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Abstract
The rationale of theoretical simulation studies of bird migration routes is to investigate and analyse factors determining the routes of migrating birds by calculating predicted trajectories according to different principles and evaluating the simulated trajectories in relation to observed routes and geographic patterns as documented by e.g. ringing results, radar and satellite tracking.

Simulation studies of bird migration routes have developed during the recent three decades along three main lines:

(1) Compass mechanisms. Assuming a certain compass mechanism (based on e.g. geomagnetic, solar or other celestial cues) and calculating the trajectories that would be the result if the birds adhere to a constant course according to this compass mechanism over long distances, provides a means to test which are the most likely compass systems used by the birds. A pioneering and most influential study is that of Kiepenheuer (1984), although the proposed compass mechanism in that study has no experimental support.

(2) Vector summation. Calculating the successive addition of flight steps according to the principles of vector summation and comparing the predicted spatial scatter at the migration front at different distances from the departure region with the observed migration pattern of different populations, serves to test if the birds are likely to be guided by navigational cues towards specific goal regions or not. The consequences of wind drift and compensation for the birds' flight routes are important in this context.

(3) Optimal routes. Predicting optimal migration routes with respect to distances, stopover and fuelling conditions, topography and barriers, wind patterns etc, makes it possible to evaluate which are the most important selective factors determining the evolution of migration routes, and also to what extent adaptive changes in routes are constrained by orientation mechanisms or colonisation history.

Studies of these three types show that there is an important role for the use of theoretical simulation of migration routes for understanding compass mechanisms, orientation and navigation performance, and the evolutionary process, in bird migration.

1. INTRODUCTION

What conclusions can we draw about the orientation of migrating birds from observations of their flight trajectories and routes? In this contribution I will review studies that have used a theoretical approach of simulating migration routes in different large-scale geographic regions and comparing the predicted trajectories with observed flight patterns in these regions. Most of our knowledge of bird migration routes relies on field observations and ringing recoveries, but more precise data about the birds' flight directions and course changes are obtained by modern techniques like radar, satellite-based telemetry and GPS. To what degree have the theoretical analyses of bird migration routes been successful in advancing our understanding of the birds' orientation on their journeys? What hopes can we have for more powerful tests and definite conclusions in the future when data of ever increasing accuracy about the flight of individual birds throughout their entire migratory journeys will become available with the new techniques?

Simulations and predictions of bird migration routes have been conducted with three main purposes of (1) testing which compass mechanisms the birds use on their flights, (2) evaluating whether naïve migrants are guided exclusively by directional information or also by navigatory (map- or coordinate-related) information, and (3) exploring adaptive orientation behaviour and routes under different optimality criteria of time and energy consumption, and survival (Table 1). Thus, attempts have been made to explain the geometry of flight paths and migration routes with respect to both their proximate and ultimate causes, from compass mechanisms to evolutionary forces.

2. MIGRATION ROUTES AND COMPASS MECHANISMS

Assuming that migrating birds use a certain compass mechanism and extrapolating an assumed or observed departure direction according to this compass, gives a predicted trajectory that can be compared and tested in relation to observed routes. Studies using this approach (Table 2) have tested a number of different magnetic and celestial compass mechanisms (cf reviews by Emlen 1975, Wiltschko and Wiltschko 1995, 2003) that differ to a larger or smaller degree in their associated routes (several studies refer to high latitudes where predicted routes according to different compasses diverge most distinctly). Routes of birds following a constant magnetic compass course over long distances are expected to gradually shift in accordance with the magnetic declination, while birds flying on a constant celestial compass course would follow loxodromes. However, if birds use their sun compass without compensating for the time shift when travelling across longitudes (their endogenous daily clock gets out of phase with local time) they will travel along routes that are quite similar to great circles (orthodromes) at high latitudes (Alerstam & Pettersson 1991). Using fixed orientation in relation to sunset (or sunrise) over longer periods will lead to shifting routes as the sunset (or sunrise) direction changes with season and latitude (Cochran 1987).

A pioneering and bold study in this field is that of Kiepenheuer (1984), who suggested a new magnetic compass mechanism where birds steer by a constant apparent angle of inclination (the magnetic inclination angle as projected on a plane perpendicular to the bird's heading). Kiepenheuer (1884) noted that many migration routes tend to show a course shift similar to that of great circle routes, and magnetoclinic orientation (the term he used for the proposed new orientation mechanism) provides a possible mechanism guiding birds along such favourably curving routes. Also course angles of monarch butterflies at different locations seemed to be in accordance with magnetoclinic orientation (Schmidt-Koenig 1985).

Table 1. *Three main types of simulation studies of bird migration routes have been employed, with differences in explanatory purpose and other characteristics.*

	Explanatory purpose	Principal matters to be tested	Focal components
1	Mechanisms	Compass mechanisms	Magnetic compasses, celestial compasses, effects of time compensation
2	Principles	Vector orientation versus navigation	Orientation scatter and route variability within and between individuals
3	Evolution	Adaptations in routes and orientation behaviour	Orientation rules in relation to wind, topography/barriers, latitude/longitude

The value of Kiepenheuer's impressive study as a source of inspiration is indeed high, setting the scene for analysing the possible relevance of orientation mechanisms for long-distance and even global flight patterns of the birds. However ingenious and elegant, the hypothesis of magnetoclinic orientation has gained further support neither from studies of magnetoreception mechanisms (Wiltschko & Wiltschko 1995) nor from analyses of migration routes in the Arctic (Table 2) or responses of migrating birds at a magnetic anomaly (Alerstam 1987).

There is certainly no universal support for any of the compass mechanisms (Table 2), and cases of disagreements between predicted and observed routes dominate over cases showing some degree of agreement (based on rather subjective evaluations of the plausibility of simulated routes in many cases where knowledge of real routes are fragmentary, poor or lacking). Radar registrations of migrating waders in arctic Siberia and Canada are in broad accordance with shifting sun compass routes, but there are distinct disagreements with this compass mechanism for routes of waders and geese in other parts of the Arctic, e.g. across Greenland.

It is remarkable and surprising that there is not a single instance of distinct support for orientation along constant magnetic compass directions, leading birds along routes where courses shift with the change in magnetic declination. This stands in stark contrast to the great advances in knowledge about animal magnetoreception and orientation responses to the magnetic field under experimental conditions (Wiltschko & Wiltschko 1995, 2003).

Most studies in Table 2 refer to distances of thousands of kilometres, and one may question if it is to be expected that migrating birds fly on a constant compass setting over so long distances. The study of highest geographic resolution is that of Gudmundsson (1994), analysing course changes recorded by radar for knots *Calidris canutus* when migrating across a few degrees of longitude (corresponding to flight distances and times of 100-300 km and 1-4 h, respectively) on a relatively broad front over sea and land in southern Scandinavia (without showing any distinct responses to local topography). Not even in this relatively short window of time and distance did the birds maintain a constant magnetic and celestial compass course. The observed gradual course changes differed significantly from predictions for all three of the main compass alternatives (Table 2)!

The most detailed agreement between observed orientation in the wild and a possible compass cue is the case of a Swainson's thrush *Catharus ustula* tracked by radio telemetry during six consecutive nocturnal flights over a total distance of 1500 km (Cochran 1987). The bird changed its northwesterly heading clockwise by a few degrees every night of migration, adding up to a cumulative change of 11 degrees, in close accordance with the 10 degree cumulative shift in sunset azimuth experienced by the bird. Recent cue-conflict experiments have supported the possibility of the thrushes establishing their orientation in relation to the

Table 2. *Studies testing the possible use of different compass mechanisms among migrating birds by calculating predicted trajectories and comparing with observed routes. Plus signs indicate that agreement was reported (with less pronounced agreement in brackets) and minus signs that disagreement (with less pronounced disagreement in brackets) between predicted and observed routes was reported.*

Reference	Region/species	Magneto-clinic orientation	Constant magnetic compass	Constant celestial compass	Shifting sun compass	Sunset compass
Kiepenheuer 1984	Holarctic/ passerines, ducks, waders, shearwaters, raptors	+				
Alerstam et al. 1990	Greenland/ waders, geese	-	-	(+)	-	
Gudmundsson 1994	S Scandinavia/ waders		-	-	-	
Sandberg & Holmquist 1998	Africa/ waders		(+)	(+)	(-)	
Sandberg & Holmquist 1998	Greenland/ waders			(+)	-	
Alerstam & Gudmundsson 1999	Siberia/ waders	-	(-)	-	+	
Alerstam et al. 2001	Arctic Canada/ waders		-	-	+	
Bingman et al. 2003	North America/ passerines		(-)			(+)
Bingman et al. 2003	Europe/ passerines		(+)			(-)
Muheim et al. 2003	North America/ passerines	-	(-)	(-)		

solar twilight azimuth, calibrating their magnetic compass relative to the sunset cues before departure and using the magnetic heading thus calibrated for maintaining the course in flight (Cochran et al. 2004). This result is in contrast to many cue-conflict experiments with caged migrants (Wiltschko & Wiltschko 1995, Muheim et al. 2004) and also other release experiments (Sandberg et al. 2000), which have indicated that the magnetic field serves as a reference for calibration of celestial compasses during migration.

Simulations of sunset compass routes, hereto considered in only one study (Bingman et al. 2003), under realistic spatial and temporal migratory schedules may help to reveal for how long distances migrants can usefully rely on a fixed orientation in relation to this possible compass cue. Spring migration routes based on such fixed sunset orientation in the Northern Hemisphere will show gradual clockwise course shifts, while autumn routes will show anticlockwise course shifts (reverse patterns of shift will hold for constant sunrise compass routes). The course changes will save distance (compared with loxodrome distance) in some cases (northeast migration in spring and southwest migration in autumn) but add to the

distance in other cases (northwest migration in spring and southeast migration in autumn), but these distance effects will be small (cf. about adaptive routes in Alerstam 2001). For birds using the compass system suggested by Cochran et al. (2004), the predicted flight trajectories will be the combined result of course changes between nights according to the sunset compass and course changes within nights according to the magnetic compass.

The variable and partly contradictory indications from the studies in Table 2 reveal a big gap between the presently advanced knowledge about compass and sensory mechanisms in birds and our understanding how these mechanisms are used in the wild and on migration. Perhaps the process of migratory orientation is extremely complex, involving frequently changing primary courses and varying roles and intercalibration of compasses, and thus being far from any expectations based on simple first principles (Muheim et al. 2003)? Perhaps will a more consistent pattern emerge in the future when more precise satellite and GPS tracking data become available for individual birds? Even if hopes to find a more universal association between compass mechanisms and the geometry of migration routes in the imaginative vein of Kiepenheuer (1984) may have declined, the fascinating task of reconciling migratory pathways with underlying orientation mechanisms will remain.

3. SCATTER OF MIGRATION ROUTES AND VECTOR ORIENTATION

In a seminal paper, Rabøl (1978) discussed whether or not migration along one (or a few) fixed directions(s) according to an inherited vector orientation program is sufficient to explain the observed orientation performance of juvenile birds on their first journeys. That such a simple vector orientation program regulates the orientation of naïve birds was suggested by the displacement and cage experiments of Perdeck (1958) and Gwinner & Wiltschko (1978), respectively, while Rabøl (1978) proposed that an element of programmed goal area navigation is involved. Rabøl (1978) pointed out that ringing recovery patterns may help to answer this question, and he showed how the scatter of routes is predicted to increase parabolically with distance for migration by simple vector summation, with a certain amount of stochastic variation between the directions of successive step vectors because of orientation error, wind influence etc. In contrast, patterns of parallel or converging scatter of recoveries along the main migration axis would indicate that guiding mechanisms dependent on external map factors (one or more coordinates) are in operation.

Rabøl (1978) concluded that recovery patterns of some passerine species in Europe, like pied flycatcher *Ficedula hypoleuca* and robin *Erithacus rubecula*, appear to be consistent with the implications of simple vector orientation, while other species did not show an expanding scatter with increasing distance, thus failing to support a program of simple vector orientation.

After a considerable time lag, these important issues eventually attracted more widespread attention in a wave of recent modelling studies (Table 3). The full implications of vector orientation for the scatter of migration routes were demonstrated and analysed by Mouritsen (1998) and Mouritsen & Mouritsen (2000). They showed that the geographic spread of extensive samples of ringing recoveries of pied flycatchers and robins in Europe indeed agree very well with the theoretical vector summation predictions. Mouritsen (1998) concluded that there is no need to involve any elements of an elusive map sense to explain the orientation performance of naïve night-migrating passerines.

In a riposte, Thorup & Rabøl (2001) demonstrated that simple vector summation apparently fails to account for the high long-distance precision of three species of trans-Saharan migrants. Other studies have given more equivocal results. Using both ringing recoveries and satellite tracking data of juvenile raptors, Thorup et al. (2003) found that simple vector orientation must be extended with an initial phase of dispersal to give a reasonable fit to data for osprey *Pandion haliaetus*, while honey buzzard *Pernis apivorus* data

Table 3. Studies comparing predicted scatter along the main orientation axis according to the effects of vector summation with observed scatter as recorded by ringing recoveries and satellite tracking results (bottom ref). Plus signs for the vector summation fit indicate agreement (inconsistent or uncertain agreement in brackets) and minus sign disagreement with the predicted scatter. Indications of deviations from predictions by overdispersion or concentration are indicated by plus signs in the two right-hand columns.

Reference	Region/species	Vector summation fit	Dispersal implied	Concentration implied
Rabøl 1978	Europe/ robin, pied flycatcher, warblers	(+)		(+)
Mouritsen 1998	Europe/ pied flycatcher	+	-	-
Sandberg & Holmquist 1998	Africa/ waders	(+)		
Mouritsen & Mouritsen 2000	Europe/ pied flycatcher, robin	+	-	-
Thorup & Rabøl 2001	Europe-Africa/ spotted flycatcher, warblers	-		+
Thorup et al. 2003	Europe-Africa/ osprey, honey buzzard	(+)	+	(+)

showed a reasonable agreement with predictions from simple vector summation. Sandberg & Holmquist (1998) illustrated the high precision required in vector orientation for birds to successfully hit their target area after long trans-oceanic flights. Actually, the birds considered in their analyses were knots, which travel in flocks and thus may improve their orientation accuracy in relation to that of single birds by group orientation as evaluated by Wallraff (1978) and recently reviewed by Simons (2004).

A most significant aspect, pointed out by Thorup et al. (2000, 2003) and Thorup & Rabøl (2001, 2004) is the sensitivity of vector summation models to the relative importance of between- and within-individual variation in orientation. If variation between individuals in preferred direction is a significant contributory cause (in addition to the within-individual variation between successive flight steps) of the observed scatter of routes along the main axis of migration, the implications of the vector summation analyses change in favour of map-related mechanisms being involved in the regulation of migration routes of juvenile birds. There are indeed strong indications of such important between-individual variation (Thorup & Rabøl 2004). The possible existence of external map-related cues in the control of juvenile orientation has gained further support from experiments indicating effects of location in geomagnetic space on orientation and fuel accumulation (Beck & Wiltschko 1988, Fransson et al. 2001) and from ringing evidence of converging orientation towards very restricted species-specific stopover areas (Fransson et al. 2005). Furthermore, the large-scale topographic effects on migratory behaviour and distribution of ringing recoveries also have to be taken into account when evaluating predictions based on vector summation models (Thorup & Rahbek 2004).

It seems as if the dogmatic view of an orientation program in juvenile birds based solely on the clock-and-compass principle is threatened, and it becomes increasingly likely that there

Table 4. *Geographic simulation models of bird migration routes that have been used to evaluate adaptations in orientation behaviour.*

Reference	Region/species	Elements in optimal orientation/routes
Erni et al. 2003a	Europe-Africa/ passerines	Inherited main direction of orientation, orientation response to coastlines, shift in main direction at certain latitude
Erni et al. 2003b	Europe-Africa/ passerines	As above with effect of wind taken into account (assuming drift, selection of altitudes with different winds)

is a role for additional navigatory mechanisms, albeit still elusive, in the control of migration routes of juveniles.

4. OPTIMAL ORIENTATION AND ROUTES

What are the adaptive values of the birds' orientation behaviour and migration routes? Are the bird migration patterns primarily adapted to present-day ecological conditions or do they rather reflect colonisation history or paleoecological conditions? To what degree is the flexibility in the development of new migration routes constrained by the structure and function of the orientation mechanisms?

Up to now it is mostly single components or characteristics of orientation behaviour and migration routes that have been evaluated, one at a time, in an evolutionary perspective. Thus, the adaptive consequences of such aspects as distance, wind response, barriers and fuel deposition rates at different stopover locations for the optimal spatial organisation of migration under different criteria of time-, energy- or risk minimisation have been analysed in a schematic and generalised way (cf. review by Alerstam & Hedenström 1998).

The more complex simulation models of Erni et al. (2003a, b; Table 4) represent a first and very interesting attempt of analysing the combined importance of several factors for the evolution of orientation behaviour and routes in a realistic geographic frame. Their model platform refers to the long-distance migration of passerines from Europe across the Mediterranean Sea and the Sahara desert to tropical winter quarters in Africa. Using a simulation technique of genetic algorithms, Erni et al. (2003a) evaluated "optimal" orientation and routes for southwesterly migration based on repeated runs of simulated migratory journeys with specified natural selection rules, and they also investigated the improvement in "fitness" by changing orientation at a certain latitude and by specified responses to coastlines and barriers. In Erni et al. (2003b) the effect of wind was also taken into account in these simulations, making southeasterly migration more favourable than southwesterly migration in many cases, although the outcome was critically dependent on the assumptions about the birds' ability to use wind at different altitudes.

One important limitation of these analyses is the fact that only autumn migration has been considered. The evolutionary success of migration directions and routes would not be expected to be determined by the autumn migration alone but also by the return spring migration. The reason is of course that the autumn migration direction will have consequences for which conditions the birds meet during the succeeding spring migration. Erni et al. (2003b) indicated that the optimal orientation is very sensitive to wind patterns, and one may therefore suspect that a wind-related advantage for one or the other main migration direction (southwest or southeast) in one season my turn into a disadvantage in the return season, or vice versa.

Still, the one-season (autumn migration) analyses by Erni et al. (2003a, b) constitute a valid and promising first step. If the challenging task of extending the analyses to cover the full

annual (autumn and spring) migration cycle will be undertaken, it would be fascinating to investigate which combinations of main optimality criteria (time-, energy- or risk minimisation) are most likely as selection factors in the evolutionary process leading to and maintaining the observed main migration routes in the European-African passerine migration systems.

One should also remember that complex models require many provisional and untested assumptions, adjusted to provide apparently realistic outcomes (more assumptions and approximations are needed the more intricately the model is developed to mirror multi-factorial reality), and this may detract seriously from the power and usefulness of the models in critically testing hypotheses. Still, there will undoubtedly be an important future role for increasingly complex and advanced computer models of bird migration.

5. CONCLUSIONS

Analyses of the geometry of bird migration routes, as reviewed above, have revealed that we are still very far from a solid understanding of the mechanisms, control principles and evolutionary forces affecting the orientation performance and routes of migrating birds under natural conditions. However, there is no reason for despair. More sophisticated techniques will in the near future allow the behaviour of individual birds to be explored with improving accuracy throughout their migratory journeys. Analytical geometric and geographic simulation techniques will also improve. It will remain an objective of foremost importance to reconcile observed flight trajectories and migration patterns of birds with underlying possible orientation mechanisms, principles and evolutionary forces. Thus, there will certainly be an important role for theoretical simulation of migration routes to accomplish this.

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