

## Estimating variation among individuals in migration direction

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Among-individual variation in mean migration directions is the basis of evolution of new migration routes and has important consequences for our understanding of the migratory orientation system. This variation in migration directions is also of interest for modelling of migratory flight paths. In test series with caged migrants, the variation among individuals is generally much smaller than the variation within individuals making the variation among individuals difficult to detect with small sample sizes. No methods exist for estimating among-individual variance for directional data. We therefore used simulations to estimate the variation among individual mean migration directions. Among-individual variation was found to be present in at least half of the 34 series analysed. In the 21 series with first-time migrants, our estimates of the variation among individuals ranged from  $r = 0.20$  (mean vector length) to  $> 0.99$ , with median 0.93 and 86% less than 1. We found slightly more variation among individuals in displaced birds and in experiments with manipulated cues. Test series with experienced migrants, presumably having varying goal areas, showed similar estimates (median 0.94 and 77% less than 1).

Variation in migration directions among individuals of the same population is to be expected (Wiltschko and Wiltschko 1996) as variation in traits is always expected in nature, and furthermore, this variation is believed to form the basis of evolution of new migratory traits (Helbig 1994, 1996, Helbig et al. 1994).

Evolution of migratory behaviour can occur very rapidly as demonstrated by observations of reduction and extension of migratoriness, changes of migration periods and migratory distance and novel migration directions and winter quarters (Berthold 1996, and references therein), and in general migratory traits have been shown to have high heritability (e.g. Pulido and Berthold 2003). A novel migration direction and winter quarter have been suggested for the apparently increased wintering population of blackcaps *Sylvia atricapilla* in Britain. Experiments by Berthold et al. (1992) and Helbig et al. (1994) suggest that the change is based on microevolutionary processes. Berthold and Terrill (1988) suggest that the new migration direction of blackcaps wintering in Britain stems from positive selection on the previously existing range of genetically

based migration directions, and the way of inheritance has been suggested to be simple (Helbig et al. 1994).

Even though rapid evolution of new migratory traits can apparently occur, studies by Bensch (1999) and Böhning-Gaese et al. (1998) indicate that development of new migration routes are constrained by the migration programme, and Bensch (1999) concluded that 'the relatively low colonisation success of migratory species into new breeding areas may be because these new areas require novel migratory programmes (migratory distance, direction and timing) for the birds to reach suitable wintering grounds'. However, in their studies, evolution of new migration routes would require jumps in the evolution of migration directions, as the new migration routes were separated by unsuitable areas for migrants from the existing migration routes.

As pointed out by Moore (1985), most studies on avian orientation do not take individual variability into account. Often only a mean direction of a sample of individuals is used for inference, and this may have important consequences for the interpretation of the

results. Variation among individuals has generally been assumed negligible and not been taken into account when modelling the orientation system, as in e.g. Mouritsen (1998). Modelling studies generally assume that birds use a vector navigation programme (a clock-and-compass strategy), where the inherited migration programme consists of 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). Studies including variation among individuals in migration direction indicate a conflict between the expectations from the vector navigation migration programme and observed (from observations, capture data and ring recoveries) concentrated migration routes and wintering areas (Thorup and Rabøl 2001, Thorup et al. 2000). It is therefore of interest to estimate the amount of variation among individuals in the inherited migration direction and investigate the consequences of this variation.

With circular data, the length of the mean vector, calculated from a sample of directions, is a measure of variation (or concentration) among the directions in the sample, with values near 1 indicating small variation and values near 0 indicating large variation. For directional data with several measurements on each of a number of individual birds, the grand mean vector is calculated as the mean vector of the individuals' mean directions, disregarding individual sample sizes and concentrations. The length of the grand mean vector has been used as an estimate of the variation among individuals (Thorup et al. 2000). However, the grand mean vector length,  $r_{\text{grand}}$ , overestimates among-individuals variation, as it contains both among-individuals and within-individuals variation. This is analogous to the among-groups variance in a linear analysis of variance model, where the among-groups mean squares term contains an error variance term (Sokal and Rohlf 1995). For circular data, although procedures, notably the Watson-Williams test, exist to test for the equality of mean directions among individuals/groups (Batschelet 1981, Fisher 1995, Mardia and Jupp 2000), we know of no method that estimates the variability among individuals/groups (in our case the variability in mean flight direction among individuals,  $r_{\text{among}}$ ). Batschelet (1981) and Zar (1999) estimate the grand mean vector length (second-order analysis), but again this is not the quantity we require. Mardia and Jupp (2000) describe an analysis of variance for circular data, but it is not clear how to estimate the variance components from this. Estimating variance components for directional vector data is further complicated by non-normality (causing massive integration and computer power requirements), circular concentrations are not variances in the usual sense, and therefore not additive as in linear models, and the variance/concentration of a sample depends on the sample size (Batschelet 1981). Another

restriction in the case of analysing published results, is that only individual mean directions and concentrations may be available, rather than all measurements. For these reasons we use simulations for the estimation of among-individuals variation.

The best data for estimating among-individuals variation in migration directions would be from following a sample of individually migrating birds. With satellite-based radio telemetry large birds can be tracked, but at present this is not possible for most individually migrating birds (mostly passerines migrating at night). However, for passerine birds data from many cage experiments provide information on directional variation at both the individual and the population level (see also Moore 1985). Ring recoveries, with only a single recovery per bird, do not provide the opportunity to distinguish the within- and the among-individuals contribution to the total variance in migration directions. Hence, we use data from published cage experiments to estimate the variation among individuals. To estimate the variation in inherited migration direction, we look at migratory naïve birds, i.e. first-time migrants. For comparison, we also analyse a similar data set on experienced migrants having performed at least one previous migration and thus presumably having specific goal areas.

## Estimating variation among individuals

We analysed cage experiments from the literature with data on the orientation of a number of individual first-time migrants each tested repeatedly (Table 1). We additionally analysed several series of similar experiments with experienced birds (Table 2). Each of these data sets thus consists of  $n_i$  direction measurements for each of  $k$  individuals with a total of  $N$  direction measurements. The mean vector length  $r$  from a sample of directions is a measure of variance (or concentration) among these directions (Batschelet 1981). We use  $r_{\text{within } i}$  to denote the mean vector length for measurements from individual  $i$ ,  $r_{\text{among}}$  for the unknown variation among individual mean directions, and  $r_{\text{grand}}$  (grand mean) for the measured variation among individual mean vectors, where the grand mean vector was calculated as the mean vector of individual mean directions. We aim to estimate  $r_{\text{among}}$  from the sample statistics  $r_{\text{within } i}$  and  $r_{\text{grand}}$  by means of simulations.

The von Mises distribution, which we assumed to generate both within-individuals and among-individuals flight directions, has the concentration parameter  $\kappa$ . The maximum likelihood estimate of  $\kappa$  is calculated from the mean vector length  $r$ , but is biased for small values of  $r$  and small sample sizes, underestimating variation (Fisher 1995, Batschelet 1981). Bias-correcting estimates exist (Fisher 1995). The presence of

Table 1. Estimates of variation among individuals,  $r_{\text{among}}$ , in preferred heading of first-time migrants tested in cages in autumn. Presence of among-individuals variation in the grand mean vector is tested using the Watson-Williams multi-sample test (Batschelet 1981; \* indicates  $P < 0.05$ , \*\* that  $P < 0.01$  and \*\*\* that  $P < 0.001$ ).  $k$  = number of individuals,  $N$  = total number of observations. Hand = handraised; Wild = wildcaught; (Wild) = caught on breeding grounds before the pre-migratory season. Estimates are based on 20,000 simulated values.

Species	Status	Available cues	k	n	$r_{\text{within}}$ (mean; range in brackets)	$r_{\text{grandobs}}$	Estimated $r_{\text{among}}$	95% CI of $r_{\text{among}}$	Reference
<i>Ficedula hypoleuca</i>	Wild	Stars and magnetic	5	22	0.87 (0.70–0.98)	0.89*	0.89	0.17–0.96	Hilkjær unpubl. data
<i>Sylvia communis</i>	(Wild)	Stars	8	25	0.78 (0.55–1.00)	0.71*	0.72	0.01–0.90	Rabøl unpubl. data
<i>Sylvia communis</i>		Stars and magnetic	9	30	0.79 (0.58–0.99)	0.88	0.94	0.53–1.00	Rabøl unpubl. data
<i>Sylvia atricapilla</i>	Hand	Sunset and magnetic	8	60	0.69 (0.53–0.87)	0.94	0.98	0.91–1.00	Helbig 1989
Forchheim–Reuth									
Frankfurt			17	143	0.68 (0.56–0.86)	0.96	>0.99	0.90–1.00	Helbig 1989
Amberg			13	88	0.75 (0.53–0.98)	0.93	0.98	0.77–1.00	Helbig 1989
Radolfzell			19	207	0.70 (0.49–0.85)	0.93	0.97	0.84–1.00	Helbig 1989
Linz			14	142	0.63 (0.55–0.83)	0.85**	0.89	0.67–0.98	Helbig 1989
SW-Germany			13	53	0.77 (0.63–0.98)	0.90	0.96	0.71–1.00	Helbig 1989
Burgenland			12	62	0.80 (0.64–0.96)	0.85**	0.88	0.53–0.95	Helbig 1989
<i>Sylvia borin</i>	Hand	Stationary ‘stellar’ sky	8	63	0.77 (0.64–0.90)	0.98	>0.99	0.80–1.00	Weindler et al. 1997
<i>Sylvia borin</i>			11	77	0.67 (0.52–0.99)	0.63***	0.64	0.08–0.85	Weindler et al. 1997
<i>Sylvia borin</i>			12	83	0.83 (0.64–0.96)	0.93*	0.95	0.73–0.99	Weindler et al. 1997
<i>Ficedula hypoleuca</i> Germany		Magnetic	11	67	0.79 (0.62–0.97)	0.83***	0.85	0.46–0.93	Weindler et al. 1995
<i>Ficedula hypoleuca</i> Latvia			7	51	0.74 (0.53–0.97)	0.35***	0.20	0.00–0.65	Weindler et al. 1998
<i>Passerculus sandwichensis</i>		Sunset, stars and magnetic	8	36	0.63 (0.53–0.78)	0.98	>0.99	0.71–1.00	Moore 1984
Displaced birds									
<i>Erithacus rubecula</i>	Wild	Stars and magnetic	5	31	0.73 (0.58–0.93)	0.87*	0.89	0.16–0.97	Rabøl 1981
<i>Sylvia borin</i>			6	22	0.75 (0.57–0.96)	0.54**	0.53	0.01–0.82	Rabøl 1993
<i>Ficedula hypoleuca</i>			8	60	0.92 (0.81–0.97)	0.90**	0.89	0.48–0.95	Rabøl 1993
Experimentals									
<i>Sylvia atricapilla</i>	Hand	Magnetic	5	49	0.79 (0.67–0.93)	0.96	0.98	0.42–1.00	Bletz et al. 1996
<i>Ficedula hypoleuca</i>		Stars	3	9	0.92 (0.84–0.98)	0.71*	0.65	0.09–0.92	Rabøl and Dabelsteen 1983

Table 2. Estimates of variation among individuals,  $r_{among}$ , in preferred heading of experienced migrants tested in cages. With one exception (Moore 1984), all experiments are from (local) spring. Otherwise as in Table 1.

Species	Status	Available cues	k	n	$r_{within}$ (mean; range in brackets)	$r_{grandobs}$	Estimated $r_{among}$	95% CI of $r_{among}$	Reference
<i>Zosterops lateralis</i>	Wild	Sunset and magnetic	8	75	0.71 (0.57–0.89)	0.98	>0.99	0.79–1.00	Wiltshcko et al. 1998
<i>Zosterops lateralis</i>			8	92	0.80 (0.55–0.95)	0.84***	0.84	0.29–0.92	Wiltshcko et al. 1999
<i>Zosterops lateralis</i>		Magnetic	6	37	0.72 (0.65–0.85)	0.80	0.82	0.13–0.95	Wiltshcko et al. 1993
<i>Zosterops lateralis</i>			5	24	0.81 (0.60–0.98)	0.90	0.93	0.18–0.98	Wiltshcko et al. 1999
<i>Zosterops lateralis</i>		Sunset	7	22	0.88 (0.64–0.99)	0.97	>0.99	0.66–1.00	Wiltshcko et al. 1999
<i>Passerculus sandwichensis</i>		Sunset, stars and magnetic	8	41	0.83 (0.55–0.94)	0.89*	0.94	0.46–1.00	Moore 1984
<i>Passerculus sandwichensis</i>			6	23	0.74 (0.55–0.88)	0.88	>0.99	0.12–1.00	Moore 1982
<i>Passerculus sandwichensis</i>			8	40	0.89 (0.77–0.98)	0.85***	0.88	0.36–0.98	Moore 1985
<i>Passerculus sandwichensis</i>			4	16	0.96 (0.89–0.98)	0.92***	0.91	0.14–0.98	Moore 1985
Experimentals									
<i>Zosterops lateralis</i>	Wild	Sunset and magnetic (cue-conflict)	10	95	0.70 (0.63–0.86)	0.94	0.97	0.72–1.00	Wiltshcko et al. 1998
<i>Zosterops lateralis</i>			6	69	0.84 (0.75–0.96)	0.96*	0.97	0.52–0.99	Wiltshcko et al. 1999
<i>Passerculus sandwichensis</i>			5	18	0.74 (0.55–0.88)	0.75	0.84	0.04–0.98	Moore 1982
<i>Zosterops lateralis</i>		Magnetic	6	31	0.78 (0.62–0.93)	0.94	0.99	0.42–1.00	Wiltshcko et al. 1993

variation among individual mean directions, i.e.  $r_{among} < 1$ , can be tested with the Watson-Williams multi-sample test (Batschelet 1981, Stephens 1972). This test assumes that individual samples are von Mises distributed, have the same concentration parameter  $\kappa$ , and that this common  $\kappa$  is reasonably large: Batschelet (1981) recommended  $\kappa > 2$ , corresponding to  $r_{within} > 0.75$ . We excluded individuals with  $r_{within}$  values  $< 0.55$  (see below) from analyses and simulations.

We estimated  $r_{within}$  and  $r_{grandobs}$  from the data:  $r_{within}$  was calculated as the weighted average of the  $k$  individual  $r_{within i}$ 's (weighted by individual sample size  $n_i$ ), assuming that all within-individual variances were equal;  $r_{grandobs}$  was calculated as the mean vector length of the  $k$  individual mean directions, where the individual mean vectors were all assumed to be of length 1 (equal weight).

Assuming equal variances for all individuals is equivalent to the condition required for the Watson-Williams test. We also ran simulations assuming that  $r_{within}$  differed among individuals, and obtained estimated  $r_{among}$  values that were on average 0.03 larger than those estimated assuming equal variances (four differences larger than 0.05; largest difference 0.19, one 0.07 and three 0.06). With the relatively small individual sample sizes, differences in  $r_{within}$  among individuals are unlikely to be detected, and thus the assumption of equal variances seems justifiable.

## Simulation details

Von Mises distributions were simulated according to Fisher (1995). We assumed that flight directions of individuals and mean flight directions among individuals both follow von Mises distributions. For each data set with  $k$  individuals, and  $r_{within}$  and  $r_{grandobs}$  estimated from the data: (1) Generate  $k$  mean flight directions from a von Mises distribution with parameters mean direction  $0^\circ$  and  $\kappa$  corresponding to  $r_{among}$  (starting with  $r_{among} = 0$ ). (2) Generate  $k$  samples of size  $n_1$  to  $n_k$ , corresponding to the sample sizes in the data set, from a von Mises distribution with means as generated in step 1 and  $\kappa$  corresponding to  $r_{within}$  (using equations in Fisher 1995, corrected for bias for small concentrations and sample sizes). (3) Calculate  $r_{grand}$  from the data generated in step 2. (4) Repeat steps 1 to 3 20,000 times. (5) Plot/tabulate the frequencies of  $r_{grand}$  (Fig. 1, we used 0.01 as category size). (6) Repeat steps 1 to 5 for all  $r_{among}$  values between 0 and 1 at 0.1 intervals, refining the interval size to 0.01 near the  $r_{among}$  that generated the highest frequency of  $r_{grandobs}$ .

Of the above frequency distributions (one for each  $r_{among}$ ), find the one that has the highest frequency (not necessarily the mode) at  $r_{grandobs}$ . We take the  $r_{among}$  corresponding to that frequency distribution as our

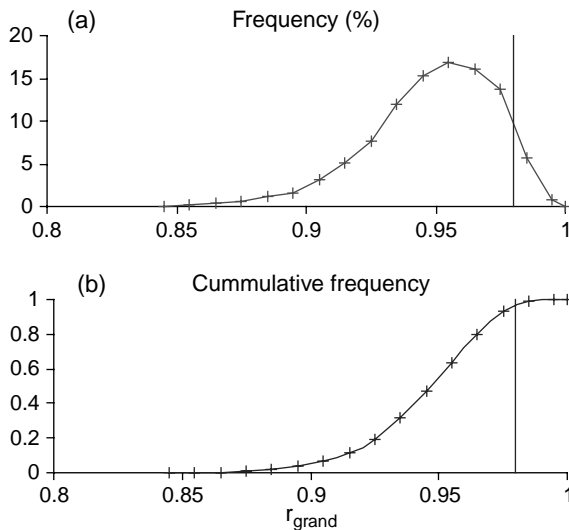


Fig. 1. Empirical (a) density function and (b) cumulative distribution function of the grand mean vector length  $r_{\text{grandmean}}$  from simulations with  $r_{\text{among}}=0.98$ . Based on 20,000 grand mean vectors calculated from 10 samples ( $k=10$ ) each with 10 directions ( $n_i=10, i=1, \dots, k$ ) generated from a within-individuals von Mises distribution with  $r_{\text{within}}=0.7$  and mean direction generated from an among-individuals von Mises distribution with ( $r_{\text{among}}=0.98$ ). The  $r_{\text{among}}$  used for these simulations is marked with a vertical line.

estimate for  $r_{\text{among}}$ . We found the 95% confidence intervals for  $r_{\text{among}}$  as follows: for each experiment, we tabulated  $r_{\text{grand}}$  for all  $r_{\text{among}}$  values from 0 to 1 (0.01 intervals). For each  $r_{\text{among}}$  we then tabulated the frequency of the simulated  $r_{\text{grand}}$  values equal to  $r_{\text{grandobs}}$ , using these frequencies as a rough estimate for the distribution of  $r_{\text{among}}$ . From this frequency distribution, we derived the (two-tailed) confidence interval.

All simulations were performed with custom-written computer programs written as Pascal code and run under Borland Delphi (Version 6.0). We used the in-built randomisation procedure to generate the random numbers needed for simulations.

### Example calculations

In the control experiments by Wiltschko et al. (1999) with eight wild-caught silvereyes *Zosterops lateralis*, having access to sunset and magnetic cues, the following mean vectors (mean direction – mean vector length) were obtained for each individual, respectively:  $123^\circ-0.81$  ( $n=15$ ),  $232^\circ-0.95$  (10),  $190^\circ-0.89$  (13),  $223^\circ-0.55$  (12),  $234^\circ-0.95$  (10),  $191^\circ-0.59$  (10),  $204^\circ-0.80$  (10) and  $220^\circ-0.86$  (12).  $r_{\text{within}}$  (calculated as the weighted mean concentration) equals 0.80 and  $r_{\text{grandobs}}$  equals 0.84. The Watson-Williams multi-

sample test strongly suggests the presence of among-individual variation ( $P < 0.001$ ,  $F_{7,84} = 10.268$ ). Our estimate from simulations for  $r_{\text{among}}$  is 0.85, with 95% CI [0.29, 0.92].

### Analysis of published cage experiments

In 17 (50%) of the 34 analysed experiments in Table 1 and 2 the Watson-Williams multi-sample test reported a significant variation among individuals, i.e.  $r_{\text{among}} < 1$ . As expected most estimated  $r_{\text{among}}$ -values were larger (closer to 1) than the corresponding  $r_{\text{grandobs}}$ . The median of estimated  $r_{\text{among}}$ -values was 0.93, compared to the median  $r_{\text{grandobs}}$  of 0.90. 82% of the estimated  $r_{\text{among}}$ -values were less than 1. Generally the estimates were close to the grand mean vector lengths, and only in four cases was our estimate of  $r_{\text{among}}$  smaller than  $r_{\text{grandobs}}$ . The largest differences were found in one case with a very small grand mean vector length ( $r_{\text{grand}} = 0.35$ ) and one case with a very small sample size ( $k=3$ ,  $n=9$ ).

The amount of variation among individuals differed only little between first-time and experienced migrants. Series with first-time migrants had a median estimated  $r_{\text{among}}$  of 0.92 and 86% less than 1 ( $n=21$ ). There was a tendency for more variation among individuals in displaced birds and in experiments with manipulated cues, and excluding these the median of estimated  $r_{\text{among}}$  was 0.94 (Fig. 2) and 81% were less than 1 ( $n=16$ ). In test series with experienced migrants the estimates were similar with median 0.94 and 77% less than 1 ( $n=13$ ).

Our estimated confidence intervals generally agreed with the significances reported by the Watson-Williams test: when the Watson-Williams test was significant, our confidence intervals did not include one, whereas one was included in the cases where the Watson-Williams test was not significant. In three cases did our

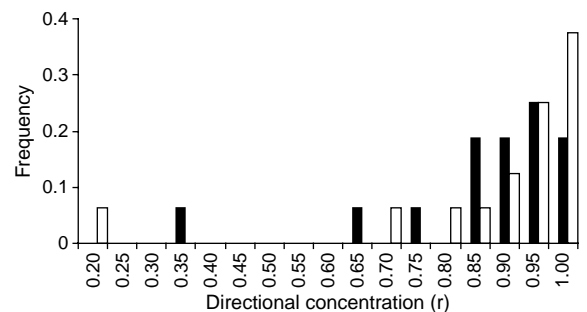


Fig. 2. Frequency distribution of the observed grand mean vector lengths (black) and estimated  $r_{\text{among}}$ -values (white) of first-time migrants in autumn ( $n=16$ ). Cue-conflict experiments and experiments with displaced birds are not included.

confidence intervals not include one, even though the Watson-Williams test was not significant, and in one case did our confidence interval include one, when the Watson-Williams test reported significance.

## Discussion

The data analysed here suggest that generally variation among individual orientation is present in cage studies: the variation among individuals contributed significantly to the total variation in half of the grand mean vectors investigated and in only 5 cases was our estimate equal to 1, i.e. no variation ( $> 0.99$  in Table 1 and 2). In a test series on the spring migratory orientation of savannah sparrows specifically performed to separate the two components of variation, among and within individuals variation, Moore (1985), using linear methods, also concluded that variation among individuals contributed significantly to the total variance of the variation among individuals, though he did not provide actual estimates of the amount of variation. The presence of among-individuals variation might have important consequences for the analysis of cage experiments, as it influences the interpretation of the mean orientation (Moore 1985).

The methods presented here can be used on most uses of directional data involving second-order mean vectors (mean of mean vectors), provided that the orientation behaviour (both at the subsample and the sample level) is unimodal (von Mises distributed). This assumption might be problematic if motivations differ among individuals (i.e. low motivation to migrate in some individuals may cause escape reactions or taxes [birds being attracted to an external stimuli, e.g. light], and differences in individual history could also introduce variation). The Watson-Williams test only requires that the individual subsamples are von Mises distributed.

### The variation among individuals in cage experiments

Variation in the inherited mean migratory/flight direction is expected as it forms the basis of evolution of migration routes. Furthermore, it is expected in experienced migrants since these presumably navigate toward different goal areas. Although the presence of among-individuals variation in cage studies cannot necessarily be directly attributed to naturally occurring variation in mean migration direction (e.g. in the case of escape reactions), it is probably a major factor in producing this variation.

Generally, large scatter is observed in orientation tests. This might partly be the result of the test

situation. According to Wiltschko and Wiltschko (1996), 'In most test series with migrants, (grand mean) vector lengths are in the range of 0.5, which does not seem to suggest a very high accuracy. However, the vectors are often based on the pooled data of several individuals, and the inter-individual differences may have contributed to the general variance'. The simulations presented here are useful for separating the large scatter in individual orientation ( $r_{\text{within}}$ ), which could increase due to the experimental situation (and experiences of individual birds such as prior wind drift), from the variation among individuals.

### Discussion of variation in migration direction among individuals

The experimental series of Helbig (1989) are particularly appropriate for finding variation among individuals in inherited migration direction in natural populations, as the birds were handraised and allowed natural cues in orientation tests. However, contrary to the expectation of the presence of variation in strongly inherited migration directions, in only 2 of 7 of these experiments did the Watson-Williams multi-sample test report a significant variation among individuals. However, this could be due to the large variation within individuals in these series. Our estimates of variation among individuals are in the range 0.86–0.98 (one  $> 0.99$ ). In these test series on blackcaps (Helbig 1989), most samples were from west or south-west migrating populations. The single sample from a south-east migrating population (Burgenland) had the largest estimate of variation among individuals.

Moore (1984) studied the orientation between first-time and experienced migrants of the same species in autumn and found more variation among individuals in experienced birds (but less variation within individuals). Overall, we found no difference between these two groups in the published experiments, but our study included different species between spring and autumn and the study by Moore (1984) involves the only experiments analysed with data on experienced birds from autumn.

In a study on ospreys *Pandion haliaetus*, Österlöv (1977) found no tendency for siblings to inherit more equal migration directions than the young from nearby nests, indicating that the migration directions taken by free-flying birds are not strongly inherited. This is in contrast to breeding and cross-breeding experiments where strong inheritance was found for most migratory traits (Berthold et al. 1992, Helbig et al. 1994), though the heritability of the migration directions is generally not tested in test series with birds held

Table 3. The proportion of birds misorienting when assuming purely endogenous vector navigation. This proportion was calculated as the number of tracks falling outside the expected band width when  $r_{\text{among}} = 0.98$  (for  $r_{\text{among}} = 0.99$  proportion given in brackets; for blackcap *Sylvia atricapilla* we used  $r_{\text{among}} = 0.87$  only). The expected band width corresponds to the width of the normal wintering area or migration route at the distance migrated from breeding areas in northwest Europe (barred warbler *Sylvia nisoria*, blackcap, collared flycatcher *Ficedula albicollis*, spotted flycatcher *Muscicapa striata*, red-backed shrike *Lanius collurio*, marsh warbler *Acrocephalus palustris*). The variation in migration direction per step ( $r_{\text{within}}$ ) is assumed to be 0, i.e.  $r_{\text{step}} = 1$  in the model of Thorup et al. (2000). A von Mises distribution with  $r_{\text{among}} = 0.98$  has 95% of the angles falling inside  $\pm 21.8^\circ$  of the mean angle. Data on red-backed shrikes and collared flycatchers were found in Zink (1973–85); barred warbler, marsh warbler and spotted flycatcher were found in Thorup and Rabøl (2001); and blackcap data were from Berthold and Terrill (1988). (W) denotes wintering area and (M) width of migration route.

Species	Area	Distance (km)	Band width (km)	Misoriented proportion
Redbacked shrike	E. Mediterranean (M)	2,700	450	0.41 (0.24)
Barred warbler	E. Africa (W)	6,100	625	0.61 (0.47)
Marsh warbler	E Africa (M)	6,800	100	0.94 (0.92)
Collared flycatcher	E/C. Africa (W)	7,500	1200	0.43 (0.26)
Spotted flycatcher	C. Africa (W)	7,700	700	0.65 (0.52)
Blackcap	W. Mediterranean (W)	4,000	1,250	0.54

in captivity (Pulido and Berthold 2003). However, such among-individuals variation in migration direction might be rather difficult to detect with small sample sizes.

### Consequences of variation among individuals

If we assume migratory birds to be guided by an entirely endogenous orientation programme without any influence of external factors, we can estimate the proportions of misoriented individuals in populations with known wintering areas or widths of migration routes. Assuming only vector navigation and a variation among individuals of 0.98, which is less variation than indicated in most of the cage tests (Fig. 2), the proportions of misoriented individuals (that is birds orienting outside their (normal) wintering range/migration route) are as shown in Table 3 for a range of species. Work by Berthold and Terrill (1988) suggests that the variation in inherited migration direction could be even larger. For Central European blackcaps, they suggested a variation in inherited migration direction spanning  $110^\circ$  inferred from ring recoveries. If we assume that this is simply among-individual variation around a population mean direction we can transform this to a von Mises distribution. A von Mises distribution with 95% of the angles falling inside this span has  $r_{\text{among}} = 0.87$ , being lower than the values we have assumed for the other species used in Table 3.

In all these cases a large proportion of misoriented individuals resulted. The above assumptions lead to unrealistically high losses for e.g. marsh warbler *Acrocephalus palustris* (94%). For this species even a very small variation (0.99) among individuals results in an unrealistically large proportion of misoriented birds, because of their concentrated migration route. This

may suggest that the migration of free-flying migrants is only partly described by their mean migration direction, and that external cues (e.g. landscape topography, or magnetic or celestial cues other than compass cues) play a larger role in guidance than previously expected.

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