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ANIMAL BEHAVIOUR, 2000, **60**, F3–F8
Article No. anbe.1999.1300, available online at http://www.idealibrary.com on IDEAL®

FORUM

Can clock-and-compass explain the distribution of ringing recoveries of pied flycatchers?

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(Received 9 June 1999; initial acceptance 28 July 1999; final acceptance 28 August 1999; MS. number: SC-1170)

Birds have a fascinating capability of finding their way on long-distance flights, and the orientation systems of migrating birds have been the subject of considerable research. Of special interest are young, inexperienced night migrants on their first migration, since they fly alone with no guidance from experienced conspecifics. These birds need a migration programme that will bring them to an area they have not been before: the species-specific winter quarters.

As Alerstam (1996) pointed out, we have extensive knowledge about birds' compass systems, but only a very limited understanding of how the actual orientation programme is carried out in free-flying birds. In the simple mechanism of the clock-and-compass model (also called 'vector orientation') 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. Much of the basis for a clock-and-compass programme has been shown to exist in birds, although Gwinner (1996) noted that current knowledge of factors influencing the length of the vector seems to indicate that the time factor alone is insufficient for reaching the winter quarters, and it is still a matter of debate whether this programme is sufficient to guide birds to their winter quarters. Birds using the simplest clock-and-compass system will not be able to correct for extensive wind drift or directional mistakes.

One way of addressing the question is to compare the expectations from a clock-and-compass programme with ringing data, as a clock-and-compass system is easy to simulate. This approach was proposed and used by Rabøl (1978) and later by Mouritsen (1998). Simulation of a simple clock-and-compass system was also used by Sandberg & Holmquist (1998), although they used survival data instead of ringing data for comparison. Mouritsen (1998) concluded that the simplest clock-and-compass system, where birds do not correct for wind drift or directional mistakes that occurred on previous nights, is sufficient to explain the distribution of ringing recoveries. However, his study ignored several factors of this system, most notably that individual mean directions may vary and that birds may use some long migratory steps. Variation between individuals is to be expected (Wiltschko & Wiltschko 1996), as this forms the basis of evolution of new migratory traits as shown by Helbig (1994, 1996) and Helbig et al. (1994), and most studies show significant differences between individual mean directions (see Discussion). Furthermore, Mouritsen's (1998) model uses a wrapped Cauchy distribution which is not commonly used to describe circular distributions occurring in nature (Mardia 1972; Batschelet 1981; Schnute & Groot 1992).

By reanalysing Mouritsen's (1998) data, we arrived at a different conclusion, and, by expanding the modelling procedures, we investigated the consequences of introducing more factors and of using the more commonly used von Mises distribution in the modelling system. We also introduce an alternative way of analysing ringing recoveries.

Methods

Analysis of circular data follows Batschelet (1981).

Modelling

Our modelling procedure corresponds to the one used by Mouritsen (1998) which calculates the directional concentration r after n migratory steps (r_n) as a function

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of the number of independent steps (n) and the directional concentration r for each step (r_{step}).

The directional scatter and the corresponding angular deviation were modelled for the wrapped Cauchy distribution using the formulas given in Mouritsen (1998).

Instead of using Mouritsen's (1998) method to estimate standard error (which results in, for example, error bars on the directional concentration r exceeding 1), we used a 95% confidence interval.

To estimate 95% confidence intervals around r_{step} we took as many angles as were used to calculate r_{step} (equal to the number of ringing recoveries in that particular distance interval), from a distribution with a specific r and calculated an r value (this calculated r value would usually be somewhat higher than the specific r value, because of the low number of angles; see Batschelet 1981). This was repeated 20 000 times. From these 20 000 trials, the 95% intervals were found. The upper limit of the 95% confidence interval around r_{step} was then estimated as the r value with a corresponding lower 95% limit of r_{step}. Similarly, the lower limit was found with a corresponding upper 95% limit of r_{step}.

The best fit was found as the r_{step} value resulting in an equal number of ringing recovery data r values above and below the r line from the model output.

We also used the von Mises distribution for modelling. The probability density of the von Mises distribution is the function,

$$f(\phi)=\frac{1}{2\pi I_0(\kappa)}\exp[\kappa\cos(\phi-\theta_1)],\quad 0\le\phi\le2\pi.$$

It has two parameters, the parameter of concentration κ ($\kappa\ge0$) and θ_1; θ_1 is the mode and the mean angle, $I_0(\kappa)$ is a constant. The distribution function is then given by

$$F(\theta)=\int_0^{\theta}f(\phi)\,d\phi,\quad 0\le\theta\le2\pi$$

where $F(0)=0$ and $F(2\pi)=1$. The inverse distribution function of random values between 0 and 1 then corresponds to random angles taken from the von Mises distribution. Given a random number $t\varepsilon[0;1]$, then a random point (x,y) on the unity circle taken from a von Mises distribution is given by

$$x=\cos[F^{-1}(t)],\ y=\sin[F^{-1}(t)].$$

Since it is presently not possible to solve the equation for F^{-1} analytically, a numerical procedure must be used. To use a specific von Mises distribution we calculated and stored the distribution function for 100 000 numbers.

In the von Mises distribution, the parameter of concentration κ is used: it can be estimated from r according to Batschelet (1981). It is then possible to check the estimated κ by running the program. In the present study we deliberately chose κ values that corresponded to a somewhat higher r value to avoid too low an r value in the computations. It is thus possible to use the von Mises distribution for modelling.

We introduced variation between individuals by choosing a realistic upper limit to the between-individuals distribution ($r_{between}$=0.98) and adjusting r_{step} ($r_{step,\ within\ individuals}=r_{step}/r_{step,\ between\ individuals}$) to an r_{step} within individual. This means using a somewhat higher r_{step} for a given r value, as $r_{between}$ cannot exceed 1. We then found the contribution of variation between individuals by adding a direction picked randomly from the chosen between-individuals distribution to the resulting sample mean vector after n migratory steps.

Ringing recoveries

We used the same ringing recovery data set and processing procedure as Mouritsen (1998). The data set consists of recoveries of pied flycatchers, *Ficedula hypoleuca* (N=1138), ringed in Denmark, Sweden, Norway and Finland and recovered within the same autumn. Only recoveries between 100 and 3549 km (loxodrome distance) from the ringing site were used, as recoveries closer than this may include dispersal and there were too few recoveries further than this for statistical analysis. The recoveries were grouped into 35 distance intervals 100–149, 150–249, 250–349, . . ., 3450–3549 according to loxodrome distances between ringing and recovery sites. The directional concentration r was calculated from the directions in each distance interval. The directional concentration r from the distance interval 100–149 km was used as the r_{step} value.

Correlation between distance and concentration of ringing recovery data

We also analysed the ringing recovery data set by calculating the mean angular deviation s (in radians) from the directional concentration r: $s=(2(1-r))^{1/2}$. From this, we calculated mean angular deviation s times distance (measured in km; this corresponds to the standard deviation of normal distributions for small angles). To test the correlation between the deviation of ringing recovery data from mean directions and distance, we calculated Spearman correlation coefficients r_s from mean angular deviation s times distance and distance.

Results

Comparing directional concentrations from the model output (r_{step}=0.665) and ringing recoveries, a sign test results in P=0.058 (R=11, N=34) when applied to the data given by Mouritsen (1998). A Wilcoxon signed-ranks test showed a nonsignificant difference (P=0.21; Mouritsen 1998). However, the data are unsuitable for use in a Wilcoxon signed-ranks test because r values can never exceed 1, which makes the data set highly skewed, and this invalidates the assumptions for application of this test. Thus, even though the value of the sign test is not significant, it indicates that the model output does not fit ringing recoveries well, and it certainly warrants further investigation.

As r values (both for predicted values and for ringing recoveries) get very close to the maximum value of 1,

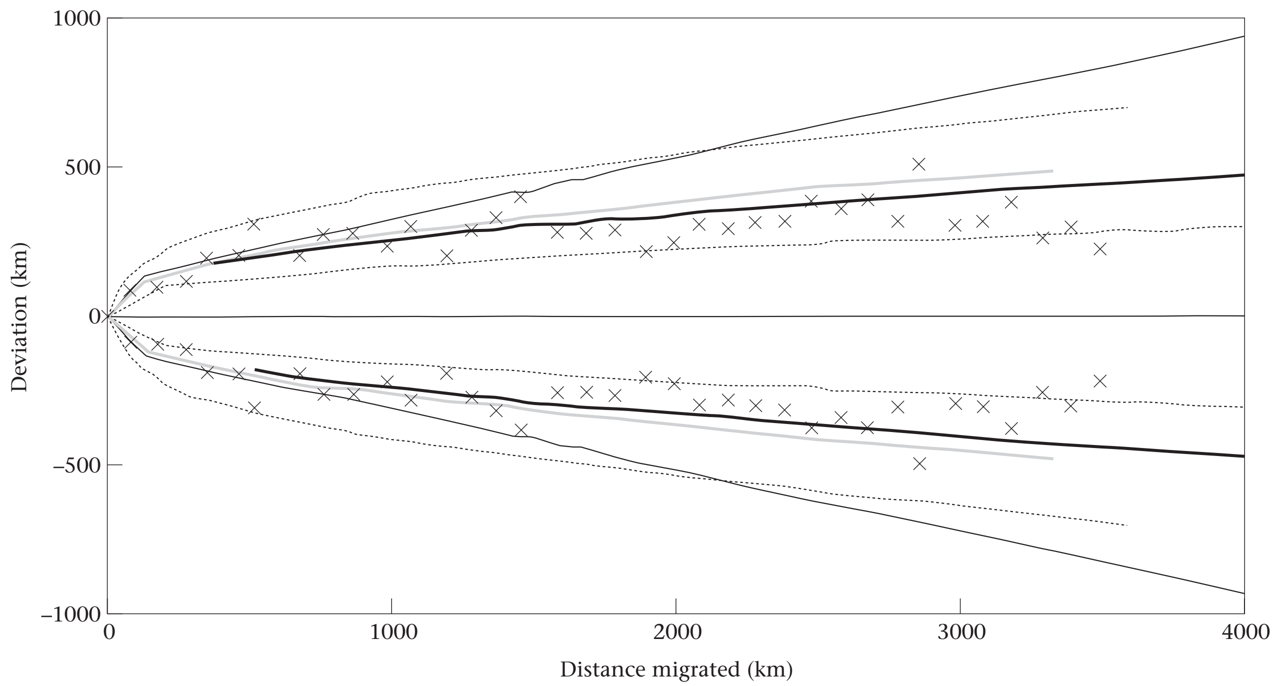

Figure 1. The output of various simulations (curved lines) compared with data from ringing recoveries (x) of pied flycatchers (same data set as used by Mouritsen 1998). Deviation: mean angular deviation *s* (in radians) times distance (km) of the data corresponding to a given distance is represented as the two points on the circle with radius equal to distance and with angle relative to the *X* axis equal to ± mean angular deviation *s*. For ringing recovery data, the points are shown as crosses. For model output, points from different distances are connected resulting in curved lines. Step length=125 km. ▬▬: wrapped Cauchy, r_{step}=0.665; -----: 95% confidence interval (r_{step}=0.835; r_{step}=0.410); ▬▬: von Mises, r_{step}=0.665; ——: wrapped Cauchy, r_{step}=0.679, $r_{between}$=0.98.

when the distance migrated is long, a clearer picture is given by multiplying *r* by distance, thereby reconstructing the mean vectors for certain distance intervals or model runs. Figure 1 shows the visually clearer corresponding mean angular deviation *s* times distance as a function of distance migrated. The angular deviation times distance does not have the upper limit of 1, and consequently lacks the inherent tendency of *r* values approaching 1 for large distances that blurs the differences in *r* between model output and ringing recovery data. This gives a clearer picture of data that are far from the start position, and it is obvious from Fig. 1 that the distant ringing recoveries deviate less from the mean direction than do the model output data. A comparison of angular deviation *s* times distance from model output with ringing recovery data yields a significant difference (confidence interval test: P<0.02). Ringing recovery data are thus more concentrated than the model predicts.

A number of ringing recovery angular deviations are smaller than the 95% confidence interval around r_{step}=0.665.

The best fit was found for r_{step} between 0.720 and 0.727.

Figure 1 also shows the output of various other runs of the model with different values of r_{step} and $r_{between}$, and with the use of the von Mises distribution. All these lines clearly produce a worse fit to the ringing recovery data than using r_{step}=0.665. The comparison between ringing recovery data and model output data yielded significantly higher deviations for model output using wrapped

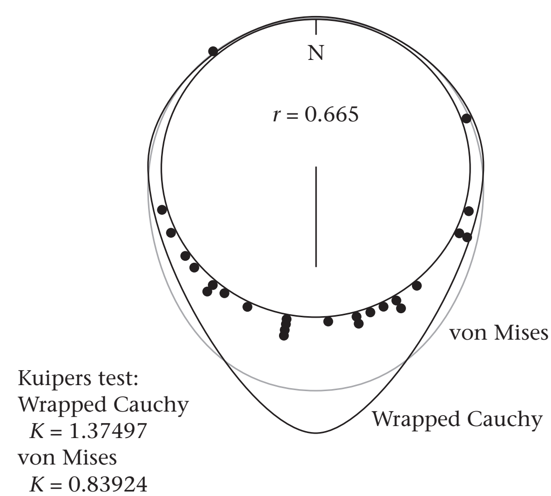

Figure 2. The directional distribution of ringing recoveries (●) in the 100–150-km interval. The corresponding circular distributions of the wrapped Cauchy and the von Mises distributions are indicated. Values of the Kuipers test statistic (*K*) are given (wrapped Cauchy: P≈0.2; von Mises: P>0.5).

Cauchy with r_{step}=0.679, $r_{between}$=0.98 (sign test: P<0.001) and for the von Mises distribution with r_{step}=0.665 (sign test: P<0.001).

Figure 2 shows how the directional distribution of the ringing recovery data from 100–150 km fits the wrapped Cauchy and the von Mises distributions. The von Mises data obviously fit the data better (as indicated by the

Kuipers test statistic *K*), although it is not significant. Figure 2 shows that the von Mises distribution seems more realistic to use, and Fig. 1 that it results in a slightly higher mean angular deviation and thus a lower directional concentration *r*.

A Spearman rank correlation coefficient r_s was calculated for all 35 points (distance, angular deviation *s* times distance) from ringing recovery data. This yielded $r_s=0.596$ ($P<0.05$), but for distances of more than 900 km (28 points), r_s was not significant ($r_s=0.316$) and r_s became negative for points with distances greater than 2000 km (16 points). For the most distant 11 points, the negative correlation actually became significant ($P<0.05$).

Discussion

As shown (Fig. 1), the ringing recovery pattern is more concentrated than expected from the clock-and-compass model (which implies that the birds are equipped with a migratory direction and an internal clock only). On the basis of the model output, we therefore conclude that birds do compensate on site for previous nights' directional mistakes and/or drift by the wind. This indicates that the concentration *r* values normally found in orientation tests in cages are lower than those of the true headings chosen by free-flying birds (cf. Wiltschko & Wiltschko 1996), since they do not include wind drift, which is included in the r_{step} value from ringing recoveries from 100–150 km.

These conclusions can be drawn only if the estimated parameters (r_{step}, $r_{between}$ and step length) are close to the true values, and if the concentration r_n values calculated from the model output give a good description of the clock-and-compass system. With the inclusion of between-individuals variation the mean vector concentration r_n can never be less than the between-individuals concentration no matter how many steps/orientational establishments are involved. Unless the between-individuals variation is extremely low ($r_{between}>0.99$), the model output cannot be made to fit the ringing recovery data by changing the other parameters. This means that, with the inclusion of $r_{between}\leq 0.99$, inclusion of compensation for wind displacement or compensation for directional mistakes cannot make the model output fit the ringing recovery data. If birds use a more advanced clock-and-compass system, then the effects of the distribution of landmasses and other topographical features will have to account for the difference. The ringing recovery data may be biased because of topographical features, as birds, by avoiding these, can be expected to be more concentrated on the Iberian Peninsula, for example, or different recovery probabilities in different areas can make recoveries more concentrated in certain areas (recoveries from the open ocean are rather unlikely, cf. Fig. 3).

The use of the more reasonable von Mises distribution makes the fit of the model worse.

Value of r_{step}

Using the wrapped Cauchy distribution we found the r_{step} value fitting the ringing recovery data best ($0.720\leq r_{step}\leq 0.727$, sign test) to be within the 95% confidence interval of the estimate of $r_{step}=0.665$, although still considerably higher.

An r_{step} of 0.665 seems a rather low directional concentration, but a simple simulation showed that if no compensation for wind drift is carried out a wind vector of two-thirds the length of the heading vector will produce $r_{step}=0.88$ when there is no within- or between-individuals variation around the standard direction (winds from all directions, i.e. for wind directions $r_{wind}=0$). If r_{within} is set to 0.88 or 0.75 and $r_{between}=1$, r_{step} decreases to 0.77 or 0.66, with one directional establishment per step. With five directional establishments per step, r_{step} is calculated as 0.83 or 0.76.

We conclude that the observed/estimated $r_{step}=0.665$ is not unreasonably low, although further research needs to be done to estimate a more realistic r_{step} of migrating birds.

Value of $r_{between}$

Both within- and between-individuals variation and wind drift are included in the ringing recovery data, and therefore in the estimate of r_{step}. The model used by Mouritsen (1998) implicitly assumes $r_{between}=1$.

The assumption of $r_{between}=1$ does not seem realistic, as variation between individuals is to be expected (Wiltschko & Wiltschko 1996), being the basis of evolution of new migratory traits (Helbig 1994, 1996; Helbig et al. 1994).

We found $r_{between}$ values of 0.93* and 0.89* (*indicates significance levels of 5%, **significance levels of 1% and ***significance levels of 1‰) in orientation cage tests with juvenile migrants: hand-reared blackcaps, *Sylvia atricapilla*, with access to sunset and magnetic cues (Helbig 1996); 0.98: wild-caught Australian silvereyes, *Zosterops l. lateralis*, with access to sunset and magnetic cues (Wiltschko et al. 1998, controls); 0.90** and 0.69***: wild-caught pied flycatchers and garden warblers, *Sylvia borin*, respectively, displaced to Kenya with access to sunset, celestial and magnetic cues (Rabøl 1993); 0.89** and 0.83**: hand-reared pied flycatchers with access to magnetic cues only (Weindler et al. 1995); 0.98 and 0.79**: hand-reared garden warblers with access to a stationary 'stellar' sky and a vertical magnetic field (Weindler et al. 1997); 0.94: wild-caught silvereyes with access to magnetic cues only (Wiltschko et al. 1993). 0.96: hand-reared blackcaps with access to magnetic cues only (Bletz et al. 1996).

The concentration of the grand mean vector *r* was considered an estimate of $r_{between}$, and the statistical significance of $r_{between}$ was tested by means of the Watson–Williams multisample test (Stephens 1972; Batschelet 1981). This test procedure may be applied if (1) r_{within} values are not too low (in the two-sample version of the Watson–Wheeler test, $r>0.75$ is recommended, Batschelet 1981), and (2) the distribution of the individual mean directions is symmetrical and unimodal (we used $r_{within}>0.60$ and/or $P<0.05$). Studies with a low r_{within} only rarely show a significant contribution to the total variance from $r_{between}$. However, this does not prove that variation between individuals is not present.

In conclusion, our estimate of r_{between}=0.98 in the calculations is probably an overestimate.

Length of migration route

Mouritsen (1998) estimated that r_{step}=0.665 implies that a flycatcher has to travel about 5000 km to cover the distance of about 3000 km from the breeding area to southern Spain. One may wonder why natural selection has not worked against so much excess in flight duration and energy expenditure. However, things may not be that simple. The 67% excess may be (much) reduced by the passive component of wind drift, where birds under varying winds should minimize the remaining distance to the goal, which means allowing a certain amount of drift (Alerstam 1979).

Step length

The model uses a step length of 125 km. If each migratory step is assumed to be more than 125 km and r_{step} is unaltered (=0.665), then r_n will be the same, but the average distance travelled will be longer. Thus, for a given distance, the resulting directional concentration *r* will be lower (and the mean angular deviation *s* higher) and the fit of the model worse. The ringing recovery data indicate that the step length might not be even throughout the migratory journey, as the recovery rate is far from equal for all distance intervals with few recoveries (7–25) from each distance interval 100–1749 km and more recoveries (29–76) from each distance interval 1750–3249 km (Mouritsen 1998). However, if we use a longer step length, the relatively low r_{step}=0.665 may not be reasonable to use, as indicated by the higher value for the distance interval 150–249 km (*r*=0.866). The effect of using a higher r_{step} will thus be counteracted by the effects of a longer step length.

Shape of the ringing recovery distribution

If we look at the ringing recovery data only, the clock-and-compass model predicts that mean angular deviation times distance should be positively correlated with distance (independent of the value of r_{step}). As shown, this seems not to be the case, as the correlation coefficient r_s for roughly the latter half of the points (distance, angular deviation times distance) is negative. This suggests that the deviations from the mean track do not increase as much as would be expected from the clock-and-compass model.

That ringing recovery data tend to become more concentrated in the last part of the journey to the western Mediterranean corresponds to the predictions of an optimal migration strategy with respect to wind drift with randomly varying winds. The birds should allow extensive drift at the beginning of the migratory journey, and then compensate more and more upon approaching the goal (Alerstam 1979; Alerstam & Hedenström 1998).

Conclusions

On the basis of the present study we find it difficult to explain the distribution of ringing recovery data by the birds using only a simple clock-and-compass system. This conclusion, though, is highly dependent on the modelling system, which includes a certain degree of uncertainty with respect to the values of the parameters used, and does not take the uneven distribution of land masses into account (Fig. 3). However, our study does contain a framework for future testing.

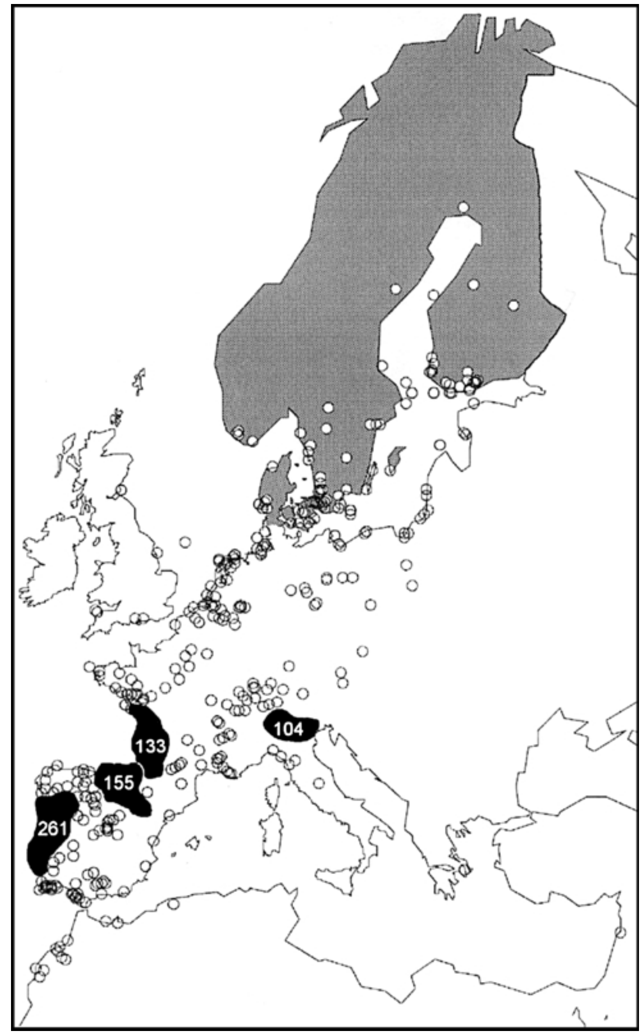

Figure 3. Recoveries of pied flycatchers ringed in Norway (122), Sweden (414), Finland (484) and Denmark (25) and recovered in the same autumn (N=1045) up to 1998. Only recoveries between 100 and 3550 km from the ringing site, and only recovery sites are shown. Recoveries in northern Italy stem mostly from Finnish birds (the large dot (104): Finland: 93; Norway, Sweden and Denmark: 11). Ringing area shown as grey shading. (Mercator projection).

We are grateful to the individual ringing schemes for their help and for permission to use their recoveries for this project. We particularly thank the following for their assistance on behalf of their schemes: Pertti Saurola and Jukka Happala (Finland), Olav Runde (Norway), Bo Sällström (Sweden), Carsten Rahbek and Kjeld T. Pedersen (Denmark). Thanks go to Henrik Mouritsen for providing us with a complete set of the directional distributions derived from the ringing recovery data. We are also grateful to Anders Thorup, Department of Mathematics, University of Copenhagen for explaining and sorting out some of the mathematics. Jette Andersen helped improve the English.

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