J Ornithol
DOI 10.1007/s10336-007-0140-6

ORIGINAL ARTICLE

Birds from the Far East in Central Europe: a test of the reverse migration hypothesis

Robert Pfeifer · Jutta Stadler · Roland Brandl

Received: 3 November 2006 / Revised: 12 February 2007 / Accepted: 15 April 2007

Abstract Every year birdwatchers throughout Europe record the arrival of a considerable number of vagrants from the eastern Palaearctic. We analysed the occurrence of such vagrants in Central Europe of the genera *Phylloscopus*, *Turdus* and *Zoothera* in Central Europe. Our results revealed that the occurrence of a species depended on total population size, but not on body size. Furthermore, the occurrence of species in Central Europe increased with distance between the breeding range and wintering range, but the distance between the breeding range and Europe had no effect. These results indicate that the migratory restlessness of species determines whether an East Asian species arrives in Europe. Overall, our data support the hypothesis that the migratory program determines vagrancy.

Keywords *Phylloscopus* · Reverse migration hypothesis · *Turdus* · Weather hypothesis · Vagrants · *Zoothera*

Communicated by A. Hedenström.

R. Pfeifer
Dilchertstr. 8, 95444 Bayreuth, Germany

J. Stadler
Department of Community Ecology,
Centre for Environmental Research Leipzig-Halle,
Theodor-Lieser-Strasse 4, 06120 Halle/Saale, Germany

R. Brandl (✉)
Department of Ecology, Philipps-University Marburg,
Karl-von-Frisch-Str, 35043 Marburg, Germany
e-mail: brandlr@staff.uni-marburg.de

Introduction

Every year birdwatchers report the occurrence of species in Europe that do not breed or regularly overwinter there. For some of these vagrants, the breeding and wintering ranges are thousands of kilometres distant from Europe. An impressive array of committees has been set up over the years which verifies and evaluates these records (van den Berg and Bosman 1999). While one trend of thought views these vagrants solely as curiosities without any deep or lasting scientific implication, others lines of thought feel that the records call for a scientific evaluation of causes and consequences (Barthel and Bezzel 1990). Firstly, vagrants may be propagules for an expansion of the distributional range. A well-known example of this is the colonization of South America by the Cattle Egret *Bubulcus ibis* (Maddock and Geering 1994; see also Veit 1997, 2000). Secondly, a study of the causes of the occurrence of individuals far away from their breeding grounds, their regular migration route and their wintering areas may facilitate scientists in gaining an understanding of the migration system of birds (Rabøl 1969, 1976; Thorup 2004). In the present study, this latter issue will be addressed from a macroecological perspective.

The documented recordings of vagrants give an impression of relative abundance as well as seasonal occurrence in Europe. A qualitative evaluation of these records reveals three general patterns. Firstly, an important group of vagrants consists of eastern Palaearctic species (especially Leaf Warblers *Phylloscopus*, Thrushes *Turdus* and *Zoothera*, Buntings *Emberiza* and Pipits *Anthus*). Secondly, the relative abundance of vagrants differs considerably between species. Thirdly, most recordings of rarities occur in the autumn. Two hypotheses have been proposed to explain these observations: the ''weather hypothesis'' and the ''reverse migration hypothesis''.

One explanation for the presence in Central Europe of Leaf Warblers from the eastern Palaearctic is that anticyclones transport the individuals to Europe (Baker and Catley 1987; see also Glutz von Blotzheim and Bauer 1991). Such weather situations are fairly common in eastern Asia during the autumn, which would explain the peak of vagrants at this time. Nevertheless, the weather hypothesis assumes implicitly that birds are not able to react actively to wind conditions (Liechti 2006). Furthermore, vagrants from the eastern Palearctic still appear in Europe in years without strong anticyclones. Hence, the weather hypothesis would not appear to be a satisfactory explanation for these vagrants. The reverse migration hypothesis has been suggested as a possible alternative. Rabøl (1969, 1976) recognized that certain vagrants of the genus *Phylloscopus* follow a great circle route during migration. An error of 180° would lead birds to Europe (Fig. 1; for a critical discussion of the reverse migration hypothesis see Gilroy and Lees 2003). Experiments with birds caught in Europe support the reverse migration hypothesis (Thorup 1998). As a mechanism for reversed migration some authors suggest reverse orientation, a phenomenon documented for many migratory species (e.g. Sandberg 1994). Other possible mechanisms include natural variation in the normal migratory direction with survival differing between directions (Alerstam 1982 as cited by Thorup 2004) or a switch from the autumn to the spring programme.

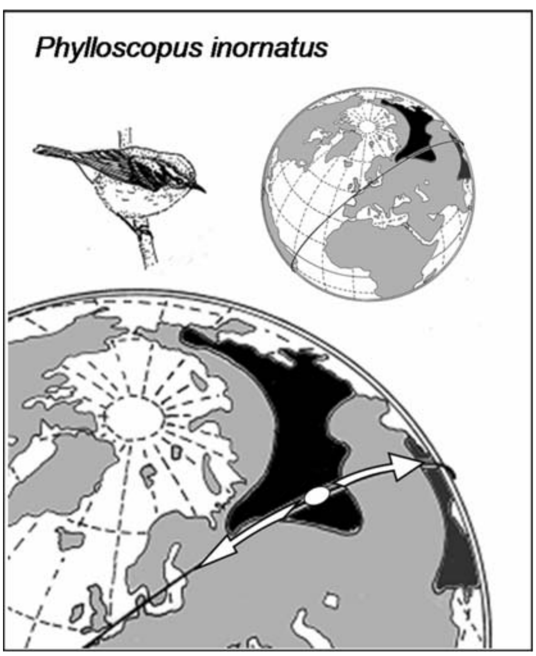


Fig. 1 Sketch of the basic idea behind the ''reverse migration hypothesis'' shown for the Yellow-browed Warbler *Phylloscopus inornatus*. If individuals follow a great *circle line* to the wintering area, a switch of 180° in the migration direction would lead them to Europe (adapted from Rabøl 1976)

If reversed orientation or a switch from the autumn to the spring programme is the principal mechanism of reversed migration, one would expect that, given a simple compass-based migration system, the occurrence of vagrants would be independent of the migratory direction (Thorup 2004). However, Thorup (2004) showed that the relative abundance of vagrants does depend on this direction, with many more vagrants from the eastern Palaearctic reaching Europe than from the Mediterranean. This results indicates that cues along the migratory routes influence the orientation system (see also Weindler et al. 1996). As well as the orientation system, the endogenous clock to terminate the migration programme should also influence vagrancy. For warblers, migration distance and migratory restlessness (''Zugunruhe'') are correlated (Gwinner 1968; Berthold 1973). Hence, only species with a sufficiently long migratory restlessness should reach Central Europe. Otherwise, species should stop along the great circle before they reach Central Europe (see Fig. 1).

To test this hypothesis, we need to consider other factors which influence the occurrence of vagrants. (1) Abundance should affect vagrancy (Thorup 2004). If, irrespective of species, all individuals have the same probability to deviate from the regular migratory direction, we expect that the number of vagrant individuals increases with total population size of the species (see also McLaren et al. 2006). Given that abundance increases with distributional range size (e.g. Gaston 1994), we would expect a positive correlation between the numbers of vagrant individuals and the distributional range size across species. Furthermore, the probability that a species (not individual!) is recorded as a vagrant should also increase with distributional range size. (2) The probability that an individual dies increases with the distance travelled. Therefore, the number of vagrant individuals and the probability that a species occurs as a vagrant should decrease with the distance between Europe and the breeding range. Thorup (2004) failed to document the latter prediction, perhaps because he considered only species with records in Europe. Therefore, to test our hypothesis that only those species with a sufficiently long migration distance arrive in Europe, we consider not only species which have arrived in Europe but also species within the same genera for which no records of vagrancy to Central Europe are available.

Material and methods

We considered species of three passerine genera (*Phylloscopus*, Sylviidae; *Turdus* and *Zoothera*, Turdidae) with a breeding range east of Central Europe (Table 1). For the

Table 1 Eastern Palaearctic species of the bird genera *Phylloscopus* (leaf warblers), *Turdus* and *Zoothera* (thrushes) are recorded every year as vagrants in Central Europe

Genus	Central Europe	Total	Eastern Palaearctic	
			Migratory	Recorded in Europe
Phylloscopus	5	29	27	8
Turdus	6	16	8	4
Zoothera	0	8	3	2

The table gives the species richness of these genera in Central Europe and in the eastern Palaearctic, the number of migrating species in the eastern Palaearctic and the number of these species which have been recorded in Central Europe

definition of species we followed Baker (1997) for *Phylloscopus* and Clement and Hathway (2000) for the two genera of Turdidae (see Appendix). Central Europe is defined as including the following countries: The Netherlands, Belgium, Luxembourg, Germany, Poland, Czech Republic, Slovakia, Hungary, Austria and Switzerland. We selected only species whose western distributional border lay to east of these countries. All species considered are migratory. The migratory direction for most of the species is to the south with little variation between species. Therefore we decided not to consider the migratory direction as a predictor variable (see Thorup 2004). For all species we extracted the following variables from the literature: body mass (g), wing length (mm), size of breeding range, distance between centre of breeding range and centre of wintering range (km) and distance between centre of breeding range and Central Europe (km) using Berlin as an arbitrary reference point.

For the morphological variables we used the data presented in Baker (1997) as well as Clement and Hathway (2000). Where these two sources reported only ranges of measurements, we used the midpoint. For some species, Baker (1997) and Clement and Hathway (2000) provide no data on body mass or wing length, and in these cases we used data given in Glutz von Blotzheim and Bauer (1985, 1988, 1991) as well as Ali and Ripley (1973). For *Turdus cardis* and *T. feae* we found no data at all on body mass. To estimate body mass for these two species, we therefore constructed a regression between wing length and body mass across 20 species of thrushes occurring in the eastern Palaearctic. We used the least square regression line [body mass (g) = –167.7 (g) + 1.965 (g mm^{-1}) wing length (mm); $r^2 = 0.79$] to estimate the expected body mass for *T. cardis* and *T. feae* from their wing length.

The variables characterizing range size, the distances between breeding and wintering ranges as well as the distance between the breeding range and Central Europe were estimated from the maps in Baker (1997) and Clement and Hathway (2000). As these maps differ in scale between species, we first used certain geographic features (e.g. estuaries, peninsulas) on these maps to estimated the scale and then measured the extent of distributional range in south–north and east–west directions as well as the distances to the centre of the wintering range and to Central Europe. These measurements were converted to kilometres. The product of the two extents provided a rough estimate of the distributional range size (in km^2). Price et al. (1997) published estimates of the distributional range sizes of *Phylloscopus* species, and our data set on distances correlated well with that of these authors [$r^2 = 0.87$; $n = 26$ excluding *P. cantator* and *P. ricketti*; Price et al. 1997 combined these two species; Price et al. (1997) and Baker (1997) combined *P. tenellipes* and *borealoides* into one species, Price et al. using the name *borealoides*).

The records of the selected species in Central Europe were extracted from Glutz von Blotzheim and Bauer (1985, 1988, 1991; see Appendix). All records were summed up, and we used this sum as an index of the relative abundance of vagrants in Central Europe. For comparison, we used information on the occurrence and abundance of passerine species from the eastern Palaearctic recorded in The Netherlands (extracted from van den Berg and Bosmann 1999). In a second step, we recoded the relative abundance into a binary variable (0 and 1). Zero indicates that a species was not recorded, whereas one indicates a species was recorded as vagrants in Central Europe. This coding allows the probability that at least one record exists to be estimated.

The distribution of the number of records, distributional range size and the distances were fairly skewed, and we $\log_{10}$-transformed these variables prior to all analyses. The data were analysed using the generalized linear model with the appropriate error distribution using R ® Development Core Team 2004). For a multivariate analysis we decided to use hierarchical partitioning (MacNally 1996, 2000) as implemented in the package HIER.PART (Walsch and MacNally 2003) within R ® Development Core Team 2004). This method does not aim to identify an appropriate regression equation, but identifies those variables that have high and independent correlations with the dependent variable and, therefore, likely to be most influential on the independent variable.

Results

Of 27 selected *Phylloscopus* species (see Appendix) and 11 species of turdids, eight and six species, respectively were recorded as vagrants in Central Europe (Table 1). In The Netherlands, the seasonal occurrence of East Asian passerines showed two peaks (Fig. 2): one in the spring and one in the autumn. The records of *Phylloscopus* and turdids followed more or less the same pattern (Fig. 3). Most individuals of the genus *Phylloscopus* were recorded during the autumn. The peak number of recordings in the spring and autumn suggests a relationship between migration and vagrancy.

The number of recordings ranged from one individual to nearly 1000 individuals (Fig. 3). Across all species recorded in Central Europe, we found a correlation between the number of recordings in Central Europe and the size of the distributional range.

We then considered the probability that a species may occur as a vagrant in Central Europe and tested simple relationships with a generalized linear model (log-link function; binomial error probability; Fig. 4). This probability increased with range size as well as with usual migration distance, but we found no relationship with the distance of the breeding range to Central Europe (Fig. 4). When the ratio of migration distance to the distance between the breeding range and Central Europe was calculated, we again found a significantly increased probability that a species may occur as a vagrant in Central Europe with increasing ratio (Fig. 4). Using hierarchical partitioning we found that size of breeding range and the ratio between migration distance and distance to Central Europe showed significant independent contributions to the probability of vagrancy (Fig. 5). Body size and taxon (warblers or trushes) did not contribute significantly to that probability.

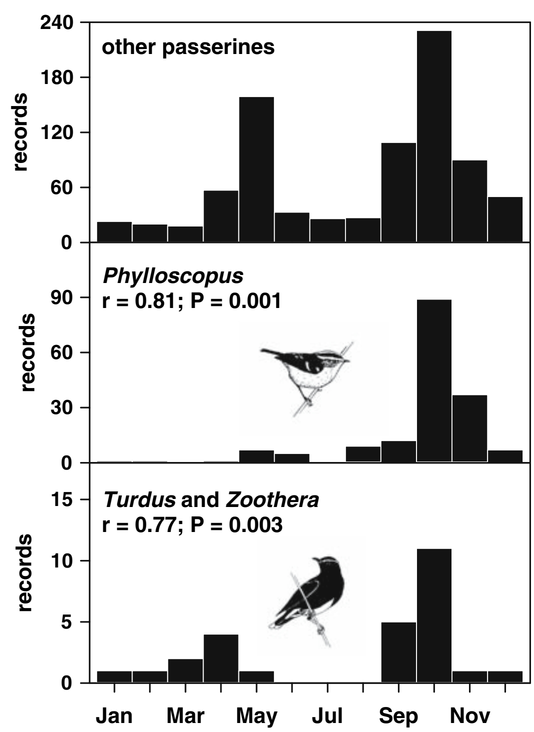


Fig. 2 Phenology of the records of East Asian passerines (excluding *Phylloscopus*, and turdids) in The Netherlands as well as the phenology of the recordings of East Asian *Phylloscopus* and thrushes of the genera *Turdus* and *Zoothera* used during this study. The correlation coefficients measure the similarity of the phenology of the records for *Phylloscopus* and thrushes with the phenology of the East Asian passerines recorded in The Netherlands

Discussion

One of the factors responsible for the transport between the breeding range and Europe are bad weather conditions. In the aftermath of storms, North American species are often recorded on the other side of the Atlantic Ocean (e.g. Hering and Alfrey 2006). One might expect small birds to be more often affected by winds than large birds. However, we found no influence of body size on the probability that a species occurs as a vagrant in Central Europe. Firstly, we found no difference in that probability between thrushes and *Phylloscopus*, although thrushes are much larger than leaf warblers. Secondly, within the genus *Phylloscopus*, body size had no influence on this probability. However, the role of body size may not be so simple (see also McLaren et al. 2006). Small birds have a higher probability of death from starvation on the way from the breeding range to Central Europe. Calder (1974) reports a positive correlation between body size and survival time of fasting birds. According to the equations reported by Calder (1974), a bird of 10 g may survive 1 day without food, a bird of 50 g almost 3 days. Clearly, small species should have a lower probability of surviving a long flight without stops for feeding than large species. Interestingly, the percentage of passerines (small birds) versus non-passerines (larger birds) in the list of vagrants differs for species from East Asia and North America. In The Netherlands (van den Berg and Bosman 1999), eight of 40 North American vagrants were passerines (20%), whereas 32 of 46 East Asian species were passerines (70%; $\chi^2 = 21.2$, $P < 0.001$). This difference in the composition of vagrants between North America and Asia indicates that the causes for the occurrence of North American and East Asian vagrants may be different.

We found that the probability that a species occurs as a vagrant in Central Europe increases with increases in the ratio of the distance between breeding and wintering range to the distance between breeding range and Central Europe. This relationship still holds when we corrected for abundance, suggesting that the migration programme and associated restlessness are important factors that determine whether a species may reach Europe. Errors in the migration programme (switch of the seasonal programme or reversed orientation in autumn) drive species on the great circle route from their breeding range to Central Europe (Alerstam and Petterson 1991). However, only those birds that are sufficiently restless arrive in Europe. Species with a short migration distance would stop far short of Central Europe.

Fig. 3 Number of records of East Asian species (genera *Phylloscopus*, *Turdus* and *Zoothera*) and correlation of the number of recordings to the distributional range size

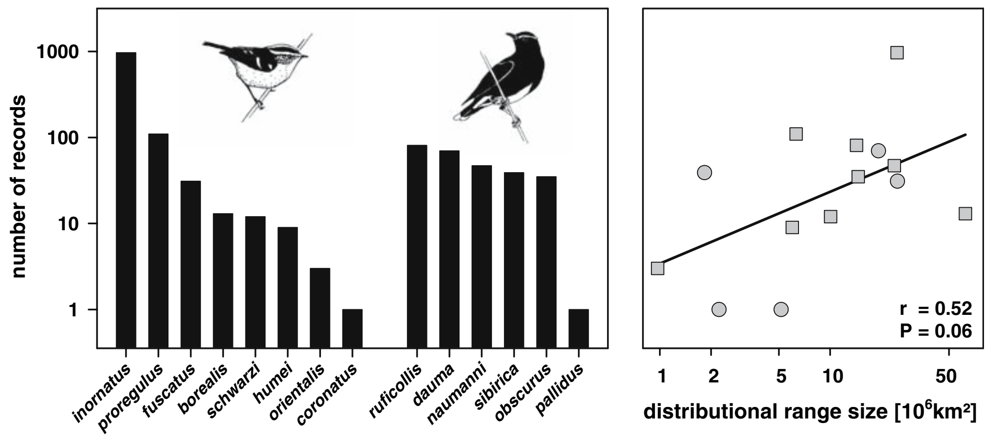
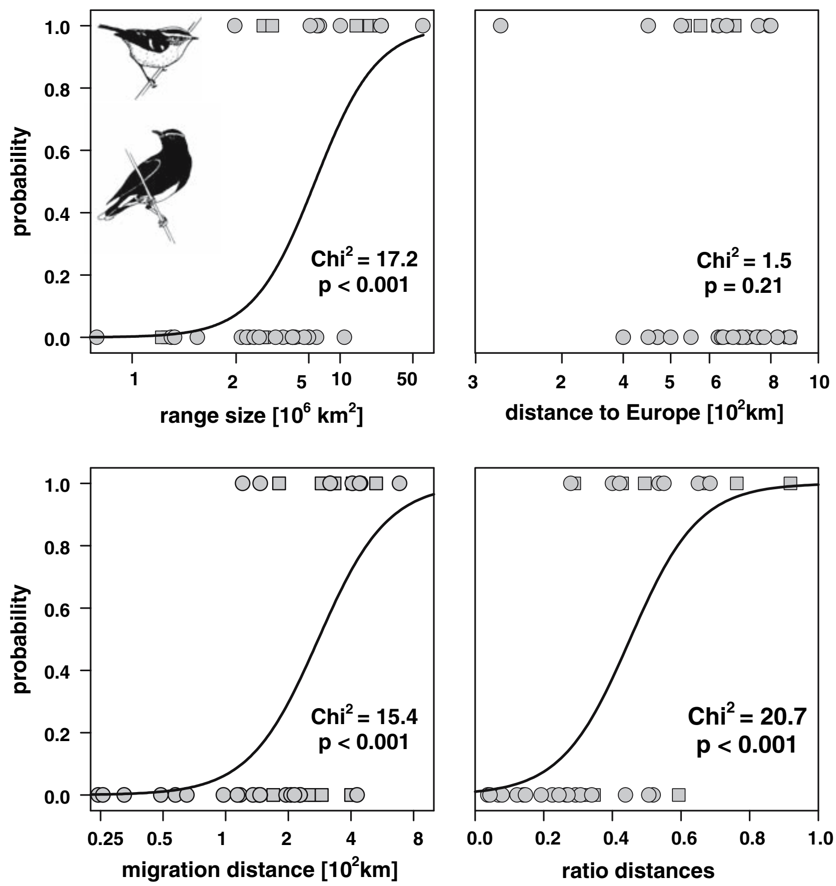


Fig. 4 Relationships between the occurrence of an East Asian species in Europe (coded as binary variable) and range size, distance between breeding range and Europe, distance between breeding and wintering range and the ratio between the latter two variables. The *curves* are significant logistic regressions and the χ^2 gives the reduction of deviance (null deviance in all models: 50.0) by entering the respective variable. Note that the ratio of distances leads to the largest drop in deviance



The hypothesis that the genetic migration programme is at least in part responsible for the occurrence of species in Central Europe leads to the idea that there may be a correlation between the occurrence of species as vagrant in Central Europe and phylogeny. We tested the leaf warblers for such a relationship using the phylogenetic tree developed by Price et al. (1997). We coded the occurrence of a species in Central Europe as a trait and mapped this trait on the tree (Fig. 6). Using parsimony, seven changes in the trait were necessary to account for the variation between species (using the software programme Mesquite; Maddison and Maddison 2004). However, randomizing species across the tips of the tree showed that this value is expected by chance (Fig. 6, inset). Although the genetic programme may be in part responsible for the occurrence of a species as a vagrant, the genetic basis of the migratory programme seems to be too liable to show a phylogenetic signal. This is not very surprising. The fascinating work of Berthold and co-workers demonstrated that the genetic migration programme changes each few years (Berthold et al. 1990).

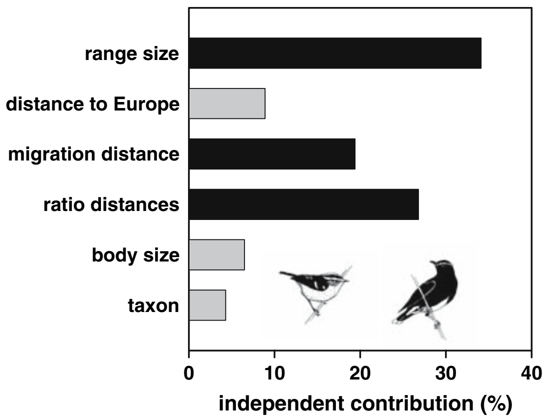


Fig. 5 The percentage distribution of independent effects (independent contribution) of several variables on the occurrence of East Asian species (*Phylloscopus* and trushes) as vagrants in Europe using the log-likelihood as goodness of fit measure. *Black bars* indicate significant independent contributions using 100 randomizations. Note that body size, genus (coded as dummy variable) as well as the distance between the breeding range and Europe had little effects on vagrancy

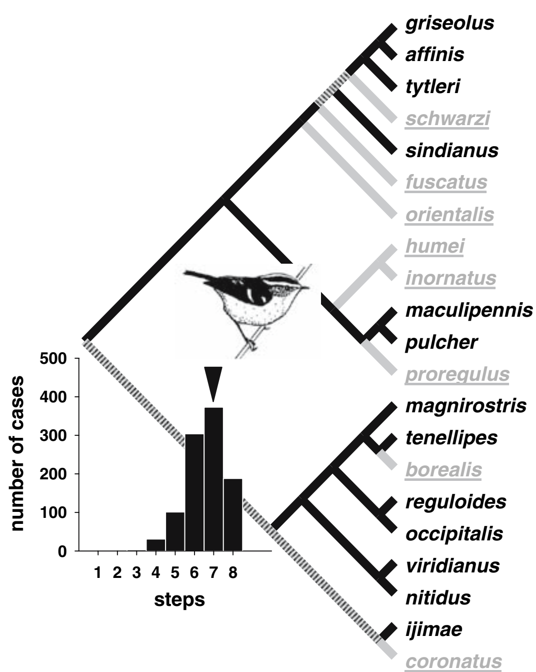


Fig. 6 Phylogeny of the genus *Phylloscopus* (from Price at al. 1997). Species in *grey* were recorded as vagrants in Europe, and the different colours of the branches indicate the evolution of the trait reconstructed using parsimony. *Hatched branches* indicate uncertain reconstructions. Overall, one needs seven changes in the state of the trait along the phylogeny to explain the distribution of species that occur as vagrants in Europe across the tree. The histogram gives the distribution of the expected number of steps generated by randomizing species across tips (10,000 runs). Note that the distribution of vagrants across the phylogeny transports no phylogenetic signal

Furthermore, Price et al. (1997) showed that the location of the distributional range of leaf warblers is also a liable trait. Obviously, fluctuations during the Pleistocene forced a rearrangement of distributional ranges and associated migration programs.

Zusammenfassung

Vögel aus Ostasien in Europa: Gründe für das Auftreten von Irrgästen

Alljährlich werden von Feldbeobachtern Irrgäste gemeldet. Wir untersuchten das Auftreten von ostasiatischen Arten der Gattung *Phylloscopus*, *Turdus* und *Zoothera* als Irrgäste in Mitteleuropa. Wir fanden, dass das Auftreten zunächst von der Häufigkeit der Arten abhängt, aber nicht von deren Körpergröße. Darüber hinaus fanden wir, dass das Auftreten einer Art als Irrgast mit zunehmendem Verhältnis zwischen der Zustrecke und der Distanz zwischen dem Brutareal und Europa wahrscheinlicher wurde. Das spricht dafür, dass letztlich die genetisch determinierte Zugunruhe dafür verantwortlich ist, ob eine Art Europa überhaupt erreicht. Das Auftreten von ostasiatischen Irrgästen beruht demnach eher auf Fehlern im Zugablauf, denn in schlechten Wetterbedingungen während des Zuges.

Acknowledgment Two anonymous referees provided valuable comments on an earlier draft of this paper. Jonathan Guest polished our language.

Appendix

List of species considered in our study. The asterisks indicate species which were recorded as vagrants in Central Europe. **Leaf Warblers** (*Phylloscopus*): *P. sindianus*, *P. neglectus*, *P. orientalis**, *P. fuscatus**, *P. fuliginventer*, *P. affinis*, *P. subaffinis*, *P. griseolus*, *P. armandii*, *P. schwarzi**, *P. pulcher*, *P. maculipennis*, *P. proregulus**, *P. subviridis*, *P. inornatus**, *P. humei**, *P. borealis**, *P. tenellipes*, *P. magnirostris*, *P. tytleri*, *P. occipitalis*, *P. coronatus**, *P. ijimae*, *P. reguloides*, *P. davisoni*, *P. cantator*, *P. ricketti*. **Thrushes** (*Zoothera*): *Z. wardii*, *Z. sibirica**, *Z. dauma**. **Thrushes** (*Turdus*): *T. pallidus**, *T. cardis*, *T. hortulorum*, *T. feae*, *T. obscurus**, *T. chrysolaus*, *T. ruficollis**, *T. naumanni**.

References

Alerstam T, Petterson S-V (1991) Orientation along great circles by migrating birds using a sun compass. J Theor Biol 152:191–202

Ali S, Ripley SD (1973) Handbook of the birds of India and Pakistan. Oxford University Press, New Delhi

Baker K (1997) Warblers of Europe, Asia and North Africa. C Helm Publ, London
Baker JK, Catley GP (1987) Yellow-browed warblers in Britain and Ireland 1968–1985. Br Birds 80:93–109
Barthel PH, Bezzel E (1990) Feststellungen seltener Vogelarten: Ihre faunistische Bewertung und wissenschaftliche Bedeutung. Vogelwelt 111:64–81
Berthold P (1973) Relationships between migratory restlessness and migration distance in six *Sylvia* species. Ibis 115:594–599
Berthold P, Mohr G, Querner U, Schlenker R (1990) Steuerung und potentielle Evolutionsgeschwindigkeit des obligaten Teilzieherverhaltens: Ergebnisse eines Zweiweg-Selektionsexperiments. J Ornithol 131:33–45
Calder WA (1974) Consequences of body size for avian energetics. In: Paynter RA (ed) Avian energetics. Nutall Ornithological Club, Cambridge, pp 86–151
Clement P, Hathway R (2000) Thrushes. C Helm Publ, London
Gaston KJ (1994) Rarity. Chapman and Hall, London
Gilroy JJ, Lees AC (2003) Vagrancy theories: are autumn vagrants really reverse migrants? Br Birds 96:427–438
Glutz von Blotzheim UN, Bauer KM (1985) Handbuch der Vögel Mitteleuropas, vol 10. Aula-Verlag, Wiesbaden
Glutz von Blotzheim UN, Bauer KM (1988) Handbuch der Vögel Mitteleuropas, vol 11. Aula-Verlag, Wiesbaden
Glutz von Blotzheim UN, Bauer KM (1991) Handbuch der Vögel Mitteleuropas, vol 12. Aula-Verlag, Wiesbaden
Gwinner E (1968) Circannuale Periodik als Ursache des jahreszeitlichen Funktionswandels bei Zugvögeln. J Ornithol 109:70–95
Hering J, Alfrey P (2006) Die Azoren als Rettungsanker für verdriftete nearktische Vogelarten – Herbst 2005. Limicola 20:65–90
Liechti F (2006) Birds: blowin' by the wind? J Ornithol 147:202–211
MacNally R (1996) Hierarchical partitioning as an interpretative tool in multivariate inference. Aust J Ecol 21:224–228
MacNally R (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between and reconciliation of 'predictve' and 'explanatory' models. Biodivers Conserv 9:655–671
Maddison WP, Maddison DR (2004) Mesquite: a modular system for evolutionary analysis, version 1.05. Available at: http://www.mesquiteproject.org
Maddock M, Geering D (1994) Range expansion and migration of the Cattle Egret. Ostrich 65:191–203
McLaren IA, Lees AC, Filed Ch, Collins KJ (2006) Origins and characteristics of Nearctic landbirds in Britain and Ireland in autumn: a statistical analysis. Ibis 148:707–726
Price TD, Helbig AJ, Richman AD (1997) Evolution and breeding distributions in the old world Leaf Warblers (Genus *Phylloscopus*). Evolution 51:552–561
R Development Core Team (2004) R: a language and environment for statistical computing, Vienna, Austria. Available at: http://www.cran.r-project.org
Rabøl J (1969) Reversed migration as the cause of westward vagrancy by four Phylloscopus warblers. Br Birds 62:89–92
Rabøl J (1976) The orientation of Pallas's Leaf Warbler *Phylloscopus inornatus* in Europe. Dansk orn Foren Tidsskr 70:5–16
Sandberg R (1994) Interaction of body condition and magnetic orientation in autumn migrating Robins, *Erithacus rubecula*. Anim Behav 47:679–686
Thorup K (1998) Vagrancy of Yellow-browed Warbler *Phylloscopus inornatus* and Pallas's Warbler *Ph. proregulus* in north-west Europe: misorientation or great circles? Ring Migr 19:7–12
Thorup K (2004) Reverse migration as a cause of vagrancy. Bird Study 51:228–238
Van den Berg AB, Bosmann CAW (1999) Zeldzame vogels van Nederland/Rare birds of the Netherlands. GMB Uitgeverij, Haarlem
Veit RR (1997) Long-distance dispersal and population growth of the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. Ardea 85:135–143
Veit RR (2000) Vagrants as the expanding fringe of a growing population. Auk 117:242–246
Walsh C, MacNally R (2003) Hierarchical partitioning. R project for statistical computing. Available at: http://www.cran.r-project.org
Weindler P, Wiltschko R, Wiltschko W (1996) Magnetic information affects the stellar orientation of young bird migrants. Nature 383:158–160