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Breeding phenology determines evolutionary transitions in migratory behaviour in finches and allies

Jácint Tökölyi and Zoltán Barta

J. Tökölyi (jtokolyi@vocs.unideb.hu) and Z. Barta, Dept of Evolutionary Zoology, Univ. of Debrecen, Egyetem tér 1, HU–4032 Debrecen, Hungary.

The breeding season of long-distance migratory birds often starts later and is shorter than in resident or short-distance species breeding at the same latitude, but the reason for this is unclear. Here we investigate the association between migration distance and breeding phenology in a group of passerine birds, the finches and their allies, using phylogenetic comparative methods. We confirm that migration distance is related to aspects of the species' breeding phenology after controlling for the effect of potentially confounding variables. Directional phylogenetic analyses suggest that evolutionary transitions in migration distance are determined by the breeding phenology. A relatively long migration distance is more likely to evolve in birds with a late, short breeding season, whereas transitions to short distance migration are more likely to occur in lineages with an early, long breeding season. These results suggest that migration distance is constrained by breeding phenology and not vice versa. Thus, breeding phenology may be an important ultimate factor shaping the evolution of migratory strategies.

The migratory behaviour of birds nesting in the temperate zone is often strikingly correlated with aspects of their breeding phenology (Kipp 1943, Böhning-Gaese et al. 2000, Bruderer and Salewski 2009, García-Peña et al. 2009). Long distance migrants start to breed later and/or have a shorter breeding season than short distant migrant or resident species breeding in several groups of birds, including raptors (Newton 2008), shorebirds (García-Peña et al. 2009) and passerines (Bruderer and Salewski 2009), among others. However, despite the widespread recognition of this phenomenon, the reason why the breeding phenology of long distance migrants differs so markedly from less migratory species breeding on the same latitude is not clear.

Possible explanations linking breeding phenology to migratory behaviour largely fall into four classes. First, life history tradeoffs between fecundity and mortality have been invoked in connection with this phenomenon, based on the observation that the shorter breeding season of long distance migrants is often associated with fewer number of broods per year, hence a lower annual fecundity (Mönkkönen 1992, Martin 1995, Böhning-Gaese et al. 2000, Bruderer and Salewski 2009). Life history theory predicts that in a population of constant size, differences in reproductive effort should be associated with different mortality rates. The reason for this is that under density dependence, any increase in reproductive investment (and hence fecundity) will intensify competition, resulting in a decrease in survivorship. High survival rates increase competition likewise, and this leads to less resources available for reproduction, ultimately selecting for lower reproductive rates (Ricklefs 1980, Martin 1995, McNamara et al. 2008, Bruderer and Salewski 2009). Thus, if the non-breeding period affects annual survival rate and mortality and fecundity are density dependent, then the behaviour of birds during the reproductive period and the non-breeding season should coevolve to reflect this tradeoff (Bruderer and Salewski 2009). Overwinter survival rates are thought to be higher in long distance migrants than in species spending the winter at northern latitudes (Greenberg 1980, Sherry and Holmes 1995, Møller 2007). On the other hand, annual fecundity is directly related to the length of the breeding season because, all else being equal, the number of broods per year and the probability of raising replacement broods after failed brood attempts should be higher when the breeding season is longer. Therefore, the fecundity-mortality tradeoff could possibly result in a correlation between migration distance and the length of breeding season because migration distance is related to overwinter survival, whereas the length of the breeding season is related to annual fecundity (the 'life history hypothesis').

Second, the migratory behaviour adopted by a given population of birds may depend directly on breeding phenology. The "time allocation hypothesis" (Greenberg 1980) proposes that with a relatively short breeding season, the benefits of wintering at a more distant site with better survival prospects may be higher, because the birds can spend more time at the favourable wintering site. The higher costs of long distance movements, according to this scenario, are more likely to be outweighed by the higher survival rate on the distant wintering ground for birds that spend more time there. Furthermore, the cost of migration could be lower for individuals migrating relatively late in the spring because they can exploit the higher food availability at that time and experience more favourable conditions during migration than birds migrating early in spring, and this lowered cost of migration could ultimately lead to longer migration distances (Bell 1996, 1997).

Third, predictability of environmental conditions on the breeding site could also affect migratory behaviour (the "spring predictability hypothesis", Alerstam and Högstedt 1980). If conditions on the breeding grounds do not change from year to year, birds can rely on their internal clock to arrive in spring at the earliest time when breeding becomes possible. Conversely, if the onset of spring is unpredictable, individuals wintering closer may predict weather conditions on the breeding grounds more accurately and respond more quickly than individuals migrating longer distances (Alerstam and Högstedt 1980). Given that weather conditions early in spring tend to be more variable than later (Newton 2008), one would predict that early breeders benefit more from staying close to the breeding grounds and have shorter migration distances.

Fourth, migratory behaviour could also affect directly the breeding phenology. Moving between the wintering and breeding grounds takes time, and some long distance migrants may need several weeks to complete the journey (Alerstam 1990). Moreover, there is a considerable mortality cost associated with migration (Sillett and Holmes 2002), and this presumably exerts a strong selection pressure on the birds to time their migration in a way that maximizes survival (e.g. by migrating late in spring and early in autumn; Bell 1996, 1997). This, in turn may affect the time available for other activities during the annual cycle, including reproductive activites, such as the number of broods per year (Bruderer and Salewski 2009), the length of the fledging period (Meiri and Yom Tov 2004), or parental activities (García-Peña et al. 2009). Thus, long distance migrants may reorganize their annual cycle and/or their reproductive behaviour such that their reproductive cycle will fit into a short summer period while simultaneously maximizing survival rate during migration (by migrating under more favourable conditions). On the other hand, short-distance migrants and residents may be less constrained by time, and could therefore freely extend their breeding season. Notice that this hypothesis does not involve life history tradeoffs because there is no change in reproductive effort per se, but it is the partition of the various reproductive activities that differs (e.g. it is possible to decrease the time spent on parental activities but increase the effort during that time, resulting in no net difference in reproductive investment). We refer to this as the 'migration time hypothesis'.

All these alternatives predict a correlation between migratory behaviour and aspects of the breeding phenology. Therefore, we have designed this study to discriminate among the possible alternatives. We collected data on the breeding phenology and migratory behaviour of a group of passerine birds (the finches and allies of the Western Palearctic and the Nearctic), and employed directional phylogenetic tests (Pagel 1994, Pagel and Meade 2006), which provide a framework to analyze the temporal order and contingency of evolutionary transitions. Given a phylogenetic hypothesis among a set of species and two traits with binary states, the method developed by Pagel (1994) determines the rate of transition among the possible combination of states. Based on these rates it is possible to determine which of the two traits is more likely to change spontaneously and whether changes in one trait are contingent upon the background state of the other. Our predictions for these directional tests were as follows: (1) if the relationship between migration and breeding phenology is mediated by life history tradeoffs, then evolutionary transitions in migratory behaviour should be contingent on breeding phenology, and vice versa, transitions in the length of the breeding season should also be contingent on migratory behaviour. (2) If either the 'time allocation' or the 'spring predictability hypothesis' is correct, the prediction is that transitions in migratory behaviour are contingent upon breeding phenology (length of breeding season and start of breeding, respectively). (3) Lastly, if the 'migration time hypothesis' is true, then both the start and the length of the breeding are predicted to be contingent upon migratory behaviour.

Methods

Data collection

We investigated the relationship between migratory behaviour and breeding phenology in the finches and their allies, a taxonomically diverse group of small to medium-sized passerines, including the families *Parulidae* (New World warblers), *Thraupidae* (tanagers), *Emberizidae* (American sparrows, Old World buntings, etc.), *Cardinalidae* (cardinals), *Icteridae* (orioles and blackbirds) and *Fringillidae* (finches). Finches are an ideal group to investigate this problem, because they include species with a wide range of migratory behaviour, including residents, short distance and long distance migrants, but the group is relatively homogenous with respect to body size and the mode of migration (they all migrate by flapping flight), thus extreme differences in the cost of migration are unlikely to bias the analyses.

Crossbills (genus *Loxia*) and cowbirds (genus *Molothrus*) were not included in this study, because the breeding season in these species cannot be determined in the same way as for the other species. Crossbills are opportunistic breeders and can breed year-round, often moving large distances between different breeding locations (Cramp and Perrins 1994, Poole 2005). Cowbirds on the other hand are brood parasites that lay in the nest of other species and their offspring are raised by foster parents (Poole 2005); as a consequence, reproductive investment per offspring is much lower in cowbirds and this could affect both the outcome of life history tradeoffs and the timing of breeding differently than in other species (i.e. cowbirds can leave immediately after egg laying). The final dataset contained 134 species (Supplementary material Appendix 1).

Data on breeding phenology was collected from several ornithological monographs and the references therein (Supplementary material Appendix 1). For most species, phenology data were available from several locations; in each case, the geographical coordinates where the study

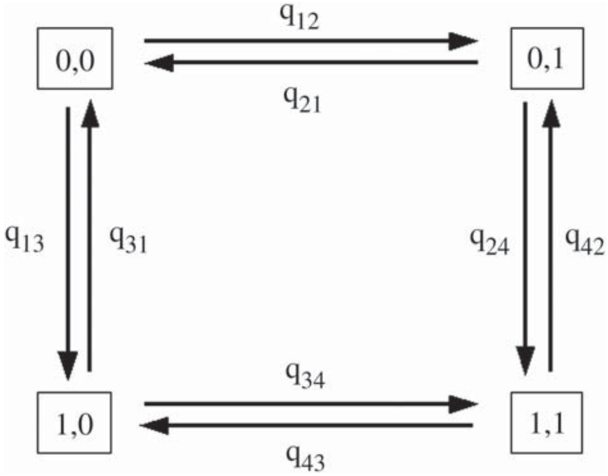

Fig. 1. Schematic representation of the transition rate parameters (q_{ij}) estimated by the directional tests. The numbers in the boxes represent the four possible combinations of two binary traits. The first number represents the state of migratory behaviour whereas the second stands for the state of either of the three explanatory variables: start of breeding season, length of breeding, adult body size or winter diet. The parameters q_{ij} denote the rate of transition among these combination of states.

was performed, the start and end of the laying period and the sample size (number of nests) was recorded. In a few cases (ten species), the dates were only given as part of the month, i.e. 'early', 'mid' or 'late' period of a month and we therefore substituted them with the 5th, 15th and the 25th day of the month, respectively. The length of the breeding season was simply taken as the difference between the end and start dates.

Data on the start and length of the breeding season originated partly from field studies of breeding biology and partly from museum collections and nest card programs encompassing larger geographic regions (US states, Canadian provinces or European countries). In this latter case, we took the midpoint of the species' distribution in that specific region, assessed from distribution maps in Cramp and Perrins (1994) and Poole (2005) to the nearest 0.5 decimal degree. Note however, that we did not include regions with a latitudinal span larger than 10 degrees, thus the lowest precision for any latitude data is about 5 degrees, and it is $<<$5 degrees in most of the cases.

Sampling intensity might introduce a bias in assessing breeding phenology, because more effort typically increases the probability that very early or very late nests are discovered. Therefore, only data based on a sample size of at least 20 nests were included in the analyses, and if more than one data point was available for a given species, we selected the one with the largest sample size. However, to maximize variation in migration distance within the sample, we also checked our results on a different dataset in which we selected the northernmost record for all species (i.e. the northernmost of all records available for a species that are based on $\geq$20 nests).

Another possible source of bias in recording breeding phenology is that different aspects of the breeding cycle may be reported. Thus, some studies report laying dates (laying of first eggs in the nest) whereas others report egg dates (dates on which viable eggs were found; McNair 1987, Peck and James 1987), and these may result in breeding periods with different start and length. To see whether this affected our phenology variables, we used the original dataset with 496 records (with a median of three records per species) to compare data originating from laying dates and egg dates. The two type of data indeed showed differences (Supplementary material Appendix 2), suggesting that the origin of phenology data needs to be taken into account in the analyses (Results).

Migratory behaviour was quantified by calculating the minimum geographical distance between the point of origin of the phenological data and the wintering range, from digitized distribution maps. We used the maps provided by Ridgely et al. (2007) for North American species and digitized the distribution of European species in our sample by hand, following range maps in Cramp and Perrins (1994). The resulting variable is the minimal distance a bird has to migrate to reach the winter quarters (where the breeding and wintering ranges overlap at the study location, the variable was set to 0). Although this measure may not represent the true migration distance of a species, (e.g. if some populations migrate to the southern end of the wintering range), we do not expect any systematic bias in this variable and assume that interspecific differences in the minimal migration distance reflect true differences in the degree of migratoriness. This assumption is supported by the very strong correlation between the minimum migration distance and the distance between the latitudinal midpoint of the breeding and wintering ranges (an approximation of the species-specific migratory behaviour; Spearman's rank correlation, $r_s = 0.865$, $p < 0.001$, $n = 134$). In addition, this variable has the important advantage of being specific to the population whose breeding phenology has been recorded.

Interspecific variation in migration distance may be affected by several other factors, such as the breeding latitude or the ability of the birds to survive harsh winter conditions. Species breeding at more northern latitudes experience harsher winters and have to migrate longer distances to enjoy the same winter conditions as birds breeding at more southern latitudes and these are more likely to be migratory (Newton 2008). In addition, birds of larger sizes can cope better with cold, because heat loss is lower compared to small animals (Bergmann's rule) and an ability to forage on seeds may also facilitate spending the winter at higher latitudes. To account for these confounding factors, we compiled data on adult body mass (the mean of male and female mass, from Dunning (2008) and winter diet, i.e. granivorous (composed primarily of seeds, 0) or insectivorous (mostly insects, 1) from Cramp and Perrins (1994) and Poole (2005), and controlled for these variables in multivariate analyses.

Breeding habitat may also confound the relationship between migration and phenology, because long distance migrants may differ in habitat use from short distance migrants and residents (Martin 1995, Böhning-Gaese and Oberrath 2003). Neotropical long distance migrants breeding in North America are more likely to inhabit forested environments, whereas Trans-Saharan migrants in

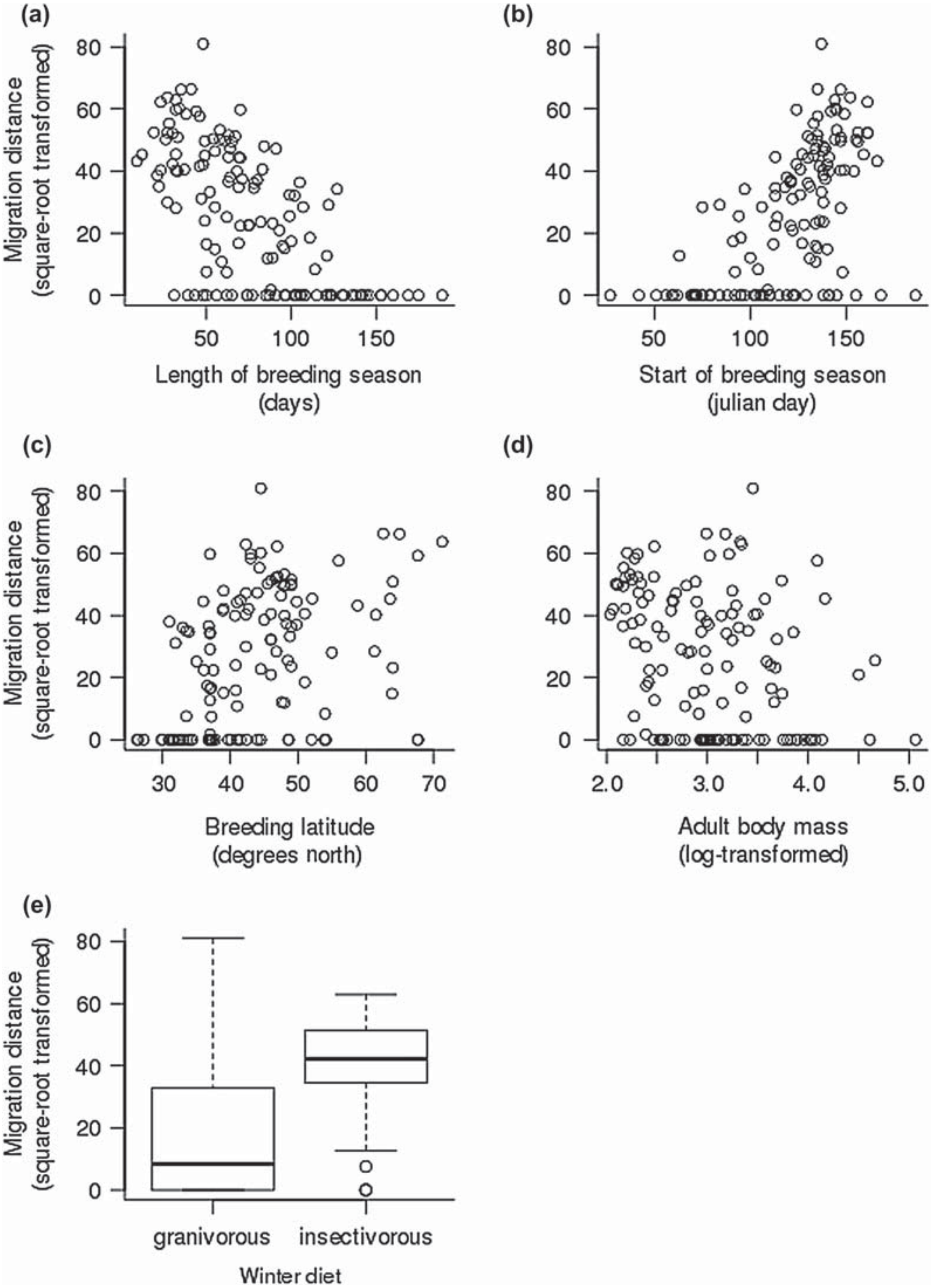

Fig. 2. Relationship between migration distance (km, square root transformed) and five explanatory variables: start (a) and length of breeding season (b), breeding latitude (c), adult body size (log-transformed for better visualization) (d) and winter diet (e). The outlier with the longest migration distance is the bobolink (*Dolychonyx oryzivorus*); excluding this species does not affect the results.

the Western Palearctic are more likely to breed in open habitats, compared to short distance or resident species in these areas. To account for any possible bias arising from these differences, we recorded the continent where the breeding phenology was studied (North America or Europe) and following Böhning-Gaese and Oberrath (2003), we assessed the type of breeding habitat based on a gradual scale ranging from closed to open habitats. Typical breeding habitat types reported in Cramp and Perrins (1994) and Poole (2005) were scored for each species on a scale from 1 to 7, as follows: 1 – closed forest; 2 – open forest; 3 – forest edge; 4 – gardens, orchards, urban areas; 5 – shrubland; 6 – open area with single trees or shrubs; and 7 – open area without trees or shrubs. If a species was reported to typically breed in more than one type of habitat, the score of these habitat types was averaged.

Comparative analyses

To find out whether the relationship between migration distance and breeding phenology is not the result of the confounding effects of breeding latitude, adult body size, winter diet, breeding habitat or continent, we performed multivariate analyses where we controlled for these confounding variables. Second, we ran directional phylogenetic tests between migratory behaviour and the explanatory variables that were significantly related to migration distance in the multivariate analyses.

Before performing the multivariate analyses, we checked whether phylogenetic correction was needed by calculating Pagel's lambda statistic for phylogenetic signal, using the 'geiger' package in the R statistical environment (Harmon et al. 2008, R Development Core Team 2008). Pagel's lambda is a measure of the phylogenetic structure in the data; a value close to zero indicates phylogenetic independence, while larger values indicate that closely related species are more similar to each other than expected by chance (Pagel 1997, 1999). Significance was estimated by comparing the log-likelihood of a model with the maximum likelihood estimate of lambda for a given trait to the log-likelihood of a model where lambda was set to zero, using likelihood ratio tests. All traits showed significant phylogenetic signal (Table 1).

The relationship between migration distance, breeding phenology and the potentially confounding variables was tested using phylogenetic generalized least squares (PGLS) in R's 'ape' package (Paradis 2006). The PGLS method accounts for the non-independence of the data points arising from their phylogenetic relationship by incorporating a matrix of covariances among the species into the model (Martins and Hansen 1997, Pagel 1997, 1999). This matrix can be adjusted to reflect the degree of phylogenetic autocorrelation in the data by incorporating the maximum likelihood estimate of Pagel's lambda (Freckleton et al. 2002). Migration distance, the dependent variable, was square-root transformed prior to the analyses, as the distribution of this variable was highly skewed due to the large number of non-migratory species in the sample. Although this transformation did not result in a normally distributed variable, the residuals of the PGLS models were normally distributed (Shapiro–Wilk tests of normality are reported along with the models). Breeding latitude, winter diet, start of breeding, length of breeding season, adult body mass, breeding habitat and continent were introduced as explanatory variables.

Table 1. Lambda statistics for phylogenetic signal for the variables investigated. Branch lengths were set to unity.

Variable	Lambda	Likelihood ratio	p
Migration distance	0.21	48.40	<0.001
Length of breeding season	0.08	44.07	<0.001
Start of breeding season	0.05	8.86	0.003
Breeding latitude	0.82	44.42	<0.001
Adult body size	0.56	107.16	<0.001
Winter diet	0.93	90.50	<0.001
Breeding habitat	0.92	82.72	<0.001

To find out the direction of evolutionary transitions and to corroborate the results of the PGLS analyses, we applied Pagel's test (Pagel 1994, Pagel and Meade 2006), using the software BayesTraits (<www.evolution.rdg.ac.uk/BayesTraits.html>). To test the correlated evolution of two binary traits on a phylogenetic tree, this method uses reversible-jump Markov chain Monte Carlo to estimate support for the hypothesis of correlated evolution between the two traits by searching among possible models conforming either to independent or correlated evolution. The dependent and independent models can be compared by means of the Bayes factor, i.e. by calculating 2[$\log_e$(harmonic mean of log likelihood of the dependent models) – $\log_e$(harmonic mean of the log likelihood of the independent models)]. A Bayes factor greater than 2 indicates positive evidence for the correlated model, greater than 5 is strong and greater than 10 is very strong evidence (Pagel and Meade 2006). Each model consists of up to eight different parameters describing the rate of transition among the four possible combination of states (Fig. 1). The posterior distribution of these transition rate parameters are simultaneously estimated by the reversible-jump Markov chain Monte Carlo algorithm. Alternative evolutionary hypotheses (such as the temporal order and contingency of evolutionary changes) can be tested by comparing critical pairs of these parameters (e.g. by looking at the posterior probability that a given parameter is zero). If transitions in one character depend on the background of the other character, then evolutionary changes in the first are contingent upon the second character (the contingent changes test). For example, if the the rate parameter for the $(0,0)\rightarrow(1,0)$ transition is higher then zero, but the rate parameter for the $(0,1)\rightarrow(1,1)$ transition is assigned a value of zero with high posterior probability, then this means that transitions in the first trait (from 0 to 1) are more likely when the background state of the other character is 0. For the analyses we have used an exponential hyperprior (0 100), which allows the estimation of the rate transition parameters from the data. The Monte Carlo algorithm was run for 10^7 iterations, with a sampling frequency of 100 iterations. The first 10^6 iterations were discarded, because the harmonic means of the log-likelihood generally did not stabilize before this. For further details on this method, see Pagel and Meade (2006) and the BayesTraits manual (<www.ams.reading.ac.uk/zoology/pagel>).

The drawback of the correlated changes test in our case is that it cannot account for the confounding effects of other variables. Thus, while two traits can be shown to conform to correlated evolution, it cannot be ruled out that transition in both traits happened because of transition in a third variable. Here, both migration distance and breeding phenology depend on breeding latitude, and transitions in the breeding range of a species may simultaneously affect both traits. To circumvent this problem, we calculated residuals between migration distance and breeding latitude and subsequently scored species with positive residuals (i.e. migration distance longer than expected for that latitude) as long distance migrants (1) and short-distance migrants (0) otherwise. The problem with taking residuals is that this categorization may depend on the species included in the analysis, or the latitude from which their migration distance is calculated. To quantify this error, we repeated the calculation the residuals using random points from within the breeding range of the species and the minimum migration distances from these coordinates. That is, for every focal species, we selected random points for all other species, but kept the original values for the focal species, calculated residuals and scored the focal species as long-distance or short distance migrant based on the residuals. This procedure was repeated 1000 times for each species. In this way, we were able to determine the rate of error of our initial categorization for each species (i.e. the number of times a species will be scored differently if the values of the other species changes). We found that our categorization is robust for most species, but 15 species received a different score at least one time (a rate of error >0). Therefore, we have repeated the directional analyses by excluding these species.

The start of breeding, length of breeding season and body mass are all continuous variables, but the correlated changes test can only be performed on binary variables. Therefore, we dichotomized these variables using their median as the cut-off value. Thus, a species was scored as a late breeder (1) if it starts breeding after 7 May and early breeder (0) otherwise; species with a breeding season longer than 69.5 days were scored as having a long breeding season (1), all others were scored as having a short breeding season (0). The median body mass in our sample was 19.55 g; species with a body size larger than this value were scored as being large (1), those with a smaller value as small (0). As this categorization may potentially introduce a bias, we repeated the analyses using two different cut-off values, the 40 and 60 percentiles of body mass, start and length of the breeding season.

The phylogenetic relationship among the species was represented by a composite phylogeny assembled from recent molecular studies (see Supplementary material Appendix 3 for the tree and the references). As the phylogenetic information was obtained from different studies performed on different gene sequences, we were not able to use branch length information. Therefore, we generated branch lengths in two ways: first, we set all branch lengths to unity (conforming to a punctuational model of evolution); second we repeated both the multivariate and the directional tests by transforming branch lengths using Grafen's method, which is similar to a gradual model of evolution (Grafen 1989, Paradis 2006).

Results

Both the start of breeding and the length of the breeding season were significantly related to migration distance and these relationships remained significant when we controlled for the potentially confounding effects (Table 2a–b). Migration distance increased with breeding latitude and decreased with adult body size, but it was not related to breeding habitat or continent (Table 2a–b). Winter diet had a significant effect in the full models, but in the minimal models it was only significant when the start of the breeding season, but not its length, was introduced as the explanatory phenology variable (Table 2a–b). The relationship between migration distance and the five significant explanatory variables is depicted in Fig. 2. When the start and length of breeding season were introduced in the same model with breeding latitude, body mass and winter diet as covariates, the start of breeding season and winter diet were not significantly associated with migration distance, whereas all other variables had a significant effect, suggesting that the length of the breeding season may be more important then its starting date. However, given the very strong correlation between

Table 2. Full and minimal phylogenetic generalized least squares models for explaining migration distance (km, square-root transformed) by (a) start of breeding season (julian day) or (b) length of breeding season (days), together with additional explanatory variables: breeding latitude (degrees north), adult body size (g), winter diet (granivorous/insectivorous), breeding habitat (for categorisation, see text) and contintent (Europe/North America). Minimal models were obtained by eliminating nonsignificant predictors from the full model in a backward stepwise manner based on the largest p-value. Branch lengths were set to unity.

(a)

Source of variance	Full model: β (SE)	t (p)	Minimal model: β (SE)	t (p)
Start of breeding season	0.126 (0.053)	2.390 (0.018)	0.142 (0.050)	2.850 (0.005)
Breeding latitude	1.182 (0.188)	6.288 (<0.001)	1.077 (0.170)	6.321 (<0.001)
Adult body size	–0.239 (0.086)	–2.776 (0.006)	–0.244 (0.088)	–2.782 (0.006)
Winter diet	11.617 (4.661)	2.492 (0.014)	10.853 (4.662)	2.328 (0.022)
Breeding habitat	0.456 (0.793)	0.575 (0.566)	–	–
Continent	–8.963 (6.018)	–1.489 (0.139)	–	–

Shapiro–Wilk test on the normality of residuals for the full model: W = 0.993, p = 0.725; for the minimal model: W = 0.988, p = 0.318.

(b)

Source of variance	Full model: β (SE)	t (p)	Minimal model: β (SE)	t (p)
Length of breeding season	–0.154 (0.038)	–4.043 (<0.001)	–0.172 (0.036)	–4.732 (<0.001)
Breeding latitude	1.124 (0.166)	6.786 (<0.001)	1.010 (0.152)	6.639 (<0.001)
Adult body size	–0.262 (0.085)	–3.118 (0.002)	–0.296 (0.088)	–3.372 (0.001)
Winter diet	9.042 (4.568)	1.980 (0.050)	–	–
Breeding habitat	0.333 (0.765)	0.437 (0.663)	–	–
Continent	–9.279 (5.757)	–1.612 (0.110)	–	–

Shapiro-Wilk test on the normality of residuals for the full model: W = 0.993, p = 0.791; for the minimal model: W = 0.989, p = 0.362.

the two phenology variables (Spearman's rank correlation, $r_s = -0.78$, $p < 0.001$, $n = 134$), multicollinearity may be a problem when these two variables are introduced into the same model and therefore the possibility that the start of breeding may also have an effect (in addition or instead of the length of the breeding season) cannot be excluded.

The PGLS analyses were repeated by including sample size (number of nests) and type of phenology data (laying dates or egg dates) as covariates, in addition to the six explanatory variables. However, neither sampling intensity nor the type of phenology data were significantly associated with migration distance, thus interspecific differences in sampling should not affect our results. Backward elimination of the nonsignificant predictors based on largest p-value resulted in the same minimum adequate model (Crawley 2007) as in the first models where these two variables have not been included, therefore they are not reported separately.

We found strong support for the correlated evolution of migratory behaviour and breeding phenology (Bayes factor for migratory behaviour – start of breeding 27.01, migratory behaviour – length of breeding season 26.12). Furthermore, the correlated evolution between migratory behaviour and adult body size and migratory behaviour and winter diet were also supported (Bayes factor 8.32 and 13.30, respectively). The transition rate parameters strongly supported the hypothesis that breeding phenology determines migratory behaviour (Table 3); transitions to long migration distance are more likely from short breeding seasons ($q_{13} >> q_{24}$) and transitions to short migration distance are more likely from a long breeding season ($q_{42} >> q_{31}$). Similarly, evolutionary transitions in migratory behaviour are contingent upon the start of breeding: transitions to long migration distance are more likely from a state of late breeding ($q_{24} >> q_{13}$) and transitions to short migration distance are more likely from a state of early breeding ($q_{31} >> q_{42}$).

The transition rate parameters for the correlated evolution between migration and body mass and migration and winter diet both showed a pattern opposite to that observed in the case of breeding phenology. Both adult body size and winter diet were found to be contingent upon migratory behaviour; thus, based on the transition rate parameters a large body size is more likely to evolve in short distance migrants ($q_{12} >> q_{34}$) and transitions to a granivorous diet are more likely from a state of short-distance migration ($q_{21} >> q_{43}$).

The PGLS analyses and the directional tests (both Bayes factors and the transition rate parameters) were qualitatively similar if the branch lengths were transformed according to Grafen's method. Moreover, the results were virtually identical when using the northernmost data points (Supplementary material Appendix 4), and were not affected by the exclusion of species with a rate of error greater than 0 in the scoring of migratory behaviour. Using the 40 or 60 percentiles as cut-off points to dichotomise the variables resulted in qualitatively similar results, with two exceptions (Supplementary material Appendix 5). In the analyses using the 60 percentiles to dichotomise the length of breeding season, three transition rate parameters were assigned a value of zero with a relatively high posterior probability: q_{24}, q_{31} and q_{34}. That is, transitions in migratory behaviour are still contingent upon the length of the breeding season, but it also appears that a very long breeding season is more likely to evolve in short distance migrants ($q_{12} >> q_{34}$). Second, in the directional test using the 40 percentiles to dichotomize body size, two rate parameters were assigned a value of zero with high posterior probability: q_{13} and q_{34} (Supplementary material Appendix 5), indicating that not only is a large body size more likely to evolve from a state of short distance migration, but also that a long distance migration is less likely to evolve from a very small body size. However, support for this test was relatively weak (Bayes factor 3.31).

Discussion

Consistent with previous studies, we found that interspecific variability in the migratory behaviour of the finches and their allies is associated with aspects of their breeding phenology. Results from the directional analyses showed that transitions from a relatively short to a relatively long migration distance are more likely when the breeding season is short and starts late, whereas the reverse transition is more likely when the breeding season is long and starts early. Although we acknowledge the difficulties associated with categorizing continuous variables into discrete traits, the results were relatively robust to different categorizations. Furthermore, while

Table 3. Mean±SD and Z-scores of the transition rate parameters, estimated from the directional tests. Migratory behaviour is the first variable in all cases, and length of breeding season, start of breeding season, adult body size and winter diet were the second character, respectively. All variables are dichotomous (see the Methods section for scoring species). Parameters which were assigned a value of 0 with high posterior probability (high Z-scores), suggesting that the given transition occurs with very low probability, are shown in bold. The meaning of the parameters is clarified in Fig. 1.

	Length of breeding season		Start of breeding season		Adult body size		Winter diet	
Parameter	Mean±SD	Z-score	Mean±SD	Z-score	Mean±SD	Z-score	Mean±SD	Z-score
q_{12}	0.56±0.43	0.00	0.41±0.09	0.00	0.19±0.08	0.00	0.05±0.02	0.04
q_{13}	0.47±0.20	0.02	**0.00±0.02**	**0.99**	0.09±0.06	0.20	0.14±0.13	0.00
q_{21}	0.39±0.12	0.00	0.42±0.13	0.00	0.16±0.07	0.00	0.22±0.13	0.00
q_{24}	**0.02±0.06**	**0.92**	0.41±0.10	0.00	0.20±0.14	0.00	0.12±0.12	0.16
q_{31}	**0.01±0.06**	**0.93**	0.42±0.10	0.00	0.10±0.04	0.00	0.26±0.13	0.00
q_{34}	0.39±0.12	0.00	0.42±0.12	0.00	**0.00±0.02**	**0.93**	0.07±0.04	0.05
q_{42}	0.46±0.20	0.03	**0.00±0.02**	**1.00**	0.21±0.14	0.00	0.06±0.03	0.00
q_{43}	0.55±0.43	0.00	0.41±0.09	0.00	0.14±0.06	0.00	**0.00±0.01**	**0.92**

the coevolution between migratory behaviour and breeding phenology may involve complex interactions between these traits, with both components affecting the other, we found a robust pattern in support of the hypothesis that the evolution of migratory behaviour is affected by the breeding phenology of the species.

The results from the directional tests provided only weak support for the hypothesis that time constraints arising from longer migration distances affect the breeding phenology, as transitions in the start and length of the breeding season were not found to be contingent upon migratory behaviour (except when we used the 60 percentiles as cut-off points for the length of breeding season). Thus, while a long migration distance may lead to less parental investment in male shorebirds (García-Peña et al. 2009) or select for shorter postembryonic developmental periods (Meiri and Yom Tov 2004), it does not lead, in general, to shorter breeding seasons or a later onset of breeding in the finches and their allies. These differences are not surprising, as the three traits are fundamentally different aspects of reproductive behaviour and each may be affected differently by time constraints. In particular, as the length of the breeding period in this study probably reflects the number of brood attempts per year (either from multiple broods or replacement broods), it may have a greater effect on reproductive success than either parental care or the length of the postembryonic developmental period. The reproductive value of second broods or replacement broods in small passerines is probably large, given their relatively short life span (Møller 2007), so it might not be advantageous to give up the opportunity to raise these broods, if the environmental conditions enable it.

Our results do not support the hypothesis that the association between migratory behaviour and breeding phenology is the result of life history tradeoffs affecting these traits simultaneously. First, while arguments based on life history theory may explain the lower number of annual broods and the corresponding shorter breeding season in long distance migrants, they cannot account for the later start of the breeding season in these species. Second, if the fecundity-mortality tradeoff would be responsible for the observed correlation between migration and breeding phenology, we would expect that evolutionary transitions in the length of the breeding season depend on the background state of migratory behaviour (i.e. transition rates to a short breeding season higher in relatively long distance migrants and transition rates to long breeding season higher in short distance migrants), a prediction not supported by our results. This is not to say that differences in annual survival due to contrasting migration strategies cannot not lead to differences in reproductive investment, because selection can affect other reproductive traits as well, e.g. clutch size (Martin 1995, Böhning-Gaese et al. 2000). However, our results make it unlikely that the shorter breeding season is the consequence of the high annual survival rate of long distance migrants, which selects for fewer broods per year (and hence a shorter breeding season). Furthermore, the fact that not all species migrate long distances (although this would supposedly increase their annual survival rate; Greenberg 1980, Bruderer and Salewski 2009), suggests that additional factors may operate which select for shorter migration distances in some species.

The most likely scenario based on our results is that reproductive phenology is determined by ecological factors, such as the species-specific type of food exploited during breeding. Reproduction in birds is an energy-demanding process and selection should act to maximally match the timing of reproduction with the peak of food availability (Lack 1968, Perrins 1970). The length and timing of this peak in food availability is likely to differ among different types of habitat, but differences may exist within habitats as well, if birds breeding at the same location rely on different types of food to feed their nestlings. The reproductive phenology in turn may determine the costs and benefits of migration, constraining migration distance such that only species with a short, late-starting breeding season can afford to migrate long distances while species with an extended breeding season can travel only short distances. The evolutionary explanation for this phenomenon could be that species with a relatively long breeding season 1) have to migrate under less favourable weather conditions early in spring and late in autumn, and 2) can spend less time on the wintering grounds, both factors decreasing the benefit of migrating long distances (Greenberg 1980, Bell 1996, 1997). In addition, a long breeding season is likely to start early in spring, when environmental conditions tend to show a higher year-to-year variability. This, in turn, could increase the benefit of staying close to the breeding grounds, as individuals can respond more quickly to improving or deteriorating conditions and have a higher fecundity as a result (Alerstam and Högstedt 1980). Unfortunately, we could not clearly discriminate among these possible mechanisms; the length of the breeding season appeared to be more important in multivariate analyses, but the start and length of breeding season were very strongly correlated. Furthermore, as most of our data points are based on data collected from multiple years, a longer breeding season may result from high year-to-year variability. Lastly, our measure of spring predictability (the start of breeding) is only indirect; unfortunately, very few long term breeding data for our species were available to enable a more thorough analysis. It is not unlikely, however, that all these mechanisms act in concert to shape the migratory behaviour of a species.

The origin and evolution of avian migration has attracted much interest and several hypotheses have been proposed to explain it (for recent reviews and discussions see Rappole and Jones 2002, Zink 2002, Alerstam et al. 2003, Helbig 2003, Salewski and Bruderer 2007). For example, the phylogenetic study of Outlaw and Voelker (2006) suggests that the increasing seasonality of the breeding environments (through the expansion of breeding ranges from southern latitudes to temperate and boreal areas) played a key role in the evolution of migratory behaviour in the pipits and wagtails (*Motacillidae*). Similarly, other studies have emphasized the importance of expanding breeding ranges for the origin of migratory behaviour (Joseph et al. 1999, Böhning-Gaese 2005, Milá et al. 2006). It is likely however, that other factors may also affect the outcome of this colonization, because closely related species, supposedly with similar biogeographical history, often show contrasting migratory behaviour. For example, in a molecular phylogenetic study, Outlaw et al. (2003) have shown that the five species of *Catharus* trushes breeding in North America most likely originate from Central or South America, and migration most likely evolved in this clade by the expansion of the breeding range, while the wintering range changed relatively little. Yet the wintering range of one of the species (*C. guttatus*), extends far more to the north than the supposed center of origin of this taxon, suggesting that the migration distance was subsequently shortened in this species (Outlaw et al. 2003). On the other hand, some species do not evolve migratory behaviour after a northward range shift, the European collared dove *Streptopelia decaocto* being a well-known example. Thus, the expansion from the tropics does not always result in long distance migration. Our results imply that the breeding phenology may explain at least partly the outcome of these range shifts, with long distance migration evolving only when breeding phenology does not constrain it. This is in accordance with current views that regard the evolution of migration as a consequence of birds exploiting the seasonal flush of food at higher latitudes for breeding yet returning to more benign environments to increase survival, but refines this scenario by highlighting ecological conditions that could determine whether the birds keep returning to these ancestral areas or adapt to the year-round occupation of the new breeding areas.

Migratory behaviour was negatively associated with adult body size and migration distance was shorter in species with a granivorous winter diet. The directional analyses revealed that transitions in adult body size and winter diet are contingent upon migratory behaviour, with a large adult body size and a granivorous diet being more likely to evolve from a state of a relatively short migration distance. Thus, in the finches and their allies, body mass and winter diet do not appear to constrain migratory behaviour, but rather, these traits adapt to increase the survival chances of birds spending the winter at high latitudes (see Pravosudov et al. 2007 for a similar conclusion on brain size).

Although the present study was restricted to the finches and allies, the relationship between phenology and migration could apply to other taxonomic groups as well. However, other factors, the cost of migration in particular, will certainly affect the outcome of the coevolution between migration and breeding phenology (Greenberg 1980). For example, swallows and martins (family *Hirundinidae*) breeding at temperate latitudes have an extended breeding season yet migrate long distances (Bruderer and Salewski 2009). As these birds are highly adapted for aerial life and can forage while in flight during migration, moving between the summer and winter quarters may be less costly for these species (both in terms of mortality and time) and a longer migration distance may be possible even with an extended breeding season. In addition, the relationship between breeding phenology and migration may apply not only to interspecific comparisons, but also to differences in the migratory behaviour of populations of the same species. Both the 'time allocation' and the 'spring predictability' hypotheses have been applied to explain leap-frog migration (the pattern in which northern populations of a species migrate longer distances than the southern ones; Alerstam and Högstedt 1980, Greenberg 1980, Bell 1996, 1997). Although alternative explanations for leap-frog migration do exist (and indeed are more commonly accepted; Greenberg 1986, Drent and Piersma 1990), our results provide phylogenetic comparative evidence that breeding phenology may also play an important role in shaping migration strategies.

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Supplementary material (available online as Appendix O18592 at www.oikos.ekol.lu.se/appendix). Appendix 1–5.