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Thomas Alerstam

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**Flight by night or day?  
Optimal daily timing of bird migration.**

Thomas Alerstam

Department of Animal Ecology, Lund University, Ecology Building, SE-22362 Lund,  
Sweden

E-mail: Thomas.Alerstam@zoekol.lu.se

Phone: 0046 462223785, Fax: 0046 462224716

Accepted manuscript

22 Abstract (294 words)

23

24 Many migratory bird species fly mainly during the night (nocturnal migrants), others  
25 during daytime (diurnal migrants) and still others during both night and day. Need to  
26 forage during the day, atmospheric structure, predator avoidance and orientation  
27 conditions have been proposed as explanations for the widespread occurrence of  
28 nocturnal migration. However, the general principles that determine the basic  
29 nocturnal-diurnal variation in flight habits are poorly known. In the present study  
30 optimal timing of migratory flights, giving the minimum total duration of the  
31 migratory journey, is evaluated in a schematic way in relation to ecological conditions  
32 for energy gain in foraging and for energy costs in flight. There exists a strong and  
33 fundamental advantage of flying by night because foraging time is maximized and  
34 energy deposition can take place on days immediately after and prior to the nocturnal  
35 flights. The increase in migration speed by nocturnal compared with diurnal migration  
36 will be largest for birds with low flight costs and high energy deposition rates. Diurnal  
37 migration will be optimal if it is associated with efficient energy gain immediately  
38 after a migratory flight because suitable stopover/foraging places have been located  
39 during the flight or if energy losses during flight are substantially reduced by thermal  
40 soaring and/or by fly-and-forage migration. A strategy of combined diurnal and  
41 nocturnal migration may be optimal when birds migrate across regions with relatively  
42 poor conditions for energy deposition (not only severe but also soft barriers).

43 Predictions about variable timing of migratory flights depending on changing foraging  
44 and environmental conditions along the migration route may be tested for individual  
45 birds by analysing satellite tracking results with respect to daily travel routines in  
46 different regions. Documenting and understanding the adaptive variability in daily

47 travel schedules among migrating animals constitute a fascinating challenge for future  
48 research.

49

50 Key words: optimal migration, nocturnal migration, diurnal migration, fly-and-forage  
51 migration, travel schedules

52

Accepted manuscript

## 52 **Introduction**

53

54 Many bird species perform their migratory flights during the night while others fly  
55 mainly during daytime and still others are flexible and may fly both during the night  
56 and day. Possible explanations for these habits have been discussed since long, mainly  
57 with the aim of understanding why so many birds fly by night.

58         Nocturnal migration brings the potential advantage that the migratory flights do  
59 not interfere with foraging during the days (for birds with diurnal foraging habits;  
60 Brewster, 1886). The idea that the daily timing of migration has evolved primarily to  
61 safeguard or maximise foraging opportunities was supported by the observations of  
62 Lank (1989) that shorebirds departed on migratory flights not only at dusk (when  
63 foraging conditions deteriorated because of the imminent darkness) but also at other  
64 times of the day when tides were rising and access to feeding areas were prevented  
65 during high tides.

66         Nocturnal migration may also be associated with more favourable flight  
67 conditions compared with diurnal migration because of the diel variation in  
68 atmospheric structure. Hence, by flying at night birds may avoid turbulence and  
69 strong winds and also reduce evaporative water losses in the cooler and more humid  
70 night time air (Kerlinger and Moore, 1989). In addition, avoidance of predators and  
71 the use of critical orientation cues at sunset or during the night have also been  
72 suggested as contributory explanations for nocturnal migration (cf. reviews by  
73 Kerlinger and Moore, 1989, Lank, 1989).

74         Among the diurnal migrants are birds that travel by thermal soaring migration  
75 like raptors, storks and cranes. Thermals develop over land during the day and the  
76 daily travel schedules of these migrants are closely associated with the daily timing of

77 thermal convection (Kerlinger, 1989). By exploiting the free lift in thermal air, these  
78 birds can use gliding flight which is much less energy-demanding than flapping flight  
79 (particularly for large birds) and thus benefit by a reduced cost of transport  
80 (Pennycuick, 1975, 1989, Kerlinger, 1989, Hedenström, 1993).

81       There are also many species of diurnal migrants that travel by sustained  
82 flapping flight just like the nocturnal migrants and the reasons for the daily timing of  
83 these migratory flights are much less clear. One interesting possibility is that the birds  
84 combine their migratory flights with foraging in a fly-and-forage migration strategy,  
85 which may be much more advantageous and widespread than generally assumed  
86 (Strandberg and Alerstam, 2007). Still another factor that may contribute to explain  
87 diurnal migration is the possibility of locating suitable stopover habitats and foraging  
88 flocks during the actual flights, thus reducing the costs of search and settling after a  
89 migratory flight. In addition, birds may change their travel schedules when passing  
90 regions with poor foraging conditions.

91       In this contribution I will evaluate and illustrate in a very simplified and  
92 schematic way some of the basic aspects that determine if nocturnal or diurnal flights,  
93 or a combination of both, are optimal in bird migration. I will evaluate the optimal  
94 solutions for time-selected migration (with minimization of total migration time as  
95 optimality criterion) but the general patterns and conclusions are also valid for  
96 energy-selected migration where the total energy costs for both flight transport and  
97 existence during the migratory period are taken into account (cf. Hedenström and  
98 Alerstam, 1997). As pointed out above, considerations for other criteria of minimal  
99 flight transport costs or predation risks have been put forward in earlier studies  
100 (Kerlinger and Moore, 1989).

101 The modern techniques of satellite tracking and GPS positioning make it  
102 possible to analyse daily travel routines of individual birds throughout their migratory  
103 journeys (Klaassen et al., 2008). This will open up new possibilities of evaluating the  
104 variation in daily timing within individuals depending on the shifting environmental  
105 conditions along the flight routes and also of comparing differences in travel  
106 schedules between individuals (e.g. between individuals infected or not infected by  
107 influenza virus; Van Gils et al., 2007), populations and species in a detailed way. The  
108 aim of my paper is to draw attention to these new possibilities of advancing our  
109 knowledge and understanding of the fascinating variation in daily travel schedules  
110 among migrating birds by providing some initial predictions for tests of optimal daily  
111 timing of bird migration.

112

#### 113 **Four basic cases of optimal daily timing of bird migration**

114

115 *Case 1: The fundamental advantage of flying by night.*

116

117 Let us consider a bird with diurnal foraging habits and assume the following changes  
118 in its energy status depending on the main activities during the periods of night and  
119 day (together making up the full 24 hr day): a migratory flight step completed either  
120 during the night (nocturnal migration) or day (diurnal migration) is associated with  
121 energy consumption  $F$ , roosting during the night with energy consumption  $N$  and  
122 foraging during daytime with net energy gain  $D$  ( $F, N, D > 0$  and  $D > N$ ). All else  
123 being equal this will bring a distinct advantage to a migrant performing its flight  
124 during the night because it can get a head start in foraging and energy gain on the  
125 succeeding day immediately after the nocturnal flight (Fig. 1). If the flight is



126 performed during daytime the migrant will have to roost first during the succeeding  
 127 night before energy replenishment can start the next day. A nocturnal migrant will  
 128 also save time by departing immediately after a day of foraging and energy  
 129 deposition, while a diurnal migrant will spend a night of roosting before departure. As  
 130 a consequence, energy restoration until the next flight will last longer and migration  
 131 speed will thus be slower for diurnal compared to nocturnal migration (Fig. 1).

132 Assuming that the bird covers distance  $Y$  in a migratory flight step, speed of  
 133 migration for a diurnal ( $S_d$ ) and nocturnal ( $S_n$ ) migrant may be calculated by dividing  
 134 distance with the time of one flight and energy replenishment cycle. The time (in 24 h  
 135 days) of one such cycle will be  $1+(F+N)/(D-N)$  for diurnal migration and  $1+(F-$   
 136  $D)/(D-N)$  for nocturnal migration (Fig. 1), giving the following resulting migration  
 137 speeds:

$$139 \quad S_d = Y \cdot \frac{(D-N)}{(F+D)} \quad (1)$$

$$141 \quad S_n = Y \cdot \frac{(D-N)}{(F-N)} \quad (2)$$

142  
 143 Thus the ratio of diurnal to nocturnal migration speed becomes:

$$145 \quad \frac{S_d}{S_n} = \frac{(F-N)}{(F+D)} \quad (3)$$

146  
 147 Under these simplified conditions nocturnal migration will always be faster and  
 148 thereby advantageous compared to diurnal migration. The relative gain in speed by

149 nocturnal migration will be largest for migrants with low relative energy consumption  
150 in flight and large relative daily energy gain in foraging (Fig. 2).

151 The scaling exponent for energy expenditure in flapping flight (flight power) in  
152 relation to body mass is expected to exceed the corresponding scaling exponent for  
153 resting metabolism (Pennycuik, 1975, 1989; but see McWilliams et al., 2004). If this  
154 holds true small birds will have more to gain by nocturnal flight than large birds. No  
155 such general size-dependence seems to exist for energy deposition rate relative to  
156 resting metabolic rate (Lindström, 1991, 2003) but there is important variation in  
157 relative energy deposition rates between populations and species migrating under  
158 different ecological conditions (Lindström, 2003).

159 The gain in migration speed by nocturnal compared to diurnal migration is  
160 often expected to be substantial. For a case of  $F=9$ ,  $N=1$ ,  $D=3$  (provisionally regarded  
161 as a typical example case),  $S_n$  will exceed  $S_d$  by 50%, and for a migrant with  
162 somewhat lower relative flight costs and higher relative foraging gain ( $F=6$ ,  $N=1$ ,  
163  $D=4$ )  $S_n$  will be twice the  $S_d$  (eq. 3).

164 Given this fundamental and strong advantage in time saving by nocturnal  
165 migration, what possible factors are there to explain the regular occurrence of diurnal  
166 migration among many species and in many situations?

167

168 *Case 2: Differential energy gain on first day(s) after flight.*

169

170 An important advantage associated with diurnal migration is the possibility for the  
171 migrants to efficiently find suitable foraging habitats and to join foraging flocks  
172 during their travel days (by combining flight with surveillance for suitable stopover  
173 sites) so that they can achieve full rates of energy gain already on the first stopover

174 day. However, combining migration flight with surveillance for suitable  
 175 stopover/foraging places will probably be associated with a cost in terms of a less  
 176 direct and effective flight towards the migratory destination. In comparison, a  
 177 nocturnal migrant will often have to spend time after landing at a new site to localise  
 178 suitable and safe foraging conditions, resulting in a lost or reduced energy gain during  
 179 its first day(s) at a new stopover site (Alerstam and Lindström, 1990). In addition,  
 180 there may be a cost of sleep deprivation after the night's flight that may contribute to  
 181 reduce foraging efficiency during the first day (Swilch et al., 2002, Fuchs et al., 2006;  
 182 but see also Rattenborg et al., 2004).

183 Assuming that the energy gain on the first day after a flight step differs between  
 184 a diurnal ( $D_{1d}$ ) and nocturnal ( $D_{1n}$ ) migrant and that the larger gain in diurnal  
 185 migration ( $D_{1d} > D_{1n}$ ) comes at a cost of reduced effective flight distance by a factor  
 186 of  $(1-c)$ , where  $c$  ( $0 \leq c < 1$ ) is a cost associated with the surveillance for  
 187 foraging/stopover opportunities, gives the following migration speeds:

$$189 \quad S_d = Y \cdot (1-c) \cdot \frac{(D-N)}{(F-D_{1d}+2D)} \quad (4)$$

$$191 \quad S_n = Y \cdot \frac{(D-N)}{(F-D_{1n}+D-N)} \quad (5)$$

$$193 \quad \frac{S_d}{S_n} = \frac{(1-c) \cdot (F-D_{1n}+D-N)}{(F-D_{1d}+2D)} \quad (6)$$

194  
 195 On the second and succeeding foraging days at a stopover site the energy gain  
 196 is assumed to be the same ( $D$ ) for diurnal and nocturnal migrants (nocturnal migrants

197 are assumed to find suitable stopover conditions after local search and settling  
198 behaviour during the first day after landing). The relationship in eq. 6 is illustrated for  
199 an example case in Fig. 3, demonstrating that for migrants with significant  
200 search/settling costs at a new stopover site leading to initial daily energy losses  
201 exceeding those during roosting, diurnal migration may be the most favourable option  
202 provided that the costs in terms of a reduced daily flight distance are not too high.  
203 These conditions may hold true among e.g. species that forage in large flocks that are  
204 widely scattered and hard to find.

205         Rather than travelling for a full day and stopping at a suitable site allowing  
206 efficient foraging the next morning, as assumed above, diurnal migrants may achieve  
207 equivalent migration speeds also by flying shorter times (and distances) between  
208 suitable foraging sites that they locate during the flights. In fact, many diurnal  
209 migrants fly mainly during morning hours, using the afternoon for foraging (Kerlinger  
210 and Moore, 1989, Newton, 2008). If the afternoon foraging will not fully compensate  
211 for the energy loss during the preceding morning flight this may lead to a pattern of  
212 migration waves, where the birds after a number of migration days will have to spend  
213 some full days for replenishing their exhausted fuel reserves and thus getting prepared  
214 for a new series of migration days (Newton, 2008).

215         Equation 6 and Fig. 3 shows that there must be a pronounced difference in  
216 settling costs in strong favour of diurnal migration to outweigh the fundamental  
217 advantage of nocturnal migration according to Case 1.

218

219 *Case 3: Reduced energy losses during diurnal flights.*

220

221 By travelling during daytime birds can reduce their energy losses during the flight in  
222 two main ways, (1) by exploiting free energy from the atmosphere in soaring flight,  
223 which is much less energy-demanding than sustained flapping flight and (2) by partly  
224 (or wholly) offsetting the flight costs by food intake using a strategy of fly-and-forage  
225 migration (birds with diurnal foraging habits).

226 Favourable conditions for thermal soaring migration, as used by e.g. raptors,  
227 storks and cranes, prevail over land during the day. Such soaring flight is associated  
228 with a marked reduction in energy consumption, particularly for large birds,  
229 compared to flapping flight which must be used when there are no thermals, during  
230 the night and over the sea (Pennycuik, 1975, 1989, Kerlinger, 1989).

231 Birds that fly extensively during their foraging, e.g. when hunting on their  
232 wings for insect or bird prey, or making search flights to locate food on the ground or  
233 in water, may combine foraging with covering migration distance. The food intake  
234 will help to offset the net energy expenditure during travelling. Rather little is known  
235 about the importance of such fly-and-forage migration, but it may well be a highly  
236 profitable and widely used strategy among many bird species (Strandberg and  
237 Alerstam, 2007, Klaassen et al., 2008).

238 These two main ways of reducing energy losses during diurnal flights are not  
239 mutually exclusive but may well be combined, as in the osprey *Pandion haliaetus* and  
240 other raptors (Strandberg and Alerstam, 2007). The advantage of fly-and-forage  
241 migration may also be combined with the related advantage of locating sites and  
242 habitats for stopover as evaluated above (Case 2). There is no sharp division line  
243 between Cases 2 and 3 for situations where localisation of stopover/foraging sites is  
244 very efficient during diurnal migratory flights, permitting the birds to travel by short  
245 hops between successive foraging sites during a day.

246 While assuming that energy costs for diurnal flight will be reduced by a factor  
 247  $(1-b)$ , where  $b$  ( $0 < b \leq 1$ ) is the relative benefit associated with soaring flight and/or  
 248 fly-and-forage migration, this benefit will usually come with a cost of a reduced daily  
 249 travel distance. Hence, the distance of a diurnal flight step is assumed to be reduced  
 250 by a factor  $(1-c)$ , where  $c$  ( $0 < c \leq 1$ ) is the relative cost of a reduced effective travel  
 251 speed (e.g. because cross-country soaring flight is often slower than sustained  
 252 flapping flight and because effective progress towards the migratory destination will  
 253 be reduced when flight is combined with searching/foraging). With these benefits and  
 254 costs the speed of diurnal migration becomes:

$$256 \quad S_d = Y \cdot (1-c) \cdot \frac{(D-N)}{[F \cdot (1-b) + D]} \quad (7)$$

257  
 258 The corresponding speed of nocturnal migration remains the same as in eq. 2. The  
 259 speed ratio thus becomes:

$$261 \quad \frac{S_d}{S_n} = \frac{(1-c) \cdot (F-N)}{[F \cdot (1-b) + D]} \quad (8)$$

262  
 263 This ratio is illustrated in the parameter space of  $b$  and  $c$  in Fig. 4. As long as  
 264 costs ( $c$ ) are not too large the advantages of reduced energy losses during flight may  
 265 make diurnal migration clearly more favourable than nocturnal migration for birds  
 266 that can exploit these advantages (in the illustrated example, diurnal migration of a  
 267 high benefit – low cost character may become more than twice as fast as nocturnal  
 268 migration).

269 Predicted size-dependent reductions of flight costs in soaring compared to  
270 flapping flight are sufficient to explain the preference among many large birds for  
271 diurnal migration by thermal soaring flight (Hedenström, 1993, Alerstam, 2000). The  
272 fly-and-forage migration strategy may also be a crucial factor to explain diurnal  
273 migration among many species, but studies of benefits and costs of this strategy are  
274 needed for critical testing of this possibility (Klaassen et al., 2008). The specific  
275 optimal behaviour for maximizing migration speed will depend on the trade-off  
276 function between benefits and costs and where this function is associated with  
277 maximum migration speed in the parameter space of  $b$  and  $c$  (cf. Alerstam and  
278 Strandberg, 2007).

279

280 *Case 4: Migration across regions with poor conditions for energy deposition.*

281

282 Flying both by day and night will lead to intermediate total migration speeds  
283 (intermediate between  $S_d$  and  $S_n$ ) for the cases considered above when energy  
284 deposition rate is assumed to be the same throughout the journey. Hence, combined  
285 nocturnal and diurnal migration will never be most beneficial in these cases.

286 However, this changes if we consider cases where birds pass regions with  
287 relatively poor conditions for energy deposition. In such cases we expect the birds to  
288 maximize their total migration speed by depositing extra energy stores in richer  
289 regions (where energy deposition rate is faster) before the passage of the poor region  
290 (and by replenishing exhausted reserves in richer regions after the passage). Hence,  
291 birds will be expected to incur a net energy loss during the passage of a poor region  
292 that will be covered by fuelling in richer regions in preparation for this passage. In the

293 extreme case of an ecological barrier where birds can find no food, they must of  
 294 course store all necessary fuel before the passage.

295 Assuming a net energy deposition rate  $B$  during a full stopover day and night  
 296 before the passage of the poor region, where  $B$  exceeds the corresponding net  
 297 deposition rate in the poor region ( $B > D-N$ ), we may compare migration speeds  
 298 between three different strategies across the poor region – (1) diurnal migration  
 299 (travelling during the day and resting during the night), (2) nocturnal migration  
 300 (travelling during the night and foraging, although with reduced gain rate, during the  
 301 day) and (3) combined diurnal and nocturnal migration (travelling during both day  
 302 and night).

303 The resulting migration speed is calculated as the distance covered during a 24  
 304 h period (day + night) divided the time of this period plus the time required for  
 305 depositing the net energy loss at deposition rate  $B$  before the passage of the poor  
 306 region. For diurnal migration the daily distance will be  $Y(1-c)$  and the associated time  
 307  $1+[F(1-b)+N]/B$ , for nocturnal migration the distance will be  $Y$  and the time  $1+(F-$   
 308  $D)/B$ , and for combined diurnal/nocturnal migration the distance will be  $Y(2-c)$  and  
 309 the time  $1+F(2-b)/B$ . This gives the following total migration speeds:

310

$$311 \quad S_d = Y \cdot (1-c) \cdot \frac{B}{[F \cdot (1-b) + N + B]} \quad (9)$$

312

$$313 \quad S_n = Y \cdot \frac{B}{(F - D + B)} \quad (10)$$

314

$$315 \quad S_c = Y \cdot (2-c) \cdot \frac{B}{[F \cdot (2-b) + B]} \quad (11)$$



316

$$317 \quad \frac{S_d}{S_c} = \frac{(1-c) \cdot [F \cdot (2-b) + B]}{(2-c) \cdot [F \cdot (1-b) + N + B]} \quad (12)$$

318

$$319 \quad \frac{S_d}{S_n} = \frac{(1-c) \cdot (F - D + B)}{[F \cdot (1-b) + N + B]} \quad (13)$$

320

$$321 \quad \frac{S_c}{S_n} = \frac{(2-c) \cdot (F - D + B)}{[F \cdot (2-b) + B]} \quad (14)$$

322

323  $S_c$  denotes the total speed of combined diurnal and nocturnal migration.

324 Depending on the degree of impoverishment of the region passed a strategy of  
 325 combined diurnal and nocturnal migration will be most favourable in a larger or  
 326 smaller part of the parameter space of  $b$  and  $c$  (Fig. 5). For ecological barriers devoid  
 327 of food, where birds will incur an energy loss if stopping to rest during the day ( $D = -$   
 328  $N$ ), the strategy of combined diurnal and nocturnal migration will be favourable under  
 329 a wide range of conditions (Fig. 5a). However, purely diurnal migration may still be a  
 330 favourable strategy for crossing such a barrier if benefits associated with e.g. thermal  
 331 soaring migration remain sufficiently large and costs remain small. These general  
 332 conclusions about the favourability of combined diurnal and nocturnal migration hold  
 333 not only for the criterion of a maximal migration speed but also for minimal total  
 334 energy costs for crossing the ecological barrier.

335 It is interesting to note that combined diurnal and nocturnal migration may be most  
 336 favourable, albeit under a more restricted range of conditions, also for birds passing a  
 337 “soft barrier” where foraging and energy deposition are still possible although at a  
 338 reduced gain rate (Fig. 5b). Such situations of soft barriers probably apply to many

339 birds like shorebirds, seabirds, geese and others that travel long distances between  
340 particularly rich staging sites, but also forage and refuel during the migration across  
341 intervening regions. In such situations we may expect to find cases of combined  
342 diurnal and nocturnal migration (as well as cases of pure diurnal or nocturnal  
343 migration; Fig. 5b).

344

## 345 **Discussion**

346

347 The first case considered above showed that nocturnal migration, by allowing  
348 maximum time for foraging, is expected to clearly surpass diurnal migration in  
349 resulting migration speed. Adding to this picture the advantages of flying by night  
350 rather than by day because of atmospheric conditions (Kerlinger and Moore, 1989), it  
351 seems that the general advantages of nocturnal migration are so pronounced and  
352 fundamental that the traditional question “why fly by night?” (e.g. Brewster, 1886,  
353 Kerlinger and Moore, 1989, Lank, 1989) should be replaced by the more puzzling  
354 “why fly by day?”.

355 The remaining three cases in the above treatment help to identify aspects that  
356 promote diurnal migration. One such factor is the benefit of an efficient start of  
357 foraging after a daytime migratory flight in comparison with the probable costs of  
358 search and settling after a nocturnal flight, possibly aggravated by the effects of sleep  
359 deprivation (Swilch et al., 2002, Rattenborg et al., 2004, Fuchs et al., 2006).

360 Of major importance to explain diurnal migration is the possibility for the birds  
361 to strongly reduce their flight costs by travelling during daytime. This is well  
362 understood for birds that use thermal soaring migration (Pennycuik, 1975, 1989,  
363 Kerlinger, 1989, Hedenström, 1993, Alerstam, 2000) but the possibilities of reducing

364 net costs for flight by a combined fly-and-forage strategy has attracted much less  
365 attention. The beneficial effects of reduced energy losses during daytime flights will  
366 in principle be the same irrespective if the reductions derive from exploitation of  
367 thermal air or from food intake during the flights.

368 Another aspect that has attracted little attention is the fact that migration across  
369 regions with relatively poor foraging conditions is expected to be best performed by  
370 flights during both nights and days, with the migrants preparing for these passages by  
371 accumulating extra energy reserves before reaching the impoverished regions. Such  
372 behaviour may be advantageous not only during the crossing of severe barriers almost  
373 devoid of food (e.g. deserts) but also of regions where foraging conditions are only  
374 mildly restricted (“soft barriers”). This is a potentially important explanation for the  
375 flexible daily flight schedules among e.g. shorebirds and waterfowl that often migrate  
376 between restricted key sites of particularly rich food abundance (e.g. wetlands, tidal  
377 mudflats; e.g. Van Gils et al., 2005). Tidal variation has a strong influence on  
378 foraging conditions of coastal birds and may constitute another important factor that  
379 explains flexible day/night migration among these birds as demonstrated by Lank  
380 (1989). However, Piersma et al. (1990) showed that the relationship between tides and  
381 migratory departures of coastal shorebirds is less consistent when comparing different  
382 stopover sites and species than the more general habit among shorebirds to depart  
383 mainly during the evening hours before or at sunset. Flying by both day and night is  
384 of course also required among birds making long non-stop flights that last more than a  
385 single night, like land birds crossing vast expanses of sea, e.g. across the Gulf of  
386 Mexico, West Atlantic, Mediterranean Sea and Pacific Ocean (Alerstam, 2001, Gill et  
387 al., 2005).

388 According to these results we expect individual birds to change their daily  
389 travel schedules when environmental conditions change along the routes, which may  
390 be tested by analysing satellite tracking data from different regions (Klaassen et al.,  
391 2008). More specifically, we predict that diurnal migrants change to nocturnal flights  
392 when travelling across regions where they cannot benefit from the gains associated  
393 with fly-and-forage and/or thermal soaring migration. When travelling across barriers  
394 and suboptimal foraging habitats they are expected to extend their schedules to  
395 include both nocturnal and diurnal flights. Likewise, nocturnal migrants are predicted  
396 to use also diurnal flights when crossing severe or soft barriers.

397 Huge numbers of birds in the Palaearctic-African migration systems fly across  
398 the Sahara Desert, a severe barrier extending over 1500-2000 km (Moreau, 1972).  
399 The desert presumably has little to offer in the form of food for the migrants and we  
400 would therefore predict that they will travel by flights during both night and day.  
401 However, available observations are contradictory to this expectation providing  
402 examples of both diurnal and nocturnal migrants maintaining their characteristic diel  
403 flight habits during this crossing.

404 Ospreys enjoy the benefit of both thermal soaring and fly-and-forage  
405 migration by travelling during daytime across Europe. They keep to their diurnal  
406 flight times, mainly between 09 and 17 hrs, also during the Sahara crossing when they  
407 fly higher and without interruption compared with their behaviour in Europe  
408 (Klaassen et al. 2008). This reflects the fact that they do not forage much during their  
409 Sahara crossing, but the gain obtained from thermal soaring migration in the desert is  
410 still sufficient to explain their strict diurnal flight habits during the desert crossing  
411 (Hedenström, 1993, Alerstam, 2000).

412           The much smaller hobby *Falco subbuteo* is less dependent on thermal soaring  
413 than larger raptors. A major reason for its diurnal migration habits, starting already at  
414 dawn, is presumably the use of fly-and-forage migration, combined with some  
415 opportunistic soaring in thermals. Surprisingly, the hobbies seem to have a similar  
416 daily flight routine during their Sahara crossing as during their travels in Europe and  
417 tropical Africa south of Sahara (Strandberg et al., in prep.). The benefit from thermal  
418 soaring in the desert is probably not a sufficient explanation since these small falcons  
419 start their daily migration very early, before the development of thermals, also in  
420 Sahara. Perhaps there is enough of insect or bird prey to make fly-and-forage  
421 migration a profitable strategy for these aerial hunters also during the desert crossing  
422 (Strandberg et al., in prep.)?

423           The majority of nocturnal passerine migrants seem to cross the Sahara primarily  
424 by nocturnal flights, landing and resting (without foraging) in the shade in the desert  
425 during daytime (Bairlein, 1985, 1988, Biebach et al., 1986, 2000, Schmaljohann et al.,  
426 2007a). The risk of excessive evaporative water loss during daytime flights over the  
427 desert is assumed to be the reason for this behaviour (Biebach, 1990, Carmi et al.,  
428 1992, Klaassen, 1995). There are even indications that some diurnal passerine  
429 migrants, like the yellow wagtail *Motacilla flava*, change to adopt this strategy of  
430 intermittent nocturnal migration for the desert passage (Biebach et al., 2000). Still,  
431 radar studies demonstrate that a significant proportion of the passerine migrants  
432 continue their flights also during the day and this proportion is larger in spring when  
433 migration takes place at higher and cooler altitudes than in autumn (Schmaljohann et  
434 al., 2007a, 2007b). Densities of such daytime passerine migration were positively  
435 correlated with favourable tailwinds, and it was suggested that the nocturnal migrants

436 prolonged their flights into daytime to exploit opportunities of particularly beneficial  
437 wind conditions (Schmaljohann et al., 2007b).

438         Such opportunistic exploitation of extra favourable winds (or other favourable  
439 conditions that are unlikely to be encountered again during the migratory journey)  
440 constitutes another possible explanation for the combination of both diurnal and  
441 nocturnal flights (besides the barrier situation of Case 4 above). However, if and to  
442 what extent nocturnal migrants prolong their flights into the day and diurnal migrants  
443 prolong their flights into the night during extra favourable winds are poorly known. It  
444 also remains to be evaluated how superior tailwinds must be on these occasions of  
445 prolonged flights in relation to expected tailwinds during future migratory flights, for  
446 such opportunistic behaviour of flight prolongation to evolve.

447         The simplified and schematic evaluations in this paper show some basic  
448 features that determine how optimal behaviour changes between nocturnal and diurnal  
449 migration depending on energy gain in foraging and energy costs in flight. This  
450 treatment may be useful as a starting-point for generating predictions about migration  
451 schedules, although additional factors, like e.g. water balance or opportunistic flight  
452 prolongation, need to be considered depending on the environmental situation, as  
453 shown by the above discussion about migration across the Sahara Desert. This general  
454 approach can be used to predict daily travel routines for interesting special cases, e.g.  
455 for seabirds that forage mainly during the night versus those foraging during the day,  
456 for full moon nights that may allow foraging by some diurnal foragers, for shorebirds  
457 that can feed only during daytime at low tide in comparison with shorebirds that feed  
458 both during the day and night, etc.

459         One should be aware that, in this schematic evaluation, the assumptions about  
460 daily timing of migration are much over-simplified. It is to be expected that there

461 exists a wide spectrum of subtle differences in timing and duration of flights, as well  
462 as in the variability of these traits, between different species and ecological  
463 conditions. However, our knowledge and understanding about these differences are  
464 still rudimentary. This may rapidly change with the new possibilities of revealing  
465 detailed daily travel schedules for individual birds based on satellite tracking and GPS  
466 techniques. It is my hope that the present evaluation will help to draw attention to the  
467 fascinating challenge of documenting and understanding the variable daily travel  
468 schedules among migrating animals. Such knowledge about the principles for daily  
469 travel timing is important for a general understanding of evolutionary possibilities and  
470 limitations in animal migration.

471

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473

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477

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479

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## FIGURE LEGENDS

560

561 Fig. 1. Change in energy level during one cycle of migratory flight and energy  
 562 restoration for nocturnal (solid line) and diurnal migration (broken line). This cycle  
 563 will be shorter for nocturnal migration because energy deposition can take place on  
 564 the day immediately after the nocturnal flight and also on the day immediately prior to  
 565 the next nocturnal flight departure. In contrast, diurnal migrants have to spend the  
 566 nights resting after and prior to the daily flights. The graph illustrates a case of  
 567 relative energy changes  $F = 9$ ,  $N = 1$ ,  $D = 3$  (see text).

568

569 Fig. 2. Ratio of speed of nocturnal versus diurnal migration in relation to  
 570 relative energy consumption in flight ( $F/N$ ) and relative energy gain during daytime  
 571 foraging ( $D/N$ ). Speed ratios in the range 1.25-3 are indicated by solid lines (based on  
 572 eq. 3, see text).

573

574 Fig. 3. Conditions of energy change during the first day after a nocturnal flight  
 575 ( $D_{1n}$ ) and cost of reduced distance during diurnal flight ( $c$ ) making diurnal or  
 576 nocturnal migration the most favourable strategy. The graph illustrates a case of  
 577 relative energy changes  $F = 9$ ,  $N = 1$ ,  $D = 3$ ,  $D_{1d} = 3$  (see text). Diurnal migration will  
 578 be most favourable if flights during the night are associated with energy losses during  
 579 the succeeding day (search/settling at a new stopover site) and if diurnal migration  
 580 costs  $c$  are not too large.

581

582 Fig. 4. Ratio of speed in diurnal versus nocturnal migration in relation to  
 583 benefits ( $b$ ) and costs ( $c$ ) in diurnal migration. Benefits ( $b$ ) refer to the proportional

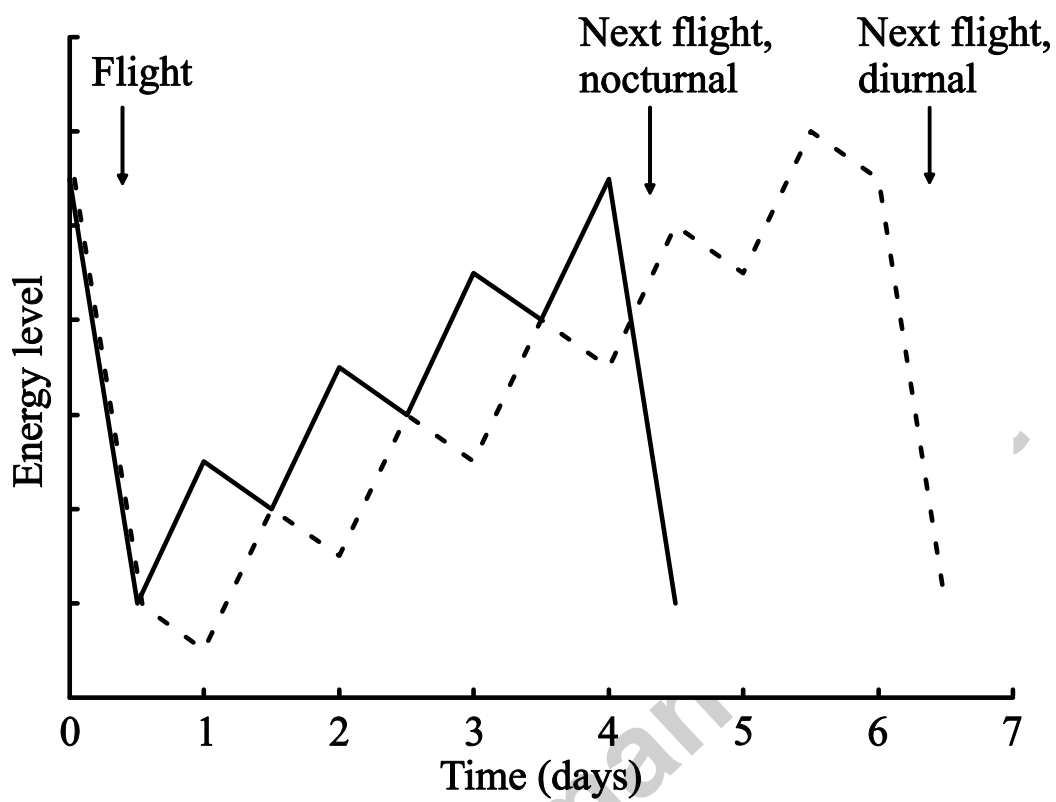
584 savings of energy costs for diurnal flights associated with thermal soaring flight  
585 and/or fly-and-forage migration and costs ( $c$ ) to the relative reduction in daily travel  
586 distance in diurnal migration. Speed ratios are indicated by solid lines at intervals of  
587 0.25 (ratios given at top of graph) with speed ratio 1 shown by a bold line, separating  
588 conditions where diurnal and nocturnal migration are most favourable. The graph  
589 illustrates a case of relative energy changes  $F = 9$ ,  $N = 1$ ,  $D = 3$  (see text).

590

591 Fig. 5. Conditions of benefits ( $b$ ) and costs ( $c$ ) in diurnal migration promoting  
592 strategies of diurnal or nocturnal migration or a combined diurnal and nocturnal  
593 migration for migration across regions where rates of energy deposition are reduced.  
594 **(a)** Migration across an ecological barrier completely devoid of food (energy change  
595 during day equals resting costs;  $D = -1$ ). **(b)** Migration across a “soft barrier” with  
596 reduced rate of energy deposition during the day ( $D = 2$ ). Calculations refer to a case  
597 with relative energy changes  $F = 9$ ,  $N = 1$  and with net energy gain  $B = 2$  (during full  
598 stopover day and night) before the passage of the poor region (see text).

599

599 Fig:1

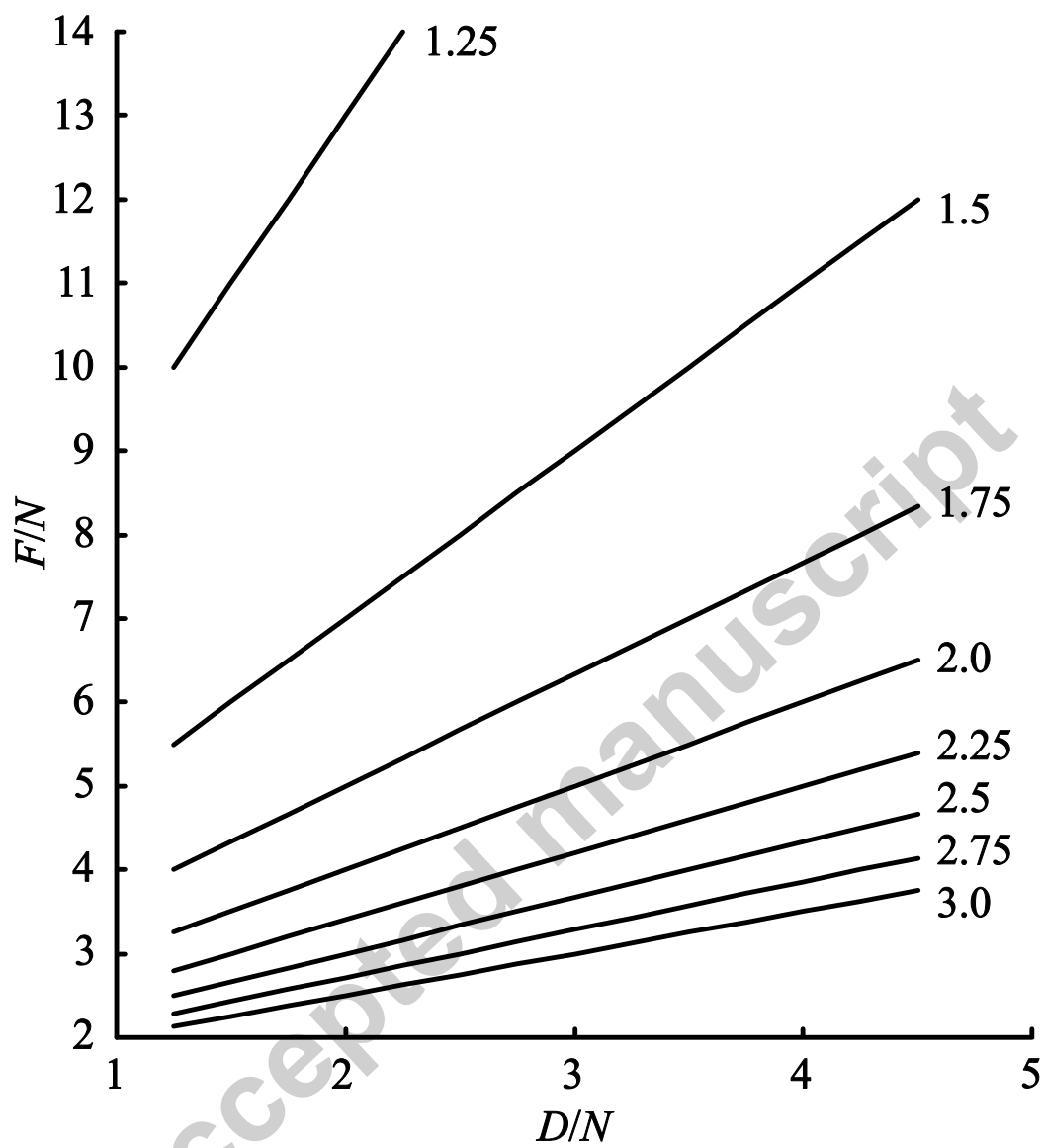


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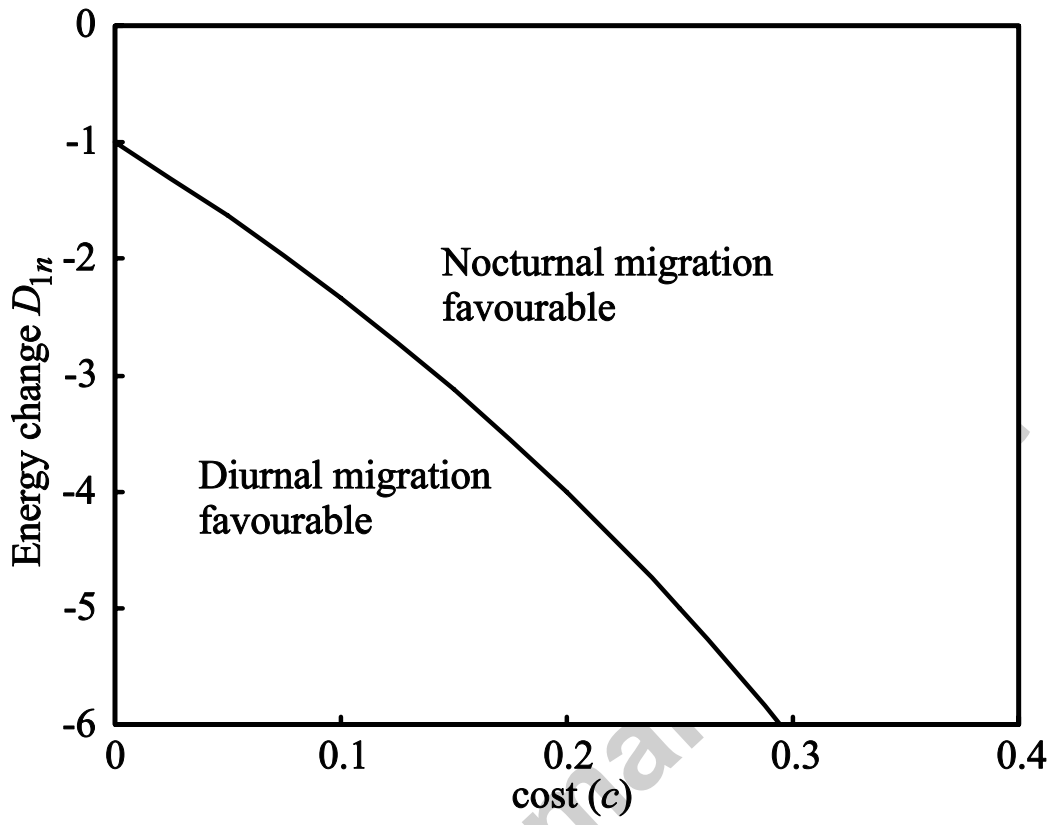
601 Fig:2



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603 Fig:3



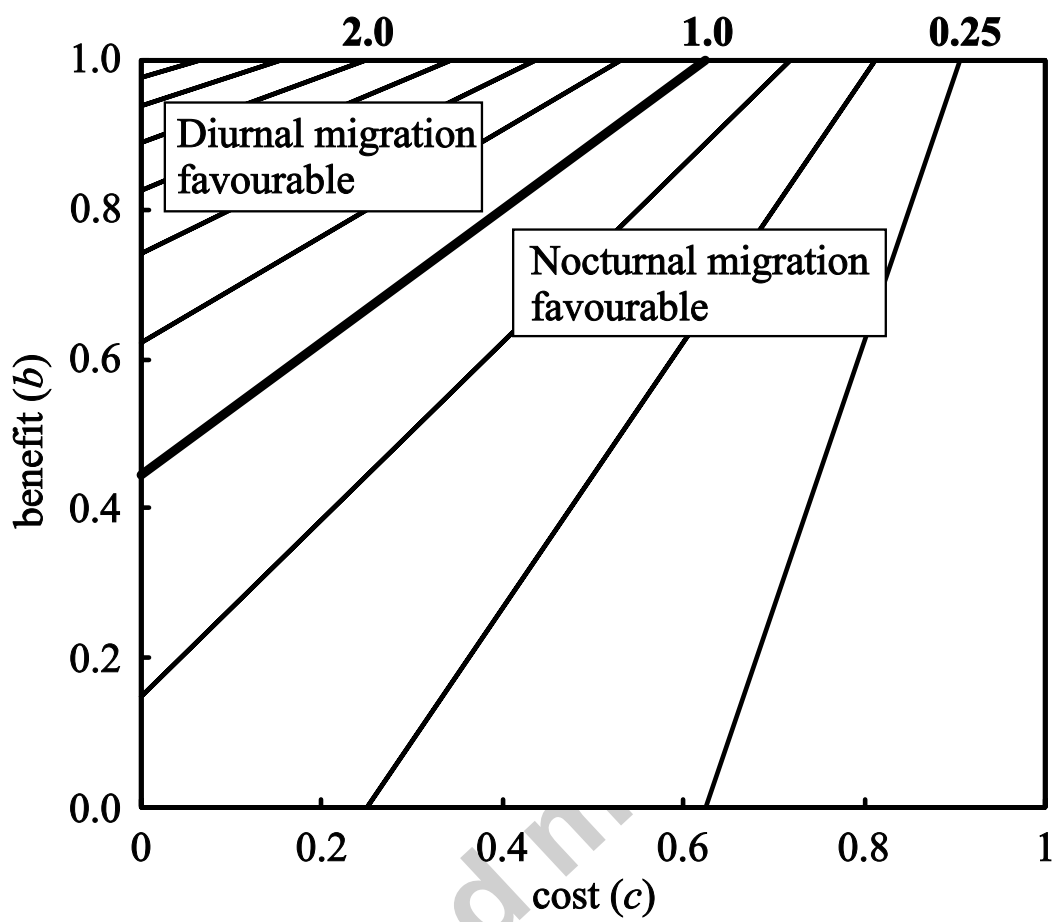
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605 Fig:4

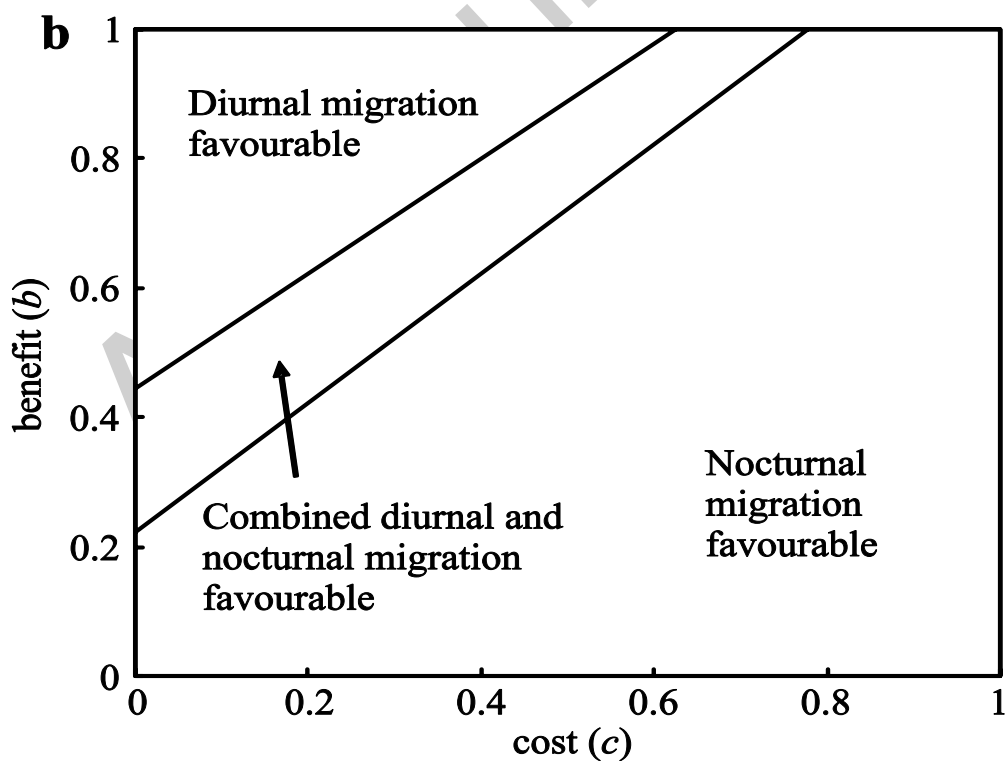
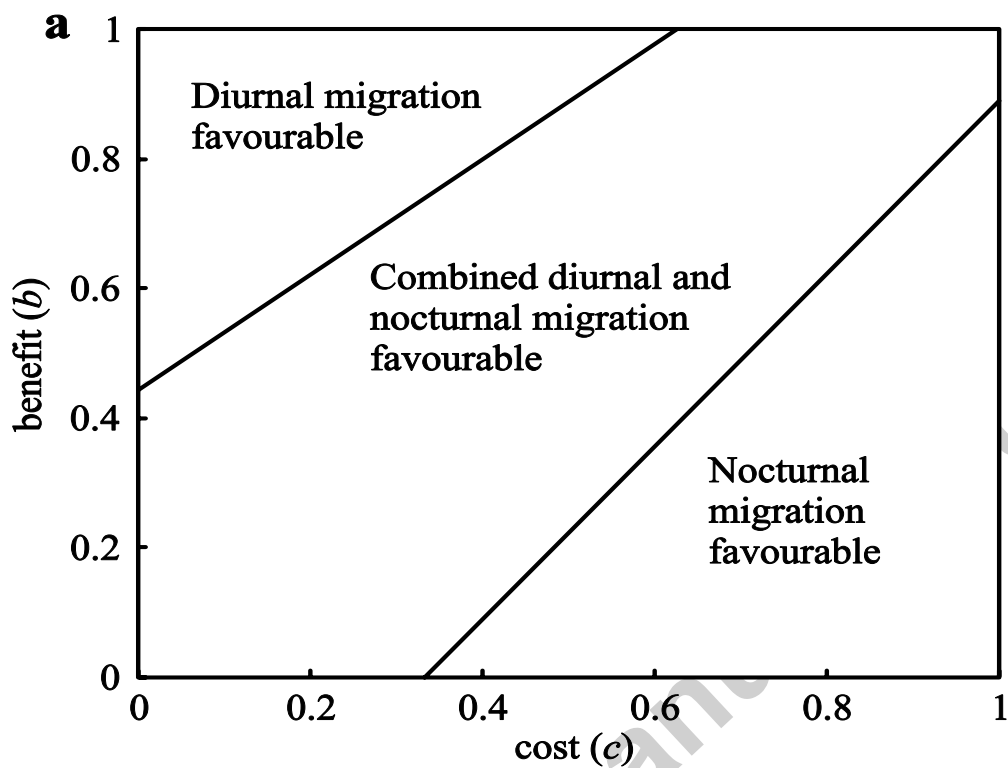


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607 Fig:5



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