



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

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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

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

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

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

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

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

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

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

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

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

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

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

Thus the ratio of diurnal to nocturnal migration speed becomes:

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

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

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

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

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

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

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

An important advantage associated with diurnal migration is the possibility for the migrants to efficiently find suitable foraging habitats and to join foraging flocks during their travel days (by combining flight with surveillance for suitable stopover 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

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

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

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

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

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.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

## Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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#### **References**

- Alerstam, T., 2000. Bird migration performance on the basis of flight mechanics and trigonometry. In: Domenici, P., Blake, R.W. (Eds.), *Biomechanics in Animal Behaviour*. BIOS Scientific Publishers, Oxford, pp 105-124.
- Alerstam, T. 2001. Detours in bird migration. *J. Theor. Biol.* 209, 319-331.

- 484 Alerstam, T., Lindström, Å. 1990. Optimal bird migration: The relative importance of  
485 time, energy , and safety. In: Gwinner, E. (Ed.), Bird migration. Physiology and  
486 Ecophysiology. Springer-Verlag, Berlin, pp 331-351.
- 487 Bairlein, F. 1985. Body weights and fat deposition of Palaearctic passerine migrants  
488 in the central Sahara. *Oecologia* 66, 141-146.
- 489 Bairlein, F. 1988. How do migratory songbirds cross the Sahara? *Trends Ecol. Evol.*  
490 3, 191-194.
- 491 Biebach, H. 1990. Strategies of trans-Sahara migrants. In: Gwinner, E. (Ed.), Bird  
492 migration. Physiology and Ecophysiology. Springer-Verlag, Berlin, pp 352-367.
- 493 Biebach, H., Friedrich, W., Heine, G. 1986. Interaction of body-mass, fat, foraging  
494 and stopover period in trans-Sahara migrating passerine birds. *Oecologia* 69, 370-379.
- 495 Biebach, H., Biebach, I., Friedrich, W., Heine, G., Partecke, J., Schmidl, D. 2000.  
496 Strategies of passerine migration across the Mediterranean Sea and the Sahara Desert:  
497 a radar study. *Ibis* 142, 623-634.
- 498 Brewster, W. 1886. Bird migration. *Memoirs Nuttall Ornithological Club* 1, Nuttall  
499 Ornithological Club, Cambridge, Massachusetts.
- 500 Carmi, N., Pinshow, B., Porter, W. P., Jaeger, J. 1992. Water and energy limitations  
501 on flight duration in small migrating birds. *Auk* 109, 268-276.
- 502 Fuchs, T., Haney, A., Jechura, T. J., Moore, F. R., Bingman, V. P. 2006. Daytime  
503 naps in night-migrating birds: behavioural adaptations to seasonal sleep deprivation in  
504 the Swaison's thrush, *Catharus ustulatus*. *Anim. Behav.* 72, 951-958.
- 505 Gill, Jr. R. E., Piersma, T., Hufford, G., Servranckx, R., Riegen, A. 2005. Crossing  
506 the ultimate ecological barrier: Evidence for an 11 000-km-long nonstop flight from

- 507 Alaska to New Zealand and eastern Australia by bar-tailed godwits. *Condor* 107, 1-  
508 20.
- 509 Hedenström, A. 1993. Migration by soaring or flapping flight in birds: the relative  
510 importance of energy cost and speed. *Phil. Trans. R. Soc. Lond. B* 342, 353-361.
- 511 Hedenström, A., Ålerstam, T., 1997. Optimum fuel loads in migratory birds:  
512 distinguishing between time and energy minimization. *J. Theor. Biol.* 189, 227-234.
- 513 Kerlinger, P. 1989. Flight strategies of migrating hawks. University of Chicago Press,  
514 Chicago.
- 515 Kerlinger, P., Moore, F. R., 1989. Atmospheric structure and avian migration. In:  
516 Power, D. M. (Ed.), *Current Ornithology Volume 6*. Plenum Press, New York, pp.  
517 109-142.
- 518 Klaassen, M. 1995. Water and energy limitations on flight range. *Auk* 112, 260-262.
- 519 Klaassen, R. H. G., Strandberg, R., Hake, M., Ålerstam, T., 2008. Flexibility in daily  
520 travel routines causes regional variation in bird migration speed. *Behav. Ecol.*  
521 *Sociobiol.* 62, 1427-1432.
- 522 Lank, D. B., 1989. Why fly by night? Inferences from tidally-induced migratory  
523 departures of sandpipers. *J. Field Ornithol.* 60, 154-161.
- 524 Lindström, Å. 1991. Maximum fat deposition rates in migrating birds. *Ornis Scand.*  
525 22, 12-19.
- 526 Lindström, Å., 2003. Fuel deposition rates in migrating birds: causes, constraints and  
527 consequences. In: Berthold, P., Gwinner, E., Sonnenschein, E. (Eds.), *Avian*  
528 *Migration*. Springer-Verlag, Berlin, pp 307-320.

- 529 McWilliams, S. R., Guglielmo, C., Pierce, B., Klaassen, M. 2004. Flying, fasting, and  
530 feeding in birds during migration: a nutritional and physiological ecology perspective.  
531 J. Avian Biol. 35, 377-393.
- 532 Moreau, R. E. G. 1972. The Palaearctic-African bird migration systems. Academic  
533 Press, London.
- 534 Newton, I. 2008. The migration ecology of birds. Elsevier, London.
- 535 Pennycuik, C. J. 1975. Mechanics of flight. In: Farner, D. S., King, J. R. (Eds.),  
536 Avian Biology Volume 5. Academic Press, New York, pp. 1-75.
- 537 Pennycuik, C. J., 1989. Bird Flight Performance. Oxford University Press, Oxford.
- 538 Piersma, T., Zwarts, L., Bruggemann, J. H. 1990. Behavioural aspects of the departure  
539 of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal  
540 timing. Ardea 78, 157-184.
- 541 Rattenborg, N. C., Mandt, B. H., Obermeyer, W. H., Winsauer, P. J., Huber, R.,  
542 Wikelski, M., Benca, R. M. 2004. Migratory sleeplessness in the white-crowned  
543 sparrow (*Zonotrichia leucophrys gambelli*). PLoS Biology 2, 924-936.
- 544 Schmaljohann, H., Liechti, F., Bruderer, B., 2007a. Songbird migration across the  
545 Sahara: the non-stop hypothesis rejected! Proc. R. Soc. B 274, 735-739.
- 546 Schmaljohann, H., Liechti, F., Bruderer, B., 2007b. Daytime passerine migrants over  
547 the Sahara – are these diurnal migrants or prolonged flights of nocturnal migrants?  
548 Ostrich 78, 357-362.
- 549 Strandberg, R., Alerstam, T., 2007. The strategy of fly-and-forage migration,  
550 illustrated for the osprey (*Pandion haliaetus*). Behav. Ecol. Sociobiol., 1865-1875.

- 551 Swilch, R., Piersma, T., Holmgren, N. M. A., Jenni, L. 2002. Do migratory birds need  
552 a nap after a long non-stop flight? *Ardea* 90, 149-154.
- 553 Van Gils, J. A., Battley, P.F., Piersma, T., Drent, R. 2005. Reinterpretation of gizzard  
554 sizes of red knots world-wide emphasises overriding importance of prey quality at  
555 migratory stopover sites. *Proc. R. Soc. B* 272, 2609-2618.
- 556 Van Gils, J. A., Munster, V. J., Radersma, R., Liefhebber, D., Fouchier, R. A. M.,  
557 Klaassen, M. 2007. Hampered foraging and migratory performance in swans infected  
558 with low-pathogenic avian influenza A virus. *PLoS ONE* 2, e184.  
559

# FIGURE LEGENDS

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

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

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

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

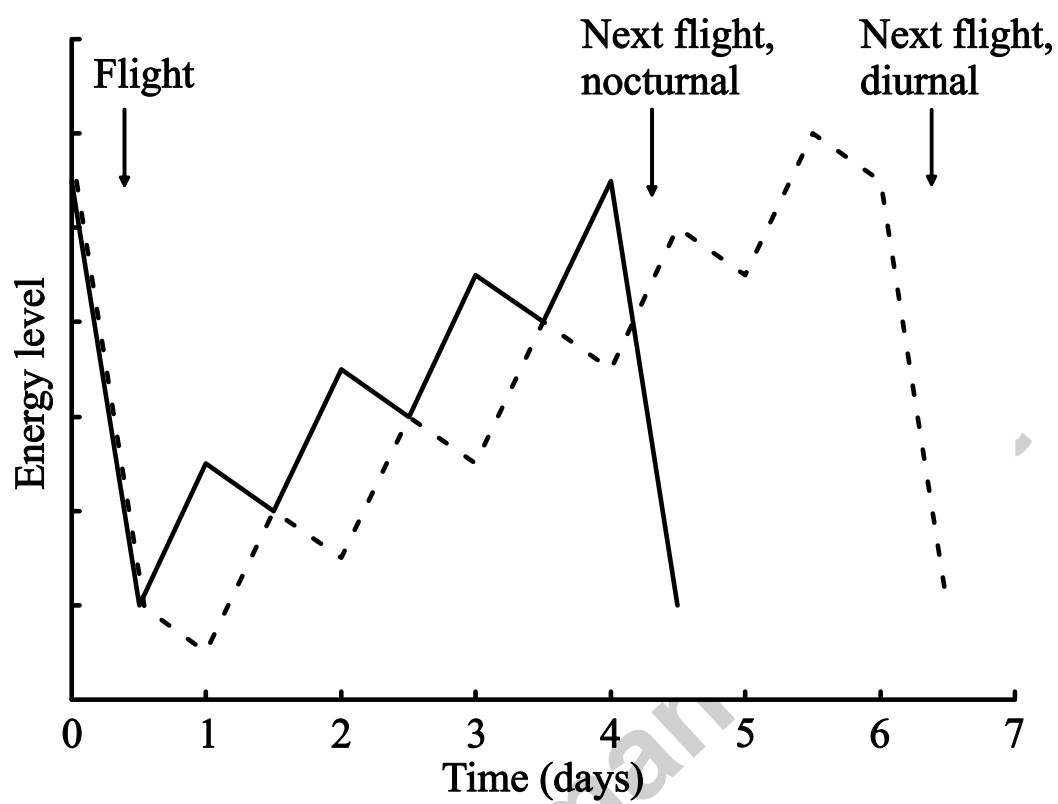
584 savings of energy costs for diurnal flights associated with thermal soaring flight  
 585 and/or fly-and-forage migration and costs ( $c$ ) to the relative reduction in daily travel  
 586 distance in diurnal migration. Speed ratios are indicated by solid lines at intervals of  
 587 0.25 (ratios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

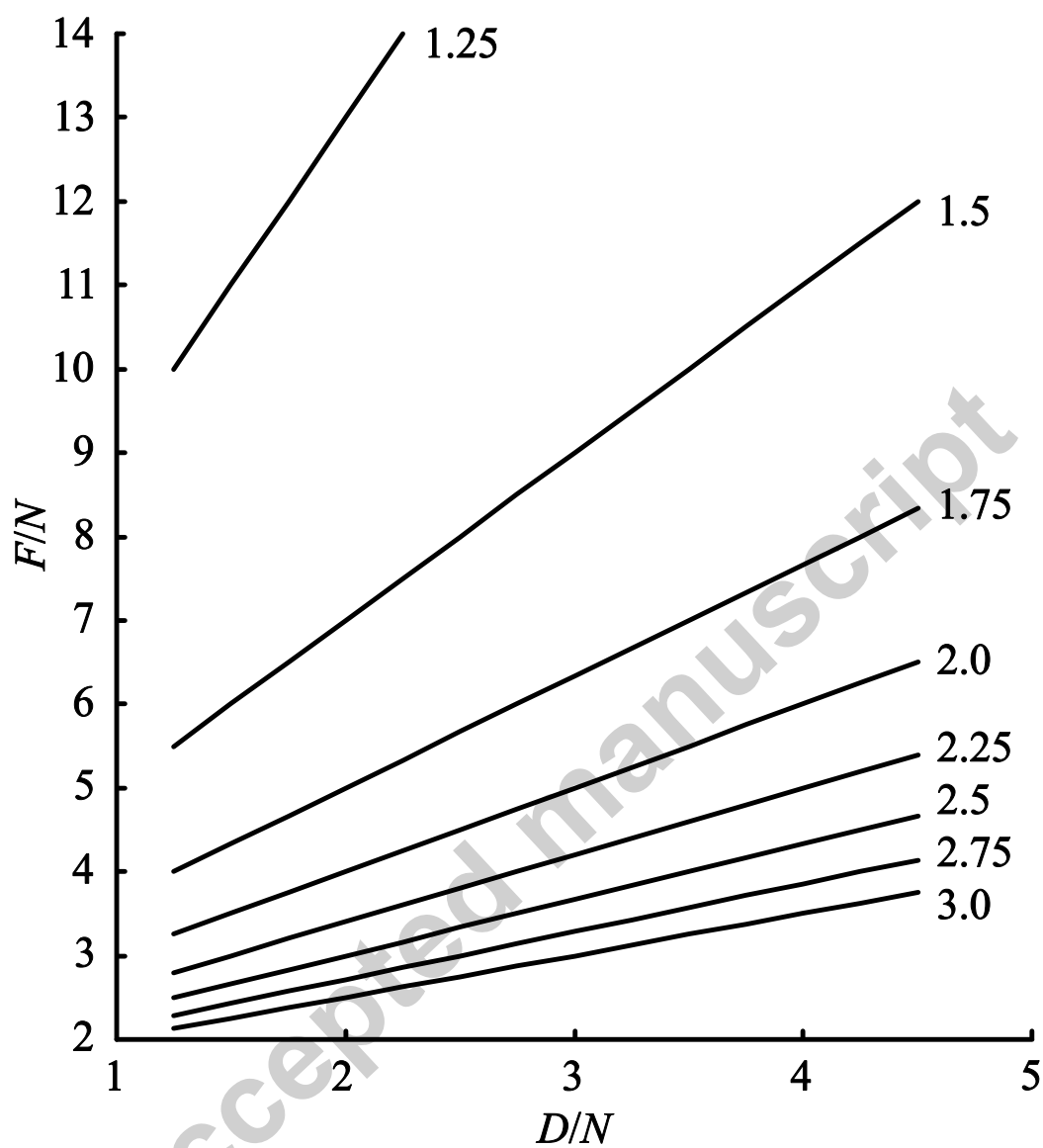
599 Fig:1



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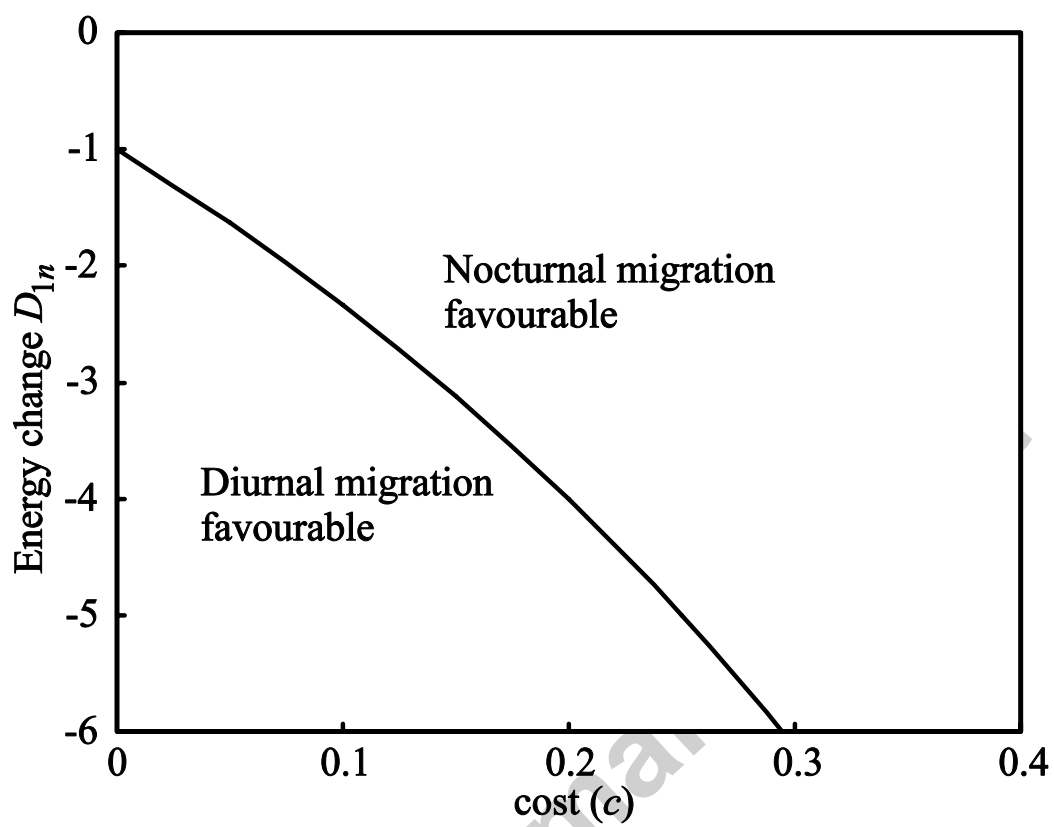
601 Fig:2



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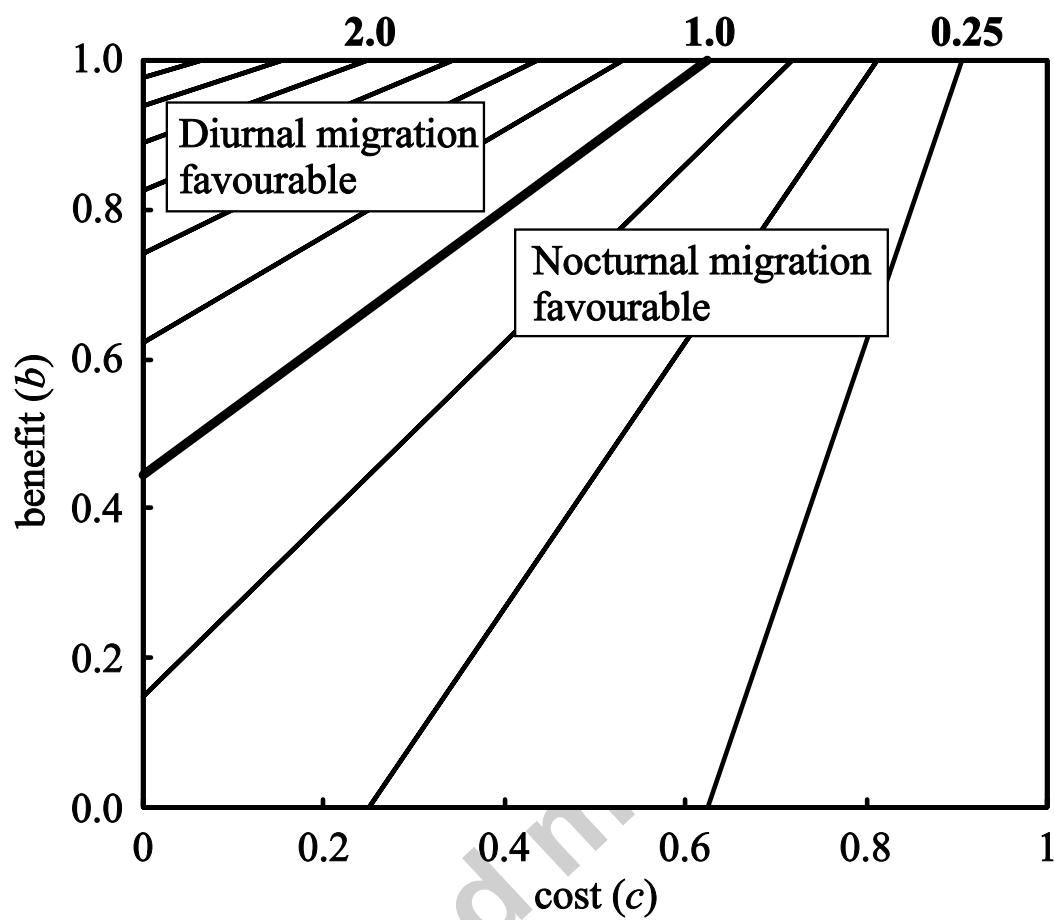
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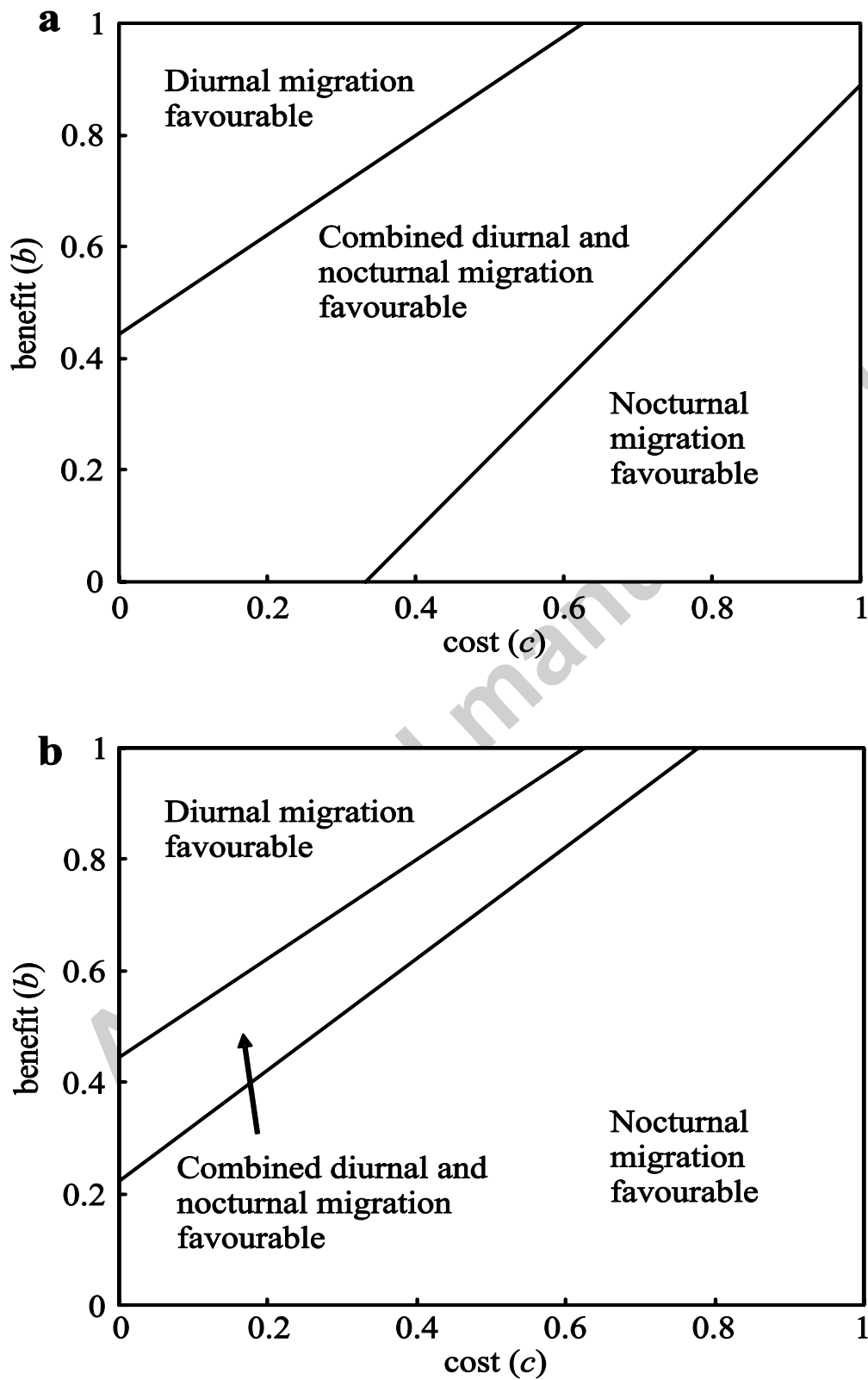
605 Fig:4



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607 Fig:5



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