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Optimal bird migration revisited

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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

35 **Introduction**

36

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

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

52 I am happy to have been contributing to generate interest in developing
53 optimization analyses in the field of bird migration, mainly starting with an article co-
54 authored with Åke Lindström (Alerstam and Lindström 1990) where we also coined
55 the concept of “optimal migration”. The use of optimization methods was not new to
56 bird migration research at that time, but such approaches were adopted mainly in
57 evaluations of e.g. partial and differential migration at population levels (cf. review by
58 Alerstam and Hedenström 1998) while, concerning birds’ behaviour on actual
59 migration, there were rather few optimization analyses, notably the work of
60 Pennycuick (1969, 1975) and Tucker (1974) on bird flight and a few attempts to
61 analyse how migrating birds could exploit winds in an optimal way (Alerstam 1979a,
62 b). At that time I was struck by our large ignorance about the adaptive values of the
63 widely variable behaviours of migrating birds and particularly by the fact that we
64 could not even tell if the birds were primarily behaving to save energy, speed up
65 migration or avoid hazards like predation. The three most important influences on our
66 ideas (Alerstam and Lindström 1990) were from flight theory (Pennycuick 1969,
67 1975, Tucker 1974), optimal foraging theory (e.g. Stephens and Krebs 1986) and the
68 notion of resulting speed of migration as calculated from ringing recoveries by Hildén

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

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

89 In the early phase of the optimal migration field, simple analytical models (e.g.
90 Pennycuick 1975; Alerstam and Lindström 1990; Weber et al. 1994) and simple
91 vector models (e.g. Alerstam 1979a, b) were used (Table 2). Such models are still
92 particularly useful for generating qualitative predictions and illustrating the main
93 principles and effects of key trade-offs. However, migratory traits do not evolve
94 deterministically in isolation in response to only a single optimization criterion, so
95 more extensive and complex models based on the techniques of stochastic dynamic
96 programming (e.g. Weber et al. 1998; Clark and Burton 1999; Bauer et al. 2008),
97 annual routine analysis (McNamara et al. 1998; Hedenström et al. 2007; Barta et al.
98 2008) and multi-objective optimization (Vrugt et al. 2007) have been used to obtain
99 more realistic predictions for different types of behavioural decisions during the
100 whole migratory journey or annual cycle. Such complex models require an extensive
101 set of assumptions about several constraints, trade-offs and stochastic effects. Being
102 applied to specific cases where there is detailed knowledge to help specifying these

103 assumptions, these models have a great potential in predicting effects on migration of
104 e.g. habitat loss at stopover sites (Weber et al. 1999) or climate change (Bauer et al.
105 2008), both immediate and long-term changes if the birds can eventually adapt in an
106 optimal way to the changed conditions. In addition, these models are important for
107 efficient conservation and management of migratory populations (Klaassen et al.
108 2008). Additional approaches such as game theory (e.g. Kokko 1999) and spatial
109 simulation models with genetic algorithms (Erni et al. 2003, 2005) have also been
110 adopted in very fruitful ways to take density-dependent and spatial effects into
111 account. I think that both simplistic and complex models have proven their usefulness
112 and are needed in a complementary way in optimization analyses of bird migration.

113

114 **Flight (speed, mode, climbing).**

115

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

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

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

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

153 It was recently demonstrated that nocturnal passerine migrants fly at
154 consistently higher airspeeds in spring than in autumn, with spring speeds exceeding
155 autumn speeds by on average 16 % (Karlsson et al. 2010). This result was based on
156 large samples of speed measurements from tracking radar studies during several years
157 at two different places in southern and northern Scandinavia, respectively. It is
158 unlikely that this difference in speed was caused by seasonal differences in body mass
159 or wing morphology and the most likely explanation is that the birds during spring fly
160 at a higher optimal speed for minimizing total duration of migration (Karlsson et al.
161 2010). This is a very exciting finding that will stimulate the exploration of seasonal
162 differences in migration strategies.

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

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

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

178

179 **Fuel deposition**

180

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

188 It has been objected (Chernetsov 2010) that recent studies in wind tunnels have
189 indicated much smaller flight costs with increasing body mass than predicted from
190 flight mechanical theory, suggesting that the range versus fuel relationship would
191 approach linearity and thus offer little as a basis for analysing and understanding the
192 birds' patterns of fuel deposition on migration. However, this conclusion seems
193 premature since the mass-dependence in airspeed has been ignored in these
194 measurements and arguments. It is the scaling of energy cost over distance (and not
195 energy cost over time) with body mass that is given from flight mechanical theory and
196 forms the basis for deriving a correct range curve. Testing this scaling relationship at
197 a fixed airspeed (Chernetsov 2010) can be very misleading and biased towards both
198 smaller and larger scaling exponents compared to the correct estimate. While I think
199 that it is premature for these and other reasons (incompatibility between metabolic
200 power measurements and mass reduction in the wind tunnel study by Kvist et al.
201 2001) to exclude the possibility that the extra cost of flying with heavy fuel burdens
202 influences the fuel deposition of birds using flapping flight, this cost may be much
203 less important and even non-existent in soaring flight for which range curves may be

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

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

224 Lindström and Alerstam (1992) suggested two possible explanations for the
225 surprisingly shallow slope – that different individuals had consistently different
226 expectations about future deposition rates or that the expected speed of migration
227 increased along the route. Further possible explanations were suggested by Klaassen
228 and Lindström (1996), that added fuel caused increased locomotion costs, and by
229 Hedenström and Alerstam (1997), that the birds were minimizing total energy costs
230 during migration, including not only costs of transport but also existence costs. A
231 particularly influential suggestion put forward by Houston (1998) was that the birds
232 adopted the experienced fuel deposition rate at each new stopover site as the expected
233 rate also for the further journey – interpreting the changing experienced deposition
234 rates as global variation in contrast to the interpretation that experienced deposition
235 rates reflect local variation in relation to an expected fixed or changing deposition rate
236 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).

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

274 The results from these tests are in agreement to a large degree – they show the
275 best fit with predictions for time minimization according to the global update rule (no.
276 2 in Fig. 1). The constant stopover duration rule (no. 3) gives a similarly good fit and
277 may have evolved as a practical control mechanism to mediate a close-to-optimal
278 outcome according to the global update rule (Bayly 2006). Results that were more in
279 accordance with an energy minimization strategy (no. 4) were reported for the robin
280 (Dänhardt and Lindström 2001) and for female wheatears (Dierschke et al. 2005)
281 showing no correlation between departure fuel load and fuel deposition rate. The
282 difference between the sexes of wheatear (Table 3) may reflect stronger time-
283 selection among males during spring migration, when the males may fly directly from
284 Helgoland to Greenland. Females on the other hand probably use a safer strategy
285 including an intermediary stopover period in Iceland (Dierschke et al. 2005).
286 Furthermore, sedge warblers migrating early in the autumn season stayed only short
287 periods at the stopover site and increased fuel loads only to a small degree with
288 increasing fuel deposition rate, while birds migrating later tended to extend their
289 fuelling duration longer and reached very large departure loads (see Fig. 2; Bayly
290 2007). Bayly (2007) suggested that this may be due to changing expectations for birds
291 migrating at different times in relation to the peak of aphid superabundance. During
292 this peak sedge warblers deposit very large fuel reserves sufficient for reaching the
293 winter quarters in West Africa without further fuelling (Bibby and Green 1981). Thus,
294 early sedge warblers behaved as if they expected aphid peak conditions at succeeding
295 stopover sites, while the late sedge warblers, being too late for the aphid peak, seemed
296 to expect less favourable feeding conditions at succeeding stopover sites (where
297 aphids were already in rapid decline) and thus stayed to exploit the local food surplus
298 reaching very large departure fuel loads (Fig. 2). This means that a prior
299 (preprogrammed) expectation about the spatial and temporal occurrence of the aphid
300 peak is a crucial element in the fuel deposition strategy of the sedge warbler (Bayly
301 2007).

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

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

324

325 **Response to predation risk**

326

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

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

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

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

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

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

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

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

401

402 **Stopover site use (and transition to breeding).**

403

404 The optimal use of different potential stopover sites separated by different distances in
405 a one-dimensional spatial migration model was first evaluated by Gudmundsson et al.
406 (1991). If birds are minimizing energy costs of transport they are expected to stop at

407 all useful sites along the route in order to minimize the costs of carrying fuel loads.
408 However, in time-selected migration the fuel deposition rates at the different sites in
409 combination with the distances between them will determine which sites should be
410 used and which sites should be skipped (by-passed) in an optimal strategy. For a bird
411 depositing fuel at a constant rate its marginal (instantaneous) speed of migration will
412 gradually decline with increasing fuel load and potential flight range because of the
413 extra costs of transport of the increasingly heavy fuel loads (Gudmundsson et al.
414 1991; Alerstam and Hedenström 1998). This means that the marginal migration speed
415 will be proportional to the fuel deposition rate devaluated by a factor that depends on
416 the potential flight range of the bird. The optimal strategy for time minimization will
417 be to consistently maintain the highest possible marginal speed of migration by using
418 only sites where this marginal speed can be improved compared to the speed at the
419 departure site devaluated for the distance between the sites. Hence, a migratory
420 journey where fuel deposition rates improve along the route is predicted to be of quite
421 another character (with the birds using all successive potential stopover sites)
422 compared to a situation with declining fuel deposition rates along the route (when
423 birds are expected to deposit large fuel reserves, make very long flights and skip
424 many sites; cf. Gudmundsson et al. 1991).

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

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

441 optimal fuel deposition rules and departure fuel loads at the sites used. It becomes
442 clear from these models that skipping of potential stopover sites may be due not only
443 to poor fuel deposition rates but also to a high risk of predation or starvation and to
444 wind conditions during the flights (Weber et al. 1998; Clark and Butler 1999). Such
445 models and considerations have proven useful for analysing why birds skip certain
446 stopover sites in case studies of e.g. Bewick's swans *Cygnus bewickii* using the White
447 Sea as stopover area in spring but not autumn (poor energy deposition rate; Beekman
448 et al. 2002), barnacle geese reducing the use of Baltic stopover sites on spring
449 migration (declining deposition rates because of increased competition and/or
450 increased predation risk; Eichhorn et al. 2009; Jonker et al. 2010) and knots *Calidris*
451 *canutus* skipping Iceland as a stopover area in autumn but not in spring (Dietz et al.
452 2010). Unpredictable wind conditions constituted the main explanation for the use or
453 by-passing of an intermediary potential stopover site at the French Atlantic coast by
454 knots travelling between West Africa and the Wadden Sea (Shamoun-Baranes et al.
455 2010).

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

463 Optimal migration models have proven to be a most valuable tool for
464 understanding the constraints and adaptations that are involved in the organization of
465 birds' migratory journeys. Applied to cases of migration systems for which there are
466 detailed information about the foraging, climate and predation conditions at the
467 potential staging sites, like the migration system of the pink-footed geese between
468 Denmark and Svalbard, these models allow the fruitful exploration of a whole range
469 of different fundamental and applied aspects of migration ecology (e.g. Bauer et al.
470 2008; Klaassen et al. 2008). Complementary individual-based simulation models may
471 be used to investigate the specific mechanisms determining the birds' migratory
472 behaviour (Duriez et al. 2009). Although such simulation models do not use an
473 optimality approach they provide information about possible decision rules and
474 response behaviour that may have evolved to allow favourable migration strategies

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

477

478 **Routes and detours**

479

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

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

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

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

509 Comparisons with observed cases of detour migration yielded support for the
510 importance of fuel transport cost minimization in most but not all cases (Alerstam
511 2001) and also in some cases of bat migration (Hedenström 2009).

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

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

537 Purcell and Brodin (2007) developed a dynamic model to evaluate three
538 alternative migration routes/strategies of black brant *Branta bernicla nigricans*
539 concentrating in early autumn at the Alaska Peninsula – (1) a direct oversea flight
540 5000 km to wintering grounds at Baja California/ Mexico, (2) detour migration along
541 the American west coast (including only a 2000 km crossing of the Gulf of Alaska)
542 and (3) staying to winter in southern Alaska. They concluded that fuelling conditions

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

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

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

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

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

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

599

600 **Daily timing and fly-and-forage migration**

601

602 Flying by night rather than by day brings the advantage that the migratory flights do
603 not interfere with daytime foraging (for birds with diurnal foraging habits). Because
604 foraging time is maximized and fuel deposition can take place on days immediately
605 after or prior to the nocturnal flights (assuming that the birds are not strongly affected
606 by sleep deprivation; cf. Rattenborg et al. 2004; Fuchs et al. 2006), the overall speed
607 of nocturnal migration may substantially exceed that of diurnal migration (Alerstam
608 2009). There are additional potential advantages associated with nocturnal flights,
609 such as avoidance of turbulence and strong winds in the atmosphere, reduced
610 evaporative water losses, avoidance of predation and facilitation of orientation

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

614 There are at least three kinds of potential advantages associated with diurnal
615 migration that may tip the optimality balance in its favour – (1) diurnal flights may
616 facilitate for the birds to locate foraging sites and to join foraging flocks, thus
617 eliminating costs of search and settling at new stopover sites, (2) birds flying by day
618 may reduce net travel costs by using thermal soaring flight or by combining energy
619 intake and flight in a strategy of fly-and-forage migration and (3) during passages
620 across regions with poor conditions for energy deposition the optimal solution may be
621 to fly both during the night and day (Alerstam 2009). Still, if benefits by e.g. thermal
622 soaring migration remain large enough it is predicted that birds continue across
623 deserts (offering no or little food) by diurnal soaring flight (stopping to rest during the
624 nights) as observed for raptors crossing the Sahara (e.g. Klaassen et al. 2008). On the
625 other hand, costs in terms of excessive evaporative water loss prevent many nocturnal
626 passerine migrants from flying also during the day across the Sahara desert (Bairlein
627 1988; Biebach 1990; Schmaljohann et al. 2007).

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

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

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

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

682

683 **Wind selectivity and wind drift**

684

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

691 Winds have a very profound influence on the transport economy of birds and
692 one may therefore argue that selection of favourable tailwinds for the migratory
693 flights is of overriding importance for the optimal migration performance (Liechti and
694 Bruderer 1998). However, there is also a cost of waiting for favourable tailwinds,
695 particularly for birds that cannot deposit fuel while they are waiting (Thorup et al.
696 2006) and if ambient temperature is low (Wikelski et al. 2003). This means that a
697 strategy of strong tailwind preference for migratory departure may or may not be
698 optimal in comparison with a strategy of no or little selectivity of winds, depending
699 on the probability of tailwinds, the variability between tail- and headwinds and the
700 relative metabolic costs of travel and resting (Thorup et al. 2006). Also in situations
701 where the birds choose between departure and continued fuel deposition is the optimal
702 policy dependent on the probability and variability of wind assistance, and birds are
703 expected to build up initial fuel reserves irrespective of wind, but later to depart under
704 tailwind conditions and even later, if tailwinds have failed and the probability of
705 tailwinds is low, to depart irrespective of wind (Weber et al. 1998, Weber and
706 Hedenström 2000).

707 Ospreys migrating between northern Europe and Africa showed no selectivity
708 of tailwinds for their travel days (Thorup et al. 2006) and also nocturnal passerine
709 migrants travelled regularly without tailwind assistance during both spring and
710 autumn migration in Scandinavia (Alerstam et al. 2011). This is in clear contrast to
711 the strong tailwind assistance gained by many shorebirds (e.g. Green 2004) as well as
712 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

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

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

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

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

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

781 (Alerstam and Pettersson 1975; Åkesson 1993; Zehnder et al. 2001; Bingman et al.
782 1982). The demonstration that juvenile raptors on their first migratory journey are
783 exposed to almost full wind drift while adults compensate for the wind drift to an
784 important degree (Thorup et al. 2003) indicates that cues learnt by adults may help to
785 reduce wind drift.

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

798

799 **Phenotypic flexibility, arrival time and moult schedules**

800

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

807 Optimization has proven to be a useful approach for analysing and
808 understanding these adaptations during migration, as a consequence of the balance
809 between benefits of having large muscles for flight and large digestive organs for
810 maximizing net energy intake, and the costs of carrying heavy organs in flight and
811 building and rebuilding the organs between flight and energy deposition phases
812 (Weber and Hedenström 2001). The adaptive variation of the gizzard size among
813 migratory knots in response to their seasonally shifting demands on eating high-
814 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

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

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

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

873

874 **Outlook**

875

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

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

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

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

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

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





