Oikos

O18592
Tökölyi, J. and Barta, Z. 2011. Breeding phenology determines evolutionary transitions in migratory behaviour in finches and allies. – Oikos 120: 184–193.

Appendix 1

Data used in the analyses.

Species	Migration distance (km)	Migratory behaviour[1]	Breeding latitude (degrees North)	Start of breeding season (Julian day)	Length of breeding season (days)	Winter diet[2]	Adult body mass (g)	Breeding habitat type[3]	Breeding phenology references
Agelaius phoeniceus	0	0	41.5	123	62	0	52.4	7	Robertson 1973
A. tricolor	0	0	36.75	71	108	0	58.7	6.5	Hamilton 1998
Aimophila aestivalis	0	0	34.36	107	131	0	19.16	3	Haggerty 1988
A. botterii	0	0	31.5	168	56	1	19.9	7	Poole 2005
A. carpalis	0	0	31.7	110	144	0	15.3	6	Bent 1968
A. cassinii	0	0	31	60	153	0	18.9	6	Poole 2005
A. quinquestriata	0	0	31.5	155	77	0	19.55	3	Poole 2005
A. ruficeps	0	0	36.85	70	121	0	18.7	6	Poole 2005
Ammodramus bairdii	1974	1	49.75	141	69	0	18.07	6	Davis 2003
A. caudacutus	253	0	40.75	134	95	1	19.25	7	Poole 2005
A. henslowii	501	1	37.5	121	70	0	12.8	7	Winter 1999
A. leconteii	1107	1	48.8	137	52	0	13	7	Poole 2005
A. maritimus	1596	1	40.7	154	33	0	23.08	7	Bent 1968
A. savannarum	228	0	39	135	96	0	17.57	6.5	Bent 1968
Amphispiza belli	806	1	46.8	75	55	0	17.07	6	Washington Birds Breeding Phenology Program
A. bilineata	0	0	29.8	79	146	0	13.5	6	Bent 1968
Arremonops rufivirgatus	0	0	27.25	75	169	0	22.45	5	Bent 1968
Bucanetes githagineus	0	0	37	51	115	0	19.4	7	Barrientos et al. 2007
Calamospiza melanocorys	576	1	40.83	136	49	0	37.6	6.5	Creighton and Baldwin 1974
Calcarius lapponicus	4059	1	71.3	152	27	0	27.85	7	Custer and Pitelka 1977
C. mccownii	1645	1	51	126	83	0	25.7	7	Poole 2005
C. ornatus	1374	1	49.75	121	80	0	20.3	7	Davis 2003
C. pictus	1865	1	58.82	166	9	0	26.7	6	Jehl 1968
Cardellina rubrifrons	968	1	31.91	122	47	1	9.8	1	Kirkpatrick and Conway 2005
Cardinalis cardinalis	0	0	44.5	103	124	0	42.65	3.8	Peck and James 1987
C. sinuatus	0	0	30	72	138	0	35.2	4.67	Bent 1968

Carduelis cannabina	808	0	61.3	106	107	0	19.55	5	Tast 1970
C. carduelis	0	0	48.6	115	102	0	16	4.33	Glück 1983
C. chloris	0	0	54	102	121	0	26	4.33	Monk 1954
C. flammea	0	0	67.7	141	65	0	13	4	Pulliainen and Peiponen 1981
C. lawrencei	302	0	36.58	91	100	0	10.95	6	Bent 1968
C. pinus	0	0	37.01	97	103	0	12.7	2	Poole 2005
C. psaltria	0	0	36.77	92	123	0	9.32	3.5	Bent 1968
C. tristis	0	0	44	186	74	0	12.8	4.33	Bent 1968
Carpodacus cassinii	0	0	42.35	138	50	0	26.5	2	Mewaldt and King 1985
C. erythrynus	4387	1	65	147	35	0	24	4	Reinikainen 1939
C. mexicanus	0	0	37	59	160	0	21.4	4.8	Bent 1968
C. purpureus	141	0	48	131	86	0	23.3	3.5	Peck and James 1998
Chondestes grammacus	0	0	31	119	39	0	49	6	Poole 2005
Coccothraustes coccothraustes	0	0	54.12	105	91	0	56.65	1	Mountfort 1957
Dendroica caerulescens	2238	1	44	139	64	1	10.15	1	Holmes et al. 1995
D. castanea	2749	1	47	156	27	1	11.8	1	Bent 1963
D. cerulea	3619	1	44.5	144	34	1	9.05	1	Peck and James 1987
D. coronata	162	0	37	63	121	1	11.87	1	Poole 2005
D. discolor	1624	1	42.3	149	23	1	7.65	3.33	Bent 1963
D. dominica	57	0	33.5	92	50	1	9.7	1	Bent 1963
D. fusca	3408	1	43	149	38	1	9.75	1	Bent 1963
D. magnolia	2520	1	45.5	155	26	1	8.15	1	Bent 1963
D. nigrescens	1340	1	36.83	121	63	1	8.7	2.67	Bent 1963
D. palmarum	1490	1	45	138	21	1	10.3	6	Bent 1963
D. pensylvanica	2834	1	48	145	58	1	9.3	3	Peck and James 1987
D. petechia	2659	1	49	135	63	1	9.52	4.5	Peck and James 1987
D. pinus	0	0	40.07	98	48	0	11.78	1	Bent 1963
D. striata	3872	1	46.87	161	23	1	11.85	1	Bent 1963
D. tigrina	2749	1	47	161	19	1	10.05	1	Bent 1963
D. virens	2447	1	48	156	65	1	8.7	1	Peck and James 1987
Dolichonyx oryzivorus	6554	1	44.5	137	48	0	31.55	7	Perlut 2007
Emberiza cirlus	0	0	39.7	84	102	0	25.6	4.33	Ponz et al. 1996
E. citrinella	0	0	54	95	153	0	29.7	4.5	Cramp and Perrins 1994b
E. hortulana	4404	1	62.56	135	41	0	19.9	5	Cramp and Perrins 1994b
E. rustica	3509	1	67.7	142	44	0	20.55	2.5	Pulliainen and Saari 1989
E. schoeniclus	70	0	54	104	114	0	18.45	6.5	Glutz von Blotzheim and Bauer (1966–1997)
Euphagus carolinus	3322	1	56	135	46	0	59.75	1	Bent 1965
E. cyanocephalus	0	0	37	88	103	0	62.65	4	Bent 1965
Fringilla coelebs	0	0	54	69	96	0	21.97	1	Newton 1964
Geothlypis trichas	1400	1	48.3	139	71	1	9.53	3	Peck and James 1987
Helmitheros vermivorus	2022	1	41.5	133	49	1	14.2	1	Poole 2005
Icteria virens	3571	1	37	124	70	1	24.9	4	Bent 1963
Icterus bullockii	271	0	37	112	50	1	37.9	6	Bent 1965
I. cucullatus	1169	1	37	97	127	1	24.3	6	Bent 1965
I. galbula	1640	1	46	138	37	1	32.85	4.5	Peck and James 1987
I. gularis	0	0	26.18	110	87	1	55.3	6	Werner 2004
I. parisorum	634	1	35	114	62	1	36.19	6	Bent 1965
I. spurius	1444	1	31	119	64	1	19.89	5	Bent 1965
Junco hyemalis	0	0	37.25	79	136	0	19.04	2	Bent 1968

J. phaeonotus	0	0	32.18	106	74	0	20.7	5	Kirkpatrick and Conway 2005
Leucosticte tephrocotis	537	0	64	134	89	0	39.47	7	Bent 1968
Limnothlypis swainsonii	1209	1	33.87	118	69	1	18.9	1	Thompson 2005
Melospiza georgiana	117	0	41	134	59	0	16.1	4.5	Poole 2005
M. lincolnii	787	0	55	147	32	0	16.6	4.67	Bent 1968
M. melodia	0	0	48.6	56	130	0	20.1	3	Smith and Arcese 1994
Miliaria calandra	0	0	54	122	97	0	48.75	6.5	Glutz von Blotzheim and Bauer (1966–1997)
Mniotilta varia	897	1	42.3	138	27	1	10.9	1	Bent 1963
Oporornis formosus	1730	1	38.9	136	46	1	14	1	Poole 2005
O. tolmiei	2535	1	47.5	132	54	1	10.4	2.5	Washington Birds Breeding Phenology Program
Parula americana	1770	1	42.67	140	48	1	7.87	1	Bent 1963
Passerculus sandwichensis	517	0	44.5	128	75	0	20.02	7	Perlut 2007
Passerella iliaca	0	0	37.37	141	48	0	33.64	3	Bent 1968
Passerina amoena	848	1	37	84	122	0	15.5	4	Bent 1968
P. caerulea	1304	1	33	130	78	0	27.4	4.4	Bent 1968
P. cyanea	2228	1	42.27	134	91	0	14.7	3.5	Payne and Payne 1998
Pheucticus ludovicianus	2625	1	46	130	67	1	42	3	Peck and James 1987
P. melanocephalus	1194	1	37	113	78	0	47.15	4.5	Bent 1968
Pinicola enucleator	0	0	67.7	145	31	0	56.4	2	Pulliainen 1979
Pipilo aberti	0	0	33.61	72	108	1	45.95	2	Finch 1984
P. chlorurus	55	0	37.24	148	62	0	29.4	4	Bent 1968
P. erythrophthalmus	1046	1	46	126	99	0	40.05	3.33	Peck and James 1987
P. fuscus	0	0	34	62	189	0	44.4	5	Bent 1968
P. maculatus	146	0	47.55	100	89	0	39	5	Washington Birds Breeding Phenology Program
Piranga ludoviciana	280	0	37.24	127	69	1	28.1	2	Bent 1965
P. olivacea	3955	1	42.3	144	32	1	28.2	1	Bent 1965
P. rubra	1228	1	33.5	131	22	1	30.1	2.5	Bent 1965
Plectrophenax nivalis	220	0	63.87	140	55	0	42.2	7	Bent 1968
Pooecetes gramineus	1029	1	46	113	102	0	25.7	6.5	Peck and James 1987
Protonotaria citrea	1982	1	36	113	63	1	14.3	1	Petit 1989
Pyrrhula pyrrhula	0	0	52.03	95	142	0	22.47	1	Bijlsma 1982
Quiscalus major	0	0	33	79	105	0	158.5	6.5	Post 1995
Q. quiscula	651	0	48.5	94	99	0	106.1	3.75	Peck and James 1987
Seiurus aurocapillus	1594	1	48	141	68	1	18.8	1	Peck and James 1987
S. novaboracensis	2465	1	49	135	49	1	16.3	2	Peck and James 1987
Serinus canaria	0	0	32.6	27	123	0	24.3	5	Voigt and Leitner 1998
S. serinus	343	0	51	95	111	0	11.2	3.5	Cramp and Perrins 1994a
Setophaga ruticilla	2469	1	48	147	61	1	8.25	1	Peck and James 1987
Spiza americana	2301	1	39	138	84	0	25.71	7	Zimmerman 1983
Spizella arborea	2588	1	64	147	33	0	17.85	6	Bent 1968
S. atrogularis	503	1	36.11	113	75	0	11.3	5	Bent 1968
S. breweri	3	0	37	109	88	0	10.9	5	Bent 1968
S. pallida	2154	1	47.5	138	55	0	11.2	4.67	Grant et al. 2005
S. passerina	1319	1	49	121	105	0	12.2	2.5	Peck and James 1987
S. pusilla	0	0	41	123	85	0	12.5	4.5	Poole 2005
Sporophila torqueola	0	0	26.4	71	175	0	8.7	7	Bent 1968
Sturnella magna	438	0	46	122	93	0	90.23	7	Peck and James 1987
S. neglecta	0	0	37	42	141	0	100.7	7	Bent 1965

Vermivora chrysoptera	3064	1	44.3	133	28	1	8.75	3	Bent 1963
V. peregrina	2718	1	46.7	161	30	1	8.9	1	Bent 1963
V. pinus	1783	1	39	124	30	1	8.9	3.33	Poole 2005
V. ruficapilla	2517	1	49	144	58	1	8.1	2	Peck and James 1987
Wilsonia canadensis	3571	1	43	145	32	1	10.05	1	Bent 1963
W. citrina	1954	1	41	130	70	1	10.55	1	Poole 2005
Xanthocephalus xanthocephalus	2063	1	52.13	127	32	0	64.5	5.5	Poole 2005
Zonotrichia albicollis	558	0	49	138	82	0	24.4	2	Peck and James 1987
Z. atricapilla	1617	0	61.5	147	32	0	32	5.5	Bent 1968
Z. leucophrys	0	0	37.8	75	106	0	28.52	4	Petrinovich Patterson 1983
Z. querula	2055	1	63.6	159	12	0	35.55	6	Norment 1992

Notes:
[1] 0 – short-distance migrant (migration distance shorter than expected for breeding latitude), 1 – long-distance migrant (migration distance longer than expected for breeding latitude)
[2] 0 – granivorous; 1 – insectivorous.
[3] 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 more than one habitat type was reported for a species, they were averaged.

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Appendix 2

Sampling bias

Differences in sampling may affect the the start and and length of the breeding season and thereby confound the relationship between breeding phenology and migration. First, sampling intensity might introduce a bias because more effort typically increases the probability of very early or very late nests to be discovered. Second, some studies report laying dates, whereas others report the dates on which viable eggs were found. Assuming identical sampling effort, earliest egg dates should not differ considerably from earliest laying dates, but the latest egg dates should be later than the latest laying dates, because the former incorporate the incubation period as well. However, egg collectors may have concentrated their efforts to specific part(s) of the breeding cycle (McNair 1987), thus the difference between the two types of data are not straightforward. To check that the two type of phenology data are indeed different and whether any kind of correction is needed, we used the original dataset with all phenology data (n = 496 records for 134 species, with a median of three records per species) to build generalized estimating equation (GEE) models. GEEs are extensions of generalized linear models (Liang and Zeger 1986, Hardin and Hilbe 2003) that can be used for correlated data (i.e. multiple data points from a single species in our case). GEE models were constructed using the 'geepack' package in the R statistical environment (Yan and Fine 2004, R Development Core Team 2008), with an exchangeable correlation structure that assumes multiple observations within clusters (species) to be equally correlated. Start and end date of the breeding season were separately used as independent variables, location (the latitude where the phenology was recorded), sample size (number of nests) and type of the data (laying date or egg date) were introduced as explanatory variables, and species as a grouping factor. These analyses showed that the end date of the breeding season does not differ significantly at the 5% level between egg dates and laying dates (after controlling for sample size and location), but that the starting date in the case of egg dates is significantly later compared to laying dates. Furthermore, sample size is negatively correlated with the start and end dates such that earlier dates were recorded for larger sample sizes). Although this is what we would expect for the start date, the direction of the relationship in the case of end dates is strange. It turns out however, that this relationship is not significant when one data point with extremely large sample size, ~500 000 nests of tricolored blackbirds *Agelaius tricolor,* is excluded.

To summarize, the start of breeding season is affected by both sampling intensity and the type of phenology data, whereas the end of the breeding season is not affected by these factors.

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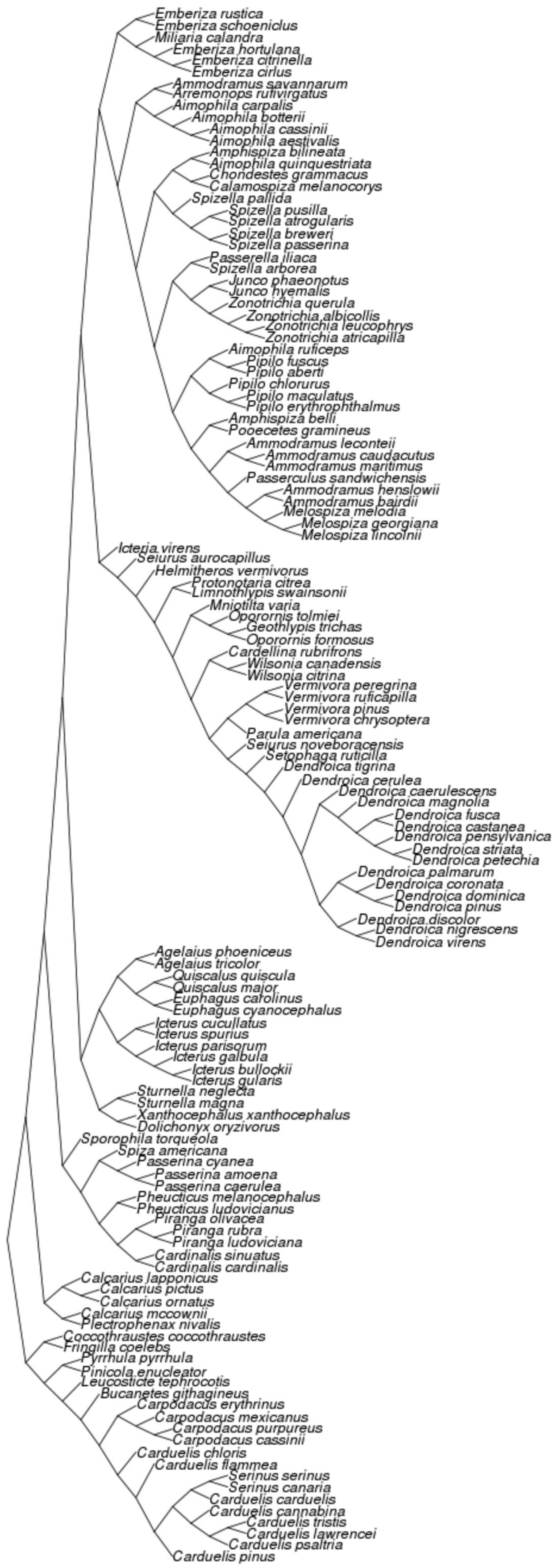
Appendix 3

The phylogenetic tree used in the analyses and the references used to compile the tree.



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Appendix 4

Results from the dataset with the northernmost phenology records. For all species where phenology data with a sample size of at least 20 nests was available from several locations, we selected the northernmost record and computed the minimum migration distance from these coordinates. Records matching these criteria were available for 54 out of 134 species. The median breeding latitude in this sample was 47.3 degrees North and the median migration distance 1137.5 km, compared to 42.55 degrees North and 642.5 km in the original sample in which data was selected based on the largest sample size. In this appendix we present the results of the multivariate analyses using this dataset with either the start (a) or the length of the breeding season (b) included as the explanatory phenology variable and the results of the directional tests (c).

(a)

Source of variance	Full model: β (SE)	t (p)	Minimal model: β (SE)	t (p)
Start of breeding season	0.187 (0.065)	2.887 (0.005)	0.210 (0.062)	3.323 (0.001)
Breeding latitude	0.935 (0.179)	5.226 (<0.001)	0.838 (0.168)	4.984 (<0.001)
Adult body size	–0.200 (0.083)	–2.399 (0.018)	–0.212 (0.087)	–2.440 (0.016)
Winter diet	11.601 (4.717)	2.459 (0.015)	10.113 (4.776)	2.118 (0.036)
Breeding habitat	0.681 (0.813)	0.838 (0.404)	–	
Continent	–9.034 (5.592)	–1.616 (0.109)	–	

Shapiro–Wilk test on the normality of residuals for the full model: W = 0.990, p = 0.422; for the minimal model: W = 0.980, p = 0.043.

(b)

Source of variance	Full model: β (SE)	t (p)	Minimal model: β (SE)	t (p)
Length of breeding season	–0.173 (0.046)	–3.774 (<0.001)	–0.193 (0.044)	–4.420 (<0.001)
Breeding latitude	0.941 (0.162)	5.811 (<0.001)	0.829 (0.153)	5.435 (<0.001)
Adult body size	–0.234 (0.082)	–2.839 (0.005)	–0.283 (0.089)	–3.166 (0.002)
Winter diet	10.699 (4.618)	2.317 (0.022)	–	
Breeding habitat	0.792 (0.796)	0.995 (0.322)	–	
Continent	–10.101 (5.358)	–1.885 (0.062)	–	

Shapiro–Wilk test on the normality of residuals for the full model: W = 0.988, p = 0.277; for the minimal model: W = 0.979, p = 0.036.

(c)

Parameter	Length of breeding season		Start of breeding season		Adult body size		Winter diet	
	Mean ± SD	Z-score	Mean ± SD	Z-score	Mean ± SD	Z-score	Mean ± SD	Z-score
q_{12}	0.46±0.17	0.00	0.63±1.10	0.00	0.20±0.10	0.00	0.05±0.02	0.00
q_{13}	0.43±0.13	0.02	0.07±0.21	0.79	0.10±0.07	0.17	0.40±1.10	0.00
q_{21}	0.42±0.11	0.00	1.10±2.85	0.00	0.20±0.09	0.00	0.30±0.22	0.00
q_{24}	0.02±0.07	0.92	0.49±0.30	0.12	0.41±1.86	0.00	0.13±0.20	0.18
q_{31}	0.00±0.03	0.98	0.55±0.44	0.06	0.10±0.04	0.00	0.45±1.12	0.00
q_{34}	0.42±0.13	0.00	1.09±2.83	0.00	0.00±0.02	0.93	0.05±0.03	0.04
q_{42}	0.44±0.12	0.01	0.02±0.07	0.91	0.42±1.86	0.00	0.05±0.02	0.00
q_{43}	0.45±0.20	0.00	0.63±1.10	0.00	0.11±0.05	0.01	0.00±0.01	0.90

Bayes factors: migratory behaviour – length of breeding season: 18.07; migratory behaviour – start of breeding season: 24.41; migratory behaviour – adult body size: 8.46; migratory behaviour – winter diet: 19.49.

Appendix 5

Mean ± SD and Z-scores of the transition rate parameters, estimated from the directional tests. In these tests, migratory behaviour was the first variable in all cases. The length of breeding season, start of breeding season and body size were the second character, respectively, and these variables were dichotomized with either the 40 (a) or the 60 percentiles (b) as cutoff points. The 40 and 60 percentiles were as follows: 62 and 82.8 days for the length of the breeding season, 30 April and 15 May for the start of the breeding season, 17.2 and 23 grams for adult body size respectively. Migratory behaviour was dichotomized by regressing breeding latitude over migration distance and setting it to 1 for species with positive residuals and to 0 for species with negative residuals.

(a)

Parameter	Length of breeding season		Start of breeding season		Adult body size	
	Mean ± SD	Z-score	Mean ± SD	Z-score	Mean ± SD	Z-score
q_{12}	0.46±0.27	0.00	0.50±0.56	0.00	0.15±0.08	0.00
q_{13}	0.45±0.21	0.00	0.01±0.03	0.96	0.06±0.06	0.37
q_{21}	0.37±0.09	0.00	0.51±0.57	0.00	0.06±0.03	0.00
q_{24}	0.00±0.02	0.99	0.40±0.11	0.00	0.22±0.37	0.00
q_{31}	0.01±0.07	0.96	0.42±0.17	0.02	0.06±0.03	0.01
q_{34}	0.45±0.40	0.00	0.41±0.23	0.01	0.04±0.03	0.38
q_{42}	0.37±0.10	0.02	0.01±0.05	0.92	0.23±0.37	0.00
q_{43}	0.44±0.40	0.00	0.34±0.12	0.00	0.14±0.07	0.00

Bayes factors: migratory behaviour – length of breeding season: 18.79; migratory behaviour – start of breeding season: 23.18; migratory behaviour – adult body size: 3.31.

(b)

Parameter	Length of breeding season		Start of breeding season		Adult body size	
	Mean ± SD	Z-score	Mean ± SD	Z-score	Mean ± SD	Z-score
q_{12}	2.44±10.95	0.00	0.38±0.09	0.00	0.17±0.06	0.00
q_{13}	0.34±0.20	0.07	0.00±0.03	0.98	0.11±0.06	0.07
q_{21}	2.19±10.86	0.00	0.61±0.40	0.00	0.17±0.06	0.01
q_{24}	0.10±0.12	0.43	0.57±0.33	0.00	0.20±0.20	0.00
q_{31}	0.07±0.09	0.56	0.38±0.11	0.02	0.11±0.05	0.01
q_{34}	0.20±0.19	0.32	0.57±0.52	0.00	0.01±0.03	0.90
q_{42}	0.75±0.77	0.06	0.01±0.07	0.96	0.20±0.20	0.00
q_{43}	1.09±1.10	0.01	0.58±0.51	0.00	0.18±0.06	0.00

Bayes factors: migratory behaviour – length of breeding season: 30.89; migratory behaviour – start of breeding season: 19.06; migratory behaviour – adult body size: 6.53.