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Migratory divides and their consequences for dispersal, population size and parasite–host interactions

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range size.

Abstract

Populations of migratory birds differ in their direction of migration with neighbouring populations often migrating in divergent directions separated by migratory divides. A total of 26% of 103 passerine bird species in Europe had migratory divides that were located disproportionately often along a longitudinal gradient in Central Europe, consistent with the assumption of a Quaternary glacial origin of such divides in the Iberian and Balkan peninsulas followed by recolonization. Given that studies have shown significant genetic differentiation and reduced gene flow across migratory divides, we hypothesized that an absence of migratory divides would result in elevated rates of gene flow and hence a reduced level of local adaptation. In a comparative study, species with migratory divides had larger population sizes and population densities and longer dispersal distances than species without migratory divides. Species with migratory divides tended to be habitat generalists. Bird species with migratory divides had higher richness of blood parasites and higher growth rates of *Staphylococcus* on their eggs during the incubation period. There was weaker cell-mediated immunity in adults and stronger cell lysis in species with migratory divides. These findings may suggest that migratory divides constitute barriers to dispersal with consequences for ecology and evolution of distributions, population sizes, habitats and parasite–host interactions. They also suggest that migratory divides may play a role in local adaptation in host–parasite interactions.

Introduction

Genetic differentiation in numerous organisms has occurred due to events during recent glacial and post-glacial periods (Hewitt, 1996, 2000). Analyses of numerous taxa have indicated post-glacial contact zones in Central Europe around longitudes 10–20°E (Hewitt, 2000). Genetic differentiation of many animals in Central Europe reflects Ice Age refugia in the Iberian Peninsula and the Balkans followed by secondary contact (Hewitt, 1996). Hence, the location of contact zones in Europe is likely to be nonrandomly distributed with disproportionately many species having such zones located in Central Europe, reflecting secondary colonization following the retreat of the ice after the last glaciations.

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The genetic consequences of Quaternary glacial periods seem to be limited. Taberlet *et al.* (1998) analysed the phylogeography of ten plant and animal taxa across Europe. Although there was evidence of post-glacial colonization routes from Iberian and Balkan refugia, there was only limited evidence for congruence, and molecular genetics have apparently only limited use in dating these events. In contrast to these findings, the amount of genetic variance in extant populations may depend on population size and number of refugia during glacial periods although that has to the best of our knowledge never been assessed. Large populations generally have more genetic variation because the product of effective population size and mutation rate determines the level of standing genetic variation (Nagylaki, 1998; Wakeley, 1998). Because all populations are finite,

genetic variability will be eroded with time through genetic drift, even in large populations. Therefore, the null expectation is that large populations will maintain greater levels of genetic variation than small populations and that any subdivision of such populations will further reduce the amount of genetic variation.

Migratory divides are defined as strict geographical boundaries between adjoining populations where one population migrates in one direction and a neighbouring population in another (see Fig. 1 for a typical example), with little or no overlap in migration directions even at small spatial scales (reviews in Mayr, 1942; Berthold, 2001; Newton, 2008). The presence of migratory divides has been ascribed to post-glacial colonization from separate glacial refugia in the Iberian and Balkan peninsulas with subsequent genetic differentiation (Mayr, 1942; Berthold, 2001; Newton, 2008). Furthermore, many migratory birds have migratory divides at the Ural Mountains with western populations migrating to Europe and/or Africa and eastern populations migrating to the Indian subcontinent or Southeast Asia. Likewise, there are migratory divides in Asia and North America (Berthold, 2001; Newton, 2008). Studies of neutral genetic markers and stable isotope profiles across migratory divides have shown conclusive evidence of significant differentiation even at short geographical scales (Chamberlain *et al.*, 2000; Berthold, 2001; Bensch *et al.*, 2009; Procházka *et al.*, 2011). Furthermore, even the winter quarters of migratory bird species differ between the two sides of a migratory divide (Chamberlain *et al.*, 2000). Such differences in migration distance will cause divergence in morphology involved in migration, and

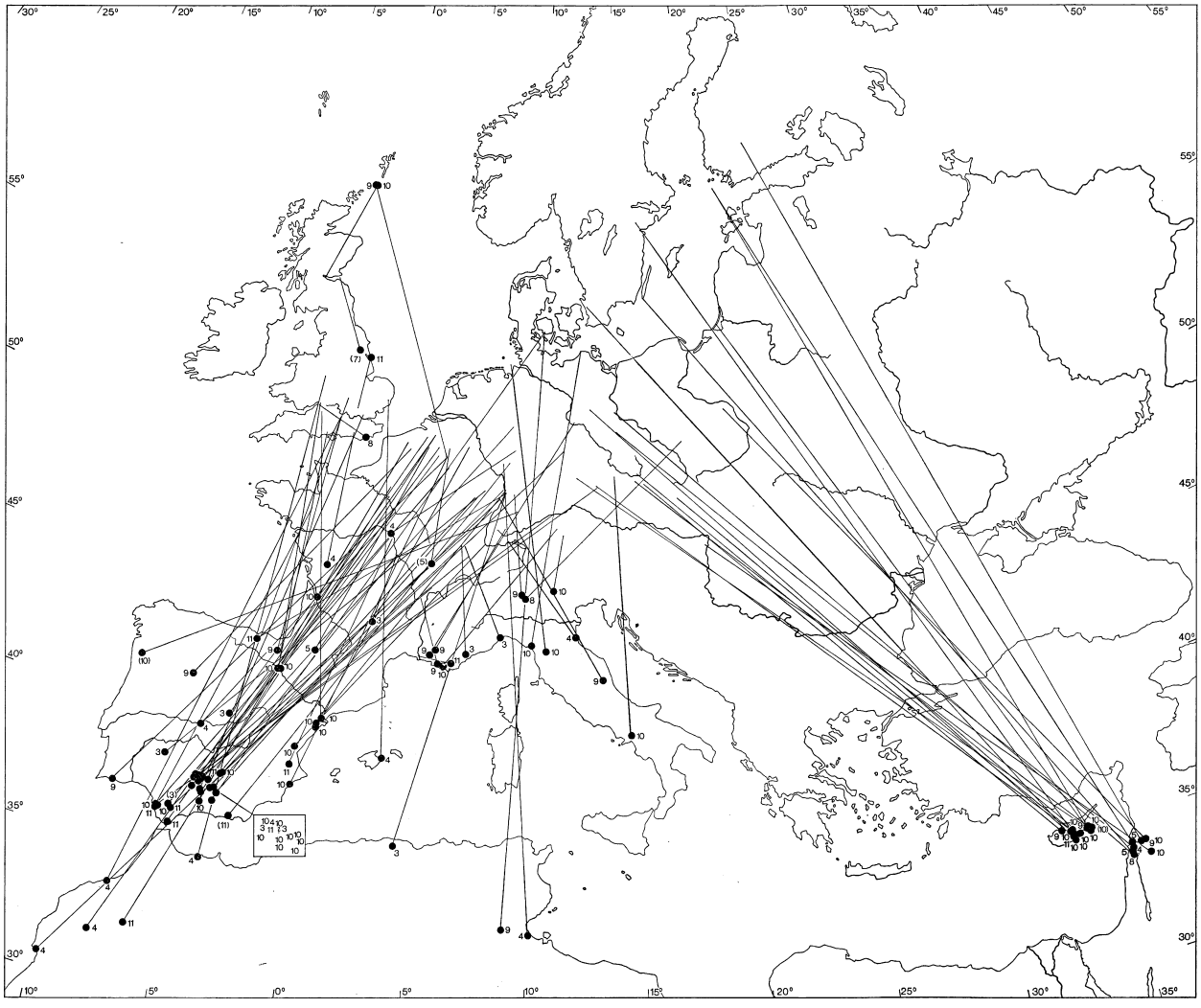

Fig. 1 A migratory divide in the blackcap *Sylvia atricapilla*, with lines connecting breeding and wintering areas of individuals. Reprinted with permission from Zink & Bairlein (1987–1995) by AULA-Verlag, Wiebelsheim, Germany.

populations with long-distance migration will as a consequence of morphological adaptations to migration also become adapted to long-distance dispersal (Belliure *et al.*, 2000). Thus, migratory divides will be associated with longer migration, morphological differentiation and extended dispersal. Genetic differentiation of populations of birds across migratory divides has produced partial reproductive isolation in at least one species, the blackcap *Sylvia atricapilla* (Rolshausen *et al.*, 2009).

Local adaptation is one of the hallmarks of evolution with organisms generally performing better under local environmental conditions, although such local adaptation can be broken up by gene flow (Fig. 2). At large spatial scales, genetic and phenotypic variation arises from mutation, genetic drift, and natural selection promoting adaptation to local environmental conditions, whereas gene flow opposes differentiation (Slatkin, 1985; Fig. 2). Accordingly, Bohonak (1999) in a review showed that dispersal ability was consistently negatively related to population structure, and estimates of gene flow were positively correlated with dispersal ability.

Gene flow may either constrain evolution by preventing adaptation to local conditions (Lenormand, 2002; Alleaume-Benharira *et al.*, 2006) or promote local adaptation through temporally variable selection by spreading new genes and combinations of genes throughout a species' range (Fig. 2; Gandon *et al.*, 1996; Morgan *et al.*, 2005; Gandon & Nuismer, 2009). Such gene flow will tend to be density dependent from more to less dense populations, preventing or delaying adaptation in the latter populations (Lenormand, 2002). In host–parasite interactions, the level of local adaptation will depend on relative migratory rates of hosts and parasites (Kaltz & Shykoff, 1998). The level of host specialization as reflected by the degree to which parasites adapt to a particular host depends on the balance between selection within and among host populations, and gene flow among host populations (Wright, 1978; Slatkin, 1985; Gandon *et al.*, 1996; Kaltz & Shykoff, 1998). Host specialization is thought to limit gene flow among parasite populations exploiting alternative hosts, thereby enhancing local adaptation and speciation (Peirce, 1981; Futuyma & Moreno, 1988; Thompson, 1994; Tripet *et al.*, 2002). Hosts are not passive victims of their parasites, but coevolve with these to provide efficient defences that limit, reduce or eliminate the damage caused by parasites (Ehrlich & Raven, 1964; Gilbert & Raven, 1975; Thompson, 1994; Combes, 2001). Phylogeographical studies of parasites and their hosts provide evidence consistent with glacial refugia in pathogens and hosts alike (Martínez *et al.*, 1999; Vercken *et al.*, 2010). However, parasites not only seem to have more and smaller refugia than hosts but also differ in large-scale dispersal, pinpointing important differences in post-glacial colonization between parasites and hosts (Vercken *et al.*, 2010).

The objectives of this study were to (i) describe the frequency and geographical distribution of migratory divides in European birds and (ii) assess ecological and evolutionary consequences of migratory divides (as outlined in Fig. 2). To this end, we used extensive information on migration patterns of European passerine birds based on banding recoveries (Zink & Bairlein, 1987–1995). We identified migratory divides and their geographical location for a large sample of species and compared the spatial distribution with a random distribution. Subsequently, we determined to which extent the presence of migratory divides correlated with dispersal, population size and range size, habitat specialization and parasite–host interactions.

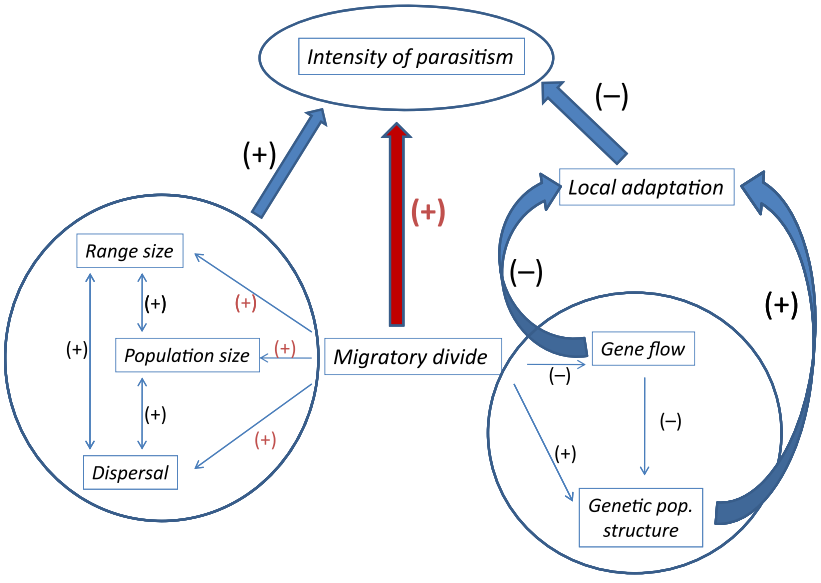

Fig. 2 Hypothetical relationships between migratory divides, gene flow, local adaptation, range size, population size and parasitism. See text for further details.

Materials and methods

Migratory divides

We classified bird species as having migratory divides or not using maps in Zink & Bairlein (1987–1995) as a source. This compilation of recoveries or recaptures of birds banded in Europe provides an atlas of more than 100 000 observations, representing the most extensive reference work for any taxon and continent. Obviously, species differ in the number of recoveries available, and this could potentially bias the conclusions if species with few recoveries were erroneously classified as not having migratory divides. We tested for this source of potential bias in two ways. First, we used the total number of recoveries listed by EURING (http://www.euring.org) as an estimate of sampling effort, assuming that a larger sample size would equal a higher probability of identifying a migratory divide. We redid the analyses in Table 1 by including $\log_{10}$-transformed number of recoveries as a covariate. None of the conclusions changed as a consequence of inclusion of this covariate. Second, we estimated northernmost, southernmost, easternmost and westernmost locations of the breeding range and determined whether they were related to the presence of a migratory divide. We did this under the assumption that species with a southern or an eastern distribution would have fewer recoveries due to smaller ringing effort. However, only the westernmost limit explained variation in the presence of migratory divides (see Results). Thus, these tests provided no evidence for bias.

Population size and range size

We obtained population sizes from Hagemeijer & Blair (1997), who reported the total number of breeding pairs in the Western Palearctic west of the Ural Mountains, derived in a consistent way from national bird census programmes in all countries. We used the arithmetic mean of the minimum and maximum estimates.

We estimated northernmost, southernmost, easternmost and westernmost locations of the breeding range, using the maps in Cramp & Perrins (1977–1994) as a source. We also estimated breeding range in the Western Palearctic and total breeding range as the area of the shape bounded by the greatest span of latitude and longitude of each species' breeding range, as published in Cramp & Perrins (1977–1994). To take into account the

Table 1 Tests of difference in phenotype between bird species without and with a migratory divide using phylogenetic generalized least-square regression. λ statistic is the estimate of the phylogenetic signal in the data. Effect size is reported as the Pearson product–moment correlation coefficient (95% confidence interval). See Materials and Methods for additional variables that were included in the analyses and for further information.

Variable	λ	P ($\lambda = 0$)	P ($\lambda = 1.0$)	F	d.f.	P	Effect size (95% CI)	Mean (SE) No migratory divide	N	Mean (SE) Migratory divide	N
Body mass	1.00	0.0001	1.000	0.50	1, 101	0.48	0.070 (–0.125, 0.259)	1.315 (0.075)	76	1.377 (0.045)	27
Natal dispersal	0.00	1.000	0.008	2.61	1, 32	0.08	0.275 (–0.064, 0.557)	0.259 (0.106)	22	0.547 (0.143)	12
Breeding dispersal	0.09	0.720	0.048	7.61	1, 29	0.017	0.456 (0.127, 0.858)	–0.372 (0.105)	19	0.093 (0.132)	12
Migration distance	0.88	0.0001	0.054	33.87	1, 100	0.008	0.503 (0.341, 0.634)	0.796 (0.068)	76	1.364 (0.114)	27
No. subspecies	0.26	0.179	0.0001	8.77	1, 100	0.0039	0.284 (0.096. 0.453)	0.713 (0.036)	76	0.500 (0.061)	27
Breeding population size	0.68	0.266	0.004	3.03	1, 100	0.019	0.171 (0.023, 0.353)	6.538 (0.078)	76	6.929 (0.132)	27
Breeding range size	0.30	0.044	0.0001	2.72	1, 100	0.076	0.163 (–0.032, 0.345)	7.473 (0.037)	76	7.596 (0.062)	27
Breeding density	0.69	0.037	0.002	2.66	1, 99	0.027	0.162 (–0.034, 0.344)	6.576 (0.075)	76	6.6822 (0.128)	27
Northernmost distribution								64.774 (0.955)	76	67.156 (1.603)	27
Southernmost distribution								29.464 (1.465)	76	29.677 (2.459)	27
Westernmost distribution								–7.149 (1.478)	76	–16.152 (2.480)	27
Easternmost distribution								114.576 (7.987)	76	127.317 (13.401)	27
No. of breeding habitats	0.22	0.110	0.0001	5.16	1, 101	0.045	0.220 (0.029, 0.396)	0.814 (0.028)	76	0.938 (0.047)	27
No. of blood parasite species	0.11	0.316	0.0001	6.36	1, 85	0.032	0.264 (0.058, 0.488)	0.448 (0.035)	60	0.604 (0.051)	27
Growth of mesophiles	0.99	0.026	1.000	0.09	1, 17	0.77	0.073 (–0.381, 0.499)	2.724 (0.431)	17	3.987 (0.468)	10
Growth of *Enterococcus*	0.00	1.000	0.11	0.30	1, 17	0.59	0.132 (–0.330, 0.542)	0.455 (0.041)	17	0.509 (0.093)	10
Growth of *Staphylococcus*	0.00	1.000	0.029	30.30	1, 17	0.0001	0.800 (0.554, 0.918)	0.346 (0.008)	17	0.316 (0.005)	10
Growth of *Enterobacteriaceae*	0.00	1.000	0.015	0.00	1, 17	0.95	0.000 (–0.441, 0.441)	1.749 (0.386)	17	2.346 (0.587)	10
Nestling cell-mediated immunity	0.00	1.000	0.0003	0.83	1, 40	0.37	0.143 (–0.165, 0.426)	–0.111 (0.053)	30	–0.206 (0.074)	13
Adult cell-mediated immunity	0.01	0.939	0.0001	5.77	1, 48	0.020	0.328 (0.058, 0.553)	–0.709 (0.044)	32	–0.865 (0.056)	19
Nestling NAbs	0.00	1.000	0.0002	0.12	1, 19	0.66	0.079 (–0.354, 0.484)	0.099 (0.063)	15	0.161 (0.138)	7
Adult NAbs	1.00	0.011	1.000	0.69	1, 16	0.51	0.203 (–0.277, 0.601)	0.420 (0.102)	11	0.555 (0.119)	8
Nestling lysis	0.00	1.000	0.0014	0.45	1, 19	0.56	0.152 (–0.288, 0.539)	0.005 (0.005)	15	0.000 (0.000)	7
Adult lysis	0.00	1.000	0.057	5.80	1, 16	0.026	0.516 (0.081, 0.786)	0.000 (0.000)	11	0.167 (0.079)	8

curvature of the earth (which was assumed to be spherical), this area was estimated by the equation

$$\text{Area} = R^2 \times (\text{Longitude}_1 - \text{Longitude}_2) \times (sin(\text{Latitude}_1) - sin(\text{Latitude}_2)),$$

where R is the radius of the earth (6366.2 km) and latitude and longitude are expressed in radians.

In widespread species, Old and New World ranges were calculated separately and subsequently summed. The method overestimates true geographical range, but the error should be random with respect to the variables investigated here. Estimates of area were strongly positively correlated with geographical range size as calculated by counting one-degree grid cells overlain on published distribution maps for a sample of 20 Palearctic and Nearctic bird species ($r = 0.87$, $P < 0.001$), and with range size as reported for a sample of 11 threatened species (Stattersfield & Capper, 2000) ($r = 0.98$, $P < 0.001$, based on log-transformed data).

Dispersal

Natal and breeding dispersal

We estimated natal and breeding dispersal distance using geometric mean dispersal distances derived from an extensive analysis of birds banded in the UK (Paradis *et al.*, 1998). These measures of dispersal distance have previously been shown to relate to subspecies richness (Belliure *et al.*, 2000), migration distance (Belliure *et al.*, 2000) and other ecologically important variables.

Migration distance

We estimated migration distance as the difference in latitude between the mean of the northernmost and the southernmost breeding distribution and the mean of the northernmost and the southernmost winter distribution, relying on information in Cramp & Perrins (1977–1994) and del Hoyo *et al.* (1992–2008).

Number of subspecies

We recorded the number of subspecies under the assumption that dispersal reduces phenotypic divergence among populations (Belliure *et al.*, 2000), using Cramp & Perrins (1977–1994) as a source. We note that only a single of the 27 of the migratory divides coincided with subspecies boundaries. The results did not change if this single subspecies was excluded from the data.

Number of breeding habitats

We estimated the number of different breeding habitats as a measure of ecological plasticity (Belliure *et al.*, 2000). We did so by relying on the habitat categories listed in the habitat section glossary of Cramp & Perrins (1977–1994) and searching the breeding habitat sections of each species.

Host–parasite interactions

Blood parasites

Parasite species richness quantified as the number of parasite species was extracted from Peirce (1981) and Scheuerlein & Ricklefs (2004) combined with information from sources listed in Møller & Haussy (2007). Although molecular techniques may be better at detecting weak infections, several studies have shown a positive association between estimates of parasite prevalence using both microscopic and molecular techniques (e.g. Waldenström *et al.*, 2004; Ricklefs *et al.*, 2005). Our own analyses of the data provided in the supplementary material in Ricklefs *et al.* (2005) showed positive consistency among the two estimates of parasite prevalence (Kendall $\tau = 0.307$, $z = 6.252$, $P < 0.001$), although analyses of blood smears only revealed 28% of what was found with PCR. Thus, analyses based on microscopy are conservative. In total, the analyses presented here were based on infection levels of 9960 adult hosts belonging to 87 species. Finally, we extracted information on the number of individuals examined for each host species to control for the potentially confounding effect of sampling effort in the analyses.

Bacteria

We sampled eggshells for bacteria twice: one at the beginning of the incubation period and another one few days before egg hatching. The first sample was taken 2–3 days after clutch completion, which assured that all sampled eggs were incubated. Briefly, trying to maintain sterile conditions and preventing inter-nest contamination, we wore latex gloves sterilized with 96% ethanol and cleaned the eggshells of the complete clutch with a sterile swab slightly wet with sterile sodium phosphate buffer (0.2 M; pH = 7.2). We introduced the swab in a microcentrifuge tube with sterile phosphate solution that was stored in a portable refrigerator at 4–6 °C. In the laboratory, samples were stored at 4 °C until processing. For a more detailed explanation of bacterial sampling protocol, see Peralta-Sanchez *et al.* (2010). After vigorously shaking microcentrifuge tubes in vortex, we performed serial dilutions until 10^{-6} times and performed microorganism cultivations by spreading homogenously 100 μL of each serial dilution in each of the four Petri dishes containing four different sterile solid growth media (Scharlau Chemie S.A. Barcelona): Tryptic Soy Agar (TSA), a broadly used general medium to grow total aerobic mesophiles; Kenner Faecal Agar (KF) for growing bacteria belonging to the genus *Enterococcus*; Vogel-Johnsson Agar (VJ) for bacteria of the genus *Staphylococcus*; and Hecktoen Enteric Agar (HK) for Gram-negative bacteria of the family *Enterobacteriaceae*. Dishes were incubated at 32 °C for 72 h, and afterwards, the number of colony-forming units (CFU) on the dish of the less-diluted solution allowing counting of colonies. For a more detailed description of protocol of bacteria cultiva-

tion, see Peralta-Sanchez *et al.* (2010). We estimated eggshell bacterial load (i.e. density) as the number of colonies that grew in our four media per surface (cm^2) of eggs sampled. Eggshell surface was estimated for each of the egg sampled according to the formula in Narushin (2005):

$$S = (3.155 - 0.0136 \times L + 0.0115 \times W) \times L \times W$$

where S is the surface in cm^2, L the length of the egg and W the width of the egg. Length and width of all eggs were measured with a calliper (accuracy 0.02 mm). Eggshell bacterial growth was estimated as the signed differences in bacterial density estimated at the end of the incubation minus that estimated at the beginning of the incubation divided by bacterial load at the beginning of the incubation. For a more detailed description of estimates of eggshell bacterial density and growth, see Peralta-Sanchez *et al.* (2010).

Immunity

Innate immunity

We collected 75 μL of blood from nestlings and adult birds in heparinized capillaries, which was stored in a cooling box at a temperature just above freezing. In the laboratory within a period of 2 h, we centrifuged the capillaries for 10 min at 4000 r.p.m. To estimate the levels of circulating natural antibodies and complement, we used a procedure developed by Matson *et al.* (2005) as modified by Møller *et al.* (2008). The agglutination part of the assay estimates the interaction between natural antibodies and antigens in rabbit blood, producing blood clumping. The lysis part of the assay estimates the action of complement from the amount of haemoglobin released from the lysis of rabbit erythrocytes. Quantification of agglutination and lysis is achieved by serial dilution in polystyrene 96-well assay plates, with the dilution step at which the agglutination or lysis reaction is stopped. Both agglutination and lysis were highly repeatable among individuals within species. See Møller & Haussy (2007) for further details.

Cell-mediated immunity

Cell-mediated immune response was measured as the response to a challenge with phytohaemagglutinin (PHA). Birds were injected with 0.05 ml of 0.2 mg PHA in one wing web and 0.05 mL of physiological water in the other wing web at premarked sites. The dose of PHA used in this study is similar to that used in other studies of free-living or captive birds (e.g. Lochmiller *et al.*, 1993; Saino *et al.*, 1997). Before injection, the thickness of the patagium in both wings was measured using a spessimeter, with an accuracy of 0.01 mm. A second measurement was taken six hours after injection in adults and 24 h after injection in nestlings. We measured adult immune response after six hours because studies of temporal change in cell immune response showed no further change after six hours (Goto *et al.*, 1978; Navarro *et al.*, 2003). See Møller *et al.* (2006) for details.

Body mass

We obtained body mass from Cramp & Perrins (1977–1994) or, if data were unavailable, from Dunning (1993). The entire data set is reported in Supporting information Table S1.

Statistical analyses

Body mass, natal and breeding dispersal distance, migration distance, number of subspecies, breeding population size, breeding range size, number of breeding habitats, number of blood parasite species, estimates of bacterial loads on eggs and immunity were all log-transformed. Eggshell bacterial loads during the incubation period were rank-transformed.

We used the presence or absence of a migratory divide as a categorical predictor variable. The variables analysed here are correlated with each other to a varying degree (Supporting information Table S2), and to avoid problems of correlations between migratory divides and different variables arising as a consequence of correlations with a third variable, we redid the analyses when correlations with a third variable exceeded 0.50. In particular, body mass was included as a covariate in the analyses of all variables, whereas breeding range size was included as a covariate in the analysis of number of subspecies and population size (the latter to provide an estimate of population density). Finally, we included measures of dispersal into analyses linking parasitism to the presence of migratory divides.

Because comparative analyses rely on discrimination between convergent evolution and similarity due to common phylogenetic descent (Harvey & Pagel, 1991), we used phylogenetic generalized least-square regression (PGLS) models (Pagel, 1997, 1999) as implemented in *R* with the appropriate libraries ('ape,' 'MASS' and 'mvtnorm') and additional functions by R. Freckleton (University of Sheffield) as implemented in the package 'caic'.

The PGLS approach characterizes evolutionary changes along each branch of a phylogeny through the variance components of traits and controls for nonindependence among species by incorporating a matrix of covariances among species based on their phylogenetic relationships (Martins & Hansen, 1997; Pagel, 1997, 1999). This phylogenetic covariance structure can be incorporated in a standard GLS regression model, by which the model parameters are estimated under the assumption that the variance–covariance matrix of the model residuals is identical to the phylogenetic covariance matrix. Model fitting in this framework relies on maximum likelihood, and PGLS model outcome (such as regression statistics, slope estimates, model likelihood and the derived model fit statistics) can be interpreted as results that take the

phylogeny of species into account. We conducted all analyses setting the degree of phylogenetic dependence (λ) to the most appropriate degree evaluated for each model. This was done by using the *pglmEstLambda* function, which automatically estimates the λ parameter simultaneously with other parameters of the model (Freckleton *et al.*, 2002). For the entire PGLS modelling, we used a conversion method that derives the phylogenetic matrix under Brownian model of evolution; thus, all models relied on the assumption of Brownian motion. Analyses for bacteria variables were weighted by sample size through a corresponding weight matrix that was combined with the phylogenetic matrix in the PGLS exercise. This was done to account for the fact that sampling effort for this variable varied considerably among species.

We used a composite molecular phylogeny based on the super-tree provided by Davis (2008) (Supporting information, Fig. S1). We arbitrarily set all branch lengths to one because the phylogeny was based on different molecular markers.

We traced the evolutionary history of migratory divides over the phylogeny of the 103 species included in the study by estimating the probability of different character states (divide or no divide) at the nodes of the phylogenetic tree. This ancestral state estimation relied on a maximum-likelihood-based approach as implemented in the program Mesquite that uses the one-parameter Markov *k*-state model of Lewis (2001). While ancestral states estimates obviously will depend on the species included, the distribution of character transitions over an incomplete phylogeny still provides an indication of the high flexibility of migratory divides.

We evaluated the magnitude of associations between predictor variables and migratory divides using effect sizes estimated as Pearson product–moment correlation coefficients. Cohen (1988) proposed explicit criteria for the evaluation of small (Pearson's $r = 0.10$, explaining 1% of the variance), intermediate (9% of the variance) and large effects (25% of the variance). To determine the strength and direction of the predicted relationships, we estimated effect sizes with the associated 95% confidence intervals (CI) for each particular relationship. We preferred to focus on effect sizes, instead of using Bonferroni adjustment of *P* values, because the latter approach has been criticized in the field of ecology and behavioural ecology for mathematical and logical reasons (Moran, 2003; Nakagawa, 2004; Garamszegi, 2006). For demonstrative purposes, we also present significance levels.

Results

Frequency and location of migratory divides

Among 103 European passerine species, migratory divides occurred in 26%. Migratory divides in Europe were located mainly in the band between 10° and 20°E, ranging from 0° to 25°E (Fig. 3). The frequency distribution in 10° longitudinal bands deviated significantly from an even distribution, with disproportionately many migratory divides at intermediate longitudes ($G_3 = 20.14$, $P < 0.0001$).

Migratory divides were dispersed across the phylogeny, and they have evolved independently several times (Fig. 4).

Migratory divides and dispersal

Species with migratory divides did not differ in body mass from species without divides (Table 1).

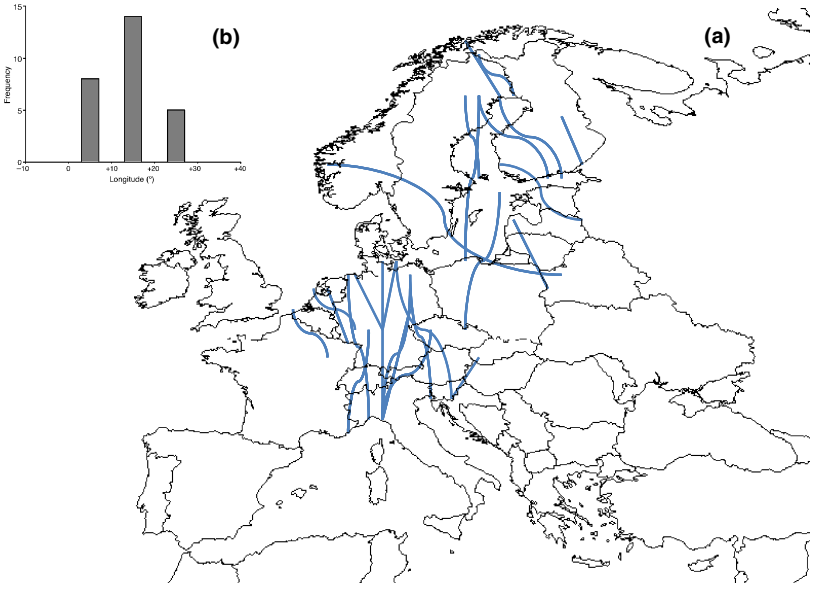

Fig. 3 (a) Location of migratory divides in European passerine birds and (b) the frequency distribution across bands of longitude.

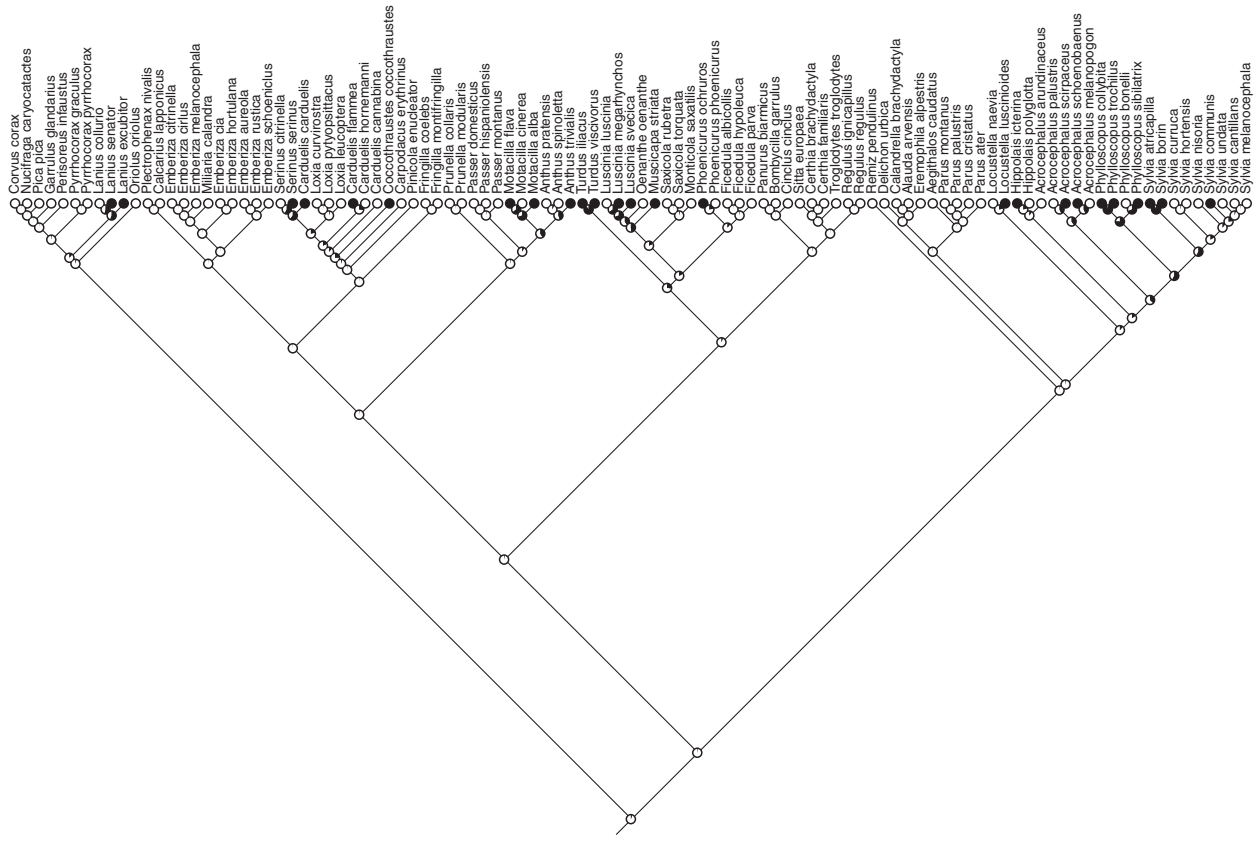

Fig. 4 Phylogenetic hypothesis of species of birds over which the evolution of character states are traced. Pie diagrams at the nodes show the probability of different character states (black: presence, white: absence of migratory divide) as estimated by the reconstruction model of ancestral states based on maximum likelihood. Pies indicate the proportional likelihood of the two character states.

We analysed four measures of dispersal propensity. Whereas natal dispersal distance did not reach statistical significance, breeding dispersal distance was longer in species with migratory divides than in species with no divides with a large effect size (Table 1). The difference for back-transformed breeding dispersal amounted to a three-fold difference. Likewise, migration distance between breeding and wintering grounds was much longer in species with than without migratory divides (Table 1), with mean values of 694 and 2566 km, respectively, or a more than three-fold difference. This effect size is large. Finally, bird species with migratory divides had fewer subspecies per unit area of the breeding distribution than species without migratory divides (Table 1), with the means being 5.2 and 3.1, respectively, or a 60% difference that equals an intermediate effect size. Note that smaller subspecies richness implies greater dispersal propensity.

Migratory divides, population size and range

With longer dispersal distances in species with migratory divides, we should expect larger breeding ranges. However, this relationship was not statistically significant (Table 1). This was entirely due to a more eastern current distribution of species with migratory divides (Table 1). Likewise, we should expect larger breeding populations for species with migratory divides, once a larger range has been occupied. Mean range size was 29.7 million km^2 for species without migratory divides and 39.4 million km^2 for species with migratory divides, or a 30% difference. Mean population size for species with migratory divides should be smaller if the range was subdivided. Indeed, population size for species with migratory divides was 3.5 millions, but for species without divides 8.5 millions, or a difference of more than a factor two (Table 1). This amounts to a small effect size.

We should expect a larger population density (i.e. population size per unit area, or density) in species with migratory divides as compared to species without such divides if reduced dispersal results in greater local adaptation. Indeed, population size was larger in species with migratory divides (Table 1), after inclusion of body mass and breeding range as additional predictor variables, with effect size being small.

Habitats

Breeding habitat diversity differed significantly between bird species with and without migratory divides (Table 1). The latter on average only had 6.5 different habitats, whereas the former had 8.6, which amounts to a difference of 30% or a small effect size.

Parasitism

If the breeding range was split up into smaller parts by migratory divides, we should expect parasitism rate to increase. Alternatively, a negative relationship could be expected if subdivided populations with partial isolation would reduce parasite transmission. That was the case for three taxa of parasites and for one category of bacteria. The number of blood parasite species was significantly higher in bird species with migratory divides (Table 1), with the mean number of blood parasite species for birds without migratory divides being 1.8 and 3.0 for species with migratory divides. This amounts to a difference of 67% or an intermediate effect. This relationship was independent of the effects of range size ($F_{1,84} = 5.46$, $P = 0.022$) and migration distance ($F_{1,84} = 7.93$, $P = 0.006$).

Growth of bacteria of the genus *Staphylococcus* differed between hosts without and with migratory divides with a large effect size (Table 1), whereas there was no significant difference for three other categories of bacteria. The difference amounted to more than an order of magnitude in the test.

Cell-mediated immunity was not related to migratory divides in nestlings, but it was weaker in adults of species with than without migratory divides, with a small to intermediate effect size (Table 1). There were no differences with respect to divides for natural antibodies, whereas for lysis adults differed in immunity between species with and without migratory divides with a large effect size (Table 1).

Discussion

Many bird species have migratory divides that separate extant populations differing consistently in migration patterns. European passerine species with migratory divides had long dispersal and migration distances because they did not follow the most direct migration route. Because of the long dispersal distances, they tended to have large range sizes, but subdivision of the range resulted in an increase in population size. Bird species with migratory divides had more diverse breeding habitats. Finally, species with migratory divides showed evidence of local adaptation with a larger diversity of blood parasites and higher bacterial growth. Finally, some components of immunity in adult birds differed between species with and without migratory divides.

The location of migratory divides in Europe was nonrandom, with most being located in Central Europe between longitudes 10° and 20°E. This location coincides well with the location of where populations with glacial refugia in the Iberian Peninsula and the Balkan Peninsula have met following post-glacial expansion (Hewitt, 1996, 2000). Whereas the frequency, location and timing of such events are well described in the literature (reviews in Hewitt, 1996, 2000), the ecological and evolutionary consequences of such subdivision of geographical ranges are only poorly understood.

Long-distance migration between breeding and wintering grounds in migratory birds and many other taxa is associated with a migratory syndrome that reflects the many different ecological and evolutionary consequences of a migratory lifestyle (Berthold, 2001; Dingle, 2006). A migratory lifestyle involves morphological and physiological adaptations to migration, and such adaptations may also have important repercussions in other contexts. Belliure *et al.* (2000) showed for common European birds that dispersal propensity was associated with the same morphological adaptations that also facilitate migration. Because migratory divides result in a four-fold increase in migration distance compared with the situation without a migratory divide, this implies that there should be morphological differences that not only facilitate flight between the two categories of species but also should affect dispersal propensity. Migratory divides affect dispersal and migration to the extent that some populations may migrate much longer distances than the shortest direct flyway between breeding and suitable wintering areas. Indeed, such cases of long-distance migration to distant winter quarters that are much longer than the closest suitable wintering area are common in birds (Sutherland, 1998). Long-distance migration in species with migratory divides implies that the genetic program of migration acts as a constraint on optimality. Long migration distances also imply large fitness costs in terms of frequent mortality due to extreme weather conditions during extended migration periods (Newton, 2007). Three of the four measures of dispersal propensity that we investigated (breeding dispersal distance, migration distance and subspecies richness) showed evidence of longer dispersal in species with migratory divides, including subspecies richness that is reduced in species with long dispersal distances (Belliure *et al.*, 2000).

Population size and range size are important determinants of genetic variation in extant populations (Møller *et al.*, 2008). Effective dispersal is an important determinant of range and hence population size because long dispersal distances assure not only that recently suitable habitats are colonized (Thomas *et al.*, 2006) but also that dispersal promotes the spread of new genes and combinations of genes throughout a species' range with consequences for the maintenance of genetic variation and local adaptation. Dispersal ability is the most obvious determinant of the ability to colonize novel environments (Clobert *et al.*, 2001). Therefore, species that disperse far on average should be closer to the limits of

the potential distribution than species that are sedentary, simply because the former species can respond more rapidly to environmental change and hence to increases in the suitable range of a species. A large range will imply a larger amount of standing genetic variation (Nagylaki, 1998; Wakeley, 1998). In fact, European birds with larger breeding ranges and larger extant population sizes have larger amounts of genetic variation (Møller *et al.*, 2008). Therefore, the prediction is that large populations will maintain greater levels of genetic variation than small populations, whereas any subdivision will reduce the amount of genetic variation. Thus, for a given geographical range, we should expect a smaller population size in species with migratory divides as compared to species without such divides. That was indeed the case despite the fact that population size and range size are positively correlated.

Phylogeographical studies of parasites and their hosts provide evidence consistent with glacial refugia in pathogens and hosts alike (Martínez *et al.*, 1999; Vercken *et al.*, 2010). However, parasites not only seem to have more and smaller refugia than hosts but also differ in large-scale dispersal, pinpointing important differences in post-glacial colonization (Vercken *et al.*, 2010). Local adaptation in host–parasite interactions depends on the relative dispersal rates by the interacting parties (Kaltz & Shykoff, 1998). The theoretical literature on local adaptation in host–parasite systems predicts either that gene flow constrains evolution by preventing adaptation to local conditions (Lenormand, 2002; Alleaume-Benharira *et al.*, 2006) or that it promotes local adaptation through coevolutionary dynamics between hosts and parasites by spreading new genes and combinations of genes throughout a species' range (Gandon *et al.*, 1996; Morgan *et al.*, 2005; Gandon & Nuismer, 2009). Because avian hosts with migratory divides have longer dispersal distances than hosts without a divide, as shown here, we should expect hosts rather than parasites enjoying an advantage in host–parasite interactions when hosts have migratory divides. However, if local adaptations are broken up by dispersal, we should expect parasites to enjoy an advantage in species with longer dispersal distances. This latter scenario may account for the observation that species richness and prevalence of parasites are greater in avian hosts with migratory divides. We note that the patterns were similar for directly transmitted and vector-transmitted parasites, suggesting that it is the behaviour of the host rather than the parasite that is causing differences between hosts with and without migratory divides. Furthermore, we note that two of the three components of immunity differed between species with and without divides, although only in adult hosts, as we found for dispersal. A consequence of differences in parasitism between hosts with and without migratory divides is that there will be further selection for maintenance of migratory divides if there are genetic bases for resistance to specific strains of parasites, and if parasites differ in their virulence among host populations on the two sides of a migratory divide (Møller & Szép, 2011). Such maintenance of migratory divides due to parasite-mediated selection can occur as a consequence of assortative mating with respect to direction of migration, resulting in partial genetic isolation (Rolshausen *et al.*, 2009). Eventually, such differentiation may give rise to speciation with parasites being the selective force promoting isolation. That seems to be the case for speciation in fleas and migratory divides in their hosts (Tripet *et al.*, 2002). The findings reported here on host–parasite interactions have similarities with recent studies of cuckoo parasitism and blood parasitism in birds in relation to heterogeneity in distribution of hosts (Soler *et al.*, 2009; Møller *et al.*, 2010). Hosts with a heterogeneous distribution constitute a resource that is more difficult to exploit for parasites, especially when considering the evolution of specialized host races. Soler *et al.* (2009) showed that cuckoos parasitizing hosts with high density and homogeneous distribution had evolved specific host races more often than cuckoos exploiting less common hosts with a heterogeneous distribution. Møller *et al.* (2010) reported similar findings for blood parasites of birds that include malaria. Here, we extend these findings by showing that heterogeneity in breeding distributions of hosts in terms of migratory divides affects prevalence, intensity of infection and diversity of parasites.

In conclusion, we have shown that bird species with migratory divides are common, affecting a fourth of all European passerines. Migratory divides have a number of consequences for dispersal, range size and population size, with consequences for local adaptation. Indeed, there was evidence of different levels of local adaptation in host species with and without migratory divides because species with migratory divides had elevated parasite loads compared with species without divides, and they also differed in immunity among adult hosts. These findings suggest a broader range of ecological and evolutionary consequences of Quaternary glacial isolation than are usually believed to be the case.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Phylogenetic relationships among the species included in this study. See Materials and Methods for further details.

Table S1 Summary information for the data set.

Table S2 Pearson product-moment correlation coefficients between the variables included in the study of migratory divides.

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