

The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns

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The requirements of the orientation system of naïve long-distance night migrants were analysed by comparing data on Barred Warbler *Sylvia nisoria*, Marsh Warbler *Acrocephalus palustris* and Spotted Flycatcher *Muscicapa striata* with data from a computer model of a clock-and-compass system. These species show, respectively, a rather restricted winter distribution in East Africa, migration through a very narrow corridor in East Africa, and rather widely distributed recoveries in the Mediterranean with more concentrated recoveries south of the Sahara. For all three species, to obtain the observed concentrations either a very high directional migratory concentration was needed in computer simulations to bring the birds successfully to their wintering areas or misorientating individuals would be subjected to a very high mortality. Neither the very high directional concentration nor the high mortality amongst misorientating individuals fit the empirical data sets. On the basis of the present study, the observed patterns seem difficult to explain by a simple clock-and-compass system only, and to account for the exceptionally precise migratory routes shown in this study it is proposed that first-time migrants might be able to use landscape topography on a regional scale in combination with corrections of directional mistakes/wind displacements.

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Migratory motivated birds have a well documented capability of orienting themselves with respect to a variety of environmental cues (e.g. Wiltschko and Wiltschko 1996; see reviews in Berthold 1991), but at the same time little is known about how the actual orientation programme is carried out in free-flying birds (Alerstam 1996). As birds are known to possess both compass systems and an endogenous circannual clock, the simple mechanism of the clock-and-compass ('vector-orientation') model has been proposed. Here the inherited migratory programme is described as a number of migratory steps with a constant compass course, the duration and length of which are defined by an endogenous circannual clock (Berthold 1996), and thus correspond to a vector with a length and a direction. The migratory programme may consist of one or more such vectors. In general, birds are believed to use a programme that includes more factors than just the

clock-and-compass, as they may have specific programmes regarding the response to e.g. ecological barriers. Fortin et al. (1999) showed that nocturnal migrants not only fly in their endogenously fixed direction, but adjust their directions more or less to their geographical position, the configuration of a coastline in relation to their innate direction, and their motivation to continue across a barrier.

So far only few attempts have aimed at testing which mechanisms are sufficient to guide inexperienced young migrants flying without guidance from older conspecifics to their species-specific winter quarters/stop-over sites. Regarding the clock part of the clock-and-compass model, Berthold and Querner (1988) found a correlation between activity and length of the expected migratory journey and that the amount of 'Zugunruhe' corresponded to the expected flight time. Gwinner et al. (1992) and Gwinner (1996), however, have pointed out

that the 'Zugunruhe' can be suppressed, and that this will not generate any later compensation and, furthermore, that the amount of 'Zugunruhe' displayed by birds is strongly affected by the way it is recorded (Gwinner 1990).

Two main approaches have aimed at testing the sufficiency of the compass orientation capability. The first approach tests whether birds on their first migration are able to correct for real or simulated displacements (e.g. Rabøl 1969, 1994, 1998, Mouritsen and Larsen 1998), and the second one compares the output from a model of the migratory programme with data from ringing recoveries (Mouritsen 1998, Thorup et al. 2000). Displacement experiments have yielded inconclusive results, though some indicate that birds are able to correct for displacements (e.g. Rabøl 1969, 1994, 1998). Modelling studies have not been conclusive either, and so far they have the severe shortcoming of not taking into account the uneven distribution of landmasses. This makes comparisons with observed data difficult, as the observed data could potentially be heavily biased by the land mass distribution.

The idea of the present study is to compare observed migration patterns with the output from a model of the clock-and-compass system, both with regard to the compass system and the endogenous circannual clock, to determine the requirements of the clock-and-compass system, and to test whether this system is sufficient to guide naïve birds on their first migratory journey, and, if not, what other systems might be involved in the migratory programme. As it is generally believed that orientation mechanisms represent phylogenetically ancient traits with only limited evolution of specific orientation mechanisms (Rodda and Phillips 1992, Berthold 1996), even the most impressive orientation capabilities should be explicable within the general model. We have searched for migration patterns that will make high demands on the migration system, as it is very difficult to separate the outcomes of different orientation systems in more simple cases. Thus, we have considered the orientation systems of long-distance migrants (Europe to Africa) with concentrated winter distributions or narrow migratory routes, as these presumably will make the highest demands with respect to precision on the inherited migratory system. To circumvent the problem with the uneven distribution of landmasses we chose only birds migrating from Europe to east or central Africa, thereby avoiding the problem of separating the effects of the Atlantic Ocean. Furthermore, the width of ecological barriers (the Mediterranean Sea and the Sahara) is similar regardless of where such migrants cross them.

In order to test the predictions of the clock-and-compass system we looked at three different cases: (1) The Barred Warbler *Sylvia nisoria*, which has a rather restricted winter distribution in East Africa. (2) The Marsh Warbler *Acrocephalus palustris*, which in East

Africa passes along a very narrow route. (3) The Spotted Flycatcher *Muscicapa striata*, which is one of very few species with many recoveries south of the Sahara. We determined the requirements of the model system to fit observed patterns, and compared them with estimated capabilities. Further, in case of (2) and (3) the model system was tested qualitatively by comparing observed patterns with the patterns emerging from modelling.

Methods

Modelling procedure

The modelling of the clock-and-compass system was done by vector summation (Rabøl 1978, Mouritsen 1998, Sandberg and Holmquist 1998), where each migratory step is considered a vector with a fixed length and a direction picked randomly (and independently) from a circular distribution. (The vector summation procedure is described in detail in Mouritsen (1998).) The basic parameters in the model are (1) the directional concentration of the circular distribution used for picking directions for each individual step (directional concentration per step r_{step}), (2) the directional concentration of the chosen between-individuals distribution (r_{between}) and (3) the step length.

In the present study, the circular distribution used is the wrapped Cauchy distribution. The basis for using this distribution is given in Mouritsen (1998). It should be noted that this distribution is not the one normally used in circular statistics and that it does have some very different properties from both the normal distribution in linear statistics and the von Mises distribution, which is otherwise normally used in circular statistics (Batschelet 1981). As shown by Thorup et al. (2000) the use of the wrapped Cauchy distribution generally generates more concentrated data than the von Mises distribution when using the same directional concentration per step, which makes the conclusions in the present study rather conservative. The advantage of using the wrapped Cauchy distribution in this case is the higher computation speed and, as the emphasis has been on finding minimum values for the parameters used, the use of the wrapped Cauchy distribution seems justified.

Variation between individuals was introduced into the model according to Thorup et al. (2000). The contribution of variation between individuals was found by adding a direction picked randomly from a chosen between-individuals distribution to the resulting sample mean vector after the chosen number of migratory steps had been added.

In modelling, two different procedures were used: (1) For a given distance from the starting point, the proportion of modelled paths falling inside \pm a given devia-

tion from the mean direction was calculated by adding vectors until the length of the sumvector exceeded the given distance. This was repeated a large number of times (100000) and the number of sumvectors falling inside the given deviation was counted. (2) For a given distance from the starting point, the number of vectors, with a corresponding mean distance from the starting point, was added. According to the central limit theorem, the distribution of vectors resulting from additions of vectors of equal length drawn randomly from a specific circular distribution will approach a normal distribution (in the plane, i.e. a bivariate normal distribution with $\sigma_x = \sigma_y$) for a large number of additions (Fig. 1). This bivariate normal distribution can then be described by standard circles (Batschelet 1981). When using this procedure, the mean and standard deviation of the points resulting from a specific number of additions were calculated. (Using the standard deviation in the Y-coordinate σ_y , where the mean direction is along the X-axis.)

A directional concentration per step of 0.7 was expected. This was chosen as a conservative value of the estimate of 0.665 found by Mouritsen (1998) for recoveries within 100–150 km of Pied Flycatcher *Ficedula hypoleuca*.

Most cases were run with two different step lengths (125 km and 250 km). When using a step length of 250 km the specific number of additions was half that for a step length of 125 km.

The modelled migratory tracks were in most cases crossing large expanses of water or desert. With a step length shorter than these expanses, the modelling corresponds to the birds continuing migrating, but with the same average ability to fly in a specific direction (i.e. wind direction should change independently) for each step flown, and the birds should determine their migratory direction independently after each step flown. In case of desert crossing evidence exists that migrants land in the desert during day-time (Biebach et al. 1986, Bairlein 1992), making this assumption less critical. This modelling is conservative in giving less scatter in tracks compared to letting birds fly long steps with unaltered ability to fly in their specific direction.

Observations in Africa (winter distribution and migration routes)

The winter distribution of the Barred Warbler was found in Cramp (1992) and Urban et al. (1997). The smallest circle that encompassed this distribution was then fitted by eye, and this was considered the goal area for Barred Warblers.

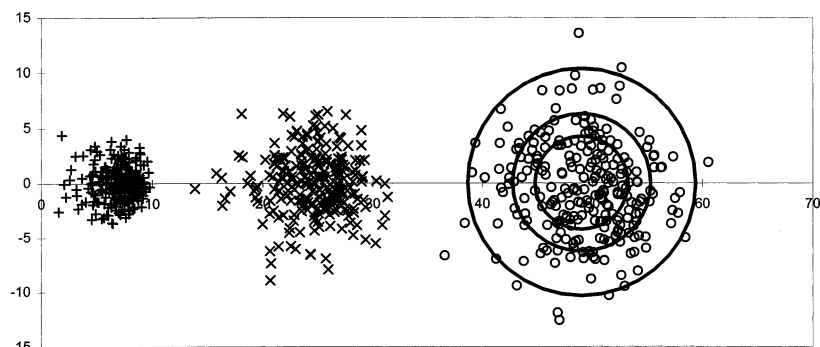
We chose a limit of at least 90% of the modelled endpoints falling inside this area for a successful model run using a single compass direction for the entire journey, and the corresponding r_{step} (with no between-individuals variation) was considered the minimum for Barred Warblers to reach their winter quarters. If the birds fly a dog-leg course (still migrating by vector summation) around the Mediterranean the distance migrated will increase and the scatter thus increase. Consequently, values found when using a single compass direction for the entire journey are minimum values. The addition of between-individuals variation was looked upon qualitatively.

The migration of the Marsh Warbler in Africa has been described quite thoroughly (Dowsett-Lemaire and Dowsett 1987) and the passage through East Africa treated in Pearson (1990), who estimates that Marsh Warblers (with a few other species) 'migrate through Kenya on a front no more than 100–200 km wide'. Using a single compass direction for the entire journey a limit of a minimum of 90% of the modelled paths falling inside a 200 km wide band was considered a successful model run, and the corresponding r_{step} (with no between-individuals variation) was considered the minimum for Marsh Warblers to migrate successfully.

Ringling recoveries (Spotted Flycatcher)

The data set consists of recoveries of Spotted Flycatcher (N = 208) ringed in Sweden and Finland and recovered in the autumn or winter (before 15 March; recoveries south of the Equator before 15 May were included as relating to 'winter'). Only recoveries more

Fig. 1. Endpoints (250) of vectors resulting from additions (equal to steps) of vectors drawn randomly from a wrapped Cauchy distribution with $r_{\text{step}} = 0.7$: +: 10 steps; ×: 35 steps; ○: 70 steps. Standard circles are shown for the distribution resulting from adding 70 vectors drawn randomly from a wrapped Cauchy with $r_{\text{step}} = 0.7$. The standard circles for normally distributed data (in the X/Y plane), which the endpoints of this vector addition approach, contain successively 40, 67 and 95% (outer) of the normally distributed data.



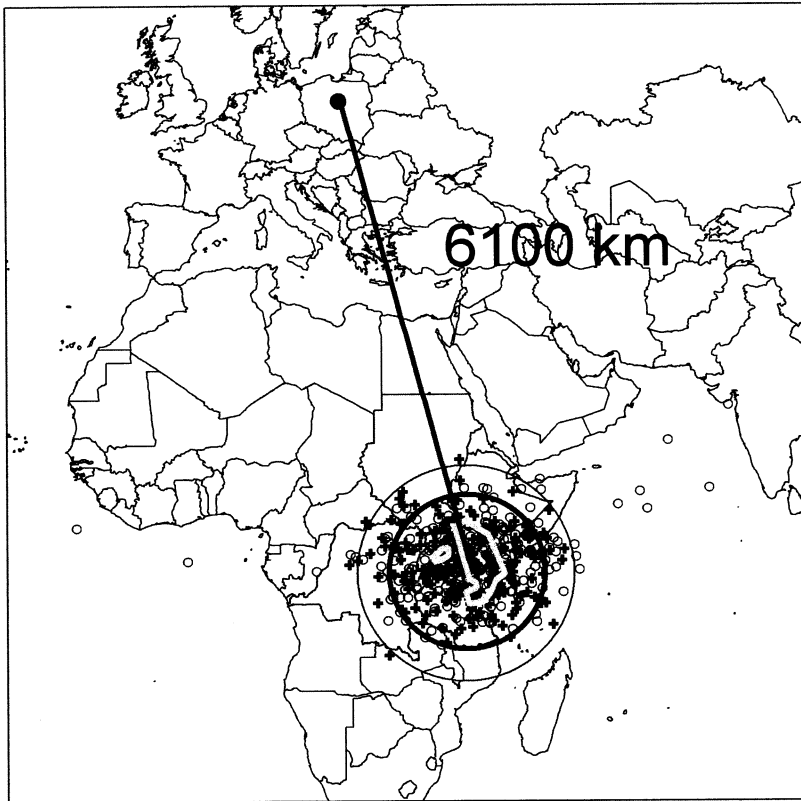


Fig. 2. Simulation of Barred Warbler migration from Poland to East Africa (6100 km) using $r_{\text{step}} = 0.7$ (wrapped Cauchy distribution). +: 250 random endpoints with no between-individuals variation ($r_{\text{between}} = 1$; 70 steps). o: small between-individuals variation added ($r_{\text{between}} = 0.99$; 70 steps). Large thick circle contains 90% of the endpoints with no between-individuals variation ($r_{\text{step}} = 0.7$; $r_{\text{between}} = 1$; step length = 125 km; radius = 1140 km; 70 steps). Thin large circle: the same with a step length of 250 km ($r_{\text{step}} = 0.7$; $r_{\text{between}} = 1$; step length = 250 km; radius = 1625 km; 35 steps). Whitish line inside circles: winter distribution of Barred Warbler. The map is a Mercator projection.

than 100 km (loxodrome distance) from the ringing sites were used, as recoveries closer than this might include dispersal.

Predictions from modelling (deviation increasing with distance)

It follows from the central limit theorem that the scatter of the endpoints of vectors resulting from vector addition increases in proportion to $(n)^{1/2}$, where n is the number of steps. It thus follows that the width of the migratory route (the deviation from mean direction) is expected to increase with distance. As the scatter increases in proportion to $(n)^{1/2}$ and step length (Y -axis on Fig. 1) it follows that the scatter for a given distance migrated will be greater when using a longer step length (corresponding to fewer steps) but unaltered directional concentration per step.

Results

Barred Warbler

Fig. 2 shows the simulated migration of Barred Warbler from Poland to East Africa (6100 km) using $r_{\text{step}} = 0.7$. With a step length of 125 km, this corresponds to

an average flight distance of 8750 km involving 70 steps, whereas the direct route is only 50 steps.

A directional concentration per step of 0.90 was required for successful migration with a step length of 125 km (with $r_{\text{step}} = 0.90$, $r_{\text{between}} = 1$ and step length = 125 km, 90% of the simulated endpoints fall inside the circle encompassing the winter distribution). With a step length of 250 km a directional concentration per step of 0.94 was needed. With a directional concentration per step of 0.70 ($r_{\text{step}} = 0.7$, $r_{\text{between}} = 1$ and step length = 125 km), 71.7% of the simulated endpoints fall inside the encircled winter distribution, whereas 58.8% fall inside with a step length of 250 km.

The addition of a small variation between individuals results in endpoints far outside the wintering area (in this case in India and far west in the Atlantic Ocean).

Marsh Warbler

Fig. 3 shows the migration of Marsh Warbler through East Africa. For successful migration a directional concentration per step of 0.996 is required with a step length of 125 km (90% of the tracks falling inside a 200 km wide band at a distance of 6800 km). With a step length of 250 km the corresponding directional concentration per step is 0.998. With a directional concentration per step of 0.70 ($r_{\text{step}} = 0.7$, $r_{\text{between}} = 1$ and step

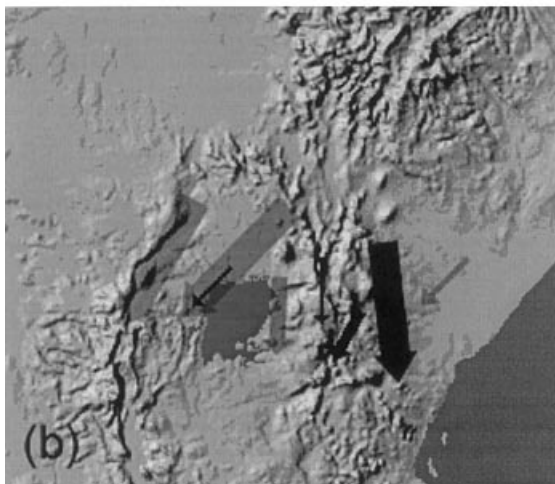
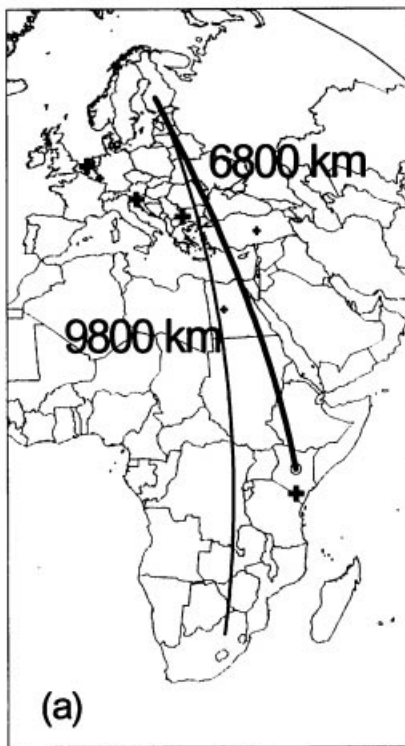


Fig. 3. Migration of Marsh Warbler. (a) Long-distance ringing recoveries from Sweden and Finland. Big crosses: recoveries within the same autumn or winter. Small crosses: additional autumn and winter recoveries. Thick line: Finland (breeding) to passage area in East Africa. Small circle: main passage area (radius = 100 km). Thin line: direct route to presumed winter area. Distances are indicated. The map is an equi-distant azimuthal projection. (b) The passage of Marsh Warblers through East Africa (Kenya and Uganda) according to Pearson (1990). Migration intensity at well covered sites in East Africa: large black arrow: up to 100+ individuals per day; small black arrow: up to 10+ per day; thin arrows: a few per year up to a few per day; grey arrows indicate migratory concentrations of all species.

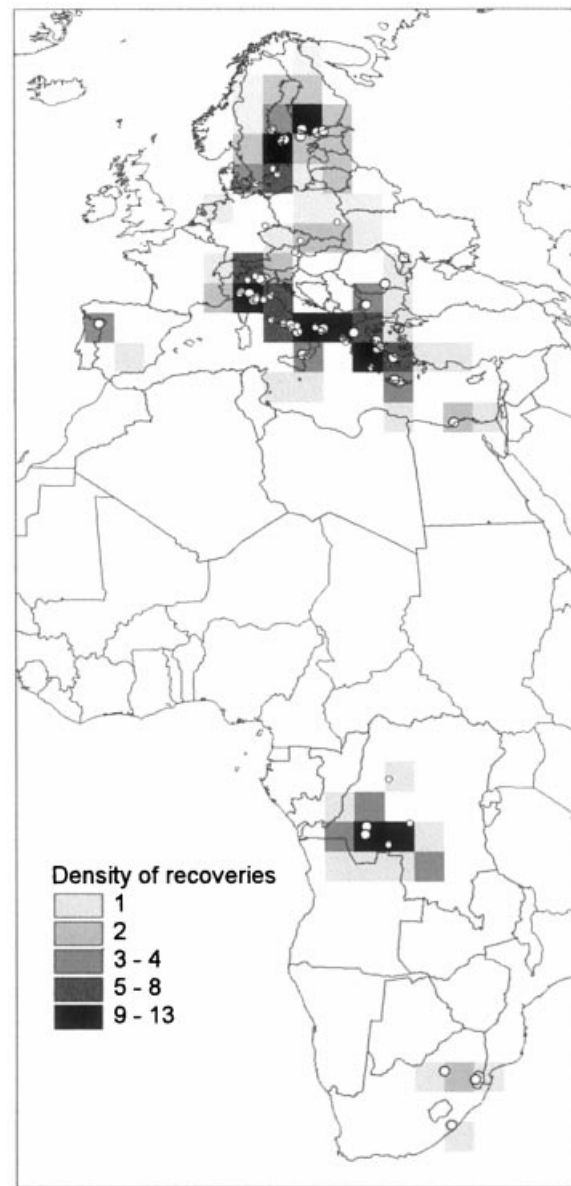


Fig. 4. Ringing recoveries of Spotted Flycatchers from Sweden and Finland, recovered on autumn migration or in the winter area (south of Sahara) (N = 208). Open circles: ringed as nestlings in Sweden (smallest circles) or Finland and recovered within the same autumn or winter (N = 66). The map is a Lambert equal-area azimuthal projection.

length = 125 km), 14.4% of the tracks fall inside the 200 km wide band, while 10.3% fall inside with a step length of 250 km.

Spotted Flycatcher

Fig. 4 shows all ringing recoveries of Swedish and Finnish Spotted Flycatchers. The overall pattern for birds ringed as nestlings is the same as when all autumn

and winter recoveries are included. From this recovery pattern three more or less distinctly different migratory directions can be identified.

Fig. 5 shows the pattern of migration in relation to different model runs. A conservative estimate of the width of the migratory route is 1400 km both in the Mediterranean and south of the Equator.

With a directional concentration per step of 0.65, 90% of the modelled paths lie inside a 1400 km wide band perpendicular to the migration direction at a distance of 2400 km from Finland (the Mediterranean) and 71.1% of the paths at a distance of 7700 km (2400 + 5300 km). With a directional concentration per step of 0.95, 95% of the modelled paths lie inside the 1400 km band at a distance of 7700 km from Finland (the northern part of the winter quarters). At a distance of 2400 km the corresponding band is then 400 km wide ($r_{\text{step}} = 0.95$).

For 90% of the birds to reach the circle in RD Congo (distance = 7700 km) a directional concentration of 0.895 is required. The corresponding standard circle in the Mediterranean (at a distance of 2400 km) has a radius of 400 km ($r_{\text{step}} = 0.895$).

On a qualitative scale the ringing recovery data have a distribution rather different from the modelled distribution, with higher concentration in the wintering area than along the migratory route.

Discussion

Summarising results

In all three cases a rather poor fit of the model to observed patterns was found. For successful model runs a directional concentration per step between 0.9 (Barred Warbler) and 0.996 (Marsh Warbler) was needed. This is much higher than the expected directional concentration per step of 0.7. Furthermore, model runs with a directional concentration per step of 0.7 yielded estimates of the survival of first-time migrants of 71.7% (Barred Warbler), 71.1% (Spotted Flycatcher) and 14.4% (Marsh Warbler), this mortality being only due to orientation mistakes and the mis-orientating fraction missing from the empirical data. The patterns emerging from the empirical data (Marsh Warbler and Spotted Flycatcher) did not fit the modelled data in any qualitative way, in that empirical data showed a tendency to be more concentrated far from the starting point, which is not expected from the model. Using a longer step length made the fit of the model even worse.

Estimated parameters (r_{step} , r_{between} , step length)

For estimates of the directional concentration per step only a single Spotted Flycatcher was recovered in the

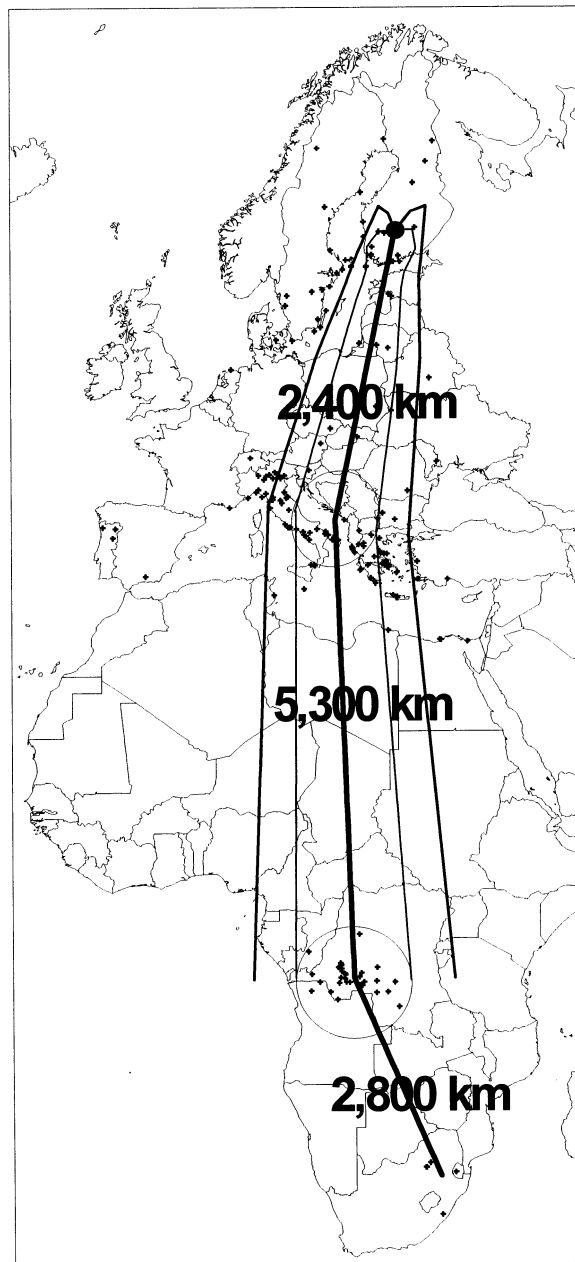


Fig. 5. The migration of Spotted Flycatcher. Crosses show ringing recoveries of birds ringed in Sweden and Finland and recovered in autumn or in the winter area (south of Sahara) (N = 208). The thick line shows the migratory route in autumn identified from ringing recoveries (cf. Fig. 4). The lengths of different migratory legs are indicated. The outer medium thick lines indicate the interval containing 90% of the modelled paths with $r_{\text{step}} = 0.65$. The thin lines indicate the interval containing 95% of the paths with $r_{\text{step}} = 0.95$. The circle centered in RD Congo contains the ringing recoveries in that region (radius = 700 km). The circle in the Mediterranean shows the standard circle at distance 2400 km ($r_{\text{step}} = 0.895$). The map is a Mercator projection.

same year in the interval 100–150 km. For Redstart *Phoenicurus phoenicurus* the directional concentration per step estimated in this way is 0.784, but it is based on only five individuals. Hake et al. (2001) estimated a directional concentration per step for juvenile Ospreys *Pandion haliaetus* followed by satellite telemetry of 0.7–0.8.

Clearly there must be some variation between individuals. This has been discussed by Thorup et al. (2000). In the present study this variation has not been included quantitatively in the model, but in all cases the fit of the model would be worse.

The step length of 125 km is the same as the one used by Mouritsen (1998). If birds use a few long migratory steps, this will have a large effect on the outcome of the model run with unaltered directional concentration per step, even if the average step length is equal to the fixed step length of 125 km, and the deviation will increase. The empirical data do suggest that birds might use some very long steps, as speeds of migration of Spotted and Pied flycatchers of more than 100 km/day have been found for birds migrating for more than 15 days (maximum 131 km/day in 23 days for a Spotted Flycatcher). As migrating birds are expected to spend most of the time staging (Alerstam and Lindström 1990, Hedenström and Alerstam 1997) a longer step length must have been used. Very slow migration speeds do not necessarily indicate that birds do not use long steps; slow migration might be the result of long stop-over times.

Difference in deviation from the mean direction between birds ringed as juveniles and as nestlings

For the Spotted Flycatcher a significant difference was found in the deviation from the mean direction of birds ringed as juveniles and as nestlings, respectively, with the mean angular deviation s of juveniles of 22.7° and of nestlings of 16.8° ($n_1 = 28$, $n_2 = 59$, $R_1 = 24.86$, $R_2 = 55.48$, $P < 0.05$, Parametric test for the concentration parameter (Batschelet 1981)). Similar results were found for Pied Flycatchers ringed in Denmark, Finland, Norway and Sweden and recovered less than 3500 km from the ringing site within the same autumn/winter, where $s = 27.7^\circ$ for juveniles and $s = 13.8^\circ$ for nestlings ($n_1 = 59$, $n_2 = 964$, $R_1 = 54.65$, $R_2 = 936.24$, $P < 0.05$).

A priori, we expected the deviation to be larger for birds ringed as nestlings, as these recoveries could include juvenile dispersal, but the results clearly indicate that juvenile dispersal is on a rather small scale. Further, the results seem strange for birds using a clock-and-compass system. A reasonable explanation would be that birds have some ability to determine whether they have strayed too far from their normal migration path. In that case we would expect a larger

deviation for birds en route (juveniles), as these birds might already have been displaced (and then compensate for the displacement), whereas birds starting migration (nestlings) will choose more or less the same direction. However, it is likely that birds caught at ringing stations do not constitute a random sample of the migratory population, but include a disproportionately high fraction of birds that have redetermined their migratory direction e.g. as a reaction to a barrier (e.g. Gauthreaux 1978, Moore 1990, Sandberg and Moore 1996).

All variation included (e.g. in step length, number of steps) gives greater deviation

Introducing more variation or more factors into the model system increases the spread of the modelled data which is not in agreement with the observed data. This is the case if we use a longer step length (all cases), introduce variation between individuals (all cases) or in number of steps (Barred Warbler only). In these cases an even higher directional concentration per step and/or a shorter step length will be necessary to counteract these effects, and still the qualitative difference will remain.

Are observed patterns real?

The distribution of migrating and wintering species in Africa has been studied in more detail during the last decades (e.g. Pearson et al. 1988), and is rather well known for most species. The Barred Warbler is easily recognisable, confined to a rather specific habitat and is very rare away from this habitat (Urban et al. 1997).

Migration in East Africa has been rather intensely studied including intensive ringing programmes (Pearson 1990), and the migratory pattern of Marsh Warblers is thus quite well known (Dowsett-Lemaire and Dowsett 1987), even though the species is not easily identifiable. A pattern such as that observed for the Marsh Warbler is found for several other species migrating through East Africa (but perhaps not quite as pronounced) e.g. Thrush Nightingale *Luscinia luscinia* and River Warbler *Locustella fluviatilis* (Pearson 1990).

The ringing recoveries of Spotted Flycatcher show a surprising distribution (Fransson 1986). Although ringing recovery data can be biased by uneven recovery probabilities, it seems highly likely that Fennoscandian Spotted Flycatchers pass through western RD Congo to winter in southern Africa, as shown by the ringing recoveries. In spite of extensive ringing programmes in East Africa, where Spotted Flycatcher is quite common (the eastern race *M. s. neumanni*), no recoveries of Fennoscandian birds have been made there nor in West Africa, where the species has a limited winter distribution only.

Can the clock-and-compass model explain the observed pattern?

If we accept the simplest clock-and-compass model, we have to accept a very high mortality of juveniles (around 30% in Barred Warbler and up to 90% in Marsh Warbler) attributable to orientation mistakes only (we expect experienced birds to be able to navigate along their previous path). Furthermore, as the width of ecological barriers is similar regardless of where they are crossed, it is difficult to explain why these misorientating individuals are not found in the observational data (e.g. Marsh Warblers in West Africa) or the ringing-recovery data (e.g. Fennoscandian Spotted Flycatchers in Kenya).

It is also possible that the directional concentration per step has been grossly underestimated, if for instance birds use some longer migratory steps, where they take wind drift into account. In that case a much higher directional concentration is possible. Still, this will not explain the qualitative difference between the model and observed data, and for the Marsh Warbler an extraordinary precision would be required.

Conclusion

Most likely naïve birds not only make use of a simple clock-and-compass system, but also of either (a) long migratory steps in selected wind directions with correction *en route* for wind drift, (b) extrinsic cues for termination of the migratory programme (Barred Warbler), (c) landscape topography, (d) correction for drift using path integration or (e) navigation (includes correction *on site* for previous wind drift) (Klein 1980, Rabøl 1980). In all cases the orientation system must be more accurate than previously thought, and only (c), (d) and (e) can explain the broad-front migration early during migration (Marsh Warbler in Europe and Spotted Flycatcher in the Mediterranean).

That first-time migrants should be able to make extensive use of landscape topography on a regional scale is difficult to comprehend, and even invoking navigation fails to fully explain the extraordinary migration of the Marsh Warbler. However, path integration or navigation in combination with the use of landscape topography might turn out to be sufficient to guide inexperienced young migrants.

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