# Co-fluctuation among bird species in their migration timing

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A b s t r a c t . Long-term spring arrival dates of 37 migratory bird species as recorded in Moravia (Czech Republic) during 103 years between 1881 and 2001 were evaluated for pairwise correlation (i.e. co-fluctuation in migratory timing) between avian species. Cluster analysis of the correlation matrix revealed a number of clusters (called 'migrons') of co-fluctuating migratory bird species. All short-distance migrants with the European (Mediterranean) winter range clustered together in migron A (*Alauda arvensis, Motacilla alba, Vanellus vanellus, Sturnus vulgaris, Corvus frugilegus, Columba palumbus, Phoenicurus ochruros, Phylloscopus collybita, Remiz pendulinus, Erithacus rubecula, Turdus philomelos, Larus ridibundus, Serinus serinus, Sylvia atricapilla*), while six other, smaller clusters were formed exclusively of long-distance migrants having an African (sub-Saharan) winter range: (B) *Cuculus canorus, Streptopelia turtur*; (C) *Hirundo rustica, Jynx torquilla, Luscinia megarhynchos, Apus apus, Sylvia curruca*; (D) *Acrocephalus schoenobaenus, Riparia riparia, Upupa epops*; (E) *Anthus trivialis, Delichon urbica, Motacilla flava, Hippolais icterina*; (F) *Ciconia ciconia, Phoenicurus phoenicurus, Ficedula albicollis, Acrocephalus arundinaceus, Lanius collurio*; (G) *Oriolus oriolus, Muscicapa striata, Locustella fluviatilis, Coturnix coturnix*. Results of the co-migration analysis pose interesting questions about possible varying underlying mechanisms of the migration timing in different migrons of birds.

**Key words:** phenology, migratory birds, spring arrival, cluster analysis

## Introduction

Mean arrival or departure dates of migratory bird species in temperate regions have been calculated and used by ornithologists and phenologists over many years (e.g., M a s o n 1995, H u d e c et al. 1999, H u b á l e k 2004, S p a r k s & M a s o n 2004). However, the analyses of co-migration patterns of the birds, i.e. the co-fluctuation of the arrival dates among species over a longer period, have seldom been used by phenologists. In general, although two species can have the same mean arrival time (computed as the arithmetic average over many years), they could differ significantly in their co-migration temporal pattern over the years as found by correlation analysis using Pearson's *r* coefficient – their arrival times fluctuate in an incongruent manner in individual years. On the other hand, two other species could have the same co-migration temporal pattern, i.e. they co-fluctuate in congruence during the period, although their mean arrival times differ significantly. Results of such studies could pose interesting questions about possible different underlying mechanisms of the migration timing in particular bird species.

In this survey, a long-term record (103 years) on spring phenology of 37 common migratory birds in Moravia, Czech Republic, was evaluated for the correlation in their timing. Two similar studies, based on restricted datasets, were published previously (H u b á l e k 1983, 1985). Surprisingly, this approach has not been tested in avian phenology since that time, although cluster analysis of correlation coefficients has been found productive in many areas of biology including ecology (S n e a t h & S o k a l 1973). There is only one exception – the study of M a s o n (1995) who found significant intercorrelations in arrival dates among several species of spring migrants in Leicestershire (U.K.), 1942–1991. Cluster analysis, however, was not applied in that study.

## Materials and Methods

### B i r d r e c o r d s

The arrival records of migratory birds in many places of Moravia (48º37‘–50º27‘N, 15º15‘–18º51‘E) between 1881 and 1960 were published in a series of yearbooks (N i e s s l 1882–1911, N o v á k & Š i m e k 1926, 1930–1938, Z í t e k 1953–1964); the records from 18 years (1907–1922, 1925, 1926) were unfortunately either inaccessible or missing. For the following period of 1961–2001, records of a number of Moravian ornithologists were used (H u b á l e k 1983, H á j e k 1992, H u d e c et al. 1999, unpublished observations). In total, 103 years were thus covered in this survey and the dataset is identical to that used in a previous paper (H u b á l e k 2004). For each bird species, the arithmetic average of the first occurrences (spring arrival), as recorded by a number of observers in different places, was calculated. However, exceptionally early and late arrival dates were omitted. In the rook (*Corvus frugilegus*), a decrease of the overwintering population by about one-half has been regarded as the spring phenological instant. When the number of records for particular species in a year did not reach three, that year was omitted. Thirty-seven common, easily recognizable (visually and/or acoustically) migratory bird species with a sufficient number of annual records (at least about 30) were selected for the correlation analysis.

### S t a t i s t i c a l a n a l y s e s

Calendar dates of phenological instants were transformed into Julian dates, i.e. sequential numbers; in leap-years, the sequential numbers were corrected by adding 1, starting from 1st March. Arithmetic average of the arrival dates as recorded by observers was calculated in each species for every year.

Correlation analysis was used to examine co-fluctuations in the phenological instants pairwise amongst all 37 bird species during the period 1881–2001. In this approach, individual years are treated as independent samples, and therefore no time series analysis and/or corrections for time trends are necessary. First, Pearson's *r* coefficient values were calculated for all species pairs (37×36/2, i.e. 666 comparisons) using SOLO 4.0 (BMDP Statistical Software, Los Angeles, CA). Second, unweighted pair-group arithmetic mean clustering (UPGMA: S n e a t h & S o k a l 1973) of the 37×37 correlation matrix was conducted with NTSYS-pc 1.60 (R o h l f 1990).

## Results

Average phenological instants were summarized in a previous paper (Table 1 in H u b á l e k 2004). However, a few species were not listed there [mean arrival ± SD (*n*)]: *Erithacus rubecula* 80.2 ± 8.44 (66), *Motacilla flava* 95.3 ± 12.02 (56), *Phoenicurus phoenicurus* 104.8 ± 9.23 (60), *Acrocephalus arundinaceus* 120.6 ± 5.96 (35), *Locustella fluviatilis*

**Table 1.** Matrix of Pearson correlation coefficients *r* (multiplied by 1,000) among 37 species of birds in their temporal co-fluctuation during spring migration in Moravia, 1881–2001. The *r* values in bold are significant at $P<0.01$. The species acronyms are formed as the first letter of the scientific generic name followed with a three-letter acronym of the specific name; e.g., 'O.ori.' is *Oriolus oriolus*.

| | Oori | Sser | Hrus | Lcol | Svul | Lme | Aarv | Hict | Aapu | Poch | Aaru | Asch | Lrid | Scur | Satr | Rpe | Atri |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| O.ori. | 1000 | | | | | | | | | | | | | | | | |
| S.ser. | 185 | 1000 | | | | | | | | | | | | | | | |
| H.rus. | 48 | 132 | 1000 | | | | | | | | | | | | | | |
| L.col. | -87 | 82 | 160 | 1000 | | | | | | | | | | | | | |
| S.vul. | 19 | 291 | 229 | 21 | 1000 | | | | | | | | | | | | |
| L.meg. | -116 | 188 | 248 | 1 | 138 | 1000 | | | | | | | | | | | |
| A.arv. | -9 | 72 | 156 | -40 | **571** | 308 | 1000 | | | | | | | | | | |
| H.ict. | 224 | -223 | 144 | 189 | 2 | -49 | 122 | 1000 | | | | | | | | | |
| A.apu. | 296 | 139 | 292 | 30 | 343 | 252 | 152 | 275 | 1000 | | | | | | | | |
| P.och. | -17 | 304 | 156 | 310 | 248 | -110 | 127 | -170 | 287 | 1000 | | | | | | | |
| A.aru. | 188 | 103 | 175 | 156 | -22 | 53 | 195 | 46 | 283 | 359 | 1000 | | | | | | |
| A.sch. | -117 | 192 | 193 | 75 | 317 | -21 | 277 | 209 | 53 | 361 | 216 | 1000 | | | | | |
| L.rid. | 171 | **448** | 294 | -58 | **447** | 3 | 278 | -78 | 166 | 316 | -83 | 153 | 1000 | | | | |
| S.cur. | 187 | 253 | 192 | -83 | 161 | 103 | 56 | 99 | **422** | 67 | 256 | 5 | -55 | 1000 | | | |
| S.atr. | 12 | **755** | 335 | 47 | 213 | 162 | -61 | -270 | 229 | 192 | 134 | -14 | 290 | 345 | 1000 | | |
| R.pen. | 227 | 321 | 50 | 57 | 406 | 176 | 324 | -125 | 338 | **549** | 16 | -8 | -33 | 243 | 444 | 1000 | |
| A.tri. | -113 | 14 | 23 | 198 | -104 | -109 | 57 | 266 | -195 | -68 | 280 | 11 | -147 | 67 | -212 | -260 | 1000 |
| M.str. | 252 | -99 | -373 | 332 | 41 | -68 | -75 | 103 | -105 | 84 | -106 | 163 | -353 | -259 | -295 | 110 | -8 |
| F.alb. | 213 | 284 | 233 | 238 | -33 | 187 | 47 | 11 | 36 | 178 | 327 | 217 | -30 | **404** | 281 | 67 | 181 |
| C.can. | **300** | 149 | 138 | 43 | 180 | 210 | 58 | 251 | 36 | -19 | 121 | 78 | 54 | -2 | 175 | 73 | -101 |
| J.tor. | 189 | 291 | **320** | 169 | 79 | 259 | 231 | 124 | **372** | 63 | 124 | -69 | 201 | 148 | 200 | 260 | 159 |
| M.fla. | -22 | -133 | -185 | 188 | -71 | -138 | -34 | **507** | -106 | -70 | -106 | 323 | -439 | -57 | -81 | 83 | 274 |
| M.alb. | 34 | 360 | **309** | 120 | **607** | 282 | **507** | -26 | 312 | 246 | 273 | 203 | **328** | 124 | **384** | 218 | 51 |
| D.urb. | 137 | -157 | **315** | 224 | 25 | 173 | 189 | **445** | 8 | -162 | 337 | 364 | -165 | 200 | -137 | -290 | 187 |
| C.pal. | 59 | 243 | -181 | 303 | **405** | -43 | **303** | 230 | 100 | 159 | -27 | 24 | -133 | 156 | 14 | **467** | 134 |
| S.tur. | 9 | 200 | 190 | -43 | 259 | 204 | 150 | -25 | 193 | 301 | 290 | 164 | 295 | 114 | 223 | 262 | -28 |
| U.epo. | -32 | -104 | 53 | 265 | **384** | -192 | 134 | 75 | 164 | **451** | 124 | 400 | 235 | 275 | -19 | 94 | -33 |
| T.phi. | 114 | **418** | 192 | 92 | **511** | 7 | **408** | 7 | 294 | 281 | 280 | 330 | **606** | -29 | 337 | 152 | -200 |
| V.van. | -166 | 302 | 204 | 202 | **554** | 226 | **545** | -31 | 151 | **328** | 5 | 140 | **487** | -66 | 232 | 294 | 99 |
| C.cic. | 131 | **443** | 89 | 261 | **358** | 9 | **306** | -83 | 68 | 225 | 91 | -109 | 27 | 162 | 269 | 217 | 160 |
| L.flu. | **631** | 225 | -149 | 328 | 275 | -395 | -212 | 119 | 286 | -46 | 148 | -12 | 41 | 19 | 222 | 299 | -121 |
| P.col. | 130 | **508** | 234 | 207 | **529** | 150 | 292 | -93 | 269 | **658** | 69 | 393 | **463** | 68 | 362 | **652** | -62 |
| R.rip. | 177 | 227 | -310 | -11 | 228 | -238 | -32 | 303 | -310 | 135 | -18 | **545** | 111 | 23 | -213 | 156 | 116 |
| E.rub. | 19 | 198 | 250 | -121 | **413** | 188 | 207 | -99 | 194 | **453** | 261 | 115 | **437** | -16 | 268 | 369 | -26 |
| C.cot. | 276 | -119 | -388 | 76 | -351 | -406 | -10 | 272 | 139 | -208 | 204 | -335 | -418 | 145 | -336 | -178 | 158 |
| P.pho. | 215 | -354 | 4 | 201 | -253 | -275 | -99 | 258 | -71 | 72 | 320 | -181 | -413 | 41 | -327 | -213 | 239 |
| C.fru. | 171 | 283 | 156 | 189 | **625** | -135 | 403 | 115 | 409 | **542** | 124 | 297 | **494** | 48 | 213 | **536** | 24 |

| | Mstr | Falb | Ccan | Jtor | Mfla | Malb | Durb | Cpal | Stur | Uep | Tphi | Vvan | Ccic | Lflu | Pcol | Rrip | Erub | Ccot | Ppho | Cfru |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| M.str. | 1000 | | | | | | | | | | | | | | | | | | | |
| F.alb. | -80 | 1000 | | | | | | | | | | | | | | | | | | |
| C.can. | 205 | -74 | 1000 | | | | | | | | | | | | | | | | | |
| J.tor. | 27 | -13 | 172 | 1000 | | | | | | | | | | | | | | | | |
| M.fla. | 95 | 119 | 207 | -179 | 1000 | | | | | | | | | | | | | | | |
| M.alb. | -57 | 113 | 166 | **303** | -212 | 1000 | | | | | | | | | | | | | | |
| D.urb. | 4 | 324 | 247 | -127 | 296 | -6 | 1000 | | | | | | | | | | | | | |
| C.pal. | 358 | 44 | 156 | 77 | **445** | 223 | 136 | 1000 | | | | | | | | | | | | |
| S.tur. | -27 | 311 | **375** | 24 | -92 | **331** | 156 | -51 | 1000 | | | | | | | | | | | |
| U.epo. | 19 | -1 | 83 | -37 | -114 | 248 | 139 | 130 | 272 | 1000 | | | | | | | | | | |
| T.phi. | -37 | -63 | 213 | 294 | -225 | **502** | -137 | 136 | 111 | 272 | 1000 | | | | | | | | | |
| V.van. | -34 | 82 | 75 | 178 | -34 | **601** | 6 | **410** | 262 | 269 | **420** | 1000 | | | | | | | | |
| C.cic. | 419 | 248 | 82 | 305 | 79 | **357** | 2 | **492** | 44 | -93 | 125 | **281** | 1000 | | | | | | | |
| L.flu. | **660** | -195 | 90 | 37 | -161 | -62 | 20 | 169 | -4 | 78 | 402 | -58 | 84 | 1000 | | | | | | |
| P.col. | 111 | 61 | 31 | 318 | -139 | 267 | -44 | 330 | 268 | 130 | **432** | 253 | **453** | 191 | 1000 | | | | | |
| R.rip. | -28 | 232 | -104 | -168 | 251 | -212 | 207 | 351 | -1 | 370 | -187 | 186 | -132 | 219 | 175 | 1000 | | | | |
| E.rub. | -126 | 177 | 68 | **363** | -247 | 259 | -66 | -7 | 316 | 214 | **407** | 136 | 219 | -123 | **558** | 75 | 1000 | | | |
| C.cot. | 454 | 50 | -104 | 151 | 332 | -360 | 109 | 251 | -356 | -265 | -163 | -323 | 324 | **691** | -128 | 4 | -505 | 1000 | | |
| P.pho. | 179 | 376 | 54 | -77 | 321 | -114 | 199 | 335 | 34 | 61 | -326 | -120 | 383 | -431 | -458 | 289 | -69 | 480 | 1000 | |
| C.fru. | 171 | -62 | 191 | 379 | 469 | 271 | -64 | **597** | 344 | 370 | **534** | **566** | 437 | 277 | **631** | 527 | 406 | -3 | -163 | 1000 |

127.0 ± 7.21 (29), *Coturnix coturnix* 136.1 ± 10.51 (48) and, in addition, *Corvus frugilegus* departure of about half of the wintering population 68.8 ± 5.56 (35).

The cluster analysis of the correlation matrix (Table 1) revealed a number of groups of bird species co-fluctuating in their arrival timing (Fig. 1). These groups have been termed 'migrons'; a migron is defined as a cluster of species with a similar pattern of co-fluctuation in migration timing. Specifically at the level of $r$ = 0.20 the migrons were: (A) all short-distance migrants with the European/Mediterranean winter range (the central part of the dendrogram): skylark *Alauda arvensis*, white wagtail *Motacilla alba*, lapwing *Vanellus vanellus*, starling *Sturnus vulgaris*, rook *Corvus frugilegus*, woodpigeon *Columba palumbus*, black redstart *Phoenicurus ochruros*, chiffchaff *Phylloscopus collybita*, penduline tit *Remiz pendulinus*, robin *Erithacus rubecula*, song thrush *Turdus philomelos*, black-headed gull *Larus ridibundus*, serin *Serinus serinus* and blackcap *Sylvia atricapilla*, while all the other six smaller clusters were formed exclusively of long-distance migrants having an African (sub-Saharan) winter range: (B) cuckoo *Cuculus canorus*, turtle dove *Streptopelia turtur*; (C) swallow *Hirundo rustica*, wryneck *Jynx torquilla*, nightingale *Luscinia megarhynchos*, swift *Apus apus*, lesser whitethroat *Sylvia curruca*; (D) sedge warbler *Acrocephalus schoenobaenus*, sand martin *Riparia riparia*, hoopoe *Upupa epops*; (E) tree pipit *Anthus trivialis*, house martin *Delichon urbica*, yellow wagtail *Motacilla flava*, icterine warbler *Hippolais icterina*; (F) white stork *Ciconia ciconia*, redstart *Phoenicurus phoenicurus*, collared flycatcher *Ficedula albicollis*, great reed warbler *Acrocephalus arundinaceus*, red-backed shrike *Lanius collurio*; and (G) golden oriole *Oriolus oriolus*, spotted flycatcher

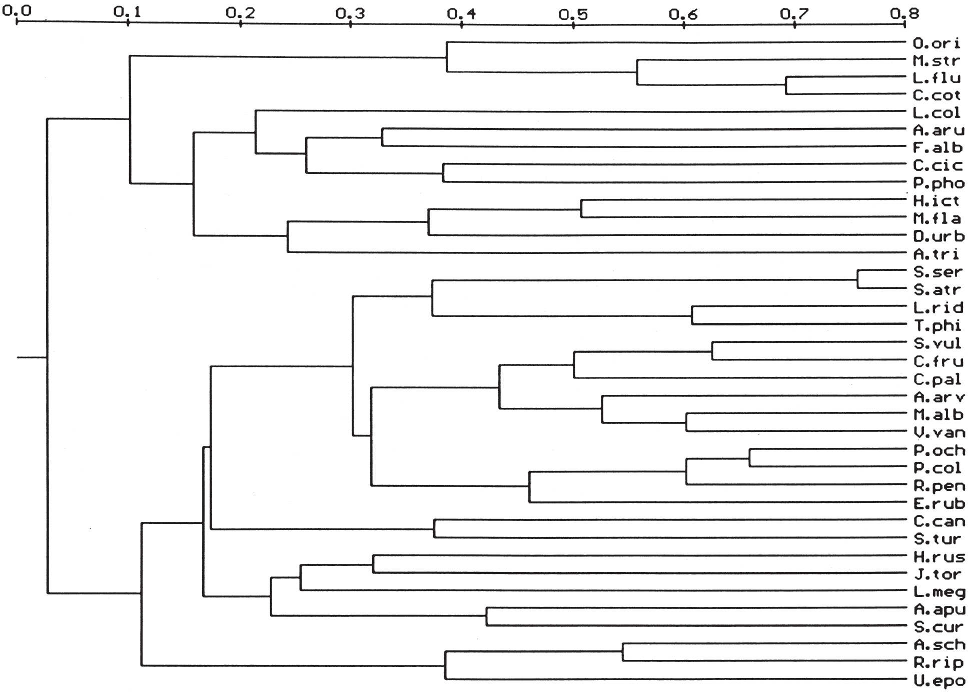


**Fig. 1.** Dendrogram of the UPGMA cluster analysis of correlations (Pearson $r$ values) in the spring arrival dates among 37 migratory bird species in Moravia, 1881–2001. The species acronyms have been formed as described in Table 1.

*Muscicapa striata*, river warbler *Locustella fluviatilis*, quail *Coturnix coturnix*. The 'African' migrons B to G differ in their dendrogram topology: whereas the groups B, C and D join the 'European' migron A at the level of $r = 0.173$, 0.166 and 0.112, respectively, the migrons E to G form a separate supercluster at the level of $r = 0.101$ that merges with the remaining migrons only at a very low level of $r = 0.028$ indicating, in fact, no relationship.

## Discussion

Arrival times used in these analyses were arithmetic means of first observations of particular avian species by a number of ornithologists in several places of Moravia. These mean instants cannot be taken as exact dates of mean arrival of the whole population of a particular bird species but for the more stringent data very extensive observation dates were necessary which are usually inaccessible. In some bird individuals exceptionally wintering close to Central Europe, an accelerated spring arrival might be expected (this is known, e.g., in white stork). This potential bias was removed by leaving out unusually early arrival dates (see Methods), differing substantially from the arrival dates of the rest of the population.

Twenty years ago, the cluster analysis of temporal patterns of avian spring migration in Moravia during 1965 to 1981 (Hubálek 1983) and 1881 to 1960 (Hubálek 1985) showed results that were very similar to those in the present study, with several migrons of avian species co-fluctuating in their migration timing: the first ('Mediterranean') migron consisted of short-distance migrants wintering in southern or western Europe (skylark, starling, chaffinch, woodpigeon, white wagtail, lapwing, song thrush, robin, woodcock), whereas the remaining migrons were called 'African' in that they only involved long-distance migrants having their winter quarters in sub-Saharan Africa (swallow, wryneck, house martin, cuckoo, nightingale, turtle dove, swift, golden oriole, quail). The present study, based on a much more extensive dataset, thus confirmed the previous conclusions. All species that are early-spring, short-distance migrants that winter in Europe or in the Mediterranean (including North Africa) clustered together. On the other hand, the remaining species, having their winter ranges largely in sub-Saharan Africa, grouped separately in a number of smaller migrons.

In a study of spring migrants in England, 1942–1991 (Mason 1995: Table 3), significant ($P<0.001$) intercorrelations in arrival dates were found among several species of birds. For instance, chiffchaff co-fluctuated with blackcap, swallow with spotted flycatcher, yellow wagtail with tree pipit, and sedge warbler with swift, etc. Only the first pair of species intercorrelated in our study – conditions for spring migration can obviously differ between England and Moravia.

The migrons generally reflect only partially the timing of arrival in particular species, i.e. the species of one migron need not be arriving either early or late (or medium). In an attempt to analyze the underlying differentiating variables of the species of 'African' migrons, it might be helpful to look at their winter ranges (Voous 1960, Moreau 1972). While the bird species of the migrons B to D generally winter over the whole territory of tropical Africa sometimes preferring its western (less southern) part (e.g., sedge warbler, sand martin), a number of migrants of the groups E to G prefer for wintering eastern, central or southern Africa (e.g., icterine warbler, white stork, collared flycatcher, red-backed shrike, golden oriole, spotted flycatcher, river warbler). However, it is difficult at present to say whether the different migrons are determined by varying wintering areas of corresponding bird species within Africa because knowledge about the detailed African winter ranges of particular Central European summer visitors is still surprisingly scarce despite the huge ringing and observatory efforts by many ornithologists. Other variables might be factors contributing to species composition of the migrons found in this study, e.g. similar feeding preferences in the winter range and/or along the migratory route of those species forming a migron; precipitation rates in the winter area and/or along the migratory route; prevailing wind conditions on the route; the method of flight during migration (migration speed, circling, using specific stop-overs on the route, etc.). These questions remain open at present but should be considered.

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