



Reverse migration as a cause of vagrancy

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Capsule Reverse migration in autumn does not occur to the same degree in all species of migrants, but is related to migratory direction.

Aims To identify factors determining degree of reverse migration and specifically to test whether it occurs in long-distance migrant species irrespective of their standard (normal) migration direction.

Methods Multiple regression analysis on the number of individuals occurring as reverse migrants observed in northwest European countries.

Results The number of reverse migrants observed in northwest European countries is strongly correlated with standard migratory direction, estimated population size and detectability, but an effect of the distance travelled from the breeding areas is not supported. The pattern holds true for subsamples of the data set, including British and Irish records or Scandinavian records only, and when controlling for phylogeny.

Conclusion Birds that migrate eastward in autumn from their breeding grounds, mostly in eastern Europe, are more likely to consistently reverse migrate than those species migrating southward mostly from southern Europe.

The overall migration pattern (direction, path and timing) is relatively well described for many bird species. For most species the species-specific wintering areas are rather restricted, at least at the population level, and, especially for long-distance migrants, ring recoveries typically reveal a general (standard) migration direction with rather little scatter around the mean on long distances (Mouritsen 1998, Thorup & Rabøl 2001). Orientation cage tests with inexperienced migrants have demonstrated equal regular species- and population-specific migratory directions. Still, there are individuals occurring far outside their normal range. Some migrants make remarkable 'mistakes': a Yellow-browed Warbler *Phylloscopus inornatus* in west Europe has flown more than 2500 km from the breeding area, to more than 7000 km away from its normal wintering area (Thorup 1998). Why do such birds keep on flying in an apparently wrong direction?

The underlying reasons for vagrancy and the possible relations to the migratory orientation system are rather poorly understood, especially for Palearctic birds. For Nearctic birds, there is evidence that the number of

vagrants is larger for species expanding their range (Patten & Marantz 1996, Veit 1997, 2000). For Palearctic birds, it has been shown that pure wind drift does not offer any satisfactory explanation for the occurrence of reverse migrants, and the explanation is more likely to be linked to the orientation system (Ullman 1989, Van Impe & Derasse 1994, Thorup 1998). Rabøl (1969, 1978) proposed that the study of occurrence-patterns of vagrants might be a method of understanding the migratory programme of birds. Hypotheses on migratory orientation systems need not only explain how birds migrate from one place to another, but they should also be able to account for the observed migration pattern, including birds occurring far outside the normal migratory range.

The occurrence of reverse orientation (also called reverse misorientation, Alerstam 1991) has often been used as an explanation for the occurrence of vagrants in autumn. High incidence of reverse orientation has been reported in a number of cage studies (Able & Bingman 1987, Sandberg 1994), however, where it is mostly believed to result from the birds' current energetic condition. Reverse migration (migration along a back azimuth) has also been reported in a number of field studies (von Haartman 1945, Alerstam

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1978, Bruderer & Liechti 1998) but the relevance of this phenomenon has not been tested in relation to the orientation system.

Many vagrants observed in northwest Europe in autumn have eastern origins, and their occurrence could be explained by reverse orientation. If reverse orientation in a simple compass-based migration system is the main reason for reverse migration, then we expect reverse orientation to occur independently of migratory direction. This expectation is tested here using the large amount of data on vagrants of long-distance migrants generated by the birding community, together with several possible confounding variables (size of the migratory population, size of the 'vagrancy area', distance to the breeding area, and the detectability of the particular species, but not poorly known data on range expansions).

METHODS

Geographical delimitation

I examined the occurrence of reversed long-distance night migrants of species breeding in Europe, for which there are extensive areas (in Europe) in the opposite direction of that to the wintering area, where the species does not breed (Appendices 1–2). The 'vagrancy area' for reversed migrants considered will thus be in north/northwest Europe. Species breeding in Siberia and Africa only were not included as their distribution and migration is generally much less well-known. The resulting sample is thus of species migrating in directions from east (species with most of the breeding population in Siberia and wintering in southeast Asia) to southwest (south European species migrating to west Africa), with rather well-known breeding distributions, migration routes and wintering distributions.

Species considered

Only species migrating solitarily at night were considered, to avoid records of birds that had possibly followed individuals of other species (as could be the case in flock-migrating species, e.g. geese and shorebirds, where vagrants often turn up with common species). Whole groups were included (rather than just species) to obtain reasonable within-group comparisons and rendering subjective and biased selection less likely. The analysis was thus restricted to passerines with warblers (Sylviini) and flycatchers (Muscicapini) as the most

typical night-migrating birds. Thrushes (Turdinae), chats (Saxicolini), accentors (Prunellinae), and shrikes (Laniidae) were also considered, though these taxa contain partly day-migrants.

Number of reverse migrants

The construction of the data set was naturally constrained by the nature of the data involved. In the analysis, I defined a record of a species as the result of reverse migration if the record was from a country more than 500 km distant from the wintering area (obtained from Cramp 1988, 1992 and Cramp & Perrins 1993) than a line tangential to the breeding area (obtained from Hagemaijer & Blair 1997) and perpendicular to the (initial) standard migratory direction (Fig. 1). This definition was dictated by the scatter in reverse directions expected from scatter in 'normal' migratory directions (e.g. for Central European Blackcaps, Berthold & Terrill 1988 suggested a variation in inherited migratory direction spanning 110° inferred from ring recoveries), the widely scattered and imperfectly known starting points of vagrants and the expected variation (over time) in the exact extent of the breeding area.

To ensure that individuals involved were on direct reverse migration (e.g. excluding birds that had over-shot during the previous spring and summered outside the breeding range) only juveniles (if separable) and records from autumn were included.

Data on vagrants

Records from Ireland, Britain, France, Belgium, The Netherlands, Germany, Denmark, Sweden, Norway, and Finland were included in the analysis as records from most other European countries are sporadic. Only records from the period 1958–92 were included in the analysis as these, for most species, are found in Rønne (1994). For the few species not included in Rønne (1994), additional information was found in Mitchell & Young (1997), Lewington *et al.* (1991), Olsen (1992), B.O. Høyland (pers. comm.) and Dymond *et al.* (1989).

The following explanatory variables were considered. (1) **Population sizes** were estimated by dividing the number of breeding pairs in the European range obtained from Hagemaijer & Blair (1997) with the proportion of the total range lying in Europe (estimated from world distributions in Cramp 1988, 1992 and Cramp & Perrins 1993). For a few species with primarily

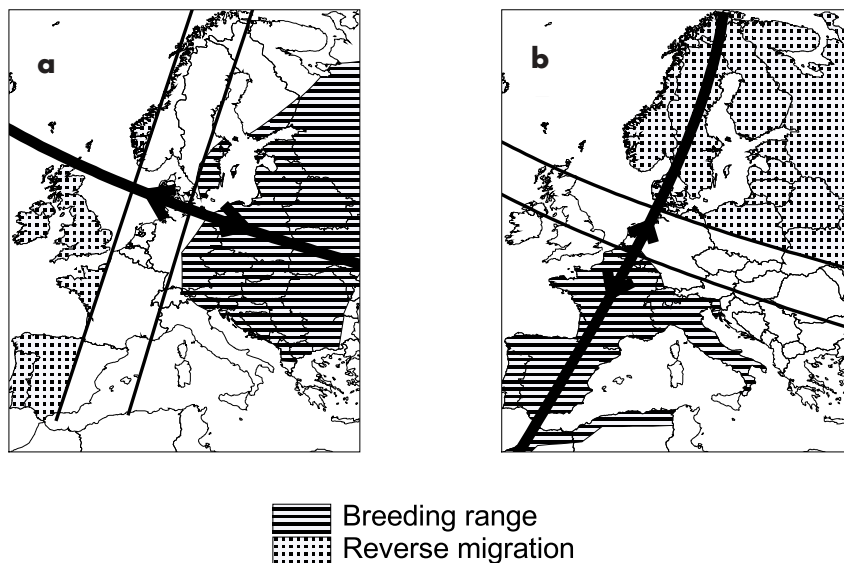


Figure 1. Definition of reverse migrants of (a) Red-breasted Flycatcher *Ficedula parva* and (b) Melodious Warbler *Hippolais polyglotta*. The thick black line shows the migratory direction to the winter quarters, as well as the direction of reverse migration. The two thin lines are separated by 500 km and are perpendicular to the migratory direction, the easternmost (for Red-breasted Flycatcher) or southernmost (for Melodious Warbler) being tangential to the breeding area. Records from countries west of the westernmost (Red-breasted Flycatcher) or north of the northernmost (Melodious Warbler) of these two lines are defined as relating to reverse migration (vagrancy area). Note that migrants from countries where only part of countries are considered reverse are not included, and that only northwestern European countries are included in the analysis.

Siberian ranges (e.g. Red-flanked Bluetail *Tarsiger cyanurus*) this method will undoubtedly underestimate the world population, but the focus of this study is the size of the population actually causing the vagrancy, which is likely to result from the nearest part of the population. For most of the populations there is only very limited information on long-term population trends or none exists. (2) **Migratory direction:** data on migratory directions were obtained from Cramp (1988, 1992) and Cramp & Perrins (1993). (3) **Detectability of each species** was assigned a number from 1 to 3 on the basis of habits and colouration: 1, very difficult to detect (cryptic colouration and secretive habits, e.g. Lanceolated Warbler *Locustella lanceolata*); 2, intermediate (cryptic colouration or secretive habits); 3, easily

detected (colourful and open-living, e.g. Rock Thrush *Monticola saxatilis*). (4) **Vagrancy area:** the size of the area of the countries included in the analysis for each species was calculated. (5) **Distance from the edge of the breeding area to the vagrancy area** was measured to the nearest 500 km.

All species included in the analysis, with relevant data used for analysis, are listed in Appendices 1–2.

Test procedure

Among the explanatory variables (migratory direction, population size, vagrancy area, distance and detectability) a few are strongly intercorrelated (Table 1). Vagrancy area and distance are expected to be auto-

Table 1. Spearman's rank correlation coefficients (r_s) between all variables included, number of reverse migrants (log), migratory direction, population size (log), detectability, size of vagrancy area (area) and distance to breeding area (distance), for all species ($n = 36$). Migratory direction is in this case entered as a quantitative variable. P values are given in parentheses without correction for autocorrelation.

	Migratory direction	Population size	Detectability	Area	Distance
Number of reverse migrants	-0.63 (< 0.0001)	0.55 (0.0007)	0.20 (0.25)	-0.23 (0.18)	-0.32 (0.06)
Migratory direction		-0.13 (0.46)	0.15 (0.37)	-0.10 (0.55)	0.04 (0.83)
Population size			0.04 (0.84)	-0.28 (0.11)	-0.18 (0.30)
Detectability				0.08 (0.65)	0.01 (0.97)
Area					0.76 (0.0001)

correlated as they basically measure the amount of land where a species does not breed. All other correlations (r_s) between explanatory variables were less than 0.3 (Table 1).

To assess the statistical evidence for the different parameters, model selection methods following Burnham & Anderson (2002) based on the Akaike information criterion (AIC) corrected for small sample size, AIC_c (Hurvich & Tsai 1989), were used. Candidate models were ranked according to AIC_c differences (Δ_i) and the likelihood of each model in the candidate set was then estimated with AIC_c weights (w_i). Inferences on the relative importance of each variable were based on the entire set of models (multi-model inference), using predictor weights, $w_+(j)$. For each variable considered, its predictor weight $w_+(j)$ is the AIC weights summed for all models containing the variable. The variable with the largest predictor weight is then estimated to be the most important and the variable with the smallest weight the least important variable.

All models^a were fitted using SAS 8.02 (SAS 1990) with additional calculation of AIC using formulas in Burnham & Anderson (2002). Migratory direction was entered as a categorical variable, the others as numerical. In addition to the information theoretic approach, the data were also analysed using analysis of covariance (ANCOVA) and multiple regression (migratory direction entered as numerical), which yielded very similar results.

To investigate a potential effect of the varying sizes of the vagrancy area and of observer bias, the analysis was additionally run with two subsets with constant size of the vagrancy area, using data from Britain and Ireland and from Scandinavia (Denmark, Norway and Sweden) separately.

Test for phylogenetic effects

The effect of phylogeny was controlled for by using permutational phylogenetic regressions (Böhning-Gaese *et al.* 2000) and the molecular phylogeny of Sibley & Ahlquist (1990) and Sibley & Monroe (1990). Significant dependence of traits on phylogeny is rarely found using this method (Böhning-Gaese & Oberrath 1999) but no better alternatives to this test exist.

RESULTS

Using species as data points, the number of reverse migrants shows strong relationships to the normal migratory direction and the population size ($P <$

0.0001), a near-significant relationship with distance to the breeding area but little correlation with detectability or size of the vagrancy area (Fig. 2, Table 1).

The global model – including migratory direction (1), population size (2), distance (3), vagrancy area (4) and detectability (5) – fitted the data extremely well ($R^2 = 0.86$; $\chi^2 = 7.79$, $P > 0.99$, $df = 29$). The most parsimonious model includes migratory direction, population size and detectability, and considerably less support was found for all other models (Table 2). Migratory direction and population size were included in all models with substantial support (Table 2). Model averaging showed very strong support for migratory direction and population size with predictor weights of more than 0.99, less support for detectability with a predictor weight of 0.92, but much less support for distance and vagrancy area with predictor weights of only 0.13 and 0.12, respectively (Table 3). The best model was $Y_{obs} = N^{0.48} \times 0.060X_{90} \times 0.29X_{113} \times 0.018X_{135} \times 0.0045X_{180} \times 0.0040X_{225} \times 1.8^{detectability} - 1$, where X_{90} , X_{113} , X_{135} , X_{180} and X_{225} are dummy variables (for X_{90} : 1 if migratory direction = 90%, 0 if migratory direction < or > 90%, etc.). This model had $R^2 = 0.856$.

Using indexed values of the population size (rounding log N to nearest integer) to control for uncertainty in estimates resulted in identical conclusions. The permutational phylogenetic regression including the phylogenetic distance matrix demonstrated no effect of phylogeny ($P = 0.59$).

For the combined data set of the two most typical night-migrating groups, warblers and flycatchers, much the same results were found although detectability was only weakly supported (Table 3). Strong support for the effects of population size and migratory direction was

Table 2. Summary of the models for the log number of reverse migrants. Variables included in the models are migratory direction (1), population size (2), distance (3), vagrancy area (4) and detectability (5). (Global model: $R^2 = 0.86$; $n = 34$). K = number of estimated parameters in the model, AIC_c = Akaike's information criterion value, AIC_c = AIC corrected for small sample size, Δ_i = AIC_c difference, w_i = AIC_c weight. Only models with $\Delta_i \leq 10$ are included, as models with $\Delta_i < 10$ have essentially no support. Models are ordered in terms of Δ_i for AIC_c .

Model parameters	K	AIC_c	Δ_i	w_i
{125}	8	9.771	0.000	0.70
{1235}	9	13.465	3.695	0.11
{1245}	9	13.704	3.933	0.10
{12}	7	14.642	4.871	0.06
{12345}	10	17.900	8.129	0.01
{124}	8	18.212	8.442	0.01

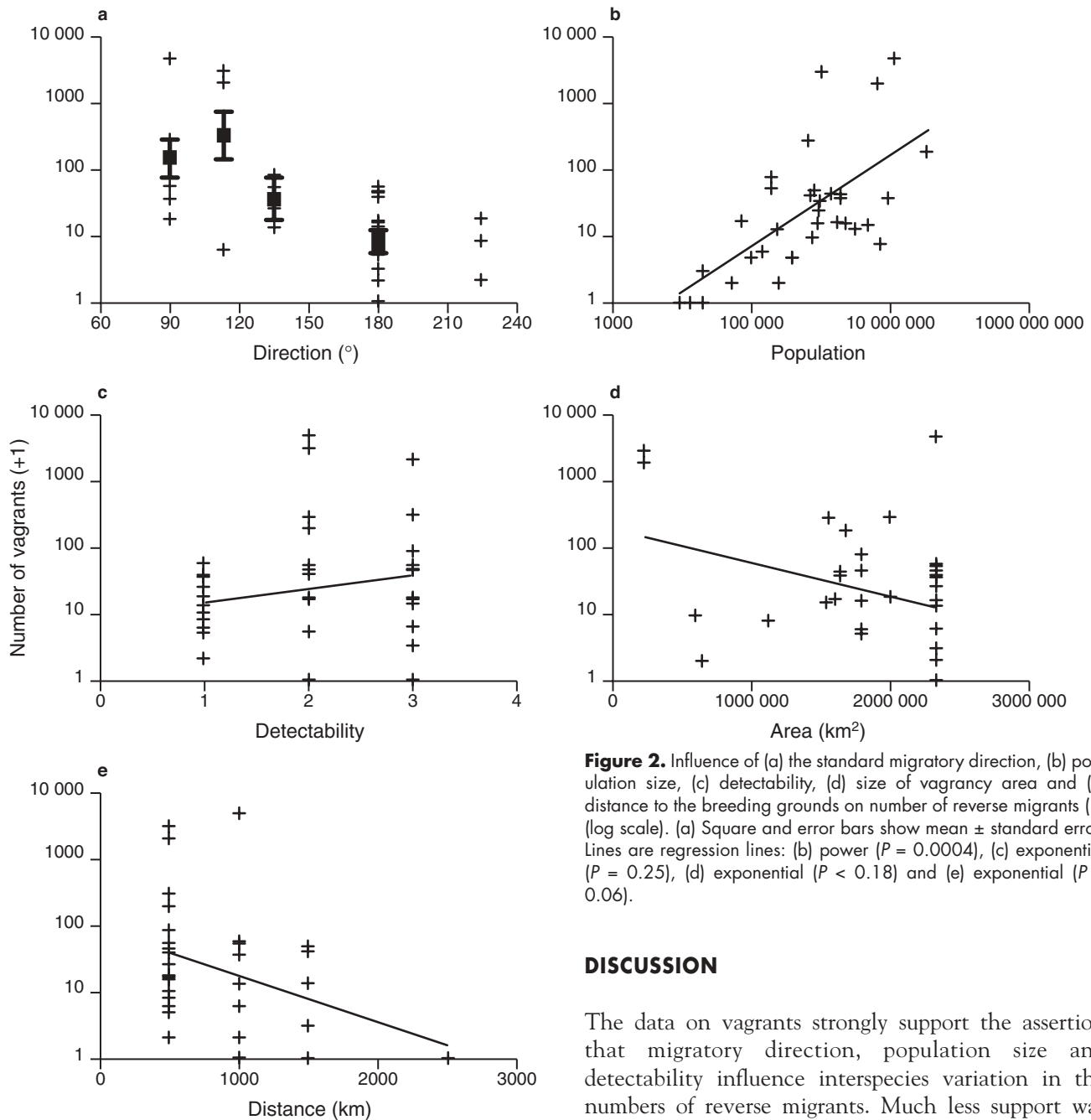


Figure 2. Influence of (a) the standard migratory direction, (b) population size, (c) detectability, (d) size of vagrancy area and (e) distance to the breeding grounds on number of reverse migrants (+1) (log scale). (a) Square and error bars show mean \pm standard error. Lines are regression lines: (b) power ($P = 0.0004$), (c) exponential ($P = 0.25$), (d) exponential ($P < 0.18$) and (e) exponential ($P = 0.06$).

DISCUSSION

The data on vagrants strongly support the assertion that migratory direction, population size and detectability influence interspecies variation in the numbers of reverse migrants. Much less support was found for effects of area and migration distance. No phylogenetic effects were found, making it reasonable to consider the results of the information theoretic approach only.

The dependence on migratory direction shows that birds migrating in an easterly direction are more likely to reverse their migratory direction than are birds migrating in a southwesterly/southerly direction. It is unlikely that this correlation should be the result of biased observer coverage as only the relationship between numbers of different species is relevant. Furthermore, migratory

also found for the British and Irish subset and for the Scandinavian subset. The Scandinavian data set also strongly supported an effect of detectability, which was less supported in the British and Irish subset (Table 3).

A traditional hypothesis testing approach gave very similar results in all cases. For the full data set, significant effects were found for migratory direction ($P < 0.0001$), population size ($P = 0.0001$) and detectability ($P = 0.01$), but not for vagrancy area ($P = 0.98$) or distance ($P = 0.68$).

Table 3. Relative importance of explanatory variables included in the analysis. Shown are predictor weights, $w_i(j)$, based on model averaging over all possible models; na, not applicable.

Data set	Migratory direction	Population size	Distance	Vagrancy area	Detectability
All species, full geography	> 0.99	> 0.99	0.13	0.12	0.92
Warblers and flycatchers, full geography	> 0.99	> 0.99	0.17	0.18	0.17
All species, British and Irish subset	> 0.99	> 0.99	0.23	na	0.54
All species, Scandinavian subset	> 0.99	> 0.99	0.24	na	0.99

direction explained significant amounts of variation when only subsamples of the data set were analysed, where observer coverage is less likely to be biased. Thus the data did not support the expectation from a simple compass-based migration system.

The effect of migratory direction was confirmed by ring recoveries reported by Zink (1973–85), when evidence of reverse migration was found only for species migrating in an easterly direction. However, this recovery database includes only few recoveries of easterly migrating species. Definite recoveries in the reverse direction have only been found for Barred Warbler *Sylvia nisoria*, Red-breasted Flycatcher *Ficedula parva* (Glutz von Blotzheim & Bauer 1991, 1993) and Yellow-browed Warbler (Folvik 1992).

Relation to the orientation system

The results indicate that prolonged reverse orientation is most common in the east–west direction. It is thus highly unlikely that east–west migrating species and southerly migrating species have basically the same circular distribution of migratory directions (differences in concentration/shape). Differential survival seems unlikely to effect the patterns much, as reverse migration of southwest migrants was not found in the ring recoveries, which even cover rather short distances (more than 100 km). Åkesson (1999) concluded that reverse migration observed for long-distance southwest migrating species was most likely due to a temporary retreat from coastal areas, and that it was of short duration and not the result of orientation errors.

On the basis of the present study, it cannot be concluded whether it is the migratory direction itself that causes the result or some correlates of the migratory direction (e.g. geographic distribution, ecology or immigration routes). Dividing the data set into eastern, southeastern and southern species according to general wintering areas (Asia, East Africa and West Africa) did not account for a significant amount of variation in numbers of vagrants. However, dividing the data set into eastern and southern species

accounted for a significant amount of variation.

The result is not consistent with the general compass models as these would imply the same circular distribution of individual migratory directions, regardless of the standard migratory direction. However, it could be related to a different availability of orientation cues along different migratory routes. Alternatively, birds could use different cues for determining east/west compared with north/south as suggested by other studies (Weindler *et al.* 1996). Magnetic cues (e.g. declination and anomalies) and weather (e.g. cloud cover relevant for using stellar cues for orientation) vary quite markedly with geography and many gradients change more markedly when moving north/south rather than east/west, e.g. temperature and daylight hours. Furthermore, the very long distances travelled by these species (for some twice the distance to the area where the migratory direction changes) raise a serious question on the sufficiency of the endogenous clock part of a vector navigation system to terminate the migratory programme, as these birds seem to lack the cue for termination.

The prolonged reverse orientation of birds normally migrating in an easterly direction is further supported by surprising numbers of some species such as Barred Warblers and Red-breasted Flycatchers being reported from Iceland (Glutz von Blotzheim & Bauer 1991, 1993). Furthermore, most Siberian species that regularly turn up in Europe in numbers in autumn (e.g. Pallas's Warbler *Phylloscopus proregulus*) are thought to have an initial east/east-southeast migratory direction (Cramp 1992), making reverse orientation a suitable explanation for the significant numbers observed in northwest Europe.

Possible mechanisms

Several (non-exclusive) mechanisms have been proposed to account for observed patterns of reversed orientation. Basically these are: (1) natural variation in the normal migratory direction (standard direction), followed by differential survival in different directions (Alerstam

1982); (2) over-representation of certain directions other than the normal migratory direction, including reverse orientation (Rabøl 1969, 1985); 'mirror-image' orientation (DeSante 1983) and environmentally induced misorientation because of magnetic anomalies (Alerstam 1991); and (3) 'vagrants as the expanding fringe of a growing population' (Veit 1997, 2000).

The effect of abundance on numbers of vagrants is consistent with all three proposed mechanisms. For the very high number of reversed migrants observed in some species, natural variation in the standard migratory direction (1) is probably a poor explanation as this would imply an unexpectedly high proportion of these species migrating in all directions (where they are not generally found), and some over-representation of specific directions other than the normal migratory direction (2) seems likely (Rabøl 1976), similar to the conclusion reached for vagrants of certain Nearctic species (DeSante 1983). This is consistent with the very high directional concentrations found for long-distance recoveries of southwest migrating species (Mouritsen 1998, Thorup & Rabøl 2001) and the very low variation found in migratory direction between individuals (Thorup *et al.* 2000).

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ENDNOTE

a. The basic underlying model for the analysis is:

$$Y = N \times P$$

where Y is number of reversed migrants, N is the size of the relevant migratory population and P is the probability of reversing migration. The probability of reversing migration will be a function of factors (e.g. night migrants and day migrants could have different probabilities of reversing migration) and confounding variables (e.g. the size of the area where migrants are counted).

Assuming that the probability of reversing migration

is dependent on the inherited migratory behaviour of a particular species, a possible model for the actually observed numbers of reversed migrants, including likely confounding variables becomes:

$$Y_{\text{obs}} = N \times f(\text{migratory behaviour, distance, vagrancy area, detectability}),$$

where migratory behaviour in this case is the standard migratory direction, detectability is a measure of probability of detecting a particular species, distance is the distance to the breeding grounds, vagrancy area is the size of the area where reversed migrants are counted, and f is a function ranging from 0 to 1. A possible influence of weather and the greater propensity of expanding species to disperse far have not been incorporated due to the lack of good data. Assuming linear dependence on confounding variables the function f could have the simple form:

$$f = f_1(\text{migratory behaviour}) \times a_1 \text{distance} \times a_2 \text{vagrancy area} \times a_3 \text{detectability}$$

where f_1 is a function and a_i are constants, and thus:

$$Y_{\text{obs}} = N \times f_1(\text{migratory behaviour}) \times a_1 \text{distance} \times a_2 \text{vagrancy area} \times a_3 \text{detectability}$$

or:

$$\ln(Y_{\text{obs}}) = \ln N + \ln [f_1(\text{migratory behaviour})] a^*_1 \ln(\text{distance}) a^*_2 \ln(\text{vagrancy area}) a^*_3 \ln(\text{detectability})$$

where $a^*_i = \ln(a_i)$.

Inserting migratory direction as a categorical variable, exponential relationships for confounding variables and substituting Y_{obs} with $(Y_{\text{obs}} + 1)$ results in the following general linear model used for analysis:

$$\ln(Y_{\text{obs}} + 1) = \beta_0 + \beta_1 \ln N + \beta_{21} X_1 + \beta_{22} X_2 \dots + \beta_{2i} X_i + \beta_3 (\text{distance}) + \beta_4 (\text{vagrancy area}) + \beta_5 (\text{detectability}) + \varepsilon$$

where X_i are dummy variables (1 if migratory direction = i , 0 if migratory direction < or > i).

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APPENDIX 1

Breeding and wintering areas and migratory direction according to Cramp (1988, 1992) and Cramp & Perrins (1993), number of breeding pairs in Europe, including Russia, according to Hagemeyer & Blair (1997), percentage of population size occurring in Europe (Eur %) estimated from Cramp (1988, 1992) and Cramp & Perrins (1993), calculated population size (World pop: breeding numbers in Europe divided by European percentage), detectability (Det., ranging from 1 to 3, where 1 = most difficult to detect and 3 = most easily detected), the size of the area of the countries included in the analysis for each species (vagrancy area in Fig. 1) and distance from the edge of the breeding area to the vagrancy area for species analysed (at least 500 km according to the definition of vagrancy area, Fig. 1).

Family	Species (subspecies)	Breeding area	Wintering area	Breeding Nos (Eur)	Eur %	
Prunellidae	<i>Prunella montanella</i>	Urals	China	16 000	0.07	
	<i>Prunella atrogularis</i>	Urals	SWC Asia	3 500	0.07	
Muscicapidae	<i>Cercotrichas galactotes</i>	S Europe	Africa	40 000	0.4	
	<i>Luscinia megarhynchos</i>	Europe	Africa	3 700 000	0.5	
	<i>Luscinia calliope</i> ¹	Urals	SC-E Asia	> 0	0.01	
	<i>Tarsiger cyanurus</i>	Finland eastwards	S China	1 000	0.01	
	<i>Saxicola torquata maura</i>	Finland eastwards	SE Asia	32 000	0.05	
	<i>Oenanthe isabellina</i>	SE Europe	Africa	650 000	0.2	
	<i>Oenanthe pleschanka</i>	SE Europe	Africa	300 000	0.2	
	<i>Oenanthe hispanica</i>	S Europe	Africa	850 000	0.9	
	<i>Zoothera dauma</i>	Urals	S Asia	20 000	0.02	
	<i>Monticola saxatilis</i>	S Europe	Africa	50 000	0.33	
	<i>Turdus ruficollis atrogularis</i>	Urals	Asia	50 000	0.06	
	<i>Ficedula p. parva</i>	E Europe	India	3 500 000	0.5	
	<i>Ficedula albicollis</i>	E Europe	Africa	5 000 000	1	
	<i>Ficedula semitorquata</i>	SE Europe	Africa	7 000	0.75	
	Sylviidae	<i>Locustella lanceolata</i>	Urals	SE Asia	6 000	0.03
		<i>Locustella fluviatilis</i>	E Europe	Africa	700 000	0.9
<i>Locustella luscinioides</i>		Europe	Africa	200 000	0.8	
<i>Acrocephalus agricola</i>		EC Europe	India	500 000	0.05	
<i>Acrocephalus dumetorum</i>		NE Europe	India	330 000	0.33	
<i>Hippolais pallida</i>		S Europe	Africa	1 800 000	0.75	
<i>Hippolais caligata</i> ²		W Russia	India	> > 0	0.2	
<i>Hippolais polyglotta</i>		SW Europe	W Africa	1 800 000	1	
<i>Hippolais olivetorum</i>		SE Europe	Africa	13 000	1	
<i>Sylvia cantillans</i>		S Europe	Africa	2 000 000	1	
<i>Sylvia mystacea</i>		SE Europe	Africa	> 0	0.33	
<i>Sylvia rüppelli</i>		SE Europe	Africa	20 000	1	
<i>Sylvia hortensis</i>		S Europe	Africa	300 000	0.75	
<i>Sylvia nisoria</i>		E Europe	E Africa	550 000	0.5	
<i>Phylloscopus trochiloides</i>		E Europe	India	350 000	0.5	
<i>Phylloscopus borealis</i>		NE Europe	SE Asia	3 000 000	0.08	
<i>Phylloscopus inornatus</i>	N Urals	SE Asia	50 000	0		
<i>Phylloscopus bonelli</i>	S Europe	Africa	2 000 000	1		
Laniidae	<i>Lanius senator</i>	SW/S Europe	Africa	700 000	0.93	
	<i>Lanius minor</i>	SE Europe	Africa	100 000	0.5	
	<i>Lanius nubicus</i>	SE Europe	Africa	17 000	0.8	

S, south; W, west; E, east; C, central. ¹Given as rare breeding bird in Hagemeyer & Blair (1997), species excluded from analysis. ²No estimates of breeding numbers found in the literature.

continued

APPENDIX 1 continued.

Family	Species (subspecies)	World pop	Migratory direction (°)		Det.	Area (km ²)	Dist. (km)	
Prunellidae	<i>Prunella montanella</i>	240 000	SE	135	1	2 349 177	1000	
	<i>Prunella atrogularis</i>	53 000	SW	225	1	2 349 177	1000	
Muscicapidae	<i>Cercotrichas galactotes</i>	100 000	S	180	1	1 802 448	500	
	<i>Luscinia megarhynchos</i>	7 400 000	SW	225	1	1 137 230	500	
	<i>Luscinia calliope</i> ¹	–	SE/E?	113	1	2 349 177	1000	
	<i>Tarsiger cyanurus</i>	75 000	E	90	1	2 015 380	500	
	<i>Saxicola torquata maura</i>	690 000	E	90	3	2 015 380	500	
	<i>Oenanthe isabellina</i>	3 300 000	S/NW	180	3	2 349 177	1500	
	<i>Oenanthe pleschanka</i>	1 500 000	S/NW	180	3	2 349 177	1500	
	<i>Oenanthe hispanica</i>	940 000	S	180	3	1 802 448	500	
	<i>Zoothera dauma</i>	1 000 000	E?	90	1	2 349 177	1000	
	<i>Monticola saxatilis</i>	150 000	S	180	3	1 802 448	500	
	<i>Turdus ruficollis atrogularis</i>	830 000	S	180	3	2 349 177	1000	
	<i>Ficedula p. parva</i>	7 000 000	ESE	113	3	2 43 137	500	
	<i>Ficedula albicollis</i>	5 000 000	S	180	3	1 549 268	500	
	<i>Ficedula semitorquata</i>	9 333	S	180	3	2 349 177	1000	
	Sylviidae	<i>Locustella lanceolata</i>	200 000	E	90	1	2 349 177	1000
		<i>Locustella fluviatilis</i>	780 000	S	180	1	602 770	500
<i>Locustella luscinioides</i>		250 000	S	180	1	650 759	500	
<i>Acrocephalus agricola</i>		10 000 000	SE	135	1	2 349 177	1500	
<i>Acrocephalus dumetorum</i>		990 000	SE	135	1	2 349 177	500	
<i>Hippolais pallida</i>		2 400 000	S	180	2	2 349 177	500	
<i>Hippolais caligata</i> ²		–	SE	135	2	2 349 177	500	
<i>Hippolais polyglotta</i>		1 800 000	SW	225	2	1 614 907	500	
<i>Hippolais olivetorum</i>		13 000	S	180	2	2 349 177	1000	
<i>Sylvia cantillans</i>		2 000 000	SW/S	180	2	1 802 448	500	
<i>Sylvia mystacea</i>		–	S	180	2	2 349 177	2500	
<i>Sylvia rüppelli</i>		20 000	S	180	2	2 349 177	1500	
<i>Sylvia hortensis</i>		400 000	S	180	2	1 802 448	500	
<i>Sylvia nisoria</i>		1 100 000	ESE	113	2	243 137	500	
<i>Phylloscopus trochiloides</i>		700 000	ESE	113	2	1 571 580	500	
<i>Phylloscopus borealis</i>		35 000 000	E	90	2	1 698 418	500	
<i>Phylloscopus inornatus</i>		12 500 000	E	90	2	2 349 177	1000	
<i>Phylloscopus bonelli</i>		2 000 000	S	180	2	1 650 400	500	
Laniidae		<i>Lanius senator</i>	750 000	SW/S	180	3	1 650 400	500
		<i>Lanius minor</i>	200 000	E/S	135	3	1 802 448	500
	<i>Lanius nubicus</i>	21 000	S	180	3	2 349 177	1500	

APPENDIX 2

Number of vagrants on reverse migration in 1958–92 in Britain and Ireland (BI), France (F), Belgium (B), The Netherlands (NL), Denmark (DK), Norway (NO), Sweden (SE), Finland (SF) and Germany (D). Records found in Rønne (1994) and additionally as indicated by superscript numbers (see footnote).

Family	Species	BI	F	B	NL	DK	NO	SE	SF	D	Total	
Prunellidae	<i>Prunella montanella</i>					1		7	4		12	
	<i>Prunella atrogularis</i>								1		1	
Muscicapidae	<i>Cercotrichas galactotes</i>	4	+								4	
	<i>Luscinia megarhynchos</i>	+	+	+	+	2	2	2	1	+	7	
	<i>Luscinia calliope</i>	1				2		1	1		5	
	<i>Tarsiger cyanurus</i>	7			2	1	2	2	+	3	17	
	<i>Saxicola torquata maura</i>	185			15	14	12	60	+ ²	3	289	
	<i>Oenanthe isabellina</i>	7				1	1	1	2		12	
	<i>Oenanthe pleschanka</i>	22				1	1	8	9	3	44	
	<i>Oenanthe hispanica</i>	6	+		1		4	2	1	1	15	
	<i>Zoothera dauma</i>	16			7		3	4	2	2	34	
	<i>Monticola saxatilis</i>	1	+					2	1	1	5	
	<i>Turdus ruficollis atrogularis</i>	19				4	3	10	4	10	50	
	<i>Ficedula p. parva</i> ³	2000	+	+	+	+	+	+	+	+	2000	
	<i>Ficedula albicollis</i>	2			3		8		+	1	+	14
	<i>Ficedula semitorquata</i>											0
Sylviidae	<i>Locustella lanceolata</i>	45					1	3	1	3	1	54
	<i>Locustella fluviatilis</i>	5	+	+	+	3	1	+	+	+	9	
	<i>Locustella luscinioides</i> ⁴	+	+	+	+	+		+	1	+	1	
	<i>Acrocephalus agricola</i>	16			10	2	1	8			37	
	<i>Acrocephalus dumetorum</i> ¹	11	1	4			5		2	1	24	
	<i>Hippolais pallida</i>	13					1		1		15	
	<i>Hippolais caligata</i>	36		1	4	3	1	2	2	2	51	
	<i>Hippolais polyglotta</i> ³	10*	+	+	+	1		2	3	16		
	<i>Hippolais olivetorum</i>											0
	<i>Sylvia cantillans</i> ³	37*	+		2			2	1	1	43	
	<i>Sylvia mystacea</i>											0
	<i>Sylvia rüppelli</i>											0
	<i>Sylvia hortensis</i>	3	+								1	4
	<i>Sylvia nisoria</i> ³	3000	+	+	+	+	+	+	+	+	+	3000
	<i>Phylloscopus trochiloides</i> ^{1,2}	220	10	2	13	15	11	11	+	+	10	281
	<i>Phylloscopus borealis</i> ¹	159	6		9	1	+	6	+	+	6	187
<i>Phylloscopus inornatus</i>	2642	427	242	450	143	50	420	336	168	168	4878	
<i>Phylloscopus bonelli</i> ²	20*	+	+	10		1	2	1	1	3	37	
Laniidae	<i>Lanius senator</i> ³	15*	+	+	10	3	5	2	5	2	42	
	<i>Lanius minor</i> ³	34	+			7		20	15	4	80	
	<i>Lanius nubicus</i>							1	1		2	

No entry in a column indicates a zero value. *Cases where a country was divided into a reverse migration and a non-reverse migration part to avoid excluding significant numbers of reverse migrants; +, the species breed in or close to the country. ¹From Mitchell & Young (1997); ²from Lewington *et al.* (1991); ³from Dymond *et al.* (1989); ⁴from B.O. Høyland (pers. comm.).