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Patterns of change in timing of spring migration in North European songbird populations

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From 1976 to 1997 passerines were mist-netted and ringed on the island of Christiansø, in the Baltic Sea. Here we present analyses of phenological changes (i.e. time of arrival) for 25 species based on the entire populations of mist-netted songbirds during spring migration. We used two approaches (least square and quantile regression) to test for changes in arrival time of first individuals and three different parts of the songbird populations (i.e. first 5%, 50% and 95% of the total number of trapped individuals corrected for trapping effort). Our results generally confirm earlier spring arrival of migratory passerines with an overall earlier arrival of 0.26 days per year. Changes in the arrival time of first individuals are often the only data available. They are typically analysed on the assumption that they are representative of their respective population. We found a unidirectional, significant change towards earlier arrival for all four measures of arrival timing which seem to support this. However, the four measures of arrival are changing at different rates. First individuals changed arrival time more rapidly than the first 5%, 50% and 95% of the spring total. Such differences are likely to be important for our understanding of population-dynamic changes in relation to climate change. These differences may also have long-term evolutionary consequences. Migration distance seems to affect the degree of change in arrival time, but we found no difference between species wintering in different regions of Africa.

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Global mean temperatures have increased during the last century (Easterling et al. 1997). In the Northern Hemisphere spring temperatures have risen during the last 30 years (Folland and Karl 2001). Ecosystems and species have changed their physiology, distribution and phenology during the last decades (e.g. Walther et al. 2002), and evidence of changes in the phenology of plants (e.g. Menzel and Fabian 1999) and animals (e.g. Beebee 1995) is gathering rapidly.

Migratory birds of Europe and North America have been subject to many studies showing evidence of changes in the timing of breeding and migration (e.g. Bairlein and Winkel 2001). Earlier egg laying dates are being reported in a number of studies (e.g. Sergio 2003, Both et al. 2004). Climatic conditions such as spring temperatures and the North Atlantic Oscillation (NAO) have been shown to correlate with the migration of birds (e.g. Forchhammer et al. 2002, Vähätalo et al. 2004).

The majority of recent phenological studies of a wide range of migratory birds report earlier spring arrivals (e.g. Hüppop and Hüppop 2003) and changes in autumn departure (Cotton 2003, Jenni and Kéry 2003). Most previous studies of migration phenology were conducted on the basis of sighting records of first arriving individuals. Typically, arrival of the first individual to breeding grounds was used (e.g. Tryjanowski et al. 2002). However, the increasing number of active birdwatchers may influence such long-term data sets, biasing the results toward earlier arrival dates.

Sparks et al. (2001) questioned looking at the earliest individuals as a reliable reflection of the overall popula-

tion timing and advocated caution when interpreting such a result. To minimise potential biases and the effect of exceptional outliers in the distributions of arrival dates, one could analyse data on other measures of arrival timing, e.g. when the first 5% of the populations had arrived. However, it is difficult, if not impossible, to obtain that kind of reliable quantitative data from most sighting data. In contrast, long-term standardised ringing programs from ringing stations monitoring migratory birds offer well-suited data sets for thorough analyses of the phenology of entire populations. The sampling procedures and efforts are often kept constant and the biases minimised. Such data are used in the analyses presented in this paper.

In a recent analysis of mean arrival dates from the ringing station at Helgoland in the North Sea, Hüppop and Hüppop (2003) found earlier spring arrival over time. They found no effect of migration distance on changes in the timing of migration, but argued that migrants following a western route are probably more affected by regional climate as expressed by the North Atlantic Oscillation (i.e. the NAO index) than migrants passing on an eastern route. Our study also examines these issues.

The aim of our study was to: (a) verify earlier spring arrival of the migratory passerines passing the Baltic Sea on route to their breeding grounds at high latitudes in Northern Europe (i.e. Scandinavia), (b) test the presumption of other studies that potential changes in arrival dates of the first (few) individual(s) constitute a sample-invariant reflection pertinent for the entire population, and (c) analyse changes in timing of different population parts and test potential phenological changes among groups of species with different migration strategies (i.e. migration distance and wintering areas). The underlying assumption for analysing arrival of different population parts (quantiles) is that the arrival of each bird reflects its breeding strategy and not just random variation from a common mean. Of course, random variation will also influence the arrival of each bird, but we assume that this is on a smaller scale than the population parts which we consider (first 5%, 50% and 95%). This view is supported by studies showing that individuals within a population follow different strategies (e.g. Bêty et al. 2004), heritability in timing of migration (Berthold and Pulido 1994) and fitness consequences related to arrival (e.g. Lozano et al. 1996).

Materials and methods

The data set used in this study is derived from 22 years of standardized mist-netting of passerine birds on the island of Christiansø (55°19′N, 15°11′E) 18 km north-east of Bornholm in the Baltic Sea. Birds were trapped from 15 March to 15 June, covering the entire spring migration period of each species. Data were collected from 1976 to 1997 when the Danish National Forest and Nature Agency operated a ringing station on Christiansø with the aim of monitoring the passing populations of migratory passerines by means of standardized mist-netting. The birds caught have their main breeding areas in Sweden and Finland and pass the isolated island twice a year during their spring and autumn migration (Rabøl and Rahbek 2002).

Migrants were trapped in mist-nets and ringed during a standardized period of five hours after sunrise. The effort (number of net-metres) was not constant, but by correcting for effort, we calculated a comparable daily figure corresponding to the number of trapped birds per 300 net-metre hours. There was a weak, negative relationship between the total number of birds trapped corrected for trapping effort (N') and total net-metre hours ($N' = -0.0145$ net-metre hours $+ 47.629$, $P < 0.001$), which was most likely caused by the closing of nets when migrants were too numerous. The general ringing activity (net-metre hours) and total number of birds trapped (N) increased in the period (slope = 5,683 net-metre hours/year, $P < 0.001$ and slope = 149.4 birds/year, $P = 0.04$, respectively), but the total number of birds trapped corrected for trapping effort (N') did not (slope = 1.21 birds/year, $P = 0.94$). Because of the isolated position of the island and the relatively constant vegetation height and thickness, trapping conditions are considered to be constant from year to year (Rabøl and Rahbek 2002).

Description of the data set

More than 568,000 individual birds were trapped and ringed on Christiansø, including more than 243,000 individuals of 149 species, during the spring migration. In our study we included all migratory passerine species of which no fewer than 10 individuals were trapped each spring season, totalling 25 species. The 25 migrants comprise three short-distance migrants wintering in north-western Europe and southern England, five medium-distance migrants wintering in south-western Europe and 17 long-distance migrants wintering in Africa south of the Sahara Desert (Table 1). For each species, the migration distance from its main wintering areas to its main breeding area (south-eastern Finland) was estimated (to the nearest 500 km; Cramp 1988, 1992, Cramp and Perrins 1993, 1994, Helbig 2003). To analyse the effects of the different migration routes, the group of sub-Saharan migrants was divided into three subgroups according to their main wintering areas in Africa (Zink 1973–1985, Zink and Bairlein 1995). The chiffchaffs *Phylloscopus collybita* and willow warblers *Phylloscopus trochilus* trapped on Christiansø belong to different

Table 1. Changes in timing of spring migration for 25 migratory species in a 22-year period (1976–1997). Arrival of first individuals and the population quantiles (first 5%, 50% and 95%) are presented using least square regression (LSR) and quantile regression (QR) including mean values of short-/median- and long-distance migrants as well as for the entire group (see Methods for details). Wintering area, total numbers trapped (N), numbers corrected for trapping effort (N′) and migration distance (km) for each species are also included. Significant trends in individual species and group means are tested using t-tests (* = P < 0.05, two-tailed; parentheses indicate non-significance (P > 0.05) when adjusting for multiple testing with the sequential Bonferroni procedure: $P_i \leq \alpha/(1+k-i)$).

	Wintering area	N	N′	Migration distance (km)	Regressions coefficients, slopes (days/year)						
					First individual	First 5%		First 50%		First 95%	
						LSR	QR	LSR	QR	LSR	QR
Short-distance migrants											
Goldcrest *Regulus regulus*	NW Europe	11,005	3,189	1,500	−0.84*	0.01	−0.29*	0.08	−0.43*	−0.28	−0.50*
Blackbird *Turdus merula*		4,923	1,929	1,500	−0.89*	−0.69(*)	−1.08*	−0.59(*)	−0.36*	−1.05(*)	−0.84*
Wren *Troglodytes troglodytes*		2,863	753	1,500	−0.88*	−0.50(*)	−0.80*	−0.35	0.00	−0.17	−0.28(*)
Medium-distance migrants											
Dunnock *Prunella modularis*	SW Europe	6,973	1,698	2,000	−0.68(*)	−0.28	−0.50*	0.06	0.00	−0.32	−0.56*
Reed bunting *Emberiza schoeniclus*		912	246	2,000	−0.75*	−0.48*	−0.82*	−0.29	−0.10	−0.12	−0.14
Robin *Erithacus rubecula*		52,265	11,231	2,500	−0.72*	−0.18	0.05(*)	−0.22	−0.13*	−0.43	−0.46*
Redwing *Turdus iliacus*		2,237	658	2,500	−0.61*	−0.45(*)	−0.59*	−0.23	−0.18*	−0.41	−0.38
Song thrush *Turdus philomelos*		8,673	2,223	2,500	−0.58(*)	−0.14	−0.33*	−0.22	−0.18*	−0.44(*)	−0.33*
Regression coefficient mean					−0.74*	−0.34*	−0.54*	−0.22*	−0.04	−0.40*	−0.44*
Long-distance migrants											
Chiffchaff *Phylloscopus collybita*	W/E Africa	2,776	656	5,500	−0.62	−0.30	−0.17	−0.26	−0.15*	0.10	0.00
Willow warbler *Phylloscopus trochilus*		42,733	10,413	7,500	−0.23	−0.26(*)	−0.13*	−0.24	−0.24*	−0.28(*)	−0.11*
Pied flycatcher *Ficedula hypoleuca*	W Africa	5,210	1,194	6,500	−0.13	−0.19	−0.17(*)	−0.02	−0.09(*)	0.04	0.08
Redstart *Phoenicurus phoenicurus*		7,980	1,692	6,000	−0.35(*)	−0.34	−0.39*	−0.25	−0.16	−0.42	−0.27*
Whitethroat *Sylvia communis*		2,949	630	6,000	−0.43(*)	−0.28	−0.25*	−0.15	−0.14(*)	−0.26	−0.15
Whinchat *Saxicola rubetra*		1,186	236	6,000	−0.32(*)	−0.26	0.00	−0.01	0.06	−0.17	0.09
Reed warbler *Acrocephalus scirpaceus*		3,268	773	6,500	−0.32	−0.46	−0.07	−0.10	−0.13*	−0.12	0.07
Icterine warbler *Hippolais icterina*	C Africa	4,223	938	9,000	−0.04	−0.04	−0.07	0.01	0.10*	−0.04	0.00
Spotted flycatcher *Muscicapa striata*		2,806	531	9,000	−0.16	−0.13	−0.15*	−0.15	−0.21*	−0.25	−0.18*
Garden warbler *Sylvia borin*		13,670	2,730	7,500	−0.01	−0.13	−0.14*	−0.19	−0.20*	−0.09	−0.08(*)
Tree pipit *Anthus trivialis*		1,625	339	7,500	−0.22	−0.07	−0.25*	−0.09	−0.07	−0.30	−0.38*
Wood warbler *Phylloscopus sibilatrix*		1,087	232	7,500	−0.39	−0.22	−0.06	0.09	−0.07	−0.01	0.09
Blackcap *Sylvia atricapilla*	E Africa	5,197	1,118	5,500	−0.67(*)	−0.35(*)	−0.25*	−0.36	−0.36*	−0.09	0.00
Lesser whitethroat *Sylvia curruca*		8,841	2,053	5,500	−0.30	−0.25	0.00	−0.29	−0.28	−0.40	−0.38
Marsh warbler *Acrocephalus palustris*		1,169	255	9,000	−0.06	−0.01	0.06	0.05	0.18*	−0.06	0.00
Thrush nightingale *Luscinia luscinia*		992	212	9,000	−0.07	−0.07	−0.18(*)	−0.17	−0.22(*)	−0.08	−0.18
Red-backed shrike *Lanius collurio*		2,223	436	9,000	−0.16	−0.25	−0.28*	−0.03	−0.27*	0.13	0.18
Regression coefficient mean					−0.24*	−0.21*	−0.15*	−0.12*	−0.13*	−0.14*	−0.07
Total number of ringed migrants:		197,786	46,366								
Overall regression coefficient means					−0.40*	−0.25*	−0.27*	−0.16*	−0.10*	−0.22*	−0.19*

subpopulations migrating southwest and southeast, respectively (Zink 1973–1985, Cramp 1992). These two species were therefore excluded from the analysis concerning the effect of migration route.

Statistical analyses

We used two different approaches to describe changes in timing of migration: (1) Least square regression (LSR) using the slope-value as a description of the phenological change over time. We used four measures of population arrival for each spring season and species; the day of trapping (in Julian days where day one = 1 January) of the first individual and the day when the first 5%, 50% and 95% of the spring total had been caught (Fig. 1A and B). (2) Quantile regression (QR) to estimate quantiles (e.g. first 5%) of arrival over all years. QR slopes also describe the phenological change over time. In this analysis the full data set consists of observations of individual birds (Julian days) as a function of year (Birds caught within the first five hours only; each bird weighted by the inverse of the relative day effort as 300 net-metres divided by the total net-metres). In QR we estimated the arrival trends of the first 5%, 50% and 95% of total number caught. Individual time trends from the two methods were compared using Pearson's product moment correlation coefficient (r).

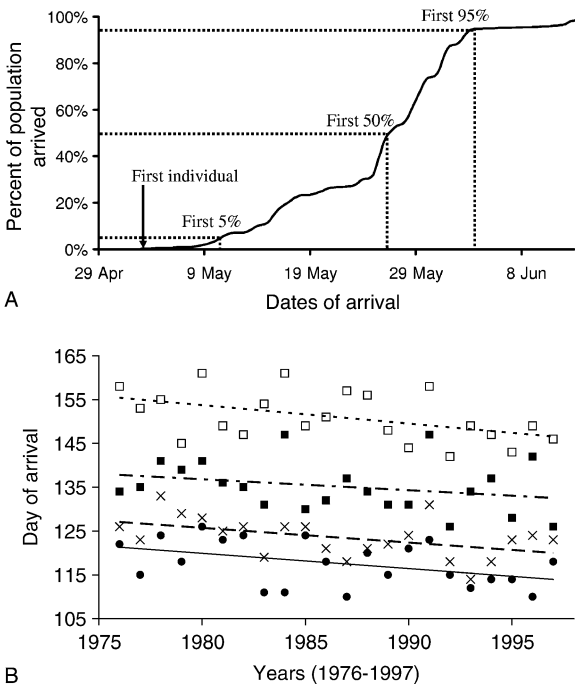

Fig. 1. (A) Illustration of the four measures of population arrival used in the (LSR) analysis. The accumulation curve describes the 1991 spring arrival of the entire population of redstart *Phoenicurus phoenicurus*. For each spring season and every species we calculated the date of trapping of the first individual, first 5%, 50% and 95% of the spring total had been caught. (B) Example of population arrival trend in the period 1976–1997 (redstart). Lines are regression lines of the arrival (in Julian days: day one = 1 January) of the first individual (closed circles; $y = -0.35x + 122$), first 5% (crosses; $y = -0.34x + 127$), 50% (closed squares; $y = -0.25x + 138$) and first 95% (open squares; $y = -0.42x + 156$).

Apart from estimating time trends for each species, we also tested effects of additional variables (other than year) in full statistical models. In LSR we estimated and tested the significance of a time trend using models with yearly arrival as the dependent variable and year as main predictor variable. Additionally, species, quantile and their interactions were included as factorial predictor variables. The variable year estimates trends in arrival dates over time. The species × quantile interaction describes differences among species in arrival of the different quantiles, the year × species interaction differences in time trends between species and the year × quantile interaction differences in time trends between quantiles. The three-way interaction, year × quantile × species, is used to test whether arrival trends differed between quantiles and species. However, quantile is a repeated measure, and thus expected to be autocorrelated. Yearly arrival is not a repeated measure, since these data are independent samples from the population, but it could still be autocorrelated due to selection in the population. Since each data point is not independent, we used appropriate repeated measures multivariate approaches when testing for an overall effect of year. Due to the autocorrelation between quantiles we used models with differences between quantiles as dependent variable in ordinary LSR to test for differences in arrival trends between quantiles. The differences between quantiles are not autocorrelated (as are the quantiles themselves).

Alternatively, these effects can be evaluated using an information-theoretic model-selection approach based on Akaike's information criterion (AIC; Burnham and Anderson 2002). In general, with AIC-based model selection the same variables were selected for inclusion in predictive models as the significant variables in ordinary and repeated measures models. AIC selection showed that there was considerable autocorrelation in the data due to correlation between quantiles. However, arrival in previous year was not included in the AIC selected best model. Repeated measures analyses were performed with quantile as repeated measures only. Since the independent variable arrival in LSR is not based on the same number of individuals (early and late quantiles are based on fewer individuals than the 50% quantile), the variances could potentially be unequal among quantiles. However, this did not seem to be the case (Unequal variances: $\chi^2 = 4.44$, df = 3, $P > 0.05$, Friedman's test; $F = 2.08$, df = 3, $P = 0.11$, ANOVA).

Effects of migration distance and wintering area were tested by inclusion in the models (with the variable species removed). We did not include the 22-year mean

arrival as a predictor variable in the analyses. Migration distance and the 22-year mean arrival are strongly correlated (first: $r = 0.93$, 5%: $r = 0.84$, 50%: $r = 0.91$, 95%: $r = 0.86$). Hence, an effect of migration distance cannot be separated from timing of arrival, and the results using either of these variables were very similar.

In QR, the effect of factorial predictor variables (quantile, species, migration distance and interactions) were tested using ANCOVA on the time trends estimated from QR. The distance × quantile interaction describes differences in arrival of the different quantiles according to migration distance, and the year × quantile × distance interaction describes differences in arrival trends of the different quantiles according to migration distance.

The two statistical approaches used to analyse the arrival of the songbird populations imply somewhat different assumptions. In QR, all trapped birds of a single species over the years are considered as belonging to the same population (Cade and Noon 2003). Thus, random variations in arrival from year to year, as expected in LSR due to, e.g. unusual weather situations, are levelled out in QR. However, more importantly this implies that later arriving birds are influencing the QR estimates, and years with many trapped birds will bias the estimates. In LSR late birds do not influence the results and all years contribute equally. Hence, with respect to the desired properties for this analysis, LSR should be favoured, even though QR does have some advantageous statistical properties (all data points considered simultaneously and not influenced by autocorrelation). Overall, the two approaches show similar results, with QR tending to show more variation in time trends (and thus more significant results for each species) than LSR. For both approaches we found significant interactions with migration distance, differences between quantiles and finally differences between quantiles with respect to migration distance (distance × quantile). However, due to the previously described potential biases introduced by QR, we generally prefer the LSR results. Thus, unless otherwise mentioned the results presented are from LSR.

Changes in migration period (difference between 5% and 95% arrival date) over time was modelled with year, species and year × species interaction as predictive variables to test for changes over time. We tested the potential effect of changing population sizes on our estimates of changes in arrival (as advocated by Tryjanowski and Sparks 2001). First, we correlated the arrival trends with the species-specific population trends (data from Rabøl and Rahbek 2002). Second, we correlated the unadjusted species-specific population indices from each year (data from Rabøl and Rahbek 2002) with the four population arrival dates from each year (first individual and first 5%, 50% and 95%).

When performing multiple similar tests (i.e. trends for each species and quantile), we adjusted the significance level, incorporating the sequential Bonferroni procedure (Rice 1989). The test results are ranked by their P-value (P_i) and will remain significant only if the inequality $P_i < \alpha/(1+k-i)$ is justified, where k = number of tests (25), i = the test result's rank and α = significance level (0.05; i.e. for smallest P-value: $P_1 < 0.05/(1+25-1) = 0.002$). All estimations and tests were performed in SAS ver. 8.2 (SAS 2000), except the quantile regressions, which were performed using the Program R (the quantreg package) (Koenker and Bassett 1978). We used Pearson's product moment correlation coefficient (r) to investigate correlations between migration distance and the 22-year mean arrival. When testing for correlations between the four quantiles and the effect of changing density on the arrival trends Spearman's rank correlation coefficient (r_s) was used instead.

Results

Arrival trends

We found an overall earlier arrival of 0.26 days per year ($SE = 0.02$, $t = -10.92$, $P < 0.0001$, LSR model with year only; for LSR model with quantile as repeated measures subject: $P < 0.0001$, Table 2). All 25 migrants showed earlier arrival dates for the first individual (Table 1) of which six species showed a significant change. The smallest change was found for garden warbler *Sylvia borin* with 0.01 days per year, and the largest for the blackbird *Turdus merula* exhibiting 0.89 days per year. The LSR results (Table 1) reveal that, the first 5% of the population showed a trend towards earlier arrival in 24 of the 25 species (goldcrest *Regulus regulus* has a delayed migration of 0.01 days/year). The figures range from 0.01 days per year for marsh warbler *Acrocephalus palustris* to 0.69 days per year for blackbird. Considering QR results (Table 1) we found earlier arrival in 22 species ranging from 0.06 for wood warbler *Phylloscopus sibilatrix* to 1.08 days per year for blackbird. The arrival of the first 50% of the population (LSR) advanced for 20 species, ranging from 0.01 days per year for icterine warbler *Hippolais icterina* to 0.59 days per year for blackbird. Considering QR results we found earlier arrival in 19 species ranging from 0.07 for tree pipit *Anthus trivialis* to 0.46 days per year for goldcrest. For 22 species, the arrival dates advanced for the first 95% of the population (LSR). With 0.08 days per year thrush nightingale *Luscinia luscinia* showed the weakest negative trend, whereas blackbird showed the largest change with 1.05 days per year. The results of the QR showed earlier arrival in 17 out of 25 species ranging from wood warbler with 0.09 days per year to blackbird with 0.84 days per year. Overall, the LSR and QR results were significantly correlated ($r = 0.76$, $P < 0.0001$, $N = 75$).

Table 2. Effects of year, quantile differences and species on arrival. For time trend in arrival multivariate p-values indicate probability levels in a multivariate model with quantile as repeated measures. The AIC selected best model was chosen between models with all different combinations of the year parameter included. In the last column; "+" indicates that the variable is included in the AIC best model while, "%" indicates that it is not included. Least square regression model including all interaction terms.

Parameter	Time trend in arrival					
	df	Mean square	F	P	Multi-variate P	AIC best model
Year	1	6044.1	201.80	<0.0001	<0.0001	+
Quantile	3	39164.1	1307.61	<0.0001	<0.0001	+
Species	24	7351.7	245.46	<0.0001	<0.0001	+
Year × quantile	3	271.9	9.08	<0.0001	<0.0001	+
Year × species	24	104	3.47	<0.0001	0.0069	%
Quantile × species	72	165.3	5.52	<0.0001	<0.0001	+
Year × quantile × species	72	22.5	0.75	0.941	0.39	%

Using year as a predictor variable to investigate overall trends in arrival dates does not imply that the relationship with year is linear. We found a non-linear relationship with year (full model analyses with year^2 as additional predictor variable: $P < 0.0001$ for year^2). The change in arrival date was slightly decelerating over years (-0.64 days/(years since starting year)^2 and 0.02 days/(years since starting year)^2, corresponding to a contribution from year of 14.1 days earlier arrival and 8.8 days later from year^2 in the 22 year period). However, there is no biological theory behind using a second-order variable and other functions could equally well describe the non-linear changes. This does not invalidate using only the first-order variable in models, and fitting a first-order relationship results in simpler models that provide easier interpretation of whether birds are arriving earlier.

Differences between measures of population arrival

The correlation coefficients for changes in timing of migration for the different measures of population arrival were all positive (ranging from 0.20 to 0.63), pointing to a unidirectional change for the four measures of arrival time. Overall, analyses using LSR showed that the four measures of arrival changed at different rates ($P = 0.0001$ for quantile × year effect in model with differences between quantiles as dependent variable). The largest changes were seen in first arrivals (-0.42 days/year, $P = 0.002$), lesser changes in 5% (-0.25 days/year, $P = 0.06$) and 95% (-0.22 days/year, $P = 0.10$) and the smallest changes in 50% arrivals (-0.16 days/year, $P = 0.24$). Even though first arrivals changed the most, similar results were obtained when omitting these from the model (Multivariate model: $P < 0.0001$ for year; $P = 0.04$ for quantile × year interaction), showing again that the three population measures were not changing equally either. However, in both cases the trend was not significant (but still negative) for the 50% quantile. Similar trends were found for the 5% and 95% quantiles, and correspondingly we found no changes in migration period over time ($P = 0.51$). We found no evidence that the differences in arrival trends between quantiles differed between species ($P = 0.21$ for year × quantile × species effect in model with differences between quantiles as dependent variable).

Migration distance

Species travelling longer distances advanced their arrival dates the least (for year × distance interaction with quantile as repeated measures subject: $P = 0.012$, Table 3). The mean effect on arrival trend of migration distance was 0.000050 days per year per km (LSR model with year, distance and interaction). For a short-distance migrant (1,500 km) this corresponds to 0.07 days per year, and for a long-distance migrant (9,000 km) to 0.45 days per year relative to the intercept of 0 km migration distance. Additionally, there were differences in arrival trends between quantiles with respect to migration distance ($P = 0.0015$ for year × quantile × distance effect in model with differences between quantiles as dependent variable). The largest differences between short-/medium-distance and long-distance migrants (Fig. 2) were seen in first arrivals (0.50 days/year) and first 95% (0.25 days/year), whereas first 5% and 50% (Fig. 3) showed less difference (0.13 and 0.10 days/year, respectively).

Different sub-Saharan wintering areas

All long-distance migrants showed earlier timing of spring migration (Table 1). Comparing the subgroups wintering in sub-Saharan Africa, we found no difference between the different wintering areas (with quantile as repeated measures subject: wintering area, $P = 0.80$; year × wintering area interaction, $P = 0.80$). The average change in arrival date for birds wintering in West, Central and East Africa was -0.23, -0.12 and -0.17 days per year, whereas birds wintering in northwest and southwest Europe advanced arrival date with -0.51 and -0.37 days per year, respectively.

Table 3. Effect of migration distance on phenological change. Least square regression model including all interaction terms. In last column; "+" indicates variable included in the AIC selected best model while "%" indicates that it is not included. "(%)" means not included in best AIC selected model but included in models with considerable support (ΔAIC <2).

Parameter	Time trend in arrival					
	df	Mean square	F	P	Multi-variate P	AIC best model
Year	1	4856.1	55.3	<.0001	<0.0001	+
Quantile	3	14929.8	169.9	<.0001	<0.0001	+
Distance	1	147047.6	1673.5	<.0001	<0.0001	+
Year × quantile	3	340.9	3.88	0.0088	<0.0001	(%)
Year × distance	1	1584.7	18	<.0001	0.012	+
Quantile × distance	3	1723.5	19.6	<.0001	<0.0001	(%)
Year × quantile × distance	3	164.4	1.87	0.133	<0.0001	%

The influence of changing population size on arrival dates

Species whose populations were declining showed the least change in arrival dates of first individuals ($r_s = -0.48$, $P = 0.02$), however, we found no significant correlations for first 5%, 50% and 95% of the total population ($r_s = -0.14$, $P = 0.50$; $r_s = -0.31$, $P = 0.14$; $r_s = -0.24$, $P = 0.25$, respectively). This pattern could not be detected on the species level. Correlating the yearly arrival date for each species (for all four measures) with the respective yearly population index results in 13 (eight positive and five negative) significant correlations (out of 100 in total). These species-specific correlations turned non-significant when adjusting for multiple tests.

Discussion

We found clear indications of overall earlier spring arrival for the 25 migratory species combined (Table 1). The change in migration timing was evident for the first arriving part of the populations (i.e. the first individual and the first 5% of the total population) and for the majority of the population (i.e. the first 50% and 95% of the population; Fig. 2). The change in arrival dates that we observed were not the result of a uniform shift in arrival dates of both early and late migrating individuals. Instead, in recent years, the earliest arriving (first individual and first 5%) as well as the last arriving (first 95%) migrants have shifted to earlier arrival at a faster rate than the median arriving migrants (Fig. 1B). The median arriving migrants now arrive relatively late compared to the onset of a species' migration, even though the migration of all individuals has become earlier. Whereas migration distance seems to affect the degree of change in arrival time (Table 3 and Fig. 3), our results point to no difference between groups of species wintering in different areas of Africa (Fig. 4).

Hüppop and Hüppop (2003) found that mean spring passage had advanced by 0.05–0.28 days per year for 23 out of 24 North European migrants trapped at Helgoland in the North Sea. Cotton (2003) found that first individuals arrived 0.03–0.76 days per year earlier for 17 out of 20 long-distance migrants breeding in the United Kingdom. Our results confirm earlier arrival of migratory passerines of Northern Europe, with dates for the first 50% of the total population advancing between 0.01–0.59 days per year for 20 out of 25 species. However, our results show that different parts of the populations are not changing arrival to the same extent. So far, most phenological studies have focused extensively, often exclusively, on analyses based on arrivals of the first individual (e.g. Tryjanowski et al. 2002, Cotton 2003). According to our study, arrival trends of first individuals should not be considered to apply to the entire population. Still, in lack

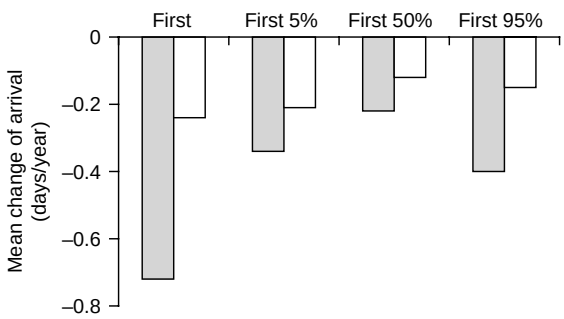

Fig. 2. Mean trends of arrival (in days/year) of the first individual, first 5%, 50% and 95% of the spring total for short-/medium- (closed bars, N = 8) and long-distance migrants (open bars, N = 17). All values are significantly different from zero, P < 0.05 (two-tailed t-test).

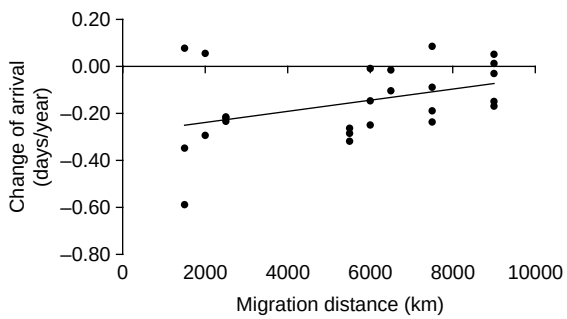

Fig. 3. The correlation between the species-specific migration distances and the arrival trends of the first 50% of the populations (r = 0.40, P = 0.05).

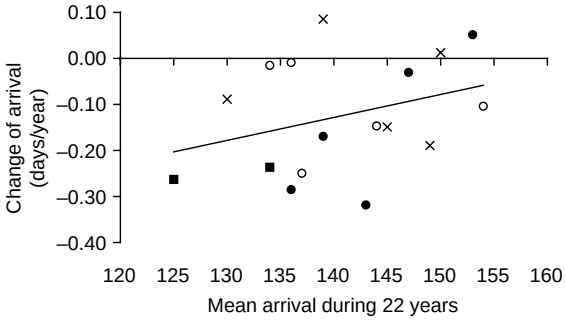

Fig. 4. The species-specific trend (days/year) of spring migration timing plotted against the 22-year mean arrival in Julian days (day one = 1 January) of the first 50% of the spring total for each of the 17 long-distance migrants. Migrants are divided in groups according to wintering areas in Africa: western Africa (open circles), central Africa (crosses) and eastern Africa (closed circles). Closed squares represent chiffchaff *Phylloscopus collybita* and willow warbler *Phylloscopus trochilus* wintering in both eastern and western Africa (see text). The line describes the trend line: $y = 0.01x - 0.83$, $r = 0.33$.

of more appropriate and comprehensive data, we find that analyses of first arriving individuals may provide a rough indication of the direction of the population timing. But beyond that, our results urge for caution in inferring too much from the results of such studies.

Jenni and Kéry (2003) showed differential changes in timing of autumn migration for short- and long-distance migrants. We found that the migration distance correlates with the degree of change in the timing of migration. Thus, it appears that migrants with a relatively short distance between breeding and wintering areas are capable of changing their timing of migration quicker than long-distance migrants. But the effect could also be caused by differential climate change earlier and late in the migration season affecting the early arrival of short-distance migrants differently from the later arrival of long-distance migrations. The first arriving individuals of a species are possibly the most northerly wintering, e.g. chiffchaff and blackcap *Sylvia atricapilla* populations wintering increasingly in north-western Europe (Berthold et al. 1992). It has been shown that birds wintering in north-western Europe are more affected by climate (NAO; Forchhammer et al. 2002, Jonzen et al. 2002), and that populations wintering in Africa are under endogenous control (biotic interactions; Gwinner 1996). However, migrants have also been shown to change migration pattern within few generations (e.g. Berthold et al. 1992). This study showed that not only the arrival dates of the first individual but also the arrival dates for the entire population has advanced (albeit at different speed). Species wintering exclusively south of the Sahara Desert (e.g. marsh warbler and redstart *Phoenicurus phoenicurus*) are also consistently arriving earlier on their breeding grounds.

Hüppop and Hüppop (2003) and Tryjanowski et al. (2002) suggested that migrants following a western route (based on migrants caught at Helgoland) are more affected by climate (NAO) and show more significant changes in migration timing than migrants following a more eastern route (e.g. migrants caught at Courish Spit, see Sokolov and Payevsky 1998). The 25 species included in this study represent a variety of migratory strategies (including migrants following both eastern and western migration routes), and we found that advanced timing of migration occurs irrespective of wintering area and migration route. Consequently, our results do not support differences between western and eastern migration routes.

The earlier arriving birds are usually males. They obtain the best territories and achieve the best mates, producing larger clutches, and hence optimise their reproductive output and may contribute disproportionately more genes to the subsequent generation (Lozano et al. 1996, Kokko 1999). The benefit related to earlier arrival should be measured against the risk of reaching the breeding areas too early for conditions to be right for breeding. There seems to be consensus that short-/medium-distance migrants are influenced by exogenous factors (e.g. weather, climate) when conducting their migratory cycle, while the onset of migration in long-distance migrants is under endogenous control (Berthold and Querner 1981, Gwinner 1996). Therefore, the pattern of migration timing of the latter is likely to remain more stable from year to year. Marra et al. (1998) argued that wintering areas and conditions during the winter period determine the conditions of the birds and thereby the timing of migration. However, this study shows that not only short-/medium-distance migrants, but also sub-Sahara migrants are able to change their timing of migration within a few generations.

Previous phenological analyses treat arrival data as a linear coherence with year. However, our findings of a non-linear relationship with year (significant year^2 relationship) indicate that non-linear relationships may be considered for a better understanding of the changes in migratory phenology.

As pointed out by Tryjanowski and Sparks (2001), changes in the population densities may directly affect (and bias the conclusion drawn from) changes in phenological data based on first arriving individuals. Our results are consistent with this conclusion and highlight the warning against widespread use of first arrivals as a good indicator of phenological changes. This is another reason why such deterministic analyses ought to be conducted more thoroughly using data encompassing the entire population. Although the arrival of first individual(s) does provide an indication of the direction of the changes in timing of migration, data and analyses of the entire migration period are necessary to get a more appropriate and precise picture of what causes the changes in timing of migration.

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