the birds use a
252 combination of expectation and experience from their latest site, weighted by distance
253 from the latest site) and the cumulative rule (where birds base their decision on
254 experienced fuel deposition at several sites), giving only small increases in
255 performance compared to the global update rule. Erni et al. (2002) suggested a simple
256 rule of constant stopover duration, and evaluated this in relation to the expectation and
257 global update rules, showing that this simple rule performed well, giving the birds a
258 close to maximum migration speed under many circumstances because of a relatively
259 low sensitivity of migration speed to variation in stopover duration (cf. Houston
260 2000).

261 This means that there are at least four different possible main rules of fuel
262 deposition that can be tested by providing migrating birds with extra food at stopover
263 sites – (1) the expectation rule for time minimization (Alerstam and Lindström 1990),
264 (2) the global update rule for time minimization (Houston 1998), (3) the constant
265 stopover duration rule (Erni et al. 2002) and (4) the constant fuel load rule for energy
266 minimization (Alerstam and Lindström 1990; also suggested as a simple threshold
267 rule by Erni et al. 2002) – with diverging predictions as illustrated in Fig. 1. Assuming
268 minimization of total energy consumption during the migratory journey as optimality
269 criterion (Hedenström and Alerstam 1997) will give predictions that are intermediate
270 between (1) and (4) in Fig. 1, i.e. often close to (2) or (3).

A number of fascinating stopover studies have tested these prediction as summarized in Table 3. An analysis of departure probabilities in relation to fuel loads and deposition rates by Schaub et al. (2008) adds to this impressive list.

The results from these tests are in agreement to a large degree – they show the best fit with predictions for time minimization according to the global update rule (no. 2 in Fig. 1). The constant stopover duration rule (no. 3) gives a similarly good fit and may have evolved as a practical control mechanism to mediate a close-to-optimal outcome according to the global update rule (Bayly 2006). Results that were more in accordance with an energy minimization strategy (no. 4) were reported for the robin (Dänhardt and Lindström 2001) and for female wheatears (Dierschke et al. 2005) showing no correlation between departure fuel load and fuel deposition rate. The difference between the sexes of wheatear (Table 3) may reflect stronger time-selection among males during spring migration, when the males may fly directly from Helgoland to Greenland. Females on the other hand probably use a safer strategy including an intermediary stopover period in Iceland (Dierschke et al. 2005). Furthermore, sedge warblers migrating early in the autumn season stayed only short periods at the stopover site and increased fuel loads only to a small degree with increasing fuel deposition rate, while birds migrating later tended to extend their fuelling duration longer and reached very large departure loads (see Fig. 2; Bayly 2007). Bayly (2007) suggested that this may be due to changing expectations for birds migrating at different times in relation to the peak of aphid superabundance. During this peak sedge warblers deposit very large fuel reserves sufficient for reaching the winter quarters in West Africa without further fuelling (Bibby and Green 1981). Thus, early sedge warblers behaved as if they expected aphid peak conditions at succeeding stopover sites, while the late sedge warblers, being too late for the aphid peak, seemed to expect less favourable feeding conditions at succeeding stopover sites (where aphids were already in rapid decline) and thus stayed to exploit the local food surplus reaching very large departure fuel loads (Fig. 2). This means that a prior (preprogrammed) expectation about the spatial and temporal occurrence of the aphid peak is a crucial element in the fuel deposition strategy of the sedge warbler (Bayly 2007).

In spite of the impressive experimental support for the global update rule, I do not think that we can safely conclude that this is the most common strategy among the passerine migrants. We cannot even be certain that the marginal effects in the

relationship between flight range and fuel constitutes the critical basis for the birds' fuelling strategies – these effects may be overruled by other factors like mass- or foraging-dependent predation risks. Still, I think that the development of the optimality analyses and tests of the birds' fuelling behaviour have opened up fascinating new perspectives and questions that will stimulate further ideas and research in this field. Is prior expectation regulating the birds' behaviour only in association with major changes in ecological conditions (e.g. at impending barrier crossings and in relation to superabundance peaks of food like the aphid peak exploited by the sedge warblers) or could it also be fine-tuned to clinal, regional and seasonal differences in fuelling conditions along the route? Why is the variation in fuelling rate between individuals at a stopover site so large, and to what degree do social interactions constrain or improve the birds' possibilities of forming expectations about fuelling success along the route? How can we understand the links between strategies and mechanisms; i.e. how do mechanisms constrain the strategies and how do the strategies promote the evolution of mechanisms (behavioural rules)? One neglected aspect in these studies is the possible existence of different strategies in spring and autumn migration (as indicated by recent flight speed results; see above). Studies making strict comparisons between the birds' behaviour during spring and autumn would be very interesting.

Response to predation risk

Predation risk is certainly a factor that could affect birds' migratory behaviour in a profound way (e.g. Lank et al. 2003). Alerstam and Lindström (1990) suggested that comparison of habitats with different levels of predator attack rate (p ; assumed to be proportional to mortality risk per time) and energy intake rate (e ; assumed to be proportional to speed of migration) may reveal if birds tend to minimize the ratio p/e (proportional to mortality risk per distance) rather than maximizing the speed of migration. Such a result was indeed obtained in a study of migrating bramblings *Fringilla montifringilla* in two different stopover habitats (beech forests versus rape fields; Lindström 1990). However, since the observed instantaneous energy intake rates were not necessarily associated with differences in the resulting sustained fuel deposition rate, one cannot be certain if the finches actually sacrificed migration speed by preferring the safer beech forest habitat (Lindström 1990). Also, the

assumption that mortality risk is proportional to predator attack rate may be misleading if the birds' antipredator behaviour differs between the habitats (Lank and Ydenberg 2003).

If predation risk is mass-dependent (e.g. Kullberg et al. 1996, Lind and Cresswell 2006) one would expect birds to depart with lower fuel loads than predicted for time-selected migration (Alerstam and Lindström 1990), and Houston (1998) demonstrated the predicted effects based on a combination of time and predation as selection criteria. Both intensity- and mass-dependent predation were included in the migration model by Weber et al. (1998) generating predictions that predation risk may lead to reductions in optimal fuel deposition rates and departure loads, as well as to avoidance of risky sites.

Analysing the body mass of passerine birds killed by predators at a stopover site (Helgoland) Dierschke (2003) demonstrated that a much larger proportion of the lean birds fell victim to predation compared to the heavier birds. This indicated that foraging intensity, leading to increased exposure, was much more important than reduced escape performance (due to heavy fuel loads) for predation risk under natural conditions (which is not to say that adaptations to minimize predation among birds with heavy fuel loads are unimportant; cf. Lank and Ydenberg 2003). Further investigations (Schmaljohann and Dierschke 2005) of the effects of variable predation risk (measured as the frequency of raptors passages) showed that birds exposed to large risks reduced their fuel deposition rate, which in turn led to slightly reduced departure loads in accordance with the global update rule (see above section), but the birds' departure probability did not increase with increased predation risk. Thus, avoidance of predation risk did not seem to be a factor outruling the time- and energy-related strategies (Schmaljohann and Dierschke 2005). It would be interesting to see under which conditions the migration model by Weber et al. (1998) would generate the pattern observed by Dierschke (2003) of lean birds falling victim to predation.

Predation is of course a factor of greatest potential importance in bird migration, with possible effects on a multitude of aspects like habitat choice, use of stopover sites, migratory schedules and geographic patterns. The possible importance of peregrine falcons *Falco peregrinus* for the migration strategies of arctic-breeding shorebirds in North America has been illuminated and investigated in a series of studies (e.g. Lank et al. 2003; Ydenberg et al. 2004, 2007; Pomeroy et al. 2006). These authors suggest that the different migration strategies of adults and juveniles

have evolved to a large degree as a consequence of differential exposure to the “spatiotemporal predation landscape”. Their studies indicate that western sandpipers *Calidris mauri* have reduced their stopover durations and fuel loads during recent decades when peregrine falcons have recovered in numbers, and experiments indicate that the sandpipers are very sensitive to danger by trading foraging intensity for safety (Pomeroy et al. 2006).

The recent recovery and expansion of the Baltic population of the white-tailed eagle *Haliaeetus albicilla* has been suggested as a possible explanation for the recent change in migratory habits of barnacle geese *Branta leucopsis* where the majority of birds no longer use stopover sites in the Baltic region that were traditionally used by the entire population (Eichhorn et al. 2009). Another possible explanation is that the strong population growth among the geese have led to increased competition which in turn have caused reduced energy deposition rates at the Baltic stopover sites below the limit of usefulness in time-selected migration (Eichhorn et al. 2009, see next section). Applying a dynamic model to this case, Jonker et al. (2010) showed in an elegant way that both explanations are possible but also that the use of the Baltic stopover area was particularly sensitive to predation danger. Predation danger had a strong threshold effect with all geese being predicted to use the Baltic stopover sites under low predation danger but with a majority (about $\frac{3}{4}$) delaying their migration and by-passing this area when predation danger increased above the threshold (Jonker et al. 2010). Empirical evidence about predation danger and fuelling rates are now needed to test these theoretical predictions and scenarios.

I think that optimality models and tests have not yet been sufficiently powerful to generate decisive evidence about the degree of importance of predation risk for the birds’ migratory behaviour. Mortality may well be high during migration compared to breeding and wintering periods (Sillett and Holmes 2002; Newton 2008) and it remains a major challenge to understand how important predation risk is as a selection factor in bird migration.

Stopover site use (and transition to breeding).

The optimal use of different potential stopover sites separated by different distances in a one-dimensional spatial migration model was first evaluated by Gudmundsson et al. (1991). If birds are minimizing energy costs of transport they are expected to stop at

all useful sites along the route in order to minimize the costs of carrying fuel loads. However, in time-selected migration the fuel deposition rates at the different sites in combination with the distances between them will determine which sites should be used and which sites should be skipped (by-passed) in an optimal strategy. For a bird depositing fuel at a constant rate its marginal (instantaneous) speed of migration will gradually decline with increasing fuel load and potential flight range because of the extra costs of transport of the increasingly heavy fuel loads (Gudmundsson et al. 1991; Alerstam and Hedenström 1998). This means that the marginal migration speed will be proportional to the fuel deposition rate devaluated by a factor that depends on the potential flight range of the bird. The optimal strategy for time minimization will be to consistently maintain the highest possible marginal speed of migration by using only sites where this marginal speed can be improved compared to the speed at the departure site devaluated for the distance between the sites. Hence, a migratory journey where fuel deposition rates improve along the route is predicted to be of quite another character (with the birds using all successive potential stopover sites) compared to a situation with declining fuel deposition rates along the route (when birds are expected to deposit large fuel reserves, make very long flights and skip many sites; cf. Gudmundsson et al. 1991).

This prediction could be extended to the transition from migration to breeding, addressing the question to what extent birds in time-selected breeding should deposit extra energy at the final stopover site (capital breeding) to get a head start in the breeding cycle. The answer depends on the differences in resource deposition rates between the final stopover site and the breeding grounds as well as on a distance-dependent devaluation factor that is slightly different from the above-mentioned devaluation factor during the pure migratory process (Alerstam 2006).

The principles for predicting optimal migration strategies along a route with a number of potential stopover sites have been greatly developed and extended in stochastic dynamic models (Weber et al. 1998; Clark and Butler 1999). These models take into account not only the effects of different fuel deposition rates and distances between the stopover sites, but also differences with respect to predation risk (type and intensity of predation), stochasticity in fuel deposition (including risk of starvation) and wind conditions, and they are based on assumptions about fitness in relation to time and body condition upon arrival at the final migratory destination. These models generate predictions about optimal site use as well as the associated

optimal fuel deposition rules and departure fuel loads at the sites used. It becomes clear from these models that skipping of potential stopover sites may be due not only to poor fuel deposition rates but also to a high risk of predation or starvation and to wind conditions during the flights (Weber et al. 1998; Clark and Butler 1999). Such models and considerations have proven useful for analysing why birds skip certain stopover sites in case studies of e.g. Bewick's swans *Cygnus bewickii* using the White Sea as stopover area in spring but not autumn (poor energy deposition rate; Beekman et al. 2002), barnacle geese reducing the use of Baltic stopover sites on spring migration (declining deposition rates because of increased competition and/or increased predation risk; Eichhorn et al. 2009; Jonker et al. 2010) and knots *Calidris canutus* skipping Iceland as a stopover area in autumn but not in spring (Dietz et al. 2010). Unpredictable wind conditions constituted the main explanation for the use or by-passing of an intermediary potential stopover site at the French Atlantic coast by knots travelling between West Africa and the Wadden Sea (Shamoun-Baranes et al. 2010).

The dynamic models are also very useful for predicting consequences of habitat loss and other temporal or spatial environmental changes for the migration habits and fitness of the migratory birds (Weber et al. 1999; Bauer et al. 2008). Model predictions about the effects of climate change for the migration system of pink-footed geese *Anser brachyrhynchus* were in general agreement with earlier spring departures from the wintering grounds and prolonged stopover times that have been observed during recent decades (Bauer et al. 2008).

Optimal migration models have proven to be a most valuable tool for understanding the constraints and adaptations that are involved in the organization of birds' migratory journeys. Applied to cases of migration systems for which there are detailed information about the foraging, climate and predation conditions at the potential staging sites, like the migration system of the pink-footed geese between Denmark and Svalbard, these models allow the fruitful exploration of a whole range of different fundamental and applied aspects of migration ecology (e.g. Bauer et al. 2008; Klaassen et al. 2008). Complementary individual-based simulation models may be used to investigate the specific mechanisms determining the birds' migratory behaviour (Duriez et al. 2009). Although such simulation models do not use an optimality approach they provide information about possible decision rules and response behaviour that may have evolved to allow favourable migration strategies

but at the same time constituting evolutionary constraints that are important to know for making penetrating optimality analyses.

Routes and detours

Changing perspective from a one-dimensional to a two- (or three-) dimensional migration system raises a number of new questions about optimal migration routes and detours that have been addressed by different optimization approaches.

First, one may ask to what extent the optimal route is a three-dimensional problem (invoking principles of spherical geometry) so that migration routes may have evolved to conform with the shortest possible trajectory between two points on the Earth's spherical surface (orthodromes or great circle routes) rather than to the path of constant geographic course (loxodrome or rhumbline; Alerstam 2000). The reduction in distance along great circles compared to rhumblines is largest at high latitudes, and radar studies in the arctic region have suggested the existence of bird migration routes similar to great circles, although with several exceptions (Alerstam et al. 2007; Alerstam 2008).

A second very basic question is to what extent migration patterns may be explained by simple distance minimization between final staging areas and breeding destinations. Calculations of sectors of closest distance from final stopover areas seemed to explain the observed circumpolar migration patterns of arctic goose and shorebird populations to a high degree (Alerstam et al. 1986). Applying a spatially explicit dynamic model to this problem showed that differences in fuel deposition and predation conditions between alternative stopover sites could cause large changes in the optimal routes and stopover sites compared to predictions based on closest distance (Bauer et al. 2010). It should be kept in mind that flight distance over ground will not reflect flights costs very accurately if wind conditions are substantially different between alternative routes. It is the air distance and not the ground distance that matters for the flight energy costs.

Long distance flights are associated with an extra cost of transporting the heavy fuel loads required for these flights. Hence, birds may minimize total energy and time costs by migrating along a detour where they can divide the journey into a number of shorter flight steps requiring smaller fuel loads during the flights, rather than flying directly towards their destination across wide ecological barriers (Alerstam 2001).

Comparisons with observed cases of detour migration yielded support for the importance of fuel transport cost minimization in most but not all cases (Alerstam 2001) and also in some cases of bat migration (Hedenström 2009).

The extraordinary flight record of bar-tailed godwits *Limosa lapponica* migrating non-stop from Alaska to New Zealand across the Pacific Ocean was considered in this perspective by Gill et al. (2009) as illustrated in Fig 3. While a two-step migration via a stopover site on the Asian coast would not reduce the energy costs for the migration compared to a direct flight, a detour involving at least 5-8 flights along the Asian coast may bring about a slight reduction in total energy cost. Gill et al. (2009) argued that other advantages, like wind conditions and absence of predators and pathogens, have tipped the evolutionary balance in favour of a direct flight. Interestingly, the godwits make a two-step detour migration via the Asian coast during spring migration, which may be beneficial for exploiting winds and for bringing extra reserves upon arrival in the breeding area (Gill et al. 2009). Since the conclusions about minimizing fuel transport costs are based on ground distances and not air distances, they remain provisional until the effects of winds on the different alternatives of direct and detour flights have been evaluated.

A remarkable geographic migration pattern has been demonstrated for juvenile sharp-tailed sandpipers *Calidris acuminata* making a detour during autumn migration that is not associated with the avoidance of a barrier but, on the contrary, includes a very long non-stop flight from Alaska to Australia across the Pacific Ocean (Handel and Gill 2010, Lindström et al. 2011). Such a detour from Siberia to Alaska before heading towards Australia, may be favourable in time-selected migration if the birds can use stopover sites in Alaska offering exceptionally high fuelling rates (in combination with low predation risk). Lindström et al. (2011) showed that the juvenile sharp-tailed sandpipers indeed attained high rates of mass increase, among the highest values recorded for wild migratory shorebirds, during their stopover in Alaska.

Purcell and Brodin (2007) developed a dynamic model to evaluate three alternative migration routes/strategies of black brant *Branta bernicla nigricans* concentrating in early autumn at the Alaska Peninsula – (1) a direct oversea flight 5000 km to wintering grounds at Baja California/ Mexico, (2) detour migration along the American west coast (including only a 2000 km crossing of the Gulf of Alaska) and (3) staying to winter in southern Alaska. They concluded that fuelling conditions

at the Alaska autumn site in combination with tailwinds were of key importance for the direct overseas migration. Furthermore, it was predicted that milder winters and reduced occurrence of tailwinds may lead to an abrupt change from long-distance migration to short-distance migration or residency. This is in fact what seems to be happening with increasing numbers of brant wintering along the Alaska Peninsula, correlated with increasing temperature and a shift in the track of the Aleutian Low pressure system (Ward et al. 2009).

The spatial models of Erni et al. (2003, 2005) represent a first and very interesting attempt of analysing the combined importance of several factors for the evolution of orientation behaviour and routes in a realistic geographic frame. Their model platform refers to the long-distance migration of passerines from Europe across the Mediterranean Sea and the Sahara desert to tropical winter quarters in Africa. Using a simulation technique of genetic algorithms, Erni et al. (2003) evaluated “optimal” orientation and routes for southwesterly migration based on repeated runs of simulated migratory journeys with specified selection rules, and they also investigated the improvement in “fitness” by changing orientation at a certain latitude and by specified responses to coastlines and barriers. In Erni et al. (2005) the effect of wind was also taken into account in these simulations, making southeasterly migration more favourable than southwesterly migration in many cases, although the outcome was critically dependent on the assumptions about the birds’ ability to use wind at different altitudes.

One important limitation of these analyses is the fact that only autumn migration has been considered. The evolutionary success of migration directions and routes would not be expected to be determined by the autumn migration alone but also by the return spring migration. The reason is of course that the autumn migration direction will have consequences for which conditions the birds meet during the succeeding spring migration. Erni et al. (2005) indicated that the optimal orientation is very sensitive to wind patterns, and one may therefore suspect that a wind-related advantage for one or the other main migration direction (southwest or southeast) in one season may turn into a disadvantage in the return season, or vice versa.

Building on the geographic model framework of Erni et al. (2003, 2005) Vrugt et al. (2007) adopted an approach of multiobjective optimization (Pareto front analysis) in an attempt to determine the relative importance of time and energy for the evolution of southwesterly autumn migration of passerines from Europe to tropical

Africa. Their results suggested that the birds' southwesterly route had evolved to minimize energy consumption per day, whereas a southeasterly route would be expected if total migration time or total energy costs were the most important optimization criteria. This result is both unexpected and surprising. If true, the key importance of keeping daily energy consumption low may reflect a secretive behaviour to reduce exposure to predation, and thus that the evolution of the southwesterly route is driven by predation avoidance rather than time or energy minimization. However, it is also possible that the results are misleading since only autumn migration and not the complete cycle of migration was considered (see above).

Thus, the challenge of analysing the importance of different optimization criteria for the evolution of routes based on effects during the full migration cycle still remains. This challenge is even more obvious in the light of findings that loop migration, where the birds travel along different routes in autumn and spring is more common than expected and it may in fact turn out to be a rule rather than exception. Such loop migration has been known since long among e.g. ocean birds and in American migration systems where its evolution has been driven by global wind patterns (e.g. Weimerskirch et al. 2000; Gauthreaux et al. 2005; Shaffer et al. 2006; Felicísimo et al. 2008). With the new tracking techniques additional cases of fascinating loop migration patterns are demonstrated (e.g. Gschweng et al. 2008; López-López et al. 2010; Klaassen et al. 2010). Optimality analysis will no doubt play a crucial role for understanding more about the evolution of bird migration routes.

Daily timing and fly-and-forage migration

Flying by night rather than by day brings the advantage that the migratory flights do not interfere with daytime foraging (for birds with diurnal foraging habits). Because foraging time is maximized and fuel deposition can take place on days immediately after or prior to the nocturnal flights (assuming that the birds are not strongly affected by sleep deprivation; cf. Rattenborg et al. 2004; Fuchs et al. 2006), the overall speed of nocturnal migration may substantially exceed that of diurnal migration (Alerstam 2009). There are additional potential advantages associated with nocturnal flights, such as avoidance of turbulence and strong winds in the atmosphere, reduced evaporative water losses, avoidance of predation and facilitation of orientation

(Kerlinger and Moore 1989). So even if many migratory bird species fly mainly during the night, why are diurnal flights of regular occurrence among other migratory species and in many situations?

There are at least three kinds of potential advantages associated with diurnal migration that may tip the optimality balance in its favour – (1) diurnal flights may facilitate for the birds to locate foraging sites and to join foraging flocks, thus eliminating costs of search and settling at new stopover sites, (2) birds flying by day may reduce net travel costs by using thermal soaring flight or by combining energy intake and flight in a strategy of fly-and-forage migration and (3) during passages across regions with poor conditions for energy deposition the optimal solution may be to fly both during the night and day (Alerstam 2009). Still, if benefits by e.g. thermal soaring migration remain large enough it is predicted that birds continue across deserts (offering no or little food) by diurnal soaring flight (stopping to rest during the nights) as observed for raptors crossing the Sahara (e.g. Klaassen et al. 2008). On the other hand, costs in terms of excessive evaporative water loss prevent many nocturnal passerine migrants from flying also during the day across the Sahara desert (Bairlein 1988; Biebach 1990; Schmaljohann et al. 2007).

Smaller birds of prey, for which the benefit of soaring flight compared to flapping flight is less pronounced than among large raptors, are inclined to travel both during the day and night during desert crossings, as observed for the Levant sparrowhawk *Accipiter brevipes* (Spaar et al. 1998) and Eleonora's falcon *Falco eleonora* (López-López et al. 2010). When crossing the Sahara desert Eleonora's falcons (recorded by satellite tracking) travelled throughout the daytime hours and also during 2/3 of the night, thus reaching an average travel time of about 20 hours per day (López-López et al. 2010). Interestingly, the small Eurasian hobby *Falco subbuteo* also extended its daily travel time into night hours when crossing the Sahara but to a smaller degree than Eleonora's falcons, reaching only 12-15 hours of travel time per day (Strandberg et al. 2009). Why do these falcons not extend their flight time to include all night hours when crossing the Sahara – are there possibilities of fly-and-forage migration in the desert that may explain the preference for flying during the light hours, especially for the hobby? There will be an important role for optimization analyses to interpret much new information about the variation of daily travel routines in bird migration that are revealed by the satellite tracking and GPS techniques.

The total migration speed is a function of the flight speed (ground speed), the net rate of energy expenditure in flight and the net rate of energy accumulation during fuel deposition, and it is given as the intercept of the abscissa in a power-versus-speed diagram (Fig. 4) as explained by Alerstam (1991; cf. also Hedenström and Alerstam 1998; Alerstam 2000, 2003). The arrows in Fig. 4a show different ways of increasing total migration speed, e.g. by increasing flight speed (tailwind assistance), reducing flight costs (changing flight mode to soaring; cf. Alerstam 2000) and increasing energy deposition rate. The total speed of migration may be increased also by combining foraging with movement in the migratory direction. The optimal solution depends on the trade-off between speed and energy for different cases as illustrated in Figs 4b and 4c – (1) a trade-off where foraging leads to serious reductions in flight speed and where efficient energy deposition cannot be combined even with slow movement in the migratory direction will make fly-and-forage migration unfavourable under all conditions, (2) a trade-off where foraging does not reduce flight speed too much and the birds do not suffer so much in energy gain rate by moving will make an exclusive fly-and-forage strategy superior for maximizing migration speed, (3) the possibility of efficiently combining foraging and movement at low but not high speed will make a mixed strategy of slow fly-and-forage migration in combination with traditional fast non-foraging flights optimal while (4) the reverse trade-off conditions at low and high speeds will make a mixed strategy of relatively fast fly-and-forage migration combined with traditional stopover periods optimal.

The conditions for fly-and-forage migration were analysed by Strandberg and Alerstam (2007). This strategy was also demonstrated for the osprey *Pandion haliaetus*, where a majority of the passing migrants deviated from their migratory tracks to visit and forage at a lake within visual range from their flights path (Strandberg and Alerstam 2007). GPS-based satellite tracking showed on a larger scale how this behaviour affected the time budget of the ospreys' migration through Europe in comparison with their uninterrupted daily soaring flight across the Sahara desert where foraging opportunities are lacking (Klaassen et al. 2008). The ospreys used a mixed strategy combining fly-and-forage movements with stationary stopover periods in Europe (case 4 above) which may also serve to accumulate surplus energy reserves for their impending passage across Sahara. Thus, observations of migrants like e.g. swallows *Hirundo rustica* spending long stationary periods of fuel accumulation before the passage of an ecological barrier (Rubolini et al. 2002) do not

exclude the possibility of fly-and-forage migration and mixed strategies during other phases of the migratory journey. Much still remains to be understood about the occurrence and importance of fly-and-forage strategies in bird migration.

Wind selectivity and wind drift

The effect of wind poses an important challenge in optimization analyses of bird migration with respect to at least four major questions: How selective of favourable winds are the migrants expected to be in their departure decisions? Once airborne, how should the flying birds adapt their airspeed to wind conditions and how should they orient in relation to the wind? How important are wind patterns for the evolution of migratory routes (see above section about routes and detours)?

Winds have a very profound influence on the transport economy of birds and one may therefore argue that selection of favourable tailwinds for the migratory flights is of overriding importance for the optimal migration performance (Liechti and Bruderer 1998). However, there is also a cost of waiting for favourable tailwinds, particularly for birds that cannot deposit fuel while they are waiting (Thorup et al. 2006) and if ambient temperature is low (Wikelski et al. 2003). This means that a strategy of strong tailwind preference for migratory departure may or may not be optimal in comparison with a strategy of no or little selectivity of winds, depending on the probability of tailwinds, the variability between tail- and headwinds and the relative metabolic costs of travel and resting (Thorup et al. 2006). Also in situations where the birds choose between departure and continued fuel deposition is the optimal policy dependent on the probability and variability of wind assistance, and birds are expected to build up initial fuel reserves irrespective of wind, but later to depart under tailwind conditions and even later, if tailwinds have failed and the probability of tailwinds is low, to depart irrespective of wind (Weber et al. 1998, Weber and Hedenström 2000).

Ospreys migrating between northern Europe and Africa showed no selectivity of tailwinds for their travel days (Thorup et al. 2006) and also nocturnal passerine migrants travelled regularly without tailwind assistance during both spring and autumn migration in Scandinavia (Alerstam et al. 2011). This is in clear contrast to the strong tailwind assistance gained by many shorebirds (e.g. Green 2004) as well as by migratory noctuid moths (Alerstam et al. 2011) departing mainly on occasions

713 providing good wind support. The birds' strategies of wind selectivity may well differ
714 between regions with different wind regimes so that e.g. nocturnal passerine migrants
715 are more prone to avoid unfavourable winds in regions with a more frequent
716 occurrence of tailwinds compared to the situation in Scandinavia where cross- and
717 opposed winds are dominating.

718 Selection of flight altitudes with the most favourable winds is an important part
719 of the birds' adaptive exploitation of winds to their benefit (e.g. Liechti 2006,
720 Schmaljohann et al. 2009). Trans-Sahara passerine migrants selected relatively low
721 flight altitudes during autumn migration, mostly below 1000 m above ground, which
722 was optimal for obtaining tailwind assistance and thus for minimizing energy costs for
723 the migratory flights, but not for minimizing water loss during the warm and dry
724 conditions (Schmaljohann et al. 2009). However, the passerines saved water by flying
725 during the nights and not during daytime and , furthermore, they seemed to be much
726 more tolerant to warm and dry flight conditions than predicted from physiological
727 models (Schmaljohann et al. 2008).

728 After departure (and selection of flight altitude) the birds are confronted with
729 the next optimization problem in relation to wind – how to orient in order to exploit
730 the winds for approaching their goals with minimal time and energy costs? If the wind
731 vector remains constant all the way to the goal, birds will minimize time and energy
732 costs for their movement by adjusting their heading into the wind in such a way that
733 they follow the shortest straight-line (“as the crow flies”) route to the goal (complete
734 compensation). However, if the wind vector varies along the route it will be optimal
735 to use a strategy of adaptive drift where the birds allow themselves to be drifted to a
736 variable degree depending on the wind pattern and distance to the destination (partial
737 drift). If the wind varies randomly between different flight steps towards the
738 destination, it will be optimal for the birds to minimize the distance remaining to the
739 goal after each flight step, which will be accomplished by allowing almost full drift
740 far away from the destination, compensating to a successively higher degree with
741 decreasing distance to the goal and finally compensating completely during the final
742 flight (Alerstam 1979a). Total energy consumption for the movement to the goal will
743 be minimized by birds that, besides changing their orientation, also vary their airspeed
744 in concert with the degree of drift/compensation (Liechti et al. 1994; Liechti 1995). If
745 winds vary in a more predictable way along the route towards the destination, the
746 optimal solution is given by the minimum time path (which is associated with the

minimum distance through the air) which involves partial drift to a variable degree and which will become increasingly similar to the above strategy of adaptive drift with increasingly random wind variation between flight steps (Alerstam 2000).

Allowing full drift is the optimal behaviour in a situation where there is a balance between crosswinds from the left and right along the route. Also if the destination area is very extensive, perhaps constituting a certain latitude rather than a narrowly defined goal area, is full drift the most favourable option. In these latter two cases the animals save energy by consistently using their full heading vector for movement along the axis of shortest distance between starting point and destination.

Differences in wind conditions between different altitudes may be exploited to save energy, not only by selection of altitudes with favourable winds (cf. above) but also by a strategy where high-altitude drift is combined with low-altitude overcompensation under certain wind directions and when wind speed at high altitude exceeds that at low altitude (Alerstam 1979b). Detour flights at low altitudes along e.g. coastlines where birds avoid wind drift over the sea and gain protection from the strongest winds (Alerstam and Pettersson 1977) could also be adaptive responses that form part of strategies to deal with the drift and exploit the winds to their best advantage.

Birds that use only their biological compasses (based on celestial or geomagnetic cues) to orient in their preferred migratory direction will be subjected to full wind drift while any behaviour of compensation (partial or complete compensation for wind drift, or overcompensation) requires that the birds not only have a compass sense but also mechanisms for directly or indirectly sensing the wind. Birds may also respond indirectly to the effect of wind if they use a map sense to regulate the progress of their movement or if they move along topographical features and landmarks. Depending on the sensory mechanisms the responses to wind may be delayed (e.g. with compensatory movements taking place only after the birds have been drifted significant distances off course) or immediate (e.g. with the bird heading into the wind to counteract drift).

Observations of differential wind drift among migrating birds that fly during the day over the sea (with a moving surface due to the wave motion) versus over land, birds that fly during the night at very low altitudes versus high altitudes or over a uniform landscape versus a landscape with prominent features suggest that visual reference to the surface plays a role for the orientation in relation to wind by the birds

(Alerstam and Pettersson 1975; Åkesson 1993; Zehnder et al. 2001; Bingman et al. 1982). The demonstration that juvenile raptors on their first migratory journey are exposed to almost full wind drift while adults compensate for the wind drift to an important degree (Thorup et al. 2003) indicates that cues learnt by adults may help to reduce wind drift.

Large numbers of studies have investigated how birds orient in relation to wind and cases of full drift, partial drift/partial compensation, complete compensation and overcompensation have been reported (Richardson 1991; Liechti 2006). Some of these results are in agreement with the theoretical predictions while other results seem to be conflicting and difficult to explain. Recent results based on satellite tracking of individual birds (ospreys and marsh harriers) during their entire migration journeys demonstrated that the birds changed responses to crosswinds between different places and times during their travels, showing a varied repertoire of different drift and compensation behaviour (Klaassen et al. 2010). This indicates that it is important to analyse the birds' responses in context of preceding and succeeding wind situations during their migratory journey, and offers hope of a new understanding of birds' orientation in relation to wind based on optimization perspectives.

Phenotypic flexibility, arrival time and moult schedules

The two main phases of bird migration, flight and energy deposition, respectively, are associated with very different demands on the birds' body and organs. Adaptations in the form of phenotypic flexibility involving changes in organ sizes have been discovered and demonstrated to an increasing degree during recent decades and this has developed into an exciting ecophysiological research field (e.g. Piersma and Lindström 1997; Piersma and van Gils 2011).

Optimization has proven to be a useful approach for analysing and understanding these adaptations during migration, as a consequence of the balance between benefits of having large muscles for flight and large digestive organs for maximizing net energy intake, and the costs of carrying heavy organs in flight and building and rebuilding the organs between flight and energy deposition phases (Weber and Hedenström 2001). The adaptive variation of the gizzard size among migratory knots in response to their seasonally shifting demands on eating high-density but hard-shelled food (cockles) to maximize net energy intake rate or on

815 eating high-quality but low-density crustacean food to balance their energy budget has
816 been explored in a particularly fascinating optimality perspective within and between
817 different migratory populations (van Gils et al. 2003, 2006; Battley et al. 2005;
818 Piersma and van Gils 2011).

819 Kokko (1999) used a game-theoretical model to predict the optimal arrival time
820 for migratory birds in relation to their individual condition. In the priority game birds
821 arriving before their competitors will have the best breeding resources (e.g. territories)
822 giving the highest fitness benefits. To obtain this benefit birds will be induced to
823 arrive before their optimal time had there been no competition, thus incurring an
824 arrival cost. A high-quality bird (in superior condition) pays a smaller cost and will
825 thus be able to advance its arrival to a larger degree and still obtain a net benefit than
826 a lower-quality competitor. In this game it is not the absolute arrival dates or the
827 length of time between arrivals that matter for the gain in priority but the arrival order
828 between competitors. The game can be extended to evaluate cascading competition
829 for early arrival between several individuals (Kokko 1999). The cascading arrival
830 game predicts that the majority of migrants, except the extreme late-comers, pay a
831 significant cost to advance their arrival before competitors, a cost of e.g. increased
832 behavioural efforts (sprint cost), resource use and mortality. If arrival before
833 competitors is more important at the breeding destination than at the winter quarters
834 one may expect important differences between spring and autumn migration, with the
835 birds migrating at higher speeds and costs during spring, perhaps even making a final
836 sprint migration to their breeding destination (Alerstam 2006).

837 While this selection for early arrival in order to obtain priority to breeding
838 resources operate within both sexes, there is additional selection on males to arrive
839 early in relation to females in order to maximize mating opportunities (with male
840 fitness typically being more strongly dependent on number of matings compared to
841 female fitness). This hypothesis was first advanced to explain protandry, i.e. the
842 emergence of males before females among insects, in an optimality analysis by
843 Wiklund and Fagerström (1977). They also pointed out that females are probably
844 selected to minimize the time spent unmated, leading to late optimal emergence in
845 relation to males, so that there is no conflict between sexes with respect to their
846 relative timing of emergence (Fagerström and Wiklund 1982). The mate opportunity
847 hypothesis can be successfully applied also to the arrival order of sexes in bird
848 migration as demonstrated by the individual-based optimality analyses by Kokko et

al. (2006). Strong sexual selection among males (high levels of sperm competition and male-biased composition of the breeding population) were predicted to promote the evolution of distinct protandry, and this was supported by the positive correlation between protandry and sexual dichromatism among trans-Saharan migratory bird species (Rubolini et al. 2004).

An urgent matter in current ecological research is to increase understanding of how ecological processes are affected by the ongoing climate and environmental change (Walther et al. 2002). This change may affect the resource peak for breeding migratory birds with respect to both mean date and variance, which will in turn affect the optimal arrival time depending on the degree of competition for territories and the risk of mortality (Jonzén et al. 2007).

A changing climate and environment will of course affect not only the optimal arrival time but the entire annual routine of the migratory birds, involving migration, breeding and moult with optimal timing decisions depending on the birds' energy reserves, breeding status, experience, flight feather quality and location. Dynamic models of the annual cycle of migratory birds (McNamara et al. 1998; Hedenström et al. 2007) have been developed to analyse the optimal moult strategies and why some passerine species moult their flight feathers while still on their breeding grounds (summer moult) while others moult in the winter quarters (winter moult; and the willow warbler moults twice a year, in both breeding and winter areas; Holmgren and Hedenström 1995, Barta et al. 2008). Annual routine models have an important potential to be applied to several different aspects in the life history of migratory birds besides the moult-migration strategies and to analyse within-individual and population processes (Barta et al. 2008).

Outlook

The above survey shows that the field of optimal bird migration during the two recent decades has matured and diversified greatly with respect to topics addressed as well as to methods and approaches used. Using optimality perspectives and arguments is now regarded as a natural and essential way of analysing and understanding adaptations and behavioural strategies. The mechanisms (proximate factors) and optimality principles (ultimate factors) are nowadays often considered in close association, which makes it obsolete to regard optimal migration as a field of its own,

but it may still represent a valid and useful concept to stress the approach and technique of analysing migratory adaptations. It is interesting to compare with the development of the field of “optimal foraging theory”, where “optimal” was soon dropped (because of misdirected criticism of the general idea of optimality), and later also “theory” was dropped in view of the development towards increasingly integrative approaches (Ydenberg et al. 2007).

It remains to be seen if and how long the concept of optimal migration will survive. A successful development where optimization analysis becomes a commonplace and indispensable component in most kinds of bird migration research will probably lead to the paradoxical outcome that it disappears as a special field and concept.

It seems clear that optimization analyses in bird migration research have produced more questions than answers. This is no weakness but shows the great strength of this approach being a superior tool to specify questions and define problems, and also to derive predictions that can be tested by observations and experiments. Making predictions that are shown to be wrong, thus leading to additional questions and ideas and to new predictions is a good way of doing science.

Field studies and tests of many of the aspects addressed in optimality analyses have revealed an unexpected large variability in the responses and strategies between and within species, populations and individuals (e.g. in fuel deposition as well as wind selectivity and drift behaviour etc.). This may seem frustrating in our striving to find general principles and patterns, but also represents a source of inspiration to understand the adaptive richness and complexity in bird migration ecology.

There will be major challenges for optimization analyses in bird migration research in the near future for at least two main reasons: (1) new tracking techniques will produce a lot of novel information about routes, timing and habits of migrating individuals that can be used to test predictions about migratory strategies, and (2) there are potentially very important but hereto largely neglected trade-offs in migration associated with e.g. digestive physiology, metabolism, immunocompetence and disease transmission (Whelan and Schmidt 2007, Hasselquist et al. 2007, Altizer et al. 2011) that must be considered in conjunction with the traditional trade-offs related to energy, time and predation risk. These new factors and perspectives may well recast our views about the fascinating phenomenon of bird migration, and optimization will be an essential approach and tool for that change.

917

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Table 1. Aspects evaluated by optimal bird migration analysis

1. Flight (speed, mode, climbing)
2. Fuel deposition
3. Response to predation risk
4. Stopover site use
5. Transition migration/breeding
6. Routes and detours
7. Daily timing
8. Fly-and-forage migration
9. Wind selectivity
10. Wind drift
11. Phenotypic flexibility
12. Arrival time
13. Moults schedules

Table 2. Methods and approaches used in optimal bird migration analysis (with examples of references)

Simple analytical/deterministic models	Alerstam & Lindström 1990
Vector/geometric analysis	Alerstam 1979, Liechti et al. 1994
Stochastic dynamic programming	Weber et al. 1998, Clark & Butler 1999
Annual routine models	MacNamara 1998, Barta et al. 2008
Multiobjective optimization	Vrugt et al. 2007
Game theory	Kokko 1999
Simulation with selection algorithm	Erni et al. 2003

Table 3. Tests of the rules for fuel deposition among birds on stopover (four possible rules are explained in the text and illustrated in Fig 1)

Species	Rule of best fit	Reference
Rufous hummingbird <i>Selasporus rufus</i>	2	Carpenter et al. 1983, Lindström & Alerstam 1992
Bluethroat <i>Luscinia svecica</i>	2	Lindström & Alerstam 1992
Whitethroat <i>Sylvia communis</i>	2	Fransson 1998, Weber et al. 1999b
European robin <i>Erithacus rubecula</i>	4	Dänhardt & Lindström 2001
Wheatear <i>Oenanthe oenanthe leucorhoa</i> , spring, males	2	Dierschke et al. 2005
Wheatear <i>Oenanthe oenanthe leucorhoa</i> , spring, females	4	Dierschke et al. 2005
Wheatear <i>Oenanthe o. oenanthe</i> , autumn	2	Schmaljohann & Dierschke 2005
Wheatear <i>Oenanthe o. oenanthe</i> , spring, males	2	Delingat et al. 2006
Wheatear <i>Oenanthe oenanthe leucorhoa</i> , autumn	2	Delingat et al. 2006
Reed warbler <i>Acrocephalus scirpaceus</i>	2 or 3	Bayly 2006
Sedge warbler <i>Acrocephalus schoenobaenus</i>	1 or 2	Bayly 2007

Figure legends.

Fig. 1. Predictions of birds' responses to increased fuel deposition rates at a stopover site according to four different rules (see text). The three curves show the increase in potential flight range in relation to fuel deposition time for three different constant rates of fuel deposition, with the lower curve corresponding to the typical natural conditions and the two upper curves showing conditions with supplementary food. The optimal solution for maximizing migration speed is found by drawing a tangent from the search/settling time on the negative side of the time axis to the range curve for the typical site. When encountering conditions allowing increased fuel deposition rates, the birds are expected to depart at the same marginal migration speed according to the expectation rule (1), at the new local optima according to the global update rule (2), after the same stopover time according to the constant stopover time rule (3) and at the same fuel load (corresponding to the same potential range) according to the constant energy threshold rule (4). A constant departure fuel load irrespective of fuel deposition rate is also predicted for energy minimization in bird migration.

Fig. 2. Relationship between departure fuel load and fuel deposition rate among reed warblers (open symbols) and sedge warblers (filled symbols) in food supplementation experiments during autumn migration in England (based on Bayly 2007). Fuel loads and rates are expressed in relation to the birds' lean body mass. The birds are long-distance migrants with winter quarters in West Africa. Both species showed a distinct positive correlation between departure fuel load and deposition rate, supporting the general importance of time minimization. However, there were also interesting differences between the two species in spite of almost identical experimental conditions. Among the sedge warblers there was an indication of two categories of individuals responding differently by storing moderate or very large fuel loads, respectively (different filled symbols). This was probably related to different expectations in relation to the peak of aphid superabundance at more southerly European latitudes (Bayly 2007).

Fig. 3. Distances for birds migrating between Alaska and New Zealand by direct flights or along detours involving two or more flight steps. The optimal route for minimization of total energy costs for the flight transport is determined by the trade-

off between costs for increasing flight distance and for transporting heavy fuel reserves. Dividing the direct journey across the Pacific Ocean into two flight steps will increase the distance by 45% while the concomitant reduction of costs for fuel transport will correspond to maximally 30% extra distance, making this option suboptimal. Dividing the journey into several flight steps will increase the distance by 55%, which matches the corresponding gain in fuel transport costs, making the total energy costs approximately equivalent for the longest and shortest routes (effect of wind not taken into account). Bar-tailed godwits make direct flights across the Pacific Ocean during the autumn while two-step migration occurs in spring (based on Gill et al. 2009).

Fig. 4. Total speed of migration can be found graphically in a power-speed diagram as the intercept of the speed axis of the line between energy gain rate on stopover and net rate of energy consumption/speed in flight (Alerstam 1991). The arrows show ways of increasing total migration speed as discussed in the text (a). Four different cases of trade-off between power and speed in fly-and-forage migration are illustrated with pure fly-and-forage migration giving maximum migration speed in case 2 while mixed strategies of slow fly-and-forage movements in combination with traditional uninterrupted flights, or fast fly-and-forage movements combined with traditional stopover periods, give maximal migration speeds in cases 3 and 4, respectively (b,c).







