Ornis Fennica 103: 00–00. 2026

Natal dispersal and migratory behaviour of juvenile kingfishers (*Alcedo atthis*) from Central Europe

Lucia Rubáčová*, Pavel Čech, Martin Čech, Mária Melišková & Martin Barka

L. Rubáčová, M. Melišková, & M. Barka, Department of Zoology, Faculty of Natural Science, Comenius University, Mlynská dolina, Ilkovičova 6, 842 15 Bratislava 4, Slovak Republic.
P. Čech, M. Čech, Czech Union for Nature Conservation, 02/19 ZO ČSOP Alcedo, Blanická 1299, 258 01 Vlašim, Czech Republic.
M. Čech, Institute for Environmental Studies, Faculty of Science, Charles University, Benátská 2, 128 01 Prague 2, Czech Republic & Biology Centre of the Czech Academy of Sciences, Institute of Hydrobiology, Na Sádkách 7, 370 05, České Budějovice, Czech Republic.
** Corresponding author's email: lucia.turcokova@uniba.sk*

Received 23 May 2025, accepted 24 March 2026

The costs and benefits of post-fledging dispersal give rise to diverse dispersal strategies in birds; however, the underlying patterns and mechanisms remain poorly understood in many species. We investigated natal dispersal and migration in juvenile Common Kingfishers (*Alcedo atthis*) originating from Czech and Slovak populations. Natal dispersal was examined by monitoring two breeding populations between 2014 and 2018. Of the 1,911 nestlings ringed during this period, 19 juveniles were subsequently recaptured, yielding a recovery rate of 0.36%. Most individuals (74%) settled within 20 km of their natal sites (median dispersal distance = 10.5 km), with no significant differences observed between populations or sexes. To assess large-scale migratory patterns, we supplemented our field data with ringing recoveries obtained from the Czech and Slovak Bird Ringing Centres (*n* = 264). In the last 50 years, migratory individuals (62%) slightly outnumbered resident birds (38%). The proportion of migrants and residents differed significantly among decades, with migrants increasingly predominating over time. Migration distance was significantly associated with fledging date: individuals fledging earlier in the breeding season (May–July) tended to migrate longer distances than those fledging later (August–September). Clear geographical variation in migratory direction was also detected. Juveniles from Bohemian and Slovak populations predominantly migrated southwest, whereas birds from Moravia generally migrated southward. Most kingfishers originating from Bohemia wintered in Western Europe, while individuals from Moravia and Slovakia were more likely to overwinter in southern Italy, the Balkans, and North Africa. It appears that juvenile Common Kingfishers exhibit a flexible migratory strategy shaped by both breeding phenology, which affects migration distance, and location of breeding sites determining migratory direction.

1. Introduction

Natal dispersal, which is the movement of an individual from its birthplace to the location where it first reproduces, plays a key role in population dynamics and evolutionary processes. Differential dispersal, where individuals with certain traits move more frequently or to specific locations, can drive evolution by creating local adaptations and rapid phenotypic differentiation. This occurs because non-random movement, influenced by factors like density, habitat quality, or competition, leads to different selection pressures in different areas (Clobert *et al*. 2001, Garant *et al*. 2005).

However, this behaviour comes with costs, such as increased energy demands and higher risk of predation during dispersal process. Dispersing individuals may face unfamiliar ecological and social conditions in new areas. This unfamiliarity can lead to less efficient resource exploitation, increased risk of predation, or diminished kin cooperation (Greenwood 1980, Emlen 1991, Pärt 1994, Smith & Metcalfe 1997, Bensch *et al*. 1998, Piper *et al*. 2008).

For migratory bird species, natal dispersal typically follows their first migration (Newton 2008). Over evolutionary time, the balance between the costs and benefits of migration has shaped different strategies within the same species (Chapman *et al*. 2011, Flack *et al*. 2016). These strategies have evolved as adaptations to seasonal changes in the environment, contributing to improved survival and reproduction by securing sufficient food resources and avoiding adverse climatic conditions (Newton 2008, Lok *et al*. 2015, Palacín *et al*. 2017).

In the Anthropocene, however, birds are increasingly responding to human-driven environmental changes such as habitat loss, fragmentation, and climate change by altering their migratory behaviour. Some species shift their wintering grounds, shorten migration distances, or stop migrating altogether and become resident (Fiedler 2003, van Vliet *et al*. 2009, Visser *et al*. 2009, Smallegange *et al*. 2010, Zuckerberg *et al*. 2011). Species that can adapt to these changes tend to experience smaller population declines than those with less flexible behaviours (Saino *et al*. 2011, Gilroy *et al*. 2016).

Due to flexible migration patterns in different conditions, the Common Kingfisher (*Alcedo atthis*) is an interesting model species for monitoring the migratory behaviour. After gaining independence, young kingfishers typically leave the parental territory within a few days and begin dispersing in apparently random directions (Čech 2009, Libois 2018). Post-fledging dispersal starts in the summer and gradually transitions into autumn migration (Cepák *et al*. 2008). Longer-distance movements during winter vary each year depending on weather severity (Morgan & Glue 1977). Birds begin returning in February, and breeding territories are usually reoccupied by March. Generally, first-time breeding kingfishers settle maximally within 250 km of their natal site, with differences in dispersal distance depending on the population (Libois 2018).

Between leaving their birthplace and settling at their first breeding site, young kingfishers stay in various locations, depending on their migratory behaviour. For example, northern European kingfishers living in regions where water bodies freeze in winter (*e.g*. Sweden, Finland, Poland) are fully migratory. In contrast, western European coastal populations follow a dispersive migration pattern, and migration is almost absent in the UK and Mediterranean peninsulas (Cramp 1990, Libois 2011, 2018).

In Central Europe, kingfishers are partial migrants. Adults usually stay close to their home range (moving no more than 25 km), while juveniles often travel much farther to overwinter in southern Europe or North Africa (*e.g*. Libya, Egypt). Among adults, females tend to migrate farther than males, likely to reduce competition for food (Cramp 1990, Cepák *et al*. 2008, Čech 2017, Libois 2018). Despite these varied strategies, juvenile kingfishers generally have very low survival rates in their first year of life (Morgan & Glue 1977, Rubáčová *et al*. 2021).

This study investigates natal dispersal and migration patterns of juvenile kingfishers from Czech and Slovak populations. We aimed (i) to determine the proportion of juvenile Common Kingfishers that return to breed and to quantify the distance between natal and first breeding sites, as well as to test for sex-specific differences in natal dispersal, with females predicted to disperse over longer distances than males. According to theories of sex-biased dispersal in birds, one sex typically disperses farther or more frequently than the other, with female-biased dispersal commonly observed in socially monogamous species. This pattern is generally attributed to males defending territories to attract mates, whereas females may benefit from dispersal by locating novel or higher-quality breeding sites; (ii) to determine the proportion of juvenile Common Kingfishers that remain near their natal sites during winter compared with those migrating long distances southward, and to assess temporal changes in this pattern over the last 50 years; (iii) to examine whether migration (recapture) distance is influenced by fledging date, with earlier-fledged juveniles, assumed to be in better condition, expected to migrate longer distances, whereas later-fledged individuals in poorer condition are predicted to remain closer to their natal areas during winter. According to the date hypothesis, offspring condition declines over the breeding season as environmental conditions for rearing young deteriorate, including seasonal reductions in food availability and variation in parental quality, with higher-quality parents typically breeding earlier in the season; (iv) to compare migratory directions of juvenile kingfishers from two Czech populations (Bohemian and Moravian) and one Slovak population. Given their Central European position, we expected the occurrence of several routes and different wintering grounds.

2. Materials and methods

To assess patterns of natal dispersal, we monitored two breeding populations of the Common Kingfisher at sites approximately 300 km apart along a west–east axis during the 2014–2018 breeding seasons. In southwestern Slovakia, approximately 55 km of the Danube River was regularly surveyed (between 48°06′13.5″N, 17°09′31.3″E and 47°52′32.1″N, 17°31′18.0″E). In the Czech Republic, the study area covered the western part of country and spanned 350 km of rivers and two reservoirs located in the Central Bohemian, South Bohemian, and Vysočina (Highland) regions (northernmost: 50°03′06″N, 14°30′25″E; southernmost: 49°15′35″N, 15°04′38″E; easternmost: 49°34′53″N, 15°11′38″E; westernmost: 49°40′46″N, 14°17′39″E).

Fieldwork was conducted from late March through to the end of September. Breeding burrows were inspected weekly using a specialized inspection camera. Surveys were carried out by walking along stream banks or in riverbeds for smaller watercourses, and by boat on reservoirs and larger rivers. Fourteen-day-old chicks were carefully extracted from the burrows using a specially adapted wire tool, measured, ringed, and returned to the nest chamber. Monitoring concluded after the final brood of the season had fledged, typically by the end of September.

To assess differences in natal dispersal distance between countries (BH: n = 13, SK: n = 6) and sexes (male: n = 13, female: n = 6), we used the Mann-Whitney U test, as the data did not meet normality assumptions.

To investigate general migration patterns of juvenile Common Kingfishers (*Alcedo atthis*), we combined data collected in Bohemia (western Czech Republic) and Slovakia with records from the Czech and Slovak Bird Ringing Centres, including data from Moravia (eastern Czech Republic), covering the period 1975–2024.

To examine temporal variation in the proportion of wintering versus migrating juveniles in the last 50 years, we analysed a subset of individuals (residents n = 93; migrants n = 154) that had been ringed as nestlings or juveniles during summer and subsequently recovered either domestically or abroad. Birds recaptured during the winter months (December–February) within a 20 km radius of their original ringing site were classified as residents. This distance threshold was selected because natal dispersal of almost 75% of juvenile kingfishers was within 20 km of their natal sites. To ensure adequate sample sizes, recovery data were pooled into decade-long intervals (1975–1984, 1985–1994, 1995–2004, 2005–2014, 2015–2024). Differences in the migrant-to-resident ratio among decades were tested using Pearson's chi-square test.

To assess whether fledging date influenced migration distance, we fitted generalized linear mixed model (GLMM) with a Gamma family and a log-link function. The response variable was the recapture distance (numeric) of juvenile kingfishers ringed as pulli at the nest, including both domestic ($n = 25$) and foreign ($n = 53$) recoveries. Fixed effect comprised fledging date, expressed as Julian date (numeric; with 1 January = 1). Year of ringing was included as a random factor to account for non-independence among individuals sampled within the same year (categorical). At first, we also included sex of the individual as a predictor in this model (categorical; 1 – female, 2 – male, 3 – unknown). The result was not significant, but the test predicted results for the unknown sex category as well, therefore we subsequently decided to remove this predictor from the analysis, because eliminating only the unknown sex category would have lost a significant part of the dataset. However, to avoid a methodological error, we decided to repeat the test with a smaller dataset ($n = 35$) containing only two categories in the case of sex predictor (female/male). The result was again not significant, so in the Results section we present outcomes of the analysis without the sex predictor, but the analyses that included sex are also presented in the Supplementary material section (Table S1, S2).

Statistical analyses were conducted in R version 4.5.1 (R Core Team, 2025) with *glmmTMB* package (Brooks *et al*. 2017, McGillycuddy *et al*. 2025). Models were validated using residual diagnostics via *DHARMa* package (Hartig 2024). We also assessed overdispersion, uniformity, zero inflation, multicollinearity using Variance Inflation Factors (VIFs), random effect assumptions, and model fit through Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), and likelihood ratio tests (LRTs).

To evaluate deviations from a uniform angular distribution, we used the Rayleigh test, which allowed us to assess whether the movements showed a predominant orientation within each region (Bohemia, Moravia, and Slovakia). We then used Watson-Williams F-test as the primary tool to test for differences in mean direction of motion between the three given regions. Before performing this test, we evaluated that samples exhibited comparable concentration parameters and underlying angular distributions were unimodal, as required by the Watson-William's test. These conditions were verified by inspecting the resulting vector lengths, concentration estimates, and graphical diagnostics. For each individual, the initial migration bearing was calculated from geodetic coordinates of the capture and recapture locations during 1947–2024 (Bohemia: $n = 89$; Moravia: $n = 56$; Slovakia: $n = 26$) with *geosphere* package (Hijmans 2024). As bearing values may be negative, they were first converted to a 0–360° scale and subsequently transformed into circular data. Using the *ggplot2* and *dplyr* packages, we created a circular (directional) diagram with estimated mean direction vectors for each region and marked azimuths for every individual. We also captured given movements on a map, where we used a raster layer (processed using *terra* package) and a shapefile layer with country borders (processed using *sf* package) as a basis. For each record, there is a colour-coded vector on the map with respect to the corresponding region, which connects sites of first capture and recapture. In some cases, the location of first capture and recapture was identical, which led to overlapping vectors on the map, so we additionally checked whether the number of records in the dataset matched the number of vectors that would be plotted on the map, despite the overlap. All circular calculations were performed using *circular* package (Agostinelli & Lund 2025).

Bayesian regression model (BRM) with a Student-t likelihood family was used to test for regional differences ($n = 171$) in the use of westward *versus* eastward migration directions, while excluding movements in other directions from the analysis, and was implemented using the *brms* package (Bürkner 2017). For each individual, longitudinal displacement (Δlongitude = $\text{lon}_2 - \text{lon}_1$) was calculated, where positive values indicated eastward movements and negative values indicated westward movements. Δlongitude was included as the response variable in the model (numeric), with region (categorical; 1 – Bohemia, 2 – Moravia, 3 – Slovakia) specified as the predictor. Model results were interpreted based on posterior credible intervals. To better assess differences

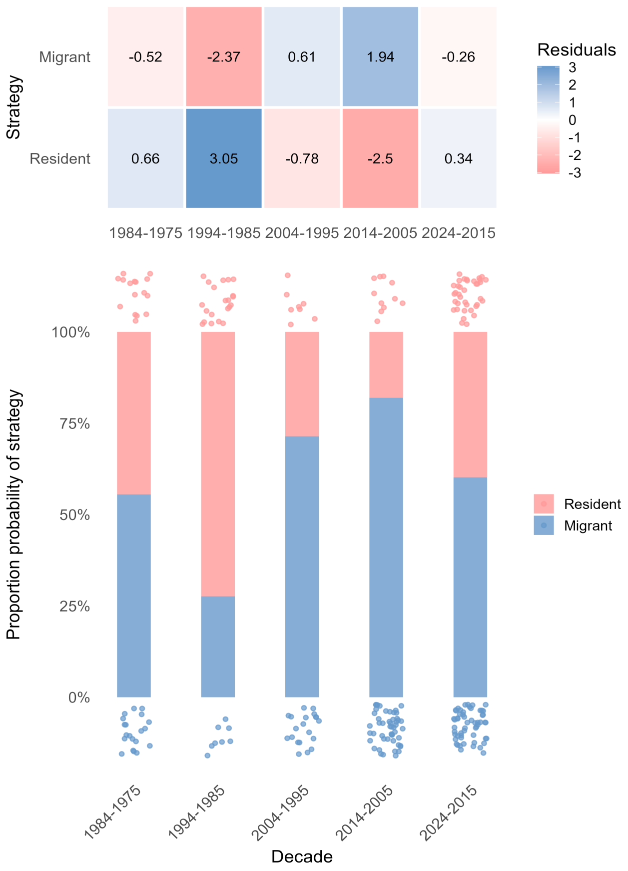

Fig. 1. Distributions of strategies across decades are shown, with Pearson residuals from a chi-square test between decade and strategy visualised as a heatmap (values with blue indicating positive residuals, red negative, and white values near zero), highlighting deviations from expected frequencies (top). Proportions of individuals adopting each strategy through different decades are displayed as stacked bars with jittered points (illustrating individual variation within each decade and strategy category; bottom).

between all groups, we also computed posterior contrasts for all pairwise comparisons, including the posterior probability of positive differences. The model was fit using 4 chains of 2000 iterations each (1000 warmup), yielding a total of 4000 post-warmup draws. Convergence diagnostics indicated that all parameters achieved Rhat = 1.0 and high effective sample sizes (Bulk_ ESS and Tail_ESS > 1700), suggesting adequate mixing and reliable posterior estimates. Posterior predictive checks further confirmed that the model adequately reproduces the observed data.

Differences among populations in the frequency of use of the western versus eastern flyways were tested using Pearson's chi-square test. Recaptures assigned to the western flyway (*n* = 89) comprised locations along and north of the northern Mediterranean coastline. Recaptures assigned to the eastern flyway (*n* = 82) included recoveries oriented toward southern Italy, the Balkan Peninsula, and North Africa.

3. Results

3.1. Natal dispersal

Out of 1,911 ringed juvenile kingfishers from both populations, 19 individuals (13 males, 68%; 6 females, 32%), representing 0.99% of the total, were recaptured in subsequent years. None of the recaptured birds returned to their exact natal burrow. Most (74%, 14 of 19) settled within 20 km of their birthplace, while the remaining 26% (5 of 19) were found at distances ranging from 22 to 74 km. The median natal dispersal distance was 10.5 km (min = 2.25 km, max = 74 km, IQR = 16.48 km, range = 71.75 km). Dispersal distances did not differ significantly between the Czech and Slovak populations (Mann-Whitney U test: z = -1.532, *p* = 0.126, *n* = 19), nor between sexes (Mann-Whitney U test: z = -1.414, *p* = 0.157, *n* = 19).

3.2. First migration

Of the 247 juvenile kingfishers recaptured during the winter months between 1975 and 2024, 93 were classified as residents (37.65%) and 154 as migrants (62.35%). The migrant-to-resident ratio

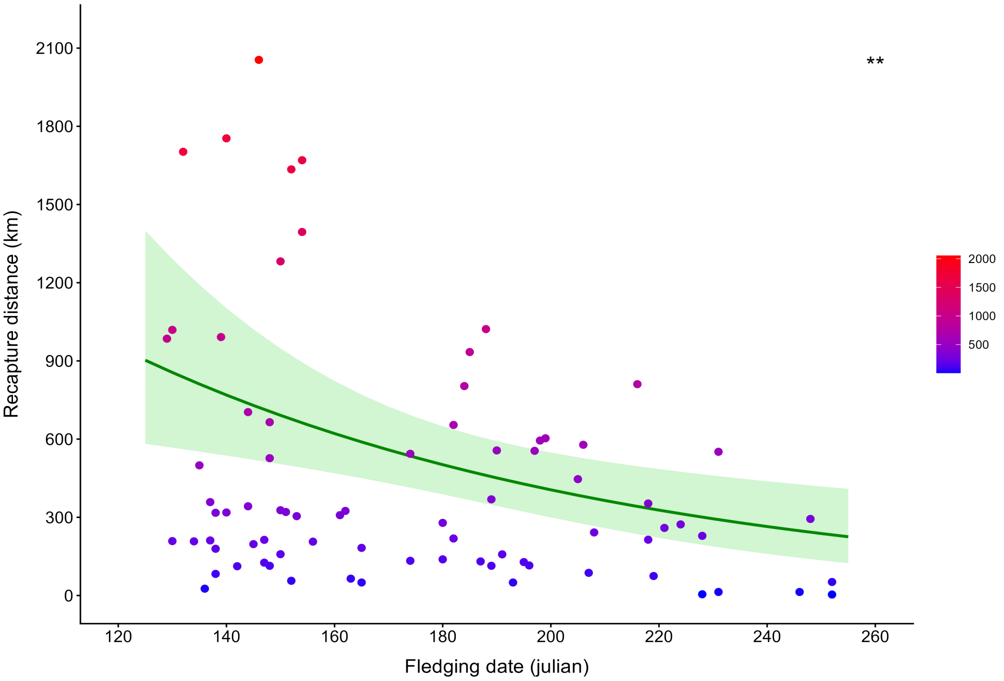

Fig. 2. Predicted relationship between recapture distance and fledging date based on GLMM. The green line shows the model predictions, with the shaded green area representing the 95% confidence interval. Points show raw observations, coloured by distance (blue–red gradient). Fledging date is expressed as a Julian date and recapture distance in kilometres. Asterisks above the prediction line indicate a significant result for the fixed effect (** *p* < 0.01).

varied significantly across decades (ANOVA: χ^2_4 = 26.801, *p* < 0.001), with migrants increasingly outnumbering residents in the last three decades. Furthermore, the decade from 1984 to 1995 differed significantly from other decades in that it was the only one in which the number of residents exceeded the number of migrants (Fig. 1).

Recapture distance was influenced by fledging date (GLMM: β = −0.011 ± 0.004, z = −3.043, *p* = 0.002), with individuals fledged earlier exhibiting longer movements than those fledged later (Fig. 2, Table 1).

Juvenile kingfishers ringed in the Czech Republic were recaptured in 17 countries, predominantly in Europe (*n* = 16) and once in Africa. The longest recorded first migration covered 2,350 km to Portugal. Eleven juveniles undertook migrations of approximately 2,000 km: one was recaptured in Portugal, two in Libya, and eight in Spain (median = 491 km, IQR = 512 km, range = 2,323 km, *n* = 145).

Juveniles from Slovakia were recaptured in nine European countries during their first migration, with the maximum distance being 1,619 km to Spain. Three individuals migrated roughly 1,000 km: one to Spain, one to Malta, and one to France (overall median = 165 km, IQR = 404 km, range = 1,596 km, *n* = 26).

Directional analyses indicated that mean

Table 1. Results of GLMM (*n* = 78) testing the effect of fixed factor (fledging date) on recapture distance of first migration in juvenile Common Kingfishers. Fledging date was expressed as a Julian date and recapture distance in kilometres. *P*-values of significant results (*p* < 0.05) are shown in bold.

Predictor	**Estimate**	**SE**	**z**	**p**
Intercept	7.869	0.634	12.421	**<0.001**
Fledging date	−0.011	0.004	−3.043	**0.002**
Random effect	**Variance**	**SD**		
Year	0.068	0.261		

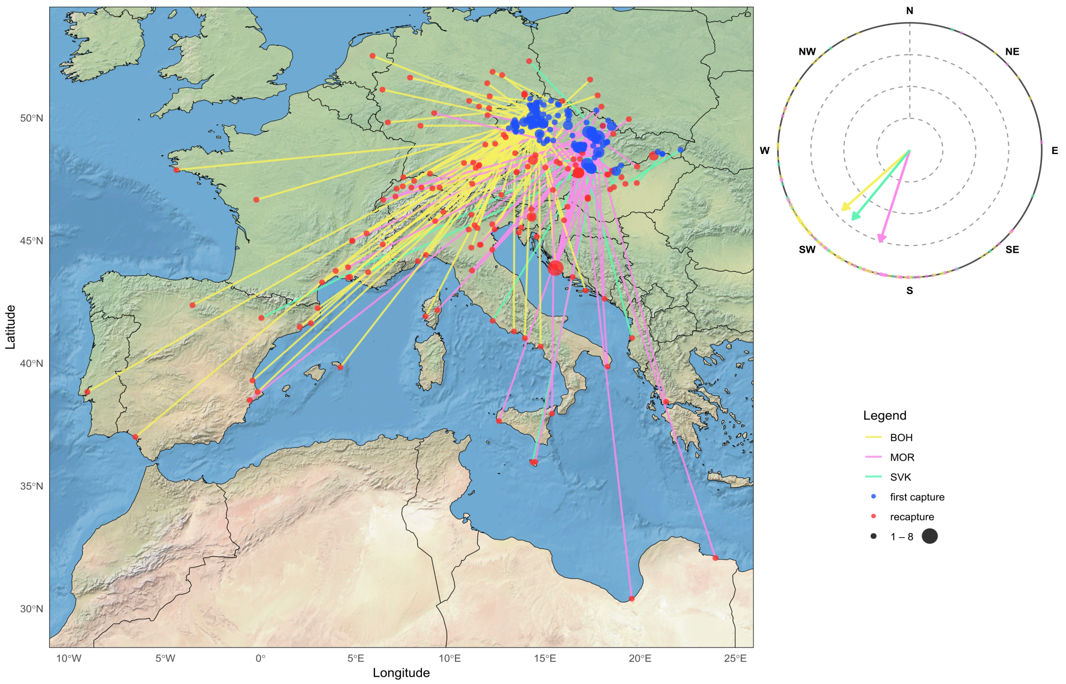

Fig. 3. Map (left) showing individual movements between first capture and recapture locations across regions. The accompanying circular (directional) plot (top right) displays regional mean movement directions, with arrow length reflecting directional concentration based on circular statistical analyses (colours correspond to regions). On the map, larger point sizes indicate locations where multiple individuals overlap, reflecting repeated use of the same sites, either first capture or recapture.

angles between regions significantly varied (WW test: $F_{2,\ 168} = 6.968$, $p = 0.001$). Juvenile kingfishers from Bohemia (mean angle = 227.327°) and Slovakia (mean angle = 218.449°) migrated predominantly in a south westerly direction, whereas individuals from Moravia (mean angle = 197.413°) tended to migrate more directly south (Fig. 3). In addition, Rayleigh tests indicated that the angles in all three regions were non-uniformly distributed, showing a significant mean direction in each group (BOH: $R = 0.693$, $p < 0.001$; MOR: $R = 0.754$, $p < 0.001$; SVK: $R = 0.695$, $p < 0.001$).

Bayesian linear models revealed that recapture locations of Bohemian juveniles were generally farther west relative to their original capture sites compared to those of Moravian (BRM: $\beta = 1.584 \pm 0.686$, 95% CrI [0.234, 2.893]) and Slovak birds (BRM: $\beta = 2.147 \pm 0.783$, 95% CrI [0.595, 3.703]; Fig. 4, Table 2). Furthermore, a higher proportion of Bohemian migrants were recaptured in Western Europe, while Moravian and Slovak birds were more frequently recaptured in Eastern Europe (ANOVA: $\chi^2_2 = 32.837$, $p < 0.001$; Fig. 5).

4. Discussion

Only 19 out of 1,911 juvenile kingfishers were re-encountered in subsequent years near their natal sites. This low number suggests low first-year survival rates (Morgan & Glue 1977, Rubáčová *et al.* 2021), but it could also reflect the possibility that some individuals dispersed beyond the range typically covered by standard bird-ringing efforts (Libois 2018). Furthermore, none of the recaptured birds returned to the exact burrow in which they hatched, likely due to competition for breeding sites with aggressive conspecifics (Johnson & Gaines 1990, McCarthy 1997, Lambin *et al.* 2001, Sutherland *et al.* 2002)

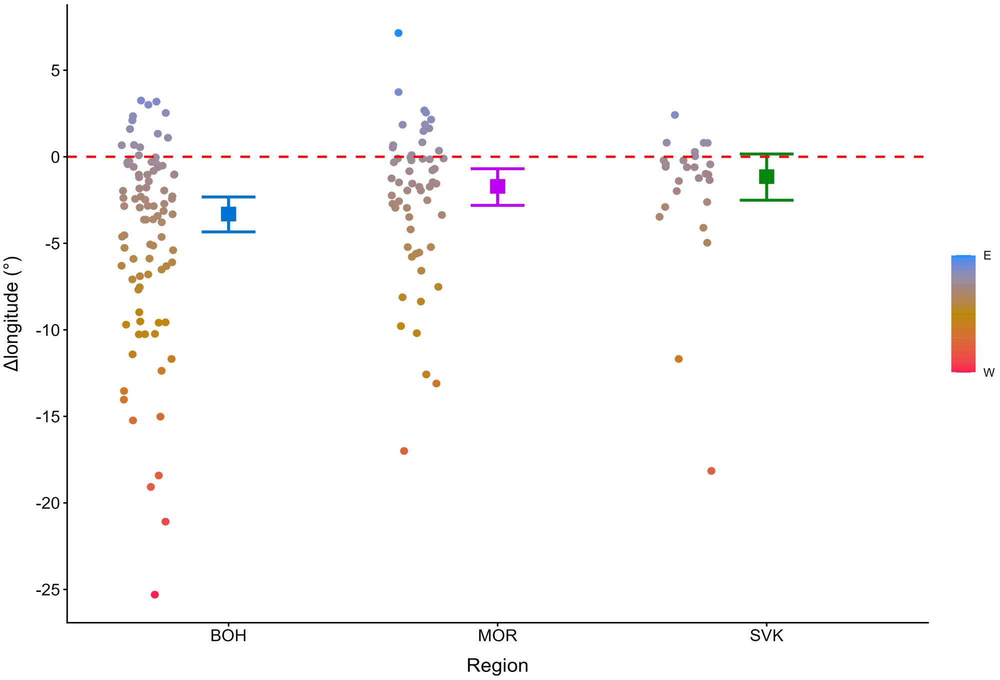

Fig. 4. Regional differences in longitudinal displacement (Δlongitude) estimated from a BRM. Coloured squares show posterior means of Δlongitude for each region with 95% credible intervals, derived from the fitted model. Individual observations are displayed as jittered points, with colour indicating the direction and magnitude of longitudinal change from westward (orange) to eastward (blue). The dashed red line marks zero displacement, separating westward and eastward movements and allowing visual assessment of directional bias within each region. Δlongitude is expressed in degrees.

or as a mechanism to avoid inbreeding (Keller & Waller 2002). The shortest recorded return distance was 2.25 km.

However, 74% of recaptured juveniles settled within 20 km of their natal site, indicating a relatively high degree of philopatry. This pattern is consistent with observations from other European populations (Libois 2018). In most bird species, except for waterfowl, natal dispersal typically occurs over longer distances than adult breeding dispersal, and females generally disperse farther than males (Greenwood & Harvey 1982, Clarke *et al.* 1997, Wolff & Plissner 1998). At our study site, adult kingfishers dispersed significantly shorter distances than juveniles, and no sex-related differences were observed in breeding dispersal (Rubáčová *et al.* 2021). Although female-biased natal dispersal has been reported in other European kingfisher populations (Libois 2018), we detected no sex-related differences in juvenile dispersal in our study. This may be due to limited statistical power resulting from a small sample size. Nevertheless, the higher proportion of returning young males (68%) compared to females (32%) suggests the possibility of sex-biased natal dispersal.

Most juvenile kingfishers undertake relatively long journeys during their first migration, with smaller proportion remaining near their natal sites to overwinter. The ratio of resident to migratory juveniles has changed over time, showing a gradual increase in the number of migrants. The only period when the number of residents exceeded the number of migrants was the decade from 1984 to 1995. During this decade in Czechia, there were three exceptionally cold winters, the average winter temperatures ranging from -4.4°C to +1.5°C. By comparison, average winter temperatures within 2005–2014 decade, during which migrants exceeded residents most, ranged from -2.8°C to +2°C (CHI historical data).

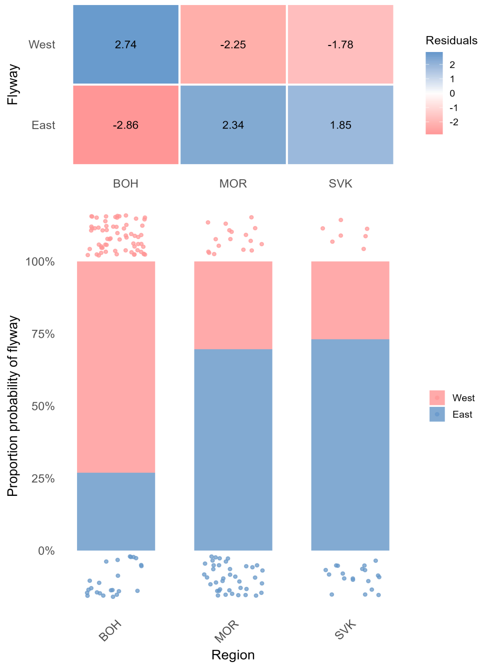

Fig. 5. Distributions of flyway strategies across regions are shown, with Pearson residuals from a chi-square test between region and flyway visualised as a heatmap (values with blue indicating positive residuals, red negative, and white values near zero), highlighting deviations from expected frequencies (top). Proportions of individuals using each flyway through different regions are displayed as stacked bars with jittered points (illustrating individual observations within each region and flyway category; bottom).

This trend contrasts with the expectation that shorter migration distances would occur under rising winter temperatures due to global warming, as observed in many other migratory bird species (Visser *et al*. 2009, Ambrosini *et al*. 2016, Curley *et al*. 2020). However, changes in one part of the annual cycle induced by climate change are likely to affect other stages as well (Heath *et al*. 2012).

Specifically, warmer winters reduce the energetic costs of surviving cold conditions, allowing adult kingfishers to remain near their breeding grounds (Cramp 1990), survive more easily (Morgan & Glue 1977), and commence breeding earlier in the season (Rubáčová *et al*. 2021). This shift in reproductive timing may in turn influence migratory behaviour, as our findings suggest that fledging date plays a key role in determining whether juvenile kingfishers migrate or remain resident. Migration distances are strongly influenced by fledging date, with early-fledged juveniles more likely to migrate, while late-fledged juveniles are more likely to remain near their natal sites.

In many bird species, a consistent decline in reproductive performance has been documented as the breeding season progresses (Crick *et al*. 1993, Svensson 1995). This decline is thought to result from deteriorating environmental conditions for offspring rearing later in the season, a concept referred to as the date hypothesis (Hatchwell 1991, Brinkhof *et al*. 1993, Moreno 1998). Two main explanations have been proposed: a seasonal reduction in food availability (food supply hypothesis; Grüebler & Naef-Daenzer 2008, Grüebler *et al*. 2008) and differences in parental quality, with higher-quality parents tending to breed earlier in the season (quality hypothesis; Parsons 1975, Hatchwell 1991, Brinkhof *et al*. 1993). A combination of both factors is also likely (Nilsson 1989, Nilsson 1999, Verhulst & Nilsson 2008). As the breeding season advances, offspring condition generally declines (Brinkhof 1997, Grüebler & Naef-Daenzer 2008), resulting in reduced survival and lower future reproductive success (Beintema & Visser 1989, Visser & Verboven 1999, Sosnovcová *et al*. 2018).

The higher proportion of migrants compared to residents may result from a combination of factors, including differences in the number of fledglings produced early versus late in the breeding season, as well as survival probabilities associated with individual fitness. Most kingfisher pairs breed early in the season and produce more offspring than those breeding later (own unpublished data). Moreover, early hatched chicks are generally considered to have higher survival rates.

Migration distance in juvenile kingfishers may also be influenced by individual condition and readiness for migration. Early-fledged chicks are typically in better physical condition and have sufficient time to further improve their condition before migration. In contrast, late-fledged individuals may lack the time and energy required for long-distance migration and are

Table 2. Results of BRM (n = 171) testing the effect of fixed factor (region) on Δlongitude as a use of westward or eastward migration directions. Δlongitude was expressed in degrees. The reference level in analysis for region predictor was BOH. The table lists posterior estimates with standard errors and 95% credible intervals, as well as pairwise contrasts between regions and posterior probabilities.

	BRM				
Predictor	**Estimate**	**est. error**	**l-95% CI**	**u-95% CI**	
Intercept	−3.294	0.498	−4.296	−2.330	
Region					
MOR	1.584	0.686	0.234	2.893	
SVK	2.147	0.783	0.595	3.703	
	Posterior pairwise comparisons				
Contrast	**Mean**	**SD**	**Q2.5**	**Q97.5**	**P(>0)**
Region					
MOR *vs*. BOH	1.584	0.686	0.234	2.98	0.989
SVK *vs*. BOH	2.147	0.783	0.595	3.72	0.998
SVK *vs*. MOR	0.563	0.839	−1.077	2.194	0.746

therefore more likely to remain near their natal areas over winter.

The decision to migrate or remain resident is also likely affected by population density, as demonstrated in many birds and mammals (Hanski *et al*. 1991, Matthysen 2005, Mueller *et al*. 2025). During the early part of the season, breeding sites are densely populated with adult kingfishers and their fledglings due to highly synchronized first breeding attempts (own unpublished data), resulting in intense competition for limited food resources. Later in the season, as some breeders and early-fledged juveniles disperse, food availability increases. This reduction in competition may decrease the pressure on late-fledged juveniles to migrate, thereby increasing the likelihood that they remain in the natal area.

Overall, most juvenile kingfishers from all studied populations that undertook longer-distance migrations travelled southwest to winter in southern Europe or, in some cases, as far as North Africa. This pattern is consistent with previous studies of European kingfishers (Cramp 1990, Cepák *et al*. 2008, Libois 2011, 2018). Similar to other populations, these juveniles covered substantial distances during their first migration to reach the Mediterranean region (Libois 2011, 2018).

Beyond confirming earlier observations, our study demonstrates that Bohemian kingfishers predominantly migrated to the western Mediterranean (*e.g*. France, Spain), whereas most individuals from Moravia followed migration routes like those from Slovakia, wintering further east (*e.g*. Croatia, southern Italy, Greece, Libya). While this does not represent a strict migratory divide, as observed in other species such as Blackcaps (*Sylvia atricapilla*; Helbig 1991), Black Storks (*Ciconia ciconia*; Literák *et al*. 2017), or Eurasian Reed Warblers (*Acrocephalus scirpaceus*; Procházka *et al*. 2018), it suggests that birds nesting within our study area select a range of wintering sites across Europe, reached via multiple migratory routes.

Among the most important findings of our study are the gradual increase in the proportion of migrant juveniles over time and the significant influence of fledging date on their migratory behaviour. Both patterns are likely linked to the broader effects of global warming on the annual cycle of birds. Future research should investigate the interactions between winter temperatures, migratory behaviour, and reproductive timing in kingfishers to improve our understanding of how ongoing climate change may shape their life-history strategies.

Keski-Euroopan nuorten kuningaskalastajien (*Alcedo atthis*) levittäytyminen synnyinpaikaltaan ensimmäiselle lisääntymispaikalle sekä muuttokäyttäytyminen

Pesästä lähdön jälkeiseen levittäytymiseen liittyvät kustannukset ja hyödyt ovat johtaneet lintujen monimuotoisiin levittäytymisstrategioihin; näiden taustalla olevat mallit ja mekanismit ovat kuitenkin monilla lajeilla yhä puutteellisesti tunnettuja. Tutkimme synnyinpaikalta tapahtuvaa levittäytymistä ja muuttokäyttäytymistä nuorilla kuningaskalastajilla (*Alcedo atthis*), jotka olivat peräisin tšekkiläisistä ja slovakialaisista populaatioista. Synnyinpaikalta tapahtuvaa levittäytymistä tarkasteltiin seuraamalla kahta pesimäpopulaatiota vuosina 2014–2018. Tänä aikana rengastetuista 1 911 poikasesta 19 nuorta yksilöä tavattiin myöhemmin uudelleen, eli kontrollien osuus oli 0,36 %. Suurin osa yksilöistä (74 %) asettui alle 20 km päähän synnyinpaikastaan (mediaani levittäytymismatka = 10,5 km), eikä populaatioiden tai sukupuolten välillä havaittu merkitseviä er oja.Laaja-alaisia muuttoreittejä arvioidaksemme täydensimme kenttäaineistoamme Tšekin ja Slovakian lintuasemilta saaduilla rengastuskontrolleilla (*n* = 264). Viimeisten 50 vuoden aikana muuttavat yksilöt (62 %) olivat hieman yleisempiä kuin paikalliset linnut (38 %). Muuttajien ja paikallisten lintujen osuudet vaihtelivat merkitsevästi vuosikymmenten välillä, ja muuttajat ovat ajan myötä selvästi yleistyneet. Muuttomatka oli merkitsevästi yhteydessä pesästä lähtöajankohtaan: pesimäkauden alkuvaiheessa (touko–heinäkuussa) pesästä lähteneet yksilöt muuttivat keskimäärin pidempiä matkoja kuin myöhemmin (elo–syyskuussa) pesästä lähteneet. Selviä maantieteellisiä eroja havaittiin myös muuttosuunnassa. Böömin ja Slovakian populaatioista peräisin olevat nuoret linnut muuttivat pääasiassa lounaaseen, kun taas Määristä lähtöisin olevat yksilöt muuttivat yleensä etelään. Suurin osa Böömistä peräisin olevista kuningaskalastajista talvehti Länsi-Euroopassa, kun taas Määristä ja Slovakiasta lähteneet yksilöt talvehtivat useammin Etelä-Italiassa, Balkanilla ja Pohjois-Afrikassa. Tulosten perusteella nuorilla kuningaskalastajilla on joustava muuttostrategia, jota muovaavat sekä pesinnän ajoitus, joka vaikuttaa muuttomatkan pituuteen, että pesimäalueen sijainti, joka määrää muuttosuunnan.

Acknowledgements. The data provided by the Bird Ringing Centre, the National Museum, Prague and the Ringing Centre of the Slovak Ornithological Society/ BirdLife Slovakia were used in this study. We would like to thank all the ringers who collected the data. While working on the manuscript, LR was supported by the Scientific Grant Agency of the Slovak Republic (VEGA 1/0134/23). In Slovakia, research was supported by grant LIFE12 NAT/SK/001137. In the Czech Republic, the research was supported by the Czech Union for Nature Conservation (Biodiversity conservation project *ALCEDO* running since 1994; the second author was the head and the coordinator of the project for the Czech Republic till 16 March 2021 when he passed away due to severe pneumonia and heart collapse caused by COVID-19), RAS Project supported by the Ringing Station of the National Museum Praha, the Czech Academy of Sciences within the programme of the Strategy AV21 (project No. RP21 – Land conservation and restoration) and by the Horizon Europe (RIA) – ProtectFish (project No. 101134976 – Protecting threatened river fish against predation).

Conflict of interest. The authors report no conflicts of interest.

Author contributions. LR: Conceptualisation, Methodology, Investigation, Funding acquisition, Project administration, Validation, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. PČ: Investigation, Validation, Writing – review & editing. MČ: Writing - review & editing. MM: Investigation, Validation, Writing – review & editing. MB: Formal analysis, Software, Visualisation, Writing – review & editing.

Ethics statement. Wild birds were captured, ringed and manipulated during this study. Manipulation of birds was provided by licenced ringers (LR, PČ), who had adequate permissions to ring and manipulate the target species from the relevant national authorities of the Ministry of the Environment of the Czech and Slovak Republic. Study methods comply with the current laws of the country in which they were performed. All field procedures employed in the present study were in accordance with Slovak and Czech legislation under license numbers: 4175/2016-2.3; 3320/2019-6.3 and followed the suggestions of Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching (ASAB Ethical Committee/ABS Animal Care Committee 2024).

Data availability. The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

References

Agostinelli, C. & Lund, U. 2025: R package 'circular': Circular Statistics. R package version 0.52. Retrieved from https://CRAN.R-project.org/package=circular.

Ambrosini, R., Cuervo, J.J., du Feu, C., Fiedler, W., Musitelli, F., Rubolini, D., Sicurella, B., Spina, F., Saino, N. & Møller, A.P. 2016: Migratory connectivity and effects of winter temperatures on migratory behaviour of the European Robin *Erithacus rubecula*: A continent-wide analysis. — Journal of Animal Ecology 85: 749–760. https://doi.org/10.1111/1365-2656.12497

Bensch, S., Hasselquist, D., Nielson, B. & Hansson, B. 1998: Higher fitness for philopatric than for immigrant males in a semi-isolated population of great reed warblers. — Evolution 52: 877–883. https://doi.org/10.1111/j.1558-5646.1998.tb03712.x

Beintema, A.J. & Visser, G.H. 1989: Growth parameters in chicks of charadriiform birds. Breeding Ecology of meadow birds (Charadriiformes). — Implications for Conservation and Management 1: 57.

Brinkhof, M.W.G., Cave, A.J., Hage, F.J. & Verhulst, S. 1993: Timing of reproduction and fledging success in the coot *Fulica atra*: evidence for a causal relationship. — Journal of Animal Ecology 62: 577–587. https://doi.org/10.2307/5206

Brinkhof, M.W.G. 1997: Seasonal decline in body size of coot chicks. — Journal of Avian Biology 28: 117–131. https://doi.org/10.2307/3677305

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H. J., Mächler, M. & Bolker, B.M. 2017: glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. — The R Journal 9: 378–400. https://doi.org/10.32614/RJ-2017-066

Bürkner, P.C. 2017: brms: An R package for Bayesian multilevel models using Stan. — Journal of Statistical Software 80: 1–28. https://doi.org/10.18637/jss.v080.i01

Cepák, J., Klvaňa, P., Formánek, J., Horák, D., Jelínek, M., Schröpfer, L., Škopek, J. & Zárybnický, J. 2008: Bird migration atlas of Czech and Slovak Republic. — Aventinum, Praha.

Chapman, B.B., Brönmark, C., Nilsson, J.Å. & Hansson, L.A. 2011: The ecology and evolution of partial migration. — Oikos 120: 1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x

Clarke, A.L., Sæther, B.E., & Røskaft, E. 1997: Sex biases in avian dispersal: a reappraisal. — Oikos 79: 429–438. https://doi.org/10.2307/3546885

Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. 2001: Dispersal. — Oxford University Press, Oxford.

Cramp J.S. (ed.) 1990: Birds of the Western Palearctic. Vol. 4. — Oxford University Press, Oxford.

Crick, H.Q.P., Gibbons, D.W. & Magrath, R.D. 1993: Seasonal changes in clutch size in British birds. — Journal of Animal Ecology 62: 263–273. https://doi.org/10.2307/5357

Curley, S.R., Manne, L.L. & Veit, R.R. 2020: Differential winter and breeding range shifts: Implications for avian migration distances. — Diversity and Distributions 26: 415–425. https://doi.org/10.1111/ddi.13036

Čech, P. 2009: Výsledky kroužkování ledňáčka říčního (*Alcedo Atthis*) na Podblanicku a středním Povltaví v období 2004–2008, příspěvek k poznání jeho populační dynamiky a migrace. — In Ledňáček říční (*Alcedo atthis*), jeho ochrana a výzkum (ed. Čech, P.): 60–70. ZO ČSOP, Vlašim. (In Czech with English abstract)

Čech, P. 2017: Příspěvek k fidelite (věrnosti k hnízdišti) a filopatrii (vazbě k rodišti) ledňáčka říčního (*Alcedo Atthis*). — In Ledňáček říční (*Alcedo atthis*), jeho ochrana a výzkum (ed. Čech, P.): 7–14. ZO ČSOP, Vlašim. (In Czech with English abstract)

Emlen, S.T. 1991: Evolution of cooperative breeding in birds and mammals. — In Behavioural ecology: Evolutionary approach (eds. Krebs, J.R., Davies, N.B.): 301–337. Blackwell Scientific Publ., London.

Fiedler, W. 2003: Recent changes in migratory behaviour of birds: A compilation of field observations and ringing data. — In Avian migration (eds. Berthold, P., Gwinner, E. & Sonnenschein E.): 21–38. Springer, Berlin, Heidelberg.

Flack, A., Fiedler, W., Blas, J., Pokrovsky, I., Kaatz, M., Mitropolsky, M., & Wikelski, M. 2016: Costs of migratory decisions: A comparison across eight white stork populations. — Science Advance 2: e1500931.

https://doi.org/10.1126/sciadv.1500931

Garant, D., Kruuk, L.E.B., Wilkin, T.A., McCleery, R.H. & Sheldon, B.C. 2005: Evolution driven by differential dispersal within a wild bird population. — Nature 433: 60–65. https://doi.org/10.1038/nature03051

Gilroy, J.J., Gill, J.A., Butchart, S.H.M., Jones, V.R. & Franco, A.M.A. 2016: Migratory diversity predicts population declines in birds. — Ecology Letters 19: 308–317. https://doi.org/10.1111/ele.12569

Greenwood, P.J. 1980: Mating systems, philopatry and dispersal in birds and mammals. — Animal Behaviour 28: 1140–1162. https://doi.org/10.1016/S0003-3472(80)80103-5

Greenwood, P.J. & Harvey, P.H. 1982: The natal and breeding dispersal of birds. — The Annual Review of Ecology, Evolution, and Systematics 13: 1–21. https://www.jstor.org/stable/2097060

Grüebler, M.U. & Naef-Daenzer, B. 2008: Fitness consequences of pre- and post-fledging timing decisions in a double brooded passerine. — Ecology 89: 2736–2745. https://doi.org/10.1890/07-0786.1

Grüebler, M.U., Morand, M. & Naef-Daenzer, B. 2008: A predictive model of the density of airborne insects in agricultural environments. — Agriculture Ecosystems and Environment 123: 75–80. https://doi.org/10.1016/j.agee.2007.05.001

Hanski, I., Peltonen, A. & Kaski, L. 1991: Natal dispersal and social dominance in the common shrew *Sorex araneus*. — Oikos 1: 48–58. https://doi.org/10.2307/3545445

Hartig, F. 2024: DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / 610 Mixed) Regression Models (Version 0.4.7) [Computer software]. 611 https://CRAN.R-project.org/package=DHARMa

Hatchwell, B.J. 1991: An experimental study of the effects of timing of breeding on the reproductive success of common guillemots (*Uria aalge*). — Journal of Animal Ecology 60: 721–736. https://doi.org/10.2307/5410

Heath, J.A., Steenhof, K. & Foster, M.A. 2012: Shorter migration distances associated with higher winter temperatures suggest a mechanism for advancing nesting phenology of American kestrels *Falco sparverius*. — Journal of Avian Biology 43: 376–384. https://doi.org/10.1111/j.1600-048X.2012.05595.x

Helbig, A.J. 1991: SE- and SW-migrating Blackcap (*Sylvia atricapilla*) populations in Central Europe: Orientation of birds in the contact zone. — Journal of Evolutionary Biology 4: 657–670. https://doi.org/10.1046/j.1420-9101.1991.4040657.x

Hijmans, R. 2024: geosphere: Spherical Trigonometry. R package version 1.5–20. Retrieved from https://github.com/rspatial/geosphere

Johnson, M.L. & Gaines, M.S. 1990: Evolution of dispersal: theoretical models and empirical tests using birds and mammals. — The Annual Review of Ecology, Evolution, and Systematics 21: 449–480. https://www.jstor.org/stable/2097033

Keller, L.F. & Waller, D.M. 2002: Inbreeding effects in wild populations. — Trends in Ecology and Evolution 17: 230–241. https://doi.org/10.1016/S0169-5347(02)02489-8

Lambin, X., Aars, J. & Piertney, S.B. 2001: Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. — In Dispersal (eds. Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D.): 110–122. Oxford University Press, New York.

Libois, R. 2011: Migration and movements of the Common Kingfisher *Alcedo atthis* in Europe. — Aves 48: 65–86.

Libois, R. 2018: Plumes d'azur. Histoire naturelle du martin-pêcheur d'Europe. — Presses Universitaires de Liége, Gembloux.

Literák, I., Kafka, P., Vrána, J. & Pojer, F. 2017: Migration of Black Storks *Ciconia nigra* at a migratory divide: two different routes used by siblings from one nest and two different routes used by one individual. — Ringing & Migration 32: 19–24. https://doi.org/10.1080/03078698.2017.1332260

Lok, T., Overdijk, O. & Piersma, T. 2015: The cost of migration: Spoonbills suffer higher mortality during trans-Saharan spring migrations only. — Biology Letters 11: 20140944. https://doi.org/10.1098/rsbl.2014.0944

Matthysen, E. 2005: Density-dependent dispersal in birds and mammals. — Ecography 28: 403–416. https://doi.org/10.1111/j.0906-7590.2005.04073.x

McCarthy, M.A. 1997: Competition and dispersal from multiple nests. — Ecology 78: 873–883. https://doi.org/10.1890/0012-9658(1997)078[0873:CADFMN]2.0.CO;2

McGillycuddy, M., Popovic, G., Bolker, B.M. & Warton, D.I. 2025: Parsimoniously fitting large multivariate random effects in glmmTMB. — Journal of Statistical Software 112: 1–19. https://doi.org/10.18637/jss.v112.i01

Moreno, J. 1998: The determination of seasonal declines in breeding success in seabirds. — Etologia 6: 17–31.

Morgan, R. & Glue, D. 1977: Breeding, mortality, and movements of Kingfishers. — Bird Study 24: 15–24. https://doi.org/10.1080/00063657709476527

Mueller, S.D., Mennill, D.J., Doucet, S.M., Dobney, S.L., Spina, H.A. & Norris, D.R. 2025: Environmental conditions and individual characteristics influence movement patterns of juvenile *Passerculus sandwichensis* (Savannah sparrow) throughout the post-fledging period. — Ornithology p.ukaf016. https://doi.org/10.1093/ornithology/ukaf016

Newton, I. 2008: The migration ecology of birds. — Academic Press, London.

Nilsson, J.Å. 1989: Causes and consequences of natal dispersal in the marsh tit, *Parus palustris*. — Journal of Animal Ecology 1: 619–636. https://doi.org/10.2307/4852

Nilsson, J.Å. 1999: Fitness consequences of timing of reproduction. — In Proceedings of the 22 International Ornithological Congress (eds. Adams, N.J. & Slotow, R.H.): 234–247. Birdlife South Africa, Durban.

Palacín, C., Alonso, J.C., Martín, C.A. & Alonso, J.A. 2017: Changes in bird-migration patterns associated with human-induced mortality. — Conservation Biology 31: 106–115. https://doi.org/10.1111/cobi.12758

Parsons, J. 1975: Seasonal variation in the breeding success of the herring gull: an experimental approach to pre-fledging success. — Journal of Animal Ecology 44: 553–573. https://doi.org/10.2307/3611

Pärt, T. 1994: Male philopatry confers a mating advantage in the migratory collared flycatcher, *Ficedula albicollis*. — Animal Behaviour 48: 401–409. https://doi.org/10.1006/anbe.1994.1254

Piper, W.H., Walcott, C., Mager, J.N. & Spilker, F.J. 2008: Nest site selection by male loons leads to sex-biased site familiarity. — Journal of Animal Ecology 77: 205–210. https://doi.org/10.1111/j.1365-2656.2007.01334.x

Procházka, P., Brlík, V., Yohannes, E., Meister, B., Auerswald, J., Ilieva, M. & Hahn, S. 2018: Across a migratory divide: divergent migration directions and non-breeding grounds of Eurasian reed warblers revealed by geolocators and stable isotopes. — Journal of Avian Biology 49: jav-012516. https://doi.org/10.1111/jav.01769

R Core Team. 2025: R: A language and environment for statistical computing (Version 4.5.1). R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rubáčová, L., Čech, P., Melišková, M., Čech, M. & Procházka, P. 2021: The effect of age, sex and winter severity on return rates and apparent survival in the Common Kingfisher *Alcedo atthis*. — Ardea 109: 15–25. https://doi.org/10.5253/arde.v109i1.a2

Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K. & Sokolov, L. 2011: Climate warming, ecological mismatch at arrival and population declines in migratory birds. — Proceedings of the Royal Society of London. Series B, Biological Sciences 278: 835–842. https://doi.org/10.1098/rspb.2010.1778

Smallegange, I.M., Fiedler, W., Köppen, U., Geiter, O. & Bairlein, F. 2010: Tits on the move: exploring the impact of environmental change on blue tit and great tit migration distance. — Journal of Animal Ecology 79: 350–357. https://doi.org/10.1111/j.1365-2656.2009.01643.x

Sosnovcová, K., Koleček, J., Požgayová, M. Jelínek, V., Šulc, M., Steidlová, P., Honza, M. & Procházka P. 2018: Timing of natal nests is an important factor affecting return rates of juvenile Great Reed Warblers. — Journal of Ornithology 159: 183–190. https://doi.org/10.1007/s10336-017-1492-1

Sutherland, W.J., Gill, J.A. & Norris, K. 2002: Density dependent dispersal in animals: concepts, evidence, mechanisms, and consequences. — In Dispersal Ecology (eds. Bulloch, J.M., Kenward, R.E. & Hails, R.S.): 134–151. British Ecological Society/Blackwell Science, Oxford.

Smith, R.D. & Metcalfe, N.B. 1997: Where and when to feed: sex and experience affect access to food in wintering snow buntings. — Behaviour 134: 143–160. https://doi.org/10.1163/156853997X00322

Svensson, E. 1995: Avian reproductive timing: when should parents be prudent? — Animal Behaviour 49: 1569–1575. https://doi.org/10.1016/0003-3472(95)90078-0

van Vliet, J., Musters, C.J.M. & ter Keurs, W.J. 2009: Changes in migration behaviour of Blackbirds *Turdus merula* from the Netherlands. — Bird Study 56: 276–281. https://doi.org/10.1080/00063650902792148

Verhulst, S. & Nilsson, J.A. 2008: The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. — Philosophical Transactions of the Royal Society B: Biological Sciences 363: 399–410. https://doi.org/10.1098/rstb.2007.2146

Visser, M.E. & Verboven, N. 1999: Long-Term Fitness

Effects of Fledging Date in Great Tits. — Oikos 85: 445–450. https://doi.org/10.2307/3546694

Visser, M.E., Perdeck, A.C., van Balen, J.H. & Both, C. 2009: Climate change leads to decreasing bird migration distances. — Global Change Biology 15: 1859–1865. https://doi.org/10.1111/j.1365-2486.2009.01865.x

Wolff, J.O. & Plissner, J.H. 1998: Sex biases in avian natal dispersal: an extension of the mammalian model. — Oikos 83: 327–330. https://doi.org/10.2307/3546844

Zuckerberg, B., Bonter, D.N., Hochachka, W.M., Koenig, W.D., DeGaetano, A.T. & Dickinson, J.L. 2011: Climatic constraints on wintering bird distributions are modified by urbanization and weather — Journal of Animal Ecology 80: 403–413. https://doi.org/10.1111/j.1365-2656.2010.01780.x

Online supplementary material

Supplementary materials available in the online version of the article.