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

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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:

188

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

190

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

192

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

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:

$$255 \quad S_d = Y \cdot (1-c) \cdot \frac{(D-N)}{[F \cdot (1-b) + D]} \quad (7)$$

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

$$260 \quad \frac{S_d}{S_n} = \frac{(1-c) \cdot (F-N)}{[F \cdot (1-b) + D]} \quad (8)$$

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

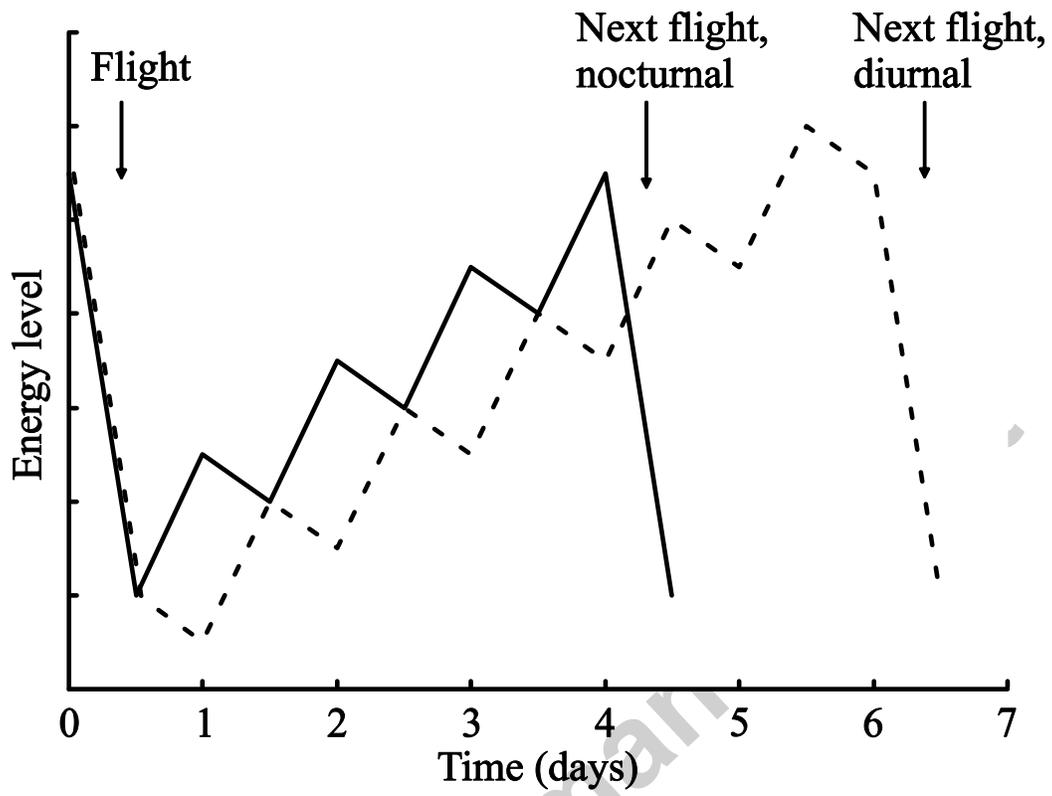
584 savings of energy costs for diurnal flights associated with thermal soaring flight
585 and/or fly-and-forage migration and costs (c) to the relative reduction in daily travel
586 distance in diurnal migration. Speed ratios are indicated by solid lines at intervals of
587 0.25 (ratios given at top 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

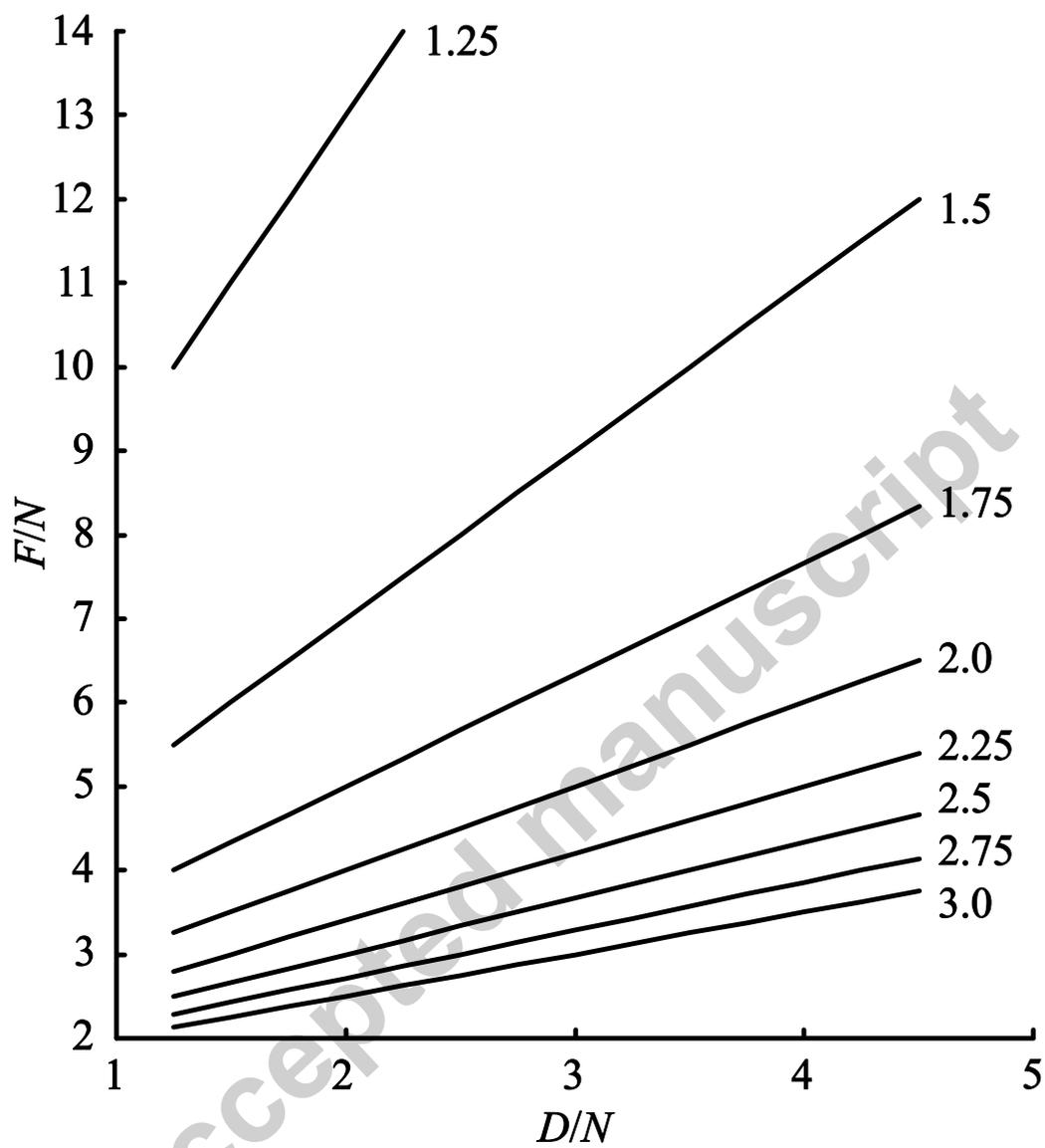


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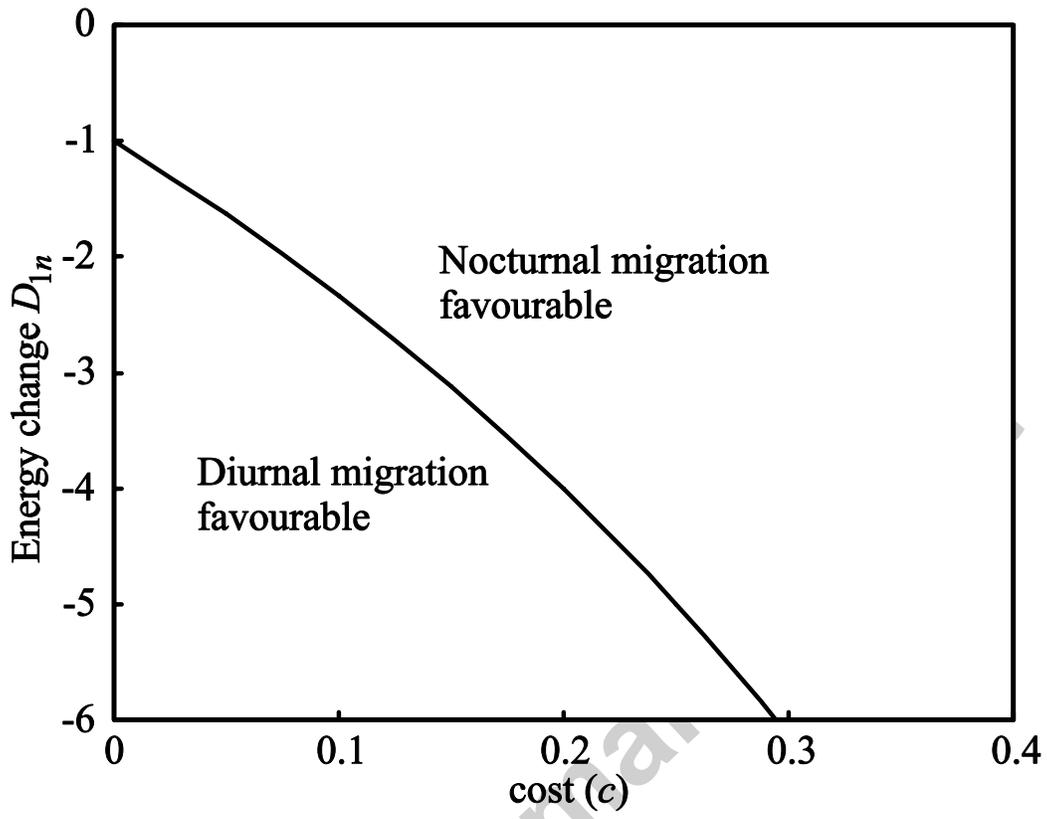
601 Fig:2



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603 Fig:3

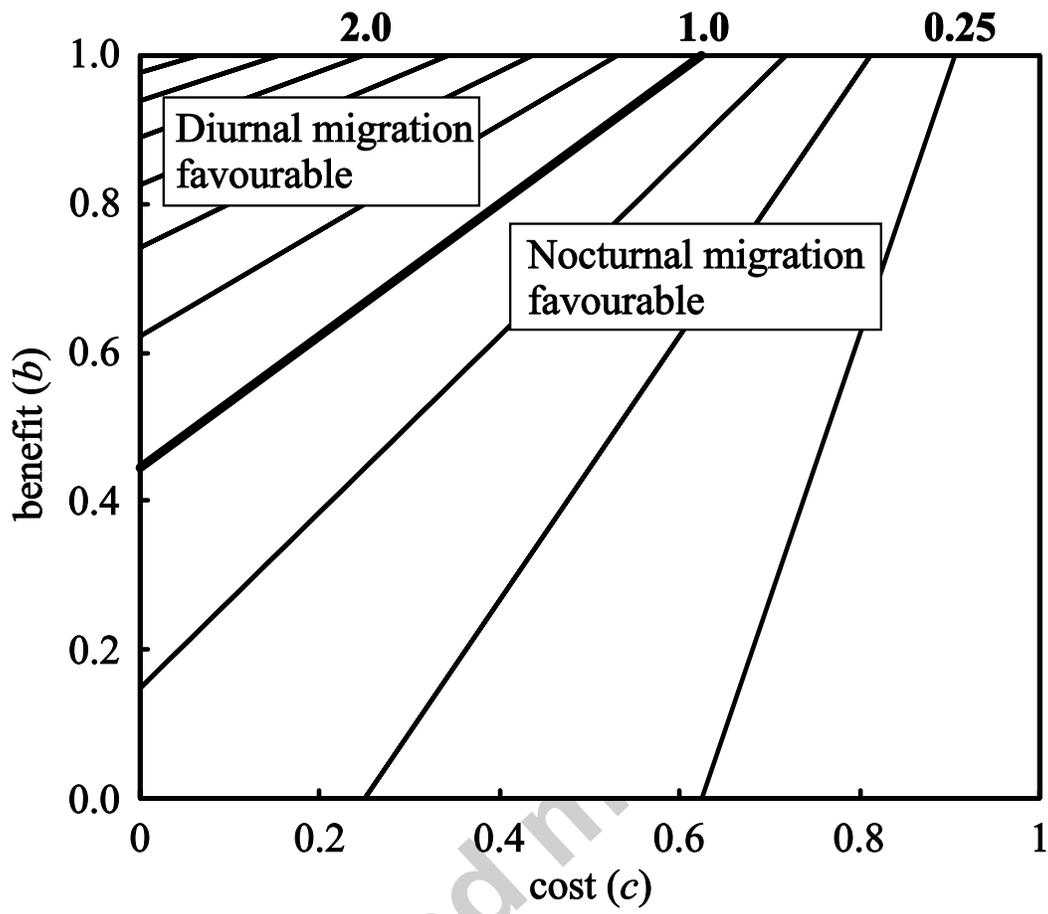


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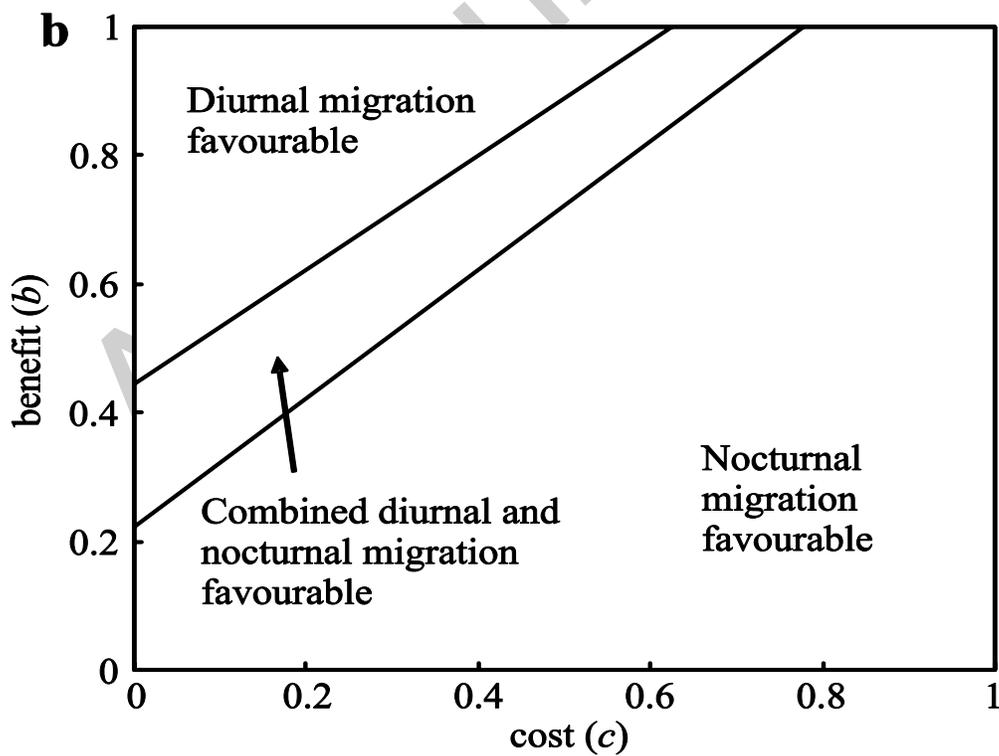
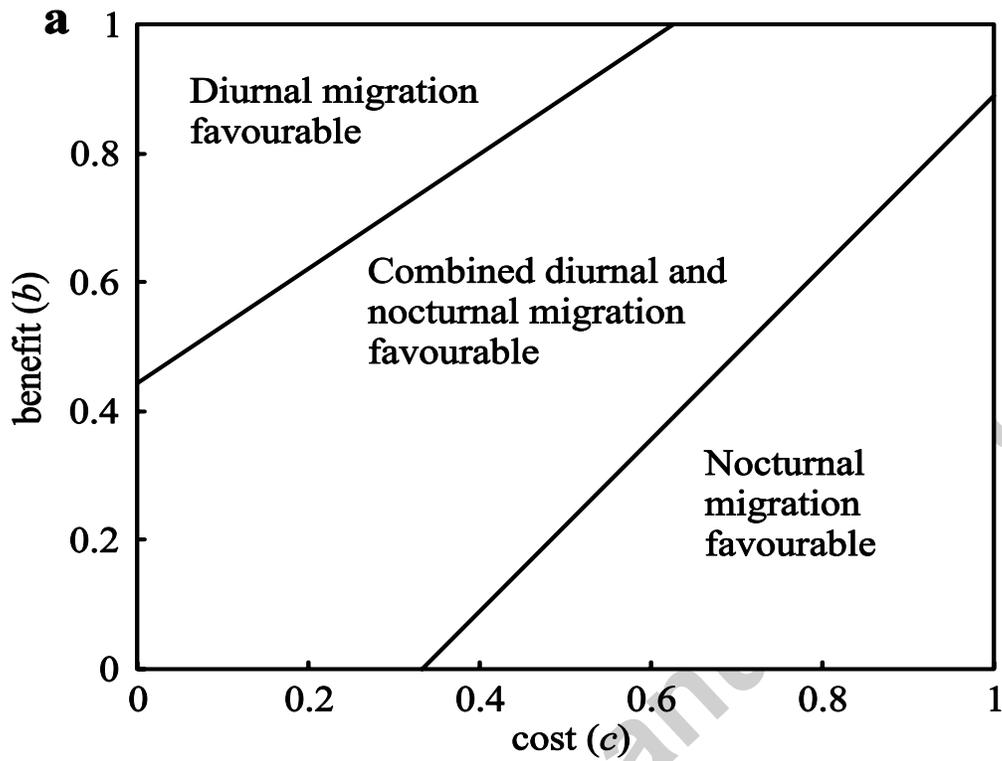
605 Fig:4



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607

607 Fig:5



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