

How do geometric constraints influence migration patterns?

K. Thorup & C. Rahbek

Thorup, K. & Rahbek, C., 2004. How do geometric constraints influence migration patterns? *Animal Biodiversity and Conservation*, 27.1: 319–329.

Abstract

How do geometric constraints influence migration patterns?— Null models exclusively invoking geometric constraints have recently been demonstrated to provide new insight as to what explains geographic patterns of species richness and range size distribution. Analyses of migration patterns have traditionally been conducted in the absence of appropriate simulations and analytical models. Here we present a null model exclusively invoking geometric constraints and a more advanced analytical model incorporating spread along a migration direction that allow investigation of the influence of physiographical and physiological boundaries for terrestrial taxa, with ocean and sea as geometric constraints, in relation to observed patterns of migration. Our models take into account the low recovery probability of terrestrial taxa over sea. The null model was not found to explain any of the directional variation in the ring-recoveries, but when comparing the distribution of data modeled using a simple clock-and-compass model with distributions of ring-recoveries, geometric constraints were found to explain up to 22% of the variation in ring-recoveries. However, the assumed directional concentrations per step used in the model were much higher than expected, and the qualitative fit of the model was rather poor even when non-terrestrial sites of recoveries were excluded.

Key words: Bird migration model, Geometric constraints, Ring-recovery probability, Pied Flycatcher, *Ficedula hypoleuca*.

Resumen

¿Cómo influyen las limitaciones geométricas en las pautas de migración?— Recientemente se ha demostrado que los modelos nulos que recurren exclusivamente a las limitaciones geométricas proporcionan nuevas aportaciones para explicar las pautas geográficas que definen la riqueza de las especies y la distribución por tamaños según el rango. Tradicionalmente, los análisis de pautas de migración se han realizado sin emplear simulaciones ni modelos analíticos apropiados. En este estudio presentamos un modelo nulo que se basa exclusivamente en limitaciones geométricas, así como un modelo analítico más avanzado que incorpora la dispersión y una dirección de migración, lo que permite investigar la influencia de los límites fisiográficos y fisiológicos en los taxones terrestres, tomando el océano y el mar como limitaciones geométricas, con relación a las pautas de migración observadas. Los modelos que hemos empleado tienen en cuenta la baja probabilidad de recuperación de los taxones terrestres en el mar. El modelo nulo no pudo explicar ninguna de las variaciones direccionales en las recuperaciones de anillas; sin embargo, al comparar la distribución de los datos modelados utilizando un modelo simple de reloj y brújula con distribuciones de recuperaciones de anillas, se constató que las limitaciones geométricas podían explicar hasta el 22% de la variación en las recuperaciones de anillas. Pese a ello, las concentraciones direccionales por pasos que se presupusieron en el modelo fueron muy superiores a lo previsto, y el ajuste cualitativo del mismo resultó bastante deficiente cuando se excluyeron los emplazamientos de recuperaciones no terrestres.

Palabras clave: Modelo de migración de aves, Limitaciones geométricas, Probabilidad de recuperación de anillas, Papamoscas cerrojillo, *Ficedula hypoleuca*.

Kasper Thorup & Carsten Rahbek, Vertebrate Dept., Zoological Museum, Univ. of Copenhagen, Universitetsparken 15, DK-2100, Denmark.

Corresponding author: K. Thorup. E-mail: kthorup@zmuc.ku.dk

Introduction

Migration is an ecological and evolutionary important phenomenon (e.g. Alerstam, 1990). Especially in some of the most mobile terrestrial animals, the birds, it is common to explore spatially separated regions by moving long distances. It is estimated that approximately half of the world's roughly 9,000 currently recognized species of birds, corresponding to individuals in a magnitude of 50,000,000,000 perform some kind of migratory movement (Berthold, 2001), and Moreau (1972) estimated that in total 5,000,000,000 Palearctic landbirds leave their breeding grounds for Africa. Similar phenomena occur between North America and Central and South America and in Asia. Such behavior poses special demands for behavioral and physiological adaptations.

Research on orientation in birds helps us to understand the constraints on evolution of bird migration, but bird migration is itself constricted by geographic boundaries. Nevertheless, most theoretical and modeling studies on bird migration, including analyses of distribution of ring-recoveries, typically assumes that the areas where birds are migrating are homogeneous or use randomly modeled landscapes (but see Erni et al., 2002). This is evidently not the case for continental and cross-continental migrants that experience dramatic changes in landscape most noticeable when facing open sea at continental coastlines.

Recently, much attention has been paid to macroecological null models to examine the expected effect of geometric constraints on patterns of many different "traits" (Colwell & Lees, 2000; Colwell et al., 2004). It has been shown that non-even distribution (i.e., a peak) of species richness along e.g. latitudinal, longitudinal and peninsular gradients and across continents (Colwell et al., 2004) can arise through simple geometric constraints on species range boundaries, in the absence of any environmental or historical mechanisms. Continental shape has also been shown to be a potential constraint on spatial distribution of ranges sizes of breeding and migratory birds (Jetz & Rahbek, 2002; Bensch, 1999; respectively).

Open sea does impose a migratory barrier of terrestrial migrants and there is a low recovery probability of terrestrial taxa over sea (e.g. Wernham et al., 2002). Hence, even the largely deterministic processes of adaptation and/or evolution of dispersal traits governing migratory choices of individuals may in principle produce geographical patterns of recoveries that have a non-deterministic (stochastic) explanation. Unless models invoking deterministic mechanisms of orientation (e.g. vector navigation) can be shown to fully predict the patterns of recoveries, geometric constraints on recoveries could emerge as a contributory explanation.

In this study we provide a framework for investigating the geometric influence of ocean and sea on observed migratory patterns (i.e. taking the very low recovery probabilities over water into account). The approach is illustrated using an

empirical data set on Pied Flycatchers *Ficedula hypoleuca*, ringed as nestlings in Scandinavia and recovered en route on their initial southwestern migration before turning south on the Iberian Peninsula to wintering grounds in West Africa. Here we investigate the predictive power of simulated migration with and without incorporating the effect of geometric constraints. As a first step (the null model) we simulate migration with birds choosing random directions. As a second step (the analytical model) we simulate migration according to the simple clock-and-compass or vector navigation hypothesis (i.e. birds migrate for an endogenously controlled period of time in an endogenously controlled direction).

Methods

Modeling procedure

The simulated data sets were constructed by using a computer model of a vector navigation system (a clock-and-compass strategy) using vector summation (Rabøl, 1978; Mouritsen, 1998; Sandberg & Holmquist, 1999; Thorup et al., 2000, 2003; Thorup & Rabøl, 2001), where each migratory step is considered a vector with a fixed length and a direction picked randomly (and independently) from a circular distribution. The circular distribution is characterized by its directional concentration measure r (where $r = 0$ for a uniform circular distribution and $r = 1$ for a unidirectional distribution without scatter; cf. Batschelet, 1981). Thus in the vector summation model the orientation is considered to vary around the inherited mean direction between each flight step according to a circular probability distribution whose concentration reflects the combined influence of internal factors (the birds capability of flying in the inherited direction) and external factors, as e.g. wind drift. The model has 3 parameters: (1) r_{step} . Variation in directional choice within individuals (between steps) with one picked for each migratory step, (2) r_{between} . Variation in directional choice between individuals, which is picked once for each modeled individual, and (3) step length, which is held constant for the whole migratory journey and for all individuals. Random directions were drawn from von Mises distributions (the distributions normally used in circular statistics), which were simulated following Fisher (1993). The mean of the directional distribution in the model is assumed to equal the mean migration direction. Variation between individuals was included by adding the direction picked from the between-individuals distribution to the resulting sample mean vector after the number of migratory steps had been summed (Thorup et al., 2000).

The simulated data sets including non-terrestrial points were constructed by simulating tracks for 5,000 birds flying each number of steps from 1 to 70 steps with a step length of 125 km, resulting in a point sky of 700,000 endpoints. These dis-

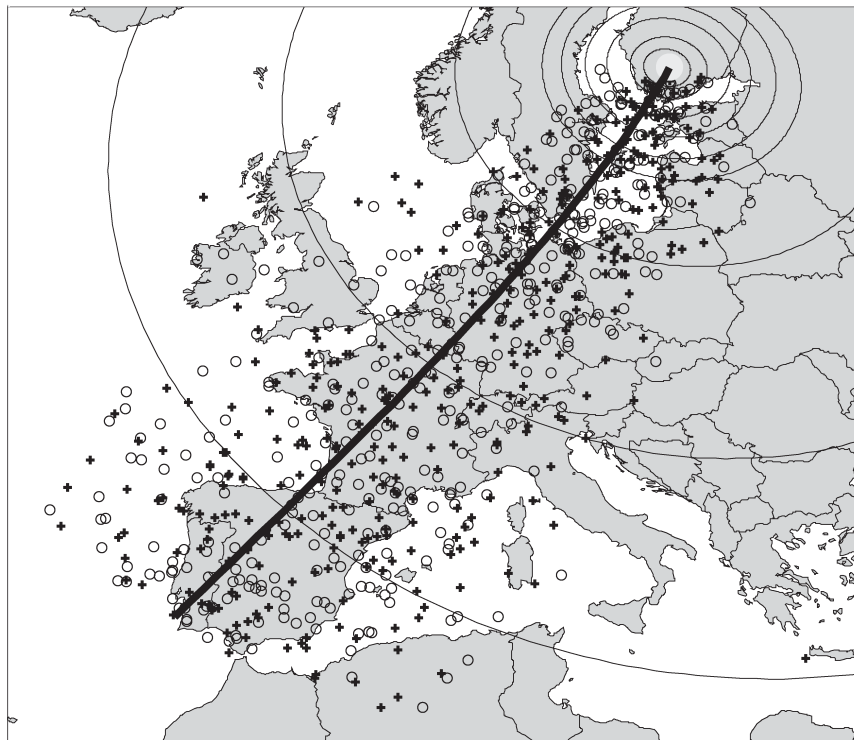


Fig. 1. Endpoints of simulated tracks of Pied Flycatchers *Ficedula hypoleuca* originating in the center of mass of ringing site locations using a directional concentration per step of 0.7: Circles. Number between–individuals variation included ($N = 401$); Plusses. A between–individuals variation of 0.99 included ($N = 401$); The thick line. Average direction used (see fig. 3). Circles show distances of 100, 150, 250, 350, 450, 550, 1,000, 2,000 and 3,000 km from the center of mass; circles from 100–550 indicate the distance intervals used.

*Fig. 1. Puntos de equivalencia de trayectorias simuladas de papamoscas cerrojillos *Ficedula hypoleuca* originadas en el centro másico de los emplazamientos de anillamiento utilizando una concentración direccional progresiva de 0,7: Círculos. Se incluye el número de la variación entre individuos ($N = 401$); Signos más: se incluye una variación entre individuos de 0,99 ($N = 401$); La línea gruesa indica la dirección media utilizada (ver la fig. 3). Los círculos indican distancias de 100, 150, 250, 350, 450, 550, 1.000, 2.000 y 3.000 km desde el centro másico. Los círculos desde 100 hasta 550 indican los intervalos de distancia empleados.*

tance coordinates were then grouped into distance intervals and used for calculation of directional concentrations. The step length considered alone is not crucial for the behavior of the model, rather it is the combination r_{step} /step length (see Thorup et al., 2003). To cope with the uncertainty in these two parameters we investigated the effects of a large range of r_{step} -values while keeping step length constant.

The step length used (125 km) is the same as the one used by Mouritsen (1998), and it is assumed to correspond to one nights migration distance. Our procedure is somewhat different from the procedure used by Mouritsen (1998), who calculates a directional concentration for a specific number of steps. However, that procedure disregards the resulting spread of the endpoints in

the migration direction (see Mouritsen & Mouritsen, 2000; Thorup & Rabøl, 2001), an effect, which the procedure used here takes into account.

To model the influence of geometric constraints as imposed by open sea, non-terrestrial points were removed using ArcView GIS 3.2 software (see fig. 1). The underlying assumption for this procedure is that birds, if not over land after completing a migratory step, embark on a new migratory step choosing direction anew from the circular distribution.

From the simulated data sets directional concentrations for comparison with the empirical data set were derived using a bootstrap method. For each distance interval, 200 estimates of the expected directional concentration were calculated by repeatedly drawing the number of random angles, corre-

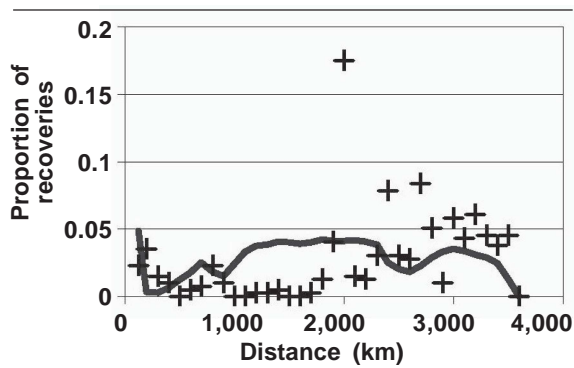


Fig. 2. Relative distribution of the number of recoveries of Pied Flycatchers *Ficedula hypoleuca* in each distance interval (+) compared with simulated data with non-terrestrial points removed (line; $r_{\text{step}} = 0.80$; $r_{\text{between}} = 1$).

Fig. 2. Distribución relativa del número de recuperaciones de papamoscas cerrojillos *Ficedula hypoleuca* en cada intervalo de distancias (+), en comparación con datos simulados en los que los puntos no terrestres habían sido eliminados (línea; $r_{\text{step}} = 0.80$; $r_{\text{between}} = 1$).

sponding to the number of ring-recoveries in the same distance category. From these directional concentrations both median and confidence intervals were derived.

Distributions resulting from this modeling approach, incorporating or excluding the effect of geometric constraints, was then compared with the ring-recovery distributions based on the assumption that all birds had been ringed at the same location defined as the center of mass of actual ringing sites (see fig. 1).

The null model

The null model was run with birds choosing random directions. First it was run as a random walk with total variation within individuals ($r_{\text{step}} = 1$) with no variation between individuals included. The model was also run with no variation in directional concentration per step ($r_{\text{step}} = 1$) but with total variation between individuals ($r_{\text{between}} = 0$).

The analytical model

The analytical model was run with a variation within individuals (r_{step}) of 0.60, 0.70, 0.80, 0.90 and 0.95 with no variation between individuals included (random walk with drift). The model was also run with no variation in directional concentration per step but with a variation between individuals (r_{between}) of 0.98 and 0.99.

Empirical data

The empirical data set consisted of ring-recoveries of Pied Flycatchers ringed as nestlings in Finland and recovered the following autumn or winter before 1 March (fig. 3; $N = 415$).

Typically, modeling studies on migratory orientation considers ring-recoveries as vectors, assuming that it is meaningful to use only the distance and direction between ringing and recovery sites regardless of the ringing site. This corresponds to parallel displacement of recovery vectors to a common, but imaginary, ringing site resulting in imaginary recoveries from non-terrestrial sites. This procedure obscures the effect of birds being ringed at different sites facing different distributions of main barriers. To avoid this bias, we assumed that all birds had been ringed at the same site. This center of mass of the latitudinal and longitudinal coordinates of the ringing sites of nestlings in Finland was used as starting location for all calculations (and as starting point for the simulated tracks, see fig. 1). The minor drawback of this approach is that it results in a too low estimate of the directional concentration on short distances (less than 500 km), but a minor (and more concentrated, see discussion) error on the estimate on long distances (contrary to parallel displacing recoveries). To reduce these biases, recoveries from a comparatively small geographical area was used (Finland).

Directional concentrations r of points were calculated for each distance interval 100–149, 150–249, 250–349, 350–449, ..., 3,850–3,949 and 3,950–4,049 km using loxodromic (constant compass courses) distances for both the empirical and the simulated data set. For the distance intervals 450–549, 550–649, 950–1,049, 1,050–1,149, ..., 1,650–1,749, 2,450–2,549, 2,650–2,749, 2,750–2,849, 3,550–3,649, 3,650–3,750 and more than 4,049 km there were less than three recoveries, and the points were therefore omitted from the analysis.

Birds recovered less than 1,000 km from the ringing site were generally from around the Baltic Sea; 1,800–2,500 km from France and Italy; 2,700–3,500 km from the Iberian Peninsula, and more than 3,500 from North Africa. We excluded the 2,600 km interval including the very aberrant recoveries in Greece (fig. 3) due to uncertainties regarding exact recovery locations.

Birds recovered more than 3,500 km from the ringing site relating to endpoints from North Africa, where we expect the birds to have changed their migration direction, were also excluded.

Statistical analysis

For comparison between simulated and empirical data, we calculated Pearson's product moment correlation coefficients between mean angular deviation (s) times distance (cf. Thorup et al., 2000) for the two data sets. Using Spearman's correlation coefficients instead yielded very similar correlation coefficients. Models were evaluated using the amount of explained variation (r^2).

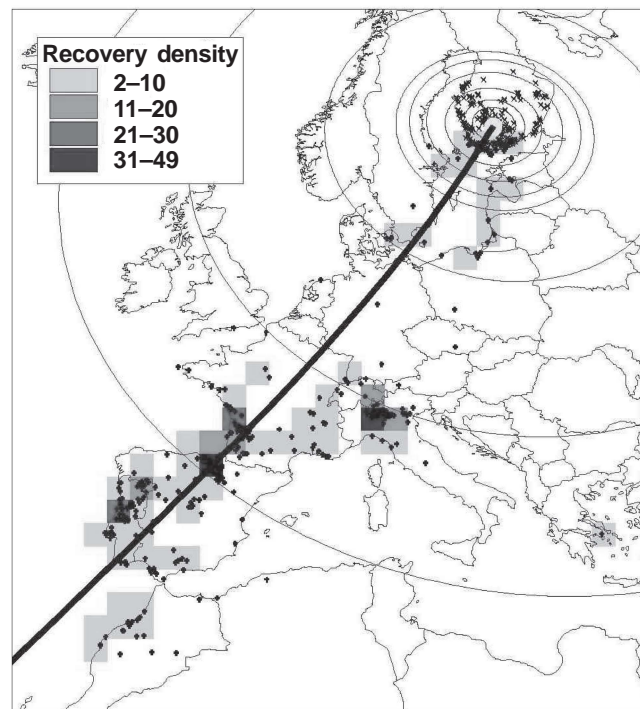


Fig. 3. Ring-recoveries of Pied Flycatchers *Ficedula hypoleuca* ringed as nestlings in Finland and recovered within the same autumn/winter ($N = 415$): Pluses. Single recoveries; Crosses. Ringing sites; Large dot. Center of mass of ringing sites; Thick line. Rhumbline (constant compass) course from center of mass of ringing sites to large concentrations of recoveries in Iberia (fitted by eye). Circles show distances from the center of mass of ringing sites of 100, 150, 250, 350, 450, 550, 1,000, 2,000 and 3,000 km; circles from 100–550 indicate the distance intervals used.

Fig. 3. Recuperaciones de anillos de papamoscas cerrojillos *Ficedula hypoleuca* que fueron anillados en Finlandia siendo crías y que se recuperaron el mismo otoño/invierno ($N = 415$): Signos más. Recuperaciones únicas; Cruces. Emplazamientos de anillamiento; Punto grande. Centro másico de emplazamientos de anillamiento; Línea gruesa. Rumbo loxodrómico (brújula constante) desde el centro másico de los emplazamientos de anillamiento hasta amplias concentraciones de recuperaciones en la península Ibérica (ajustados visualmente). Los círculos indican distancias desde el centro másico de los emplazamientos de anillamiento de 100, 150, 250, 350, 450, 550, 1.000, 2.000 y 3.000 km. Los círculos desde 100 hasta 550 indican los intervalos de distancia empleados.

There was a rather low correspondence between the number of recoveries in each distance category compared to modeled numbers. Figure 2 shows this for a model run with a moderate directional concentration per step, no variation between individuals in migration direction ($r_{\text{step}} = 0.80$; $r_{\text{between}} = 1$, respectively) and with non-terrestrial points removed. This strongly suggests, that migrants use some longer steps or alternatively, shorter stopover times, in the first part of the migration. The model procedure then corresponds to birds using a constant interval of changing directions throughout the migratory journey.

Results

The ring-recoveries of Finnish Pied Flycatcher nestlings show a distinct southwest migration through Europe (fig. 3). The null models with random orientation do not explain significant amounts of the observed directional variation in the ring-recoveries (table 1, fig. 4). In general only little directional variation is explained by the analytical model even with non-terrestrial points removed (table 1, fig. 5).

When non-terrestrial points are included (fig. 5A), none of the directional concentrations per step explained any amount of directional variation. The

Table 1. Pearson's product moment correlation coefficient (r) and explained variation (r^2) between mean angular deviation times distance for empirical and simulated data, respectively. Data for various model runs with different values of r_{step} and r_{between} (see methods) when non-terrestrial points are included or removed. The aberrant 2,600 km distance interval with two outlying Greek recoveries has been excluded (see text). If r -values are less than 0 only signs are given. Only P -values less than 0.10 are given.

Tabla 1. Coeficiente de correlación momento-producto (r) de Pearson y variación (r^2) explicada entre el promedio de distancia de tiempos de la desviación angular para datos empíricos y simulados, respectivamente. Los datos correspondientes a varios modelos presentan valores diferentes de r_{step} y r_{between} (ver los métodos), según se hayan incluido o eliminado los puntos no terrestres. Se ha excluido el intervalo de distancias atípicas de 2.600 km con dos recuperaciones periféricas Greek (consultar el texto). Si los valores r son inferiores a 0, sólo se indican los signos. Únicamente se facilitan los valores P inferiores a 0,10.

	r_{step}	r_{between}	Including non-terrestrial			Excluding non-terrestrial		
			Pearson r	P	r^2	Pearson r	P	r^2
Null models	1	0	–			–		
	0	1	–			–		
Analytical models	0.60	1	–			0.261		0.07
	0.70	1	–			0.293		0.09
	0.80	1	–			0.382	0.07	0.15
	0.90	1	–			0.469	0.02	0.22
	0.95	1	0.024			0.376	0.08	0.14
	1	0.98	–			–		
	1	0.99	–			0.119		0.01

addition of even a small amount of variation between individuals (fig. 5C) results in a too large scatter on long distances (more than 2,500 km) corresponding to the birds having reached as far as the Iberian Peninsula. With non-terrestrial points removed (fig. 5B), the qualitative fit tends to be somewhat better, especially if the very aberrant point at 2,600 km (resulting from two recoveries in Greece) is removed, with model output lines mirroring the shape of the ringing recovery points, but only the directional concentrations per step of 0.8, 0.90 and 0.95 had significant Spearman rank correlation coefficients and explained 0.15, 0.22 and 0.14, respectively of the directional variation (table 1). However, these models tend to fit well neither in France and Italy nor on the Iberian peninsula (fig. 6). Still the addition of small amounts of variation between individuals results in a too large scatter on long distances (more than 2,500 km) even with non-terrestrial points removed (fig. 5D).

Due to the use of the center of mass as reference point, the scatter of the recoveries closer than 500 km is expected to be too large, but removing these from analysis did not change the pattern. Though simulated data sets with non-terrestrial points removed generally explained small amounts of the observed directional variation the correlation coeffi-

cients were significantly larger than without removing the non-terrestrial points (mean $r = -0.093$ and 0.169 , with terrestrial points included and removed, respectively; $P = 0.007$; paired t -test)

Discussion

Despite decades of research, we still lack knowledge about how free-flying birds orientate on migration (Alerstam, 1996). Since Perdeck's (1957) paradigmatic displacement experiments and the formulation of the "clock-and-compass" hypothesis we have learned much about behavioral responses in caged migrants from controlled experiments using mostly Emlen funnels (e.g. Berthold, 1996, 2001). Additional theories and hypotheses on how birds perform migratory navigation—such as "goal-area navigation" (Rabøl, 1978)—have been formulated, but only recently have research been directed at testing these at larger scales (Wehner, 2001). Because controlled, manipulative experiments are usually impossible or impractical at large scales in nature for more than a few species, factorial designs intended to evaluate the role of competing explanations for large-scale dispersal, migration and orientation, are limited to what nature happens

to have produced. In that respect, the vast amount of ring-recoveries (more than 1 million from birds ringed in Britain and Ireland alone, Wernham et al., 2002) provide unique opportunities to build predictive models to evaluate hypotheses. Extensive effort has been done recently to evaluate orientation hypotheses using ring-recoveries (Mouritsen, 1998; Mouritsen & Mouritsen, 2000; Thorup et al., 2000, 2003), but none of these has taken into account the potential effect of geometric constraints.

Summing up

With the analytical model simulating a simple migratory orientation strategy, geometric constraints were found to explain up to 22% for the best fitted model, which did not include any variation between individuals and had a rather low variation per step ($r_{step} = 0.90$). Assuming no variation between individuals is, however, unrealistic as variation between individuals forms the basis of evolution of new migratory traits (Helbig, 1994, 1996; Helbig et al., 1994). Furthermore, overall removing non-terrestrial points lead to more explained variation (table 1). This indicates that a significant amount of the observed concentration of migratory paths is explained by geometric constraints and shows the importance of including geometric constraints in future studies on large-scale migration patterns. Previous modeling studies on land bird migratory orientation have generally not taken this into account and it is usually not included in studies on optimal migration.

However, we also found a presumably important general pattern of qualitative lack of fit of the presented models, with the empirical data being more concentrated than simulated either in the middle part of the migration or in the last part. Possible reasons for this lack of fit could be biased empirical data, birds using more of the landscape geometry than included in this study or that the underlying migration model (here the clock-and-compass strategy) used is not reasonable or it is insufficient.

Are observed patterns real

Due to differences in reporting rates between different regions it is often questioned to what degree ring-recoveries do reflect the true migratory patterns (summarized in e.g. Perdeck, 1977; Nichols, 1996). However, quite pronounced species-specific differences in ring recoveries, even for species with rather similar migratory routes do exist. Furthermore, such differences can be detected even at a fine scale (within regions). An example of this is shown on figure 7, which shows the distributions of ring-recoveries of Scandinavian Pied Flycatchers and Scandinavian and Finnish Redstarts for comparison with those of the Finnish Pied Flycatchers (fig. 3). A significant difference in the recovery patterns is evident from these maps, with Scandinavian Pied Flycatchers showing more recoveries to the north-west compared to the Finnish, and recoveries of Scandinavian and Finnish

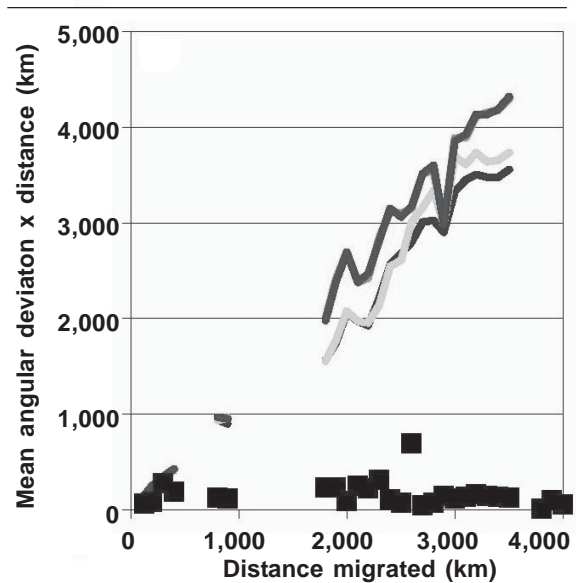


Fig. 4. Comparison of spread of empirical data set (ring-recoveries of Pied Flycatchers *Ficedula hypoleuca*; filled squares) with values from various null models (lines). Terrestrial points have been removed in the two lower lines. Lines being above squares indicate a larger spread of modeled data than observed in the empirical data set at that particular distance.

Fig. 4. Comparación de la dispersión del conjunto de datos empíricos (recuperaciones de anillos de papamoscas cerrojillos *Ficedula hypoleuca*; cuadros negros) con valores procedentes de varios modelos nulos (líneas). Los puntos terrestres se han eliminado en las dos líneas inferiores. Las líneas situadas encima de los cuadros indican una mayor dispersión de datos modelados en comparación con lo observado en el conjunto de datos empíricos a esa distancia concreta.

Redstarts being concentrated south-east of the Finnish Pied Flycatchers. This indicates, that ring recovery patterns do reflect the migratory patterns, and that they are suitable for an analysis of the concentration of the migratory route.

This is important for the general use of ringing data in studies of migration. Ringing data are currently being used for a lot of different kinds of analyses, as it is, for most species, the only possible method for gathering data. Furthermore, bird ringing has been performed for more than 100 years, which means that an impressive amount of data has already been collected (Bairlein, 2001). This makes it possible to use existing data for analysis of migratory patterns, which has become important in the case of possible effects of climate change.

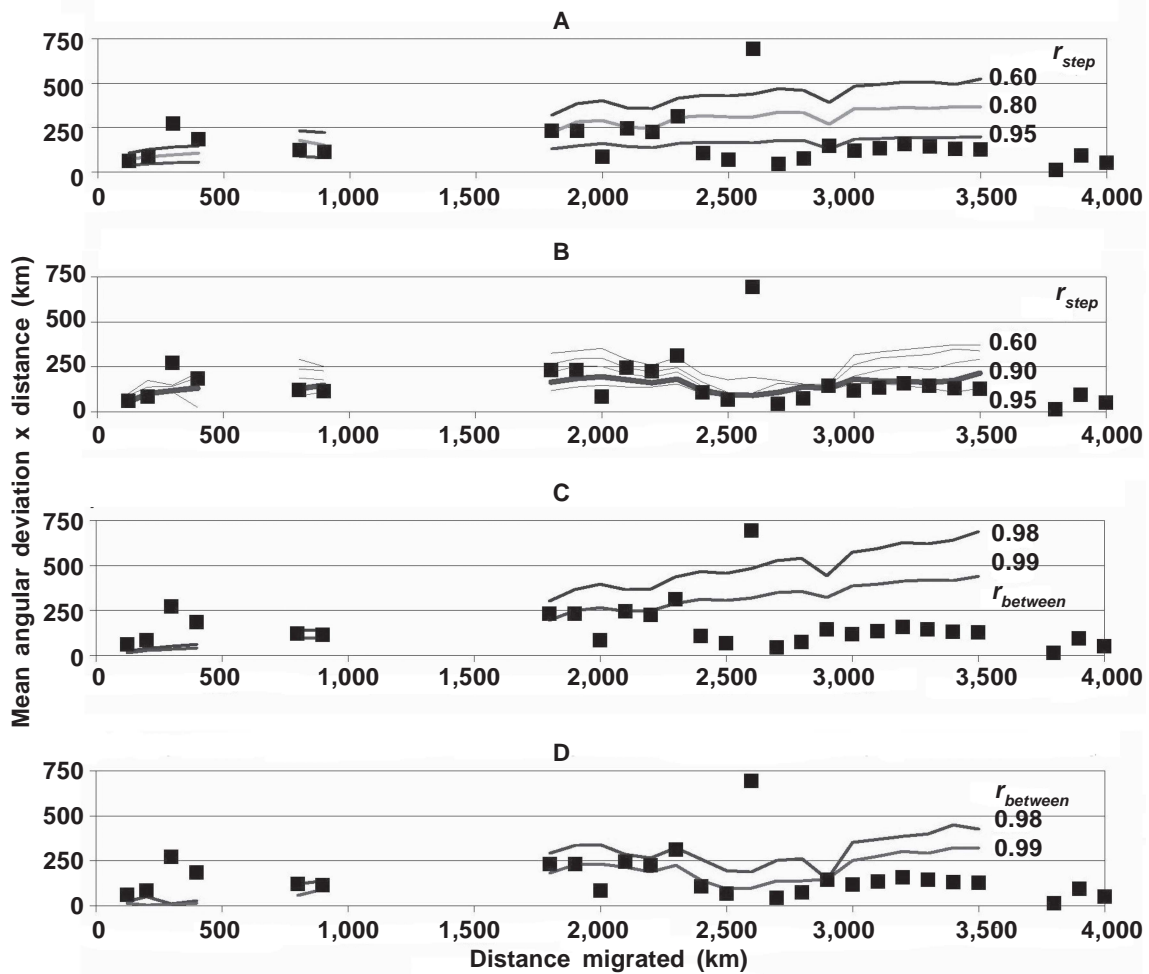


Fig. 5. Comparison of deviation of empirical data set (ring-recoveries of Pied Flycatchers *Ficedula hypoleuca*) with values from various model runs. Lines show modeled values for indicated $r_{step}/r_{between}$ values and filled squares show ring-recoveries. Lines being above squares indicate a larger spread of modeled data than observed in the empirical data set at that particular distance: A. No variation between individuals; non-terrestrial points included; B. No variation between individuals; non-terrestrial points removed; C. Variation between individuals included; non-terrestrial points included; D. Variation between individuals included; non-terrestrial points removed.

Fig. 5. Comparación de la desviación del conjunto de datos empíricos (recuperaciones de anillos de papamoscas cerrojillos *Ficedula hypoleuca*) con valores procedentes de varias aplicaciones de modelos. Las líneas indican valores modelados para los valores $r_{step}/r_{between}$ indicados, mientras que los cuadros negros indican recuperaciones de anillos. Las líneas situadas encima de los cuadros indican una mayor dispersión de datos modelados en comparación con lo observado en el conjunto de datos empíricos a esa distancia concreta: A. Ninguna variación entre individuos; puntos no terrestres incluidos; B. Ninguna variación entre individuos; puntos no terrestres eliminados; C. Variación entre individuos incluida; puntos no terrestres incluidos; D. Variación entre individuos incluida; puntos no terrestres eliminados.

Implications for our understanding of the migratory orientation program

The rather low scatter of ring recoveries described in this study suggests that the rather wide scatter found in the study by Mouritsen (1998) could be

caused partly by not taking geography into account (i.e. by using the parallel displacement of recoveries). Most studies of free-flying migrants do find a much higher directional concentration of tracks of migrants (Bäckman & Alerstam, 2003). However, this cannot explain the amount of variation on

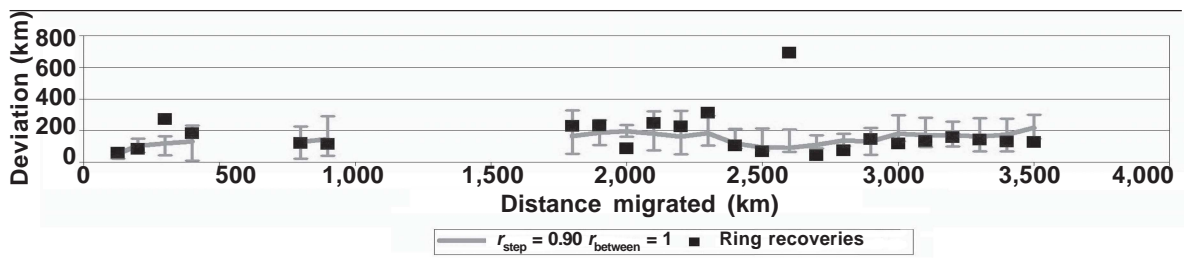


Fig. 6. Confidence intervals for the best fitting model with little variation within individuals and no variation between individuals ($r_{step} = 0.90$ and $r_{between} = 1$). For explanation see figure 5.

Fig. 6. Intervalos de confianza para el modelo que presenta un mejor ajuste, con escasa variación en el conjunto de los individuos y ninguna variación entre individuos ($r_{step} = 0,90$ y $r_{between} = 1$). Para detalles al respecto, ver la figura 5.

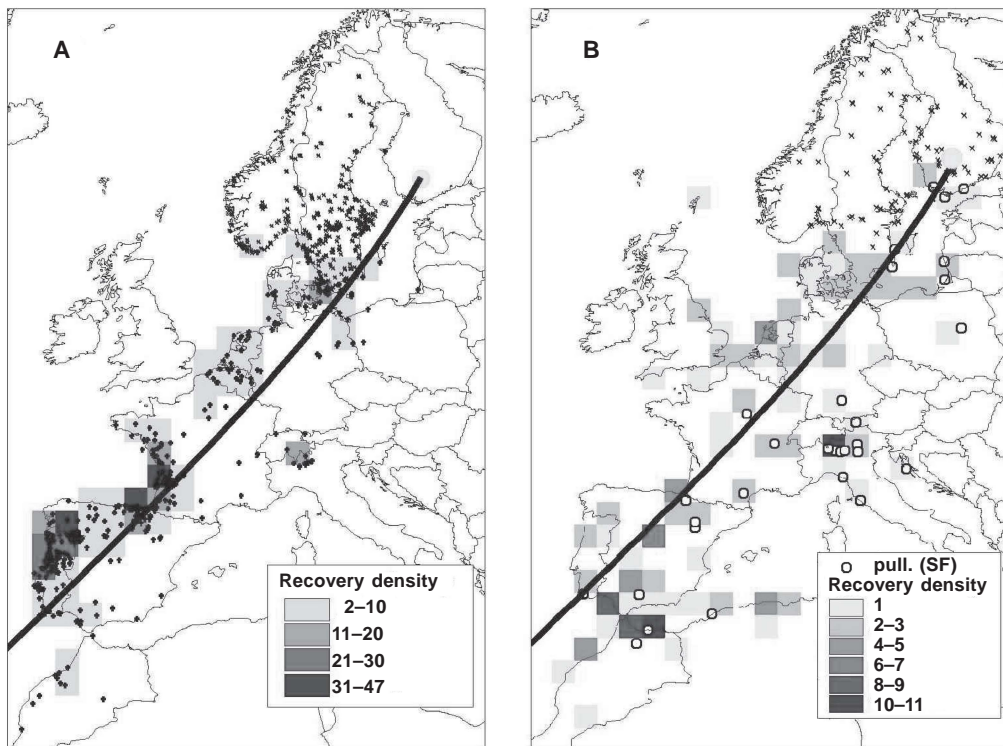


Fig. 7. Ring-recoveries of: A. Pied Flycatchers *Ficedula hypoleuca* ringed as nestlings in Scandinavia ($N = 486$); B. Redstarts *Phoenicurus phoenicurus* ringed as first-years ($N = 93$) or nestlings ($N = 82$) in Scandinavia or Finland, and recovered within the same autumn/winte: Crosses. Ringing sites; Pluses. Single recoveries; Open circles. Ringed as nestling in Finland (Redstart only; $N = 32$). Large dot and thick line as for figure 2.

Fig. 7. Recuperaciones de anillos de: A. Papamoscas cerrojillos *Ficedula hypoleuca* que fueron anillados en Escandinavia siendo crías ($N = 486$); B. Colirrojos reales *Phoenicurus phoenicurus* anillados durante el primer año de vida ($N = 93$) o como crías ($N = 82$) en Escandinavia o Finlandia, y recuperados el mismo otoño/invierno. Cruces: emplazamientos de anillamiento. Signos más: recuperaciones únicas. Círculos blancos: anillados siendo crías en Finlandia (sólo colirrojos reales; $N = 32$). El punto grande y la línea gruesa significan lo mismo que en la figura 2.

short-distance recoveries, which is nevertheless found in the ring-recoveries (Mouritsen, 1998).

It is generally believed that young migrants use a vector navigation program for finding their species-specific wintering area, and the present study is based on such a program. The rather high concentration of migratory steps needed to provide a reasonable fit suggests that following coastlines could play a significant role in guiding migrants. However, this is contradicted by e.g. Redstarts *Phoenicurus phoenicurus* being concentrated away from coastal areas within the Iberian Peninsula (fig. 7B). Thus the lack of qualitative fit for the model may indicate that a simple form of vector navigation program is only part of the program used by free-flying migrants. Moreover, the assumptions underlying the best fitted model are not realistic (i.e. no variation between individuals in migratory direction: $r_{\text{between}} = 0$), but the degree as to how much this assumption is violated is not yet known (Thorup & Rabøl, 2000; Thorup et al., 2003). The combined effect of geography and simple factors, such as compensation for previous drift, to correct their course along the migration route, can probably account for the failure of the simple vector navigation program to satisfactorily encompass the observed patterns.

Importance of taking geometry into account

The present study shows a significant role of geometric constraints, thereby stressing the importance of including such constraint in analyses. It is possible to extend the modeling procedure used here to include most factors important in migration (e.g. flight range) and to use mortality for evaluating the model. Such a model has already been employed (Erni et al., 2002), though the primary focus of that model is physiological and not the migratory orientation program. However, at present estimates of mortality are heavily dependent on estimated flight ranges, which in turn rely on equations whose parameters are difficult to estimate (Pennycuik et al., 1996; Rayner & Maybury, 2003). Furthermore, the actual mortality associated with migration is very difficult to assess (Nichols, 1996), though recent estimates suggest that it is high (Silleet & Holmes, 2002). Nevertheless such approaches are likely to improve our understanding of the migratory orientation program and can guide further research.

Acknowledgements

We are especially grateful to the Finnish ringing scheme (Pertti Saurola and Jukka Happala) for help and permission to use their recoveries for this project. Also we wish to thank Jesper Johannes Madsen for his help with obtaining the recovery data, and the Swedish ringing scheme (Bo Sällström) for permission to use their recoveries for this project.

References

- Alerstam, T., 1990. *Bird Migration*. Cambridge University Press.
- 1996. The geographical scale factor in orientation of migrating birds. *Journal of Experimental Biology*, 199: 9–19.
- Bairlein, F., 2001. Results of bird ringing in the study of migration routes and behaviour. *Ardea*, 89 (special issue): 7–19.
- Bensch, S., 1999. Is the range size of migratory birds constrained by their migratory program? *Journal of Biogeography*, 6: 1225–1237.
- Berthold, P., 2001. *Bird Migration. A General Survey* (2nd ed.). Oxford University Press, Oxford.
- 1996. *Control of Bird Migration*. Chapman & Hall, London.
- Bäckman, J. & Alerstam, T., 2003. Orientation scatter of free-flying nocturnal passerine migrants: components and causes, *Animal Behaviour*, 65: 987–996.
- Colwell, R. K. & Lees, D. C., 2000. The mid-domain effect: Geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, 15(2): 70–76.
- Colwell, R. K., Rahbek, C. & Gotelli, N. J., 2004. The mid-domain effect and species richness patterns: What have we learned so far? *American Naturalist*, 163: E1–E23.
- Erni, B., Liechti, F. & Bruderer, B., 2002. Stopover Strategies in Passerine Bird Migration: A Simulation Study. *Journal of Theoretical Biology*, 219: 479–493.
- Fisher, N. I., 1993. *Statistical analysis of circular data*. Cambridge University Press, Cambridge.
- Helbig, A. J., 1994. Genetic basis and evolutionary change of migratory directions in a European passerine migrant *Sylvia atricapilla*. *Ostrich*, 65: 151–159.
- 1996. Genetic basis, mode of inheritance and evolutionary changes of migratory directions in palearctic warblers (Aves: Sylviidae). *Journal of Experimental Biology*, 199: 49–55.
- Helbig, A. J., Berthold, P., Mohr, G. & Querner, U., 1994. Inheritance of a novel migratory direction in central European Blackcaps (Aves: *Sylvia atricapilla*). *Naturwissenschaften*, 81: 184–186.
- Jetz, W. & Rahbek, C., 2002. Geographic Range Size and Determinants of Avian Species Richness. *Science*, 297: 1548–1551.
- Moreau, R. E., 1972. *The Palaearctic–African Bird Migration Systems*. Academic Press, London.
- Mouritsen, H., 1998. Modelling migration: the clock-and-compass model can explain the distribution of ringing recoveries. *Animal Behaviour*, 56(4): 899–907.
- Mouritsen, H. & Mouritsen, O., 2000. A mathematical expectation model for bird navigation based on the clock-and-compass strategy. *Journal of theoretical Biology*, 207: 283–291.
- Nichols, J. D., 1996. Sources of variation in migratory movements of animal populations: Statistical inference and a selective review of

- empirical results for birds. In: *Population dynamics in ecological space and time*: 147–197 (D. E. Rhodes, R. K. Chesser & M. H. Smith, Eds.). The University of Chicago Press.
- Pennycook, D. J., Klaassen, M., Kvist, A. & Lindström, Å., 1996. Wingbeat frequency and the wingbeat frequency and the body drag anomaly: wind-tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). *Journal of Experimental Biology*, 199: 2757–2765.
- Perdeck, A. C., 1958. Two types of orientation in migrating starlings, *Sturnus vulgaris* L., and chaffinches *Fringilla coelebs* L., as revealed by displacement experiments. *Ardea*, 46: 1–37.
- 1977. The analysis of ringing data: pitfalls and prospects. *Vogelwarte*, 29 Sonderheft: 33–44.
- Rabøl, J., 1978. One-direction orientation versus goal area navigation in migratory birds. *Oikos* 30, 216–223.
- Rayner, J. M. & Maybury, W. J., 2003. The drag paradox: Measurements of flight performance and body drag in flying birds. In: *Avian Migration*: 543–562 (P. Berthold, E. Gwinner & E. Sonnenschein, Eds). Springer Verlag.
- Sandberg, R. & Holmquist, B., 1998. Orientation and long-distance migration routes: An attempt to evaluate compass cue limitations and required precision. *Journal of Avian Biology*, 29(4): 626–636.
- Sillett, T. S. & Holmes, R. T., 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology*, 71: 296–308.
- Thorup, K. & Rabøl, J., 2001. The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns. *Journal of Avian Biology*, 32: 111–119.
- Thorup, K., Rabøl, J. & Madsen, J. J., 2000. Can clock-and-compass explain the distribution of ringing recoveries of pied flycatcher? *Animal Behaviour*, 60: F3–F8.
- Thorup, K., Alerstam, T., Hake, M. & Kjellén, N., 2003. Can vector summation describe the orientation system of juvenile ospreys and honey buzzards? – An analysis of ring recoveries and satellite tracking. *Oikos*, 103: 350–362.
- Wehner, R., 2001. Bird navigation – computing orthodromes. *Science*, 291: 264–265.
- Wernham, C. V., Toms, M. P., Marchant, J. H., Clark, J. A., Siriwardene, G. M. & Baillie, S. R., Eds., 2002. *The Migration Atlas: movements of the birds of Britain and Ireland*. T & A D Poyser, London.
-