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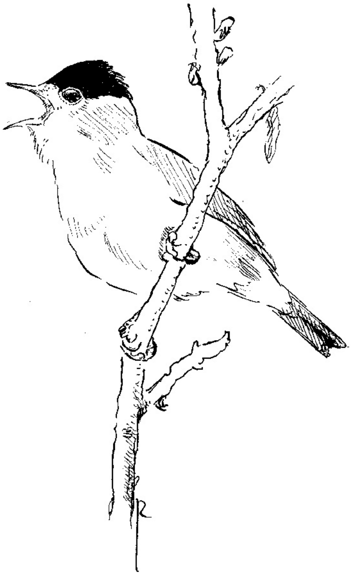
Changes in timing of autumn migration in North European songbird populations

Anders P. Tøttrup[1,*], **Kasper Thorup**[1,2] & **Carsten Rahbek**[1]



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Although studies of changes in the timing of passerine spring migration are numerous, less is known about timing of their autumn departure. We present phenological data on 22 species based on mist-netted birds caught on the Baltic island of Christiansø during autumn migration between 1976 and 1997. We used least square and quantile regression to test for changes in departure time of the last individuals and the date at which 5%, 50% and 95% of the season total remaining to be trapped (corrected for catch effort). For the entire group of 22 migrants there was no overall change in median departure (–0.0426 days year^{-1}, P = 0.40). Testing the 12 species for which the entire migration period was included (thus excluding many long-distance migrants), we found an overall earlier departure (–0.18 days year^{-1}, P = 0.007). Short-distance migrants tended to show earlier departure, while long-distance migrants only showed advanced departure amongst the last individuals to leave. The magnitude of change in departure time was correlated with migration distance, longer distance migrants showing the least change. Overall, timing of autumn migration was more variable between species than the unidirectional change reported in studies of spring arrival.

Key words: autumn migration, Northern Europe, passerines, phenology, population parts

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INTRODUCTION

Global temperatures have increased (Easterling *et al.* 1997) and the phenology of plant (Menzel & Fabian 1999) and animal schedules (Beebee 1995) has advanced in the Northern Hemisphere in recent decades. The timing of avian migration is under endogenous control, which is influenced by the photoperiodic cycle (Rowan 1926, Gwinner 1996). However, external factors such as spring temperatures and the North Atlantic Oscillation (NAO) have been shown to correlate with observed changes in timing of spring migration (Forchhammer *et al.* 2002, Vähätalo *et al.* 2004) and evidence for earlier spring arrival of migratory birds is gathering rapidly (Lehikoinen *et al.* 2004). Most studies, but not all (Both *et al.* 2004), show evidence of earlier egg laying in northern Europe (Bairlein & Winkel 2001). Clearly, understanding how climate change affects migration phenology is important, as migration is linked to breeding performance and thereby population dynamics.

Less is known about changes in timing of autumn migration. Previous work gives an equivocal picture of phenological changes, with advanced and delayed autumn departure for long- and short-distance migrants, respectively (Bairlein & Winkel 2001, Cotton 2003, Jenni & Kéry 2003, Thorup *et al.* 2007). The timing of autumn migration has been shown to depend on the start of breeding, which is determined by year to year fluctuations of spring temperatures (Ellegren 1990, Sokolov *et al.* 1999). Warmer spring temperatures and earlier breeding initiation in northern Europe potentially enable migrants to complete their reproductive cycle earlier. An advancement in autumn migration phenology might therefore be expected. However, predicted responses in adoption of breeding strategies and hence autumn departure times are likely to be species-specific. For example, short-distance migrants would be expected to commence southward migration earlier to achieve better winter territories while long-distance migrants may stay longer in the breeding areas to optimise their physical condition prior to migration. Long-distance migrants (or a larger part of the populations) may also take advantage of the warmer climate to produce an additional clutch, increasing their reproductive output.

Long time-series of standardised data are essential for the study of the phenology of bird migration. Greatest insight can be gained from situations where regular trapping of birds covers an entire migration episode for any given population. Twenty-two years of such data are available from the standardized mist-netting of passerines birds on the island of Christiansø in the Baltic Sea during 1976–1997. We recently reported advanced timing of the first, median and last population parts in timing of spring migration using these data (Tøttrup *et al.* 2006). Here, we use comparable data from Christiansø covering the entire autumn period and the same analytical approach to examine phenological changes in departure time for populations of northern European passerines passing the island and relate these to migration distance of the different species.

METHODS

Standardised mist-netting was conducted during 1976–1997 on the Danish island of Christiansø (55°19'N, 15°11'E), 18 km northeast of Bornholm in the Baltic Sea. Here, the Danish National Forest and Nature Agency operated a ringing station to monitor passing migratory passerine populations. These migrants mainly breed in Sweden and Finland, passing the isolated island twice a year during spring and autumn migration (Rabøl & Rahbek 2002).

Migrants were trapped in mist-nets and ringed during the first five hours from sunrise. Catch effort was standardised to 300 net-metre hours per day. Only birds ringed from 2 August to 4 November were included in the analysis. There was a weak, negative relationship between the total number of birds trapped corrected for trapping effort (N') and total net-metre hours ($N' = -0.0230$ net-metre hours year^{-1} + 61.199, $P < 0.001$), which was most likely caused by the closing of nets when migrants were too numerous to process. Ringing activity (net-metre hours) increased in the period (slope was 2833 net-metre hours year^{-1}, $P < 0.003$) and the total number of birds trapped (N) showed a tendency to increase (the slope was 230 birds year^{-1}, $P = 0.16$). However, the total number of birds trapped corrected for trapping effort (N') did not change over the years (slope 0.274 birds year^{-1}, $P = 0.995$). Because of the isolated position of the island and the relatively constant vegetation height and thickness, trapping conditions were considered constant during the period (Rabøl & Rahbek 2002).

Description of the data set

During 1976 to 1997, more than 568 000 individual birds of 184 species were trapped and ringed on Christiansø, more than 325 000 birds of 155 species during autumn. Our analysis includes all migrant species exceeding a minimum catch of 10 individuals (with standard effort) every autumn season (22 species, Table 1). Data from the autumns of 1979 and 1980 were excluded because of interrupted coverage of the migration period, resulting in 20 autumn seasons. Species migration

Table 1. Changes in timing of autumn migration for 22 migratory passerine species in a 22-year period (1976–1997). Changes in departure time of last individual and three different parts of the songbird populations using least square regression including mean values for the entire group (see Methods for details). A positive value indicates delayed autumn departure. Total number of individuals caught (*N*), number of individuals corrected for trapping effort (*N*'), and migration distance (km) for each species are included. Trends over the years 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: $P_i < \alpha / (1 + k - i)$).

			Migration distance	Percent of the total population remaining (days year^{-1})			
	N	*N*'	(km)	95%	50%	5%	Last bird
Short-distance migrants:							
Goldcrest *Regulus regulus*	83 354	25 163	1 500	–0.14	–0.22	–0.13	0.03
Blackbird *Turdus merula*	4 644	1 241	1 500		0.03		
Wren *Troglodytes troglodytes*	3 984	1 101	1 500	–0.17	0.00		
Dunnock *Prunella modularis*	4 731	1 197	2 000	–0.36$^{(*)}$	–0.53$^{(*)}$	–0.32	–0.08
Reed Bunting *Emberiza schoeniclus*	1 690	411	2 000	–0.03	–0.39	–0.47$^{(*)}$	0.12
Robin *Erithacus rubecula*	8 212	19 906	2 500	–0.33	–0.45	–0.16	–0.13
Redwing *Turdus iliacus*	2 530	730	2 500	–0.54	–0.22		
Song Thrush *Turdus philomelos*	21 877	5 643	2 500	–0.37	–0.26	–0.26	–0.01
Long-distance migrants:							
Blackcap *Sylvia atricapilla*	5 450	1 541	5 500	0.03	–0.62(*)	–0.54	–0.32
Lesser Whitethroat *Sylvia curruca*	5 940	1 449	5 500	0.07	–0.02	–0.29	–0.13
Chiffchaff *Phylloscopus collybita*	3 473	961	5 500	0.07	0.11	–0.41$^{(*)}$	–0.22
Redstart *Phoenicurus phoenicurus*	7 534	1 851	6 000	0.10	–0.29	–0.45	–0.47
Whitethroat *Sylvia communis*	1 618	352	6 000		0.33	0.10	–0.46
Reed Warbler *Acrocephalus scirpaceus*	998	273	6 500		–0.11	–0.57	0.17
Pied Flycatcher *Ficedula hypoleuca*	12 650	2 941	6 500		0.21	–0.34	–1.04*
Tree Pipit *Anthus trivialis*	1 478	405	7 500	–0.04	–0.04	–0.09	–0.19
Garden Warbler *Sylvia borin*	8 837	2 049	7 500		–0.09	–0.88*	–0.19
Wood Warbler *Phylloscopus sibilatrix*	2 755	608	7 500		0.53$^{(*)}$	0.11	0.01
Willow Warbler *Phylloscopus trochilus*	33 389	7 918	7 500	0.26$^{(*)}$	0.41*	–0.25	–0.18
Icterine Warbler *Hippolais icterina*	952	239	9 000		0.32	–0.04	–0.34
Spotted Flycatcher *Muscicapa striata*	4 818	1 170	9 000	0.18	0.07	–0.69*	–0.40
Red-backed Shrike *Lanius collurio*	3 763	830	9 000		0.28	–0.14	–0.88
Total number of ringed migrants:	**299 677**	**77 979**					
Overall regression coefficient mean				**–0.09**	**–0.03**	**–0.31***	**–0.25***

distance was estimated (to the nearest 500 km) from the main breeding areas (southwestern Finland) to the main wintering areas (Cramp 1988, 1992, Cramp & Perrins 1993, 1994, Helbig 2003). The 22 migrants included eight short-distance migrants wintering in Europe and 14 long-distance migrants wintering south of the Sahara Desert (Zink 1973–85, Zink & Bairlein 1995).

Statistical analyses

We used two approaches to describe changes in timing of migration (Tøttrup *et al.* 2006). (1) Least square regression (LSR) using the slope-value as a description of phenological change over time. We used four measures of population departure for each autumn season and species; the day (in Julian days, where day one = 1 January) was

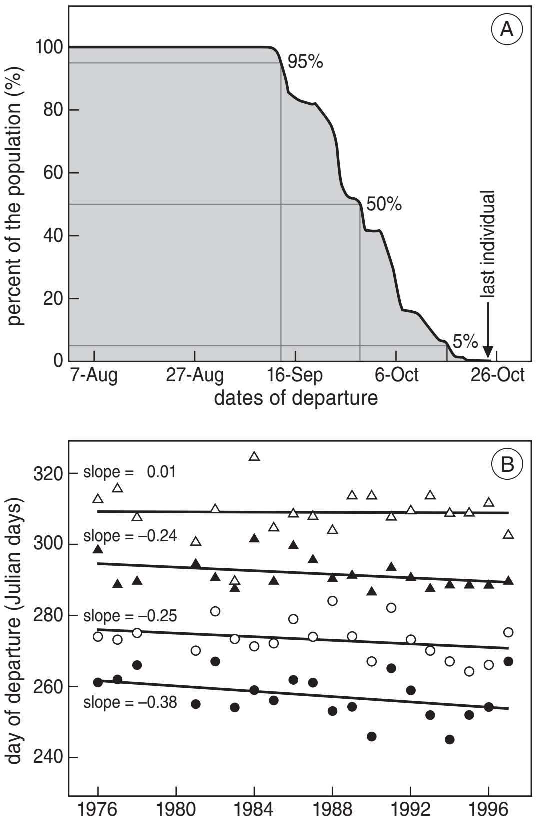

Figure 1. (A) Illustration of the four measures of population departure used in the least square regression analysis. The figure describes the 1985 autumn departure of the entire population of Song Thrush *Turdus philomelos*. For each autumn season we calculated dates of trapping when 95, 50 and 5% of the season total remained to be trapped. (B) Population departure trend in the period from 1976 to 1997 (Song Thrush). Lines are regression lines describing the change in departure for 95% (closed circles; slope: –0.38), 50% (open circles; slope: –0.25), 5% of the total population remaining to be trapped (closed triangles; slope: –0.24) and last individual (open triangles; slope: 0.01).

calculated when 95, 50 and 5% of the total number remained to be trapped (Fig. 1A and B). (2) Quantile regression (QR) to estimate quantiles (e.g. 5% remaining) of departure over all years. QR slopes also describe the phenological change over time. In QR analysis the full data set consists of observations of individual birds using Julian days as a function of year. The LSR and QR analyses imply somewhat different assumptions. As earlier caught birds do not influence the results and all years contribute equally in LSR, this method should be favoured. However, QR has advantageous statistical properties, because all data points are considered simultaneously and are therefore not influenced by autocorrelation (Tøttrup *et al.* 2006). Overall, the two approaches provide similar results, with QR tending to show more variation in time trends (and thus more significant results for each species) than LSR. Results from LSR and QR results were significantly correlated ($r = 0.85$, $P < 0.0001$ Pearson's product coefficient). Due to the potential biases introduced by QR, we present LSR results in the text but include QR results in Appendix 1.

Visual inspection showed that seven long-distance migrants and one short-distance migrant (Blackbird *Turdus merula*) initiated autumn migration before the start of ringing activities at Christiansø. Three short-distance migrants continued their migration period beyond the last date of season coverage. This implies that the measures of population departure for the species mentioned above were biased by the missing individuals. Therefore, we have excluded the measures of departure for 95% of the populations remaining on the breeding areas for the first group. For the latter group the measures of departure for 5% of the population remaining have likewise been excluded from the analysis.

We tested the effects of additional variables such as *species, quantile* and interactions in full statistical models. The following interactions were included as factorial predictor variables: *quantile* x *species* (describing differences between species in departure of the different quantiles), *year* x *species* (differences in time trends between species), *year* x *quantile* (differences in time trends between quantiles) and *year* x *quantile* x *species* (to test whether departure trends differed between quantiles and species). Since each data point is not independent due to autocorrelation between e.g.

quantiles, we used *quantile* as a repeated measure in multivariate approaches when testing for an overall effect of year (cf. Tøttrup *et al.* 2006).

Testing for differences in departure trends for different quantiles is equivalent to testing whether there are trends in the differences in departure between quantiles. The differences between quantiles are not autocorrelated (as are the quantiles themselves), and thus, to test for departure trends between quantiles, we applied ordinary LSR to the differences.

We tested the effects of migration distance and wintering area by inclusion of these variables in full statistical models with the variable *species* excluded. The effect of factorial predictor variables (*quantile, species, migration distance* and interactions) were tested using ANCOVA. The *quantile* x *distance* interaction describes differences in departure of the different quantiles according to migration distance, and the *year* x *quantile* x *distance* interaction describes differences in departure trends of the different quantiles according to migration distance.

Changes in population size can affect phenological trends as discussed by Tryjanowski & Sparks (2001). We tested the four measures of population departures and mean departure trends of each migrant against the species-specific population indices from Rabøl & Rahbek (2002). To investigate this further, we correlated the four yearly departure days of each species with the species-specific population indices of each year.

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 version 8.2 (SAS 2000), except the quantile regressions, which were performed using the Quantreg package of the Program R (Koenker & Bassett 1978). When testing the effect of changing density on the departure trends, Spearman's rank correlation coefficient (r_s) was used.

RESULTS

We found no overall change in timing of autumn migration for median departure of the 22 species (50% quantile: –0.043 days year^{-1}, $P = 0.40$). However, the change in timing differed between species ($P = 0.03$ for *year* x *species* interaction). For the 12 species where the entire migration period was included and thus excluding most long-distance migrants, we found an overall earlier median departure (–0.18 days year^{-1}, $P = 0.007$).

The 22 species showed an overall earlier mean departure when 50% of the populations remained in the breeding area of 0.03 days per year ranging from Blackcap *Sylvia atricapilla* with an advanced departure of 0.62 days per year to Wood Warbler *Phylloscopus sibilatrix* departing 0.53 days per year later (Table 1). The 14 species for which the 95% quantile could be reported showed a mean earlier departure of 0.09 days year^{-1} (range: –0.52 to 0.26 days year^{-1}). For the 19 species included in analysis of departure for 5% of the populations exhibited an overall earlier departure of 0.31 days year^{-1} (range: –0.88 to 0.11 days year^{-1}). The 19 species included in the last record analysis showed an overall change in timing of 0.25 days year^{-1} earlier (LSR) (range: –0.88 to 0.28 days year^{-1}).

Differences among population parts

Overall, analyses showed that the four measures of departure were changing differently (i.e. significant *year* x *quantile* effect in Table 2B). However, we found no evidence that the differences in departure trends between quantiles differed between species (i.e. no significant *year* x *quantile* x *species* interaction, Table 2B).

Migration distance

Longer migration distance tended to correlate with less advanced timing of median departure ($P = 0.051$; 22 species data set; Fig. 2). The mean effect

Table 2. Effects of year, quantile differences and species on departure for all four population measures (95, 50, 5% and last) included (12 species). (A) For time trend in departure multivariate, P-values indicate probability levels in a multivariate model with quantile as repeated measures. (B) For differences between quantiles, quantile differences are used. Hence, the year parameter does not describe a change in departure, but an overall trend in differences between quantiles, which does not necessarily imply a change in overall departure. Least square regression model including all interaction terms.

	A	Time trend in departure				**B**	Differences between quantiles		
Parameter	*df*	Mean square	*F*	*P*	Multivariate *P*	*df*	Mean square	*F*	*P*
Year	1	1479.0	30.69	<0.0001	<0.0001	1	29.5	0.57	0.45
Quantile	3	272.5	5.65	0.0008	0.0015	2	976.4	19.0	<0.0001
Species	21	65.6	1.36	0.13	0.72	11	193.6	3.78	<0.0001
Year x quantile	3	239.6	4.97	0.002	0.0029	2	297.1	5.79	0.0032
Year x species	21	61.8	1.28	0.18	0.76	11	28.9	0.56	0.86
Quantile x species	49	59.7	1.24	0.13	0.44	22	72.4	1.41	0.10
Year x quantile x species	49	59.7	1.24	0.13	0.45	22	57.2	1.12	0.32

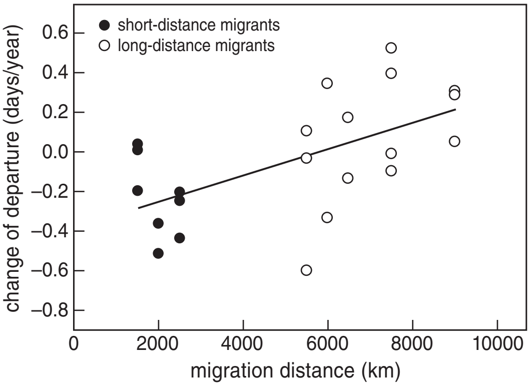

Figure 2. The effect of migration distance on the change in the timing of departure for 50% of the populations still remaining in the breeding areas ($r^2 = 0.34$, $P < 0.01$).

on departure trend of migration distance was –0.000065 days year^{-1} km^{-1}. For a short-distance migrant (1500 km) this corresponds to 0.10 days year^{-1}, and for a long-distance migrant (9000 km) to 0.59 days year^{-1}.

No overall effect of migration distance was seen in the smaller data set including only species with coverage of the full migration period (i.e. *year* x *distance* interaction with quantile as repeated measures subject; $P = 0.80$, Table 3A).

However, there were differences in departure trends between quantiles with respect to migration distance (i.e. *year* x *quantile* x *distance* interaction in Table 3B). The largest differences between short-distance and long-distance migrants were seen for 95, 50% remaining and last record (Fig. 3) (0.37, 0.31 and 0.35 days year^{-1}, respectively), whereas 5% remaining showed less difference (0.07 days year^{-1}).

Impact of changing population sizes on migration timing

The population indices showed no correlation with any of the four measures of population timing (95%: $r_s = 0.06$, $P = 0.81$; 50%: $r_s = 0.10$, $P = 0.65$; 5%: $r_s = –0.05$, $P = 0.86$; last record: $r_s = 0.20$, $P = 0.40$). Correlating the species-specific departure dates for all four measures and the respective population indices resulted in five (three positive and two negative) significant correlations out of 74 in total. However, the latter correlations turned non-significant when adjusting for multiple tests.

Table 3. Effect of migration distance category (short/long) on phenological change based on least square regression model including all interaction terms. For details, see Table 2.

	A Time trend in departure					**B** Differences between quantiles			
Parameter	*df*	Mean square	*F*	*P*	Multi-variate *P*	*df*	Mean square	*F*	*P*
Year	1	1162.5	5.94	0.015	0.11	1	6.8	0.11	0.74
Quantile	3	112.5	0.57	0.63	0.011	2	888.5	14.64	< 0.0001
Distance	1	89.7	0.46	0.50	0.76	1	589.9	9.72	0.0019
Year x quantile	3	98.3	0.50	0.68	0.015	2	272.7	4.49	0.012
Year x distance	1	60.73	0.31	0.58	0.80	1	271.3	4.47	0.035
Quantile x distance	3	320.7	1.64	0.18	0.032	2	80.2	1.32	0.27
Year x quantile x distance	3	319.4	1.63	0.18	0.032	2	92.3	1.52	0.22

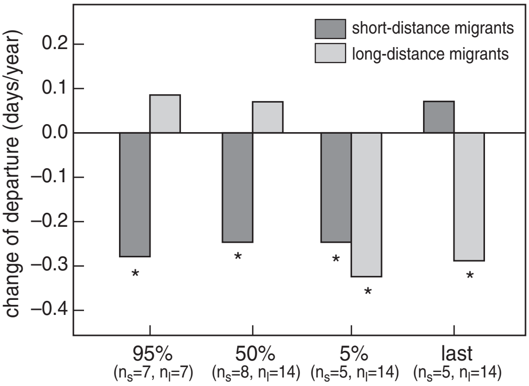

Figure 3. Mean trends of autumn departure (1976–1997) for 95, 50 and 5% of the total populations still remaining to be trapped and last record for short- and long-distance migrants. n_s = number of short-distance migrants included, n_l = number long-distance migrants included and ‘*’ indicate values significantly different from zero ($P < 0.05$, *t*-tests, two-tailed).

DISCUSSION

We found clear indications of changes in autumn migration phenology. Short-distance migrants showed earlier departure for all three population measures (95, 50 and 5% remaining) while the departure of the last individual showed no change. Long-distance migrants showed no change for the first population parts (95% and 50% remaining) while the last population parts (5% remaining and last individual) advanced autumn departure time. Our results show that degree of change in departure time differed between different population parts and between species with different migration strategies (long- vs. short-distance migrants). The results also indicate that migration distance seems to affect the degree of change in departure (longer distance less change).

Previous work on timing of autumn migration gives an equivocal picture of phenological changes (Bairlein & Winkel 2001). Sokolov *et al.* (1999) analysed mean departure dates for 26 short- and long-distance migrants showing a tendency towards later departure in the 1990s compared with the 1980s, while the 1980s showed earlier departure than the 1970s. Nowalowski (2000) showed later median departure time for Blackcap *Sylvia atricapilla*, but no changes for Garden Warbler *Sylvia borin*, Whitethroat and Lesser Whitethroat *Sylva curruca* from 1985 to 1998. Cotton (2003) found advanced last individual departure for a group of 20 long-distance migrants while Jenni & Kéry (2003) found an overall advanced autumn median departure for 25 long-distance migrants and delayed median departure for 40 short-distance migrants. However, Thorup *et al*. (2007) showed consistent intra-specific patterns throughout Europe with much of the previous reported variation explained by each species' migratory status.

We found no evidence of the potential effect of changing population size on phenological data when correcting for multiple tests. Hence, an effect of changing population density on autumn migration phenology is unlikely to significantly influence our results. However, a potential time lag effect on changes in timing of migration is a possibility and studies incorporating e.g. autocorrelation models could bring more knowledge to this topic.

Our analyses show that different parts of the populations change timing of migration differently. This suggests that the different population parts may follow different strategies or react differently to for example a change in climate. Data on last individual departures have been used as indicators of changing phenology in entire migrant populations. However, data on last birds could reflect sick, mis-programmed or otherwise aberrant individuals, biasing the results. Since this study indicates that different elements of populations may respond differently in their timing of migration, caution should be exercised when analysing data based on such data sets.

Conditions in the wintering areas and on migratory stopover sites probably also influence the timing of migration. When conducting protection programmes and conservation strategies for migratory birds, analyses on entire migrant populations are of high value and could improve the understanding of changes and dynamics at population level in relation to climate change. Furthermore, the understanding of short-term changes in migration timing may also improve the understanding of long-term evolutionary consequences of changing climate.

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SAMENVATTING

Over het tijdstip van de najaarstrek is veel minder bekend dan over het tijdstip van de voorjaarstrek. Dit artikel beschrijft de veranderingen die zijn opgetreden in het tijdstip van de herfsttrek van 22 zangvogelsoorten op het eilandje Christiansø in de Oostzee. De vogels werden met mistnetten gevangen gedurende de jaren 1976–1997. Rekeninghoudend met de vangstinspanning (lengte van de netten in combinatie met het aantal vanguren) werd de dag bepaald waarop – gesommeerd over het seizoen – 5%, 50% en 95% van de vogels waren gevangen. De vogels trokken over de twintigjarige onderzoeksperiode gemeten wel eerder door, maar de trend was verre van significant (een verandering van slechts –0,0426 dag per jaar). Sommige soorten begonnen echter al door te trekken voor de jaarlijkse ringactiviteiten startten. Wanneer deze soorten buiten beschouwing werden gelaten, bleek sprake te zijn van een forse vervroeging van de herfsttrek (–0,18 dag per jaar). Hoe korter de afstand tussen broed- en overwinteringsgebied was, hoe sterker het effect van de vervroeging van de trek. Bij langeafstandstrekkers was alleen van vervroeging sprake bij de laatste doortrekkers. Geconcludeerd wordt dat de mate van verandering in de herfsttrek meer variatie tussen vogelsoorten vertoont dan in het voorjaar, wanneer sprake is van een meer eenduidige vervroeging van de trek.

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Appendix 1. Changes in timing of autumn migration for 22 migratory passerine species in a 22-year period (1976–1997). Comparison of the results using least square regression (LSR) and quantile regression (QR) (see Methods for details). A positive value indicates delayed autumn departure. Trends in in time 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: $P_i < \alpha / (1 + k - i)$).

	Percent of the total population remaining (days year^{-1})					
	95%		50%		5%	
	LSR	QR	LSR	QR	LSR	QR
Short-distance migrants:						
Goldcrest *Regulus regulus*	–0.14	–0.5	–0.22	–0.27*	–0.13	–0.25*
Blackbird *Turdus merula*			0.03	–0.14*		
Wren *Troglodytes troglodytes*	–0.17	–0.11	0.00	0.06		
Dunnock *Prunella modularis*	–0.36$^{(*)}$	–0.40*	–0.53$^{(*)}$	–0.33*	–0.32	–0.36$^{(*)}$
Reed Bunting *Emberiza schoeniclus*	–0.03	–0.24*	–0.39	0.07	–0.47$^{(*)}$	–0.22
Robin *Erithacus rubecula*	–0.33	–0.62*	–0.45	–0.54*	–0.16	–0.46*
Redwing *Turdus iliacus*	–0.54	–0.56*	–0.22	0.00		
Song Thrush *Turdus philomelos*	–0.37	–0.46*	–0.26	–0.33*	–0.26	–0.24*
Long-distance migrants:						
Blackcap *Sylvia atricapilla*	0.03	0	–0.62$^{(*)}$	–0.50*	–0.54	–0.50*
Lesser Whitethroat *Sylvia curruca*	0.07	0.25	–0.02	0.13	–0.29	–0.44*
Chiffchaff *Phylloscopus collybita*	0.07	0.21	0.11	–0.05	–0.41$^{(*)}$	–0.42*
Redstart *Phoenicurus phoenicurus*	0.10	0.22*	–0.29	–0.16$^{(*)}$	–0.45	–0.42*
Whitethroat *Sylvia communis*			0.33	0.50*	0.10	–0.05
Reed Warbler *Acrocephalus scirpaceus*			–0.11	0.00	–0.57	–0.5
Pied Flycatcher *Ficedula hypoleuca*			0.21	0.20*	–0.34	–0.31*
Tree Pipit *Anthus trivialis*	–0.04	0.00	–0.04	0.05	–0.09	0.00
Garden Warbler *Sylvia borin*			–0.09	0.01	–0.88*	–0.60*
Wood Warbler *Phylloscopus sibilatrix*			0.53$^{(*)}$	0.40*	0.11	0.07
Willow Warbler *Phylloscopus trochilus*	0.26$^{(*)}$	0.33*	0.41*	0.50*	–0.25	–0.08
Icterine Warbler *Hippolais icterina*			0.32	0.29	–0.04	–0.09
Spotted Flycatcher *Muscicapa striata*	0.18	0.22	0.07	0.07	–0.69*	–0.06
Red-backed Shrike *Lanius collurio*			0.28	0.33*	–0.14	–0.30$^{(*)}$
Overall regression coefficient mean	**–0.09**	**–0.09**	**–0.03**	**0.01**	**–0.31***	**–0.28***