AGE STRUCTURE OF LESSER BLACK-BACKED GULLS *LARUS FUSCUS* DURING AUTUMN MIGRATION IN ICELAND SUGGESTS INDEPENDENT MIGRATION BY JUVENILES

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ABSTRACT

Hallgrimsson, G. T. (2026). Age structure of Lesser Black-backed Gulls *Larus fuscus* during autumn migration in Iceland suggests independent migration by juveniles. *Marine Ornithology*, *54*(2), 367–371. http://doi.org/10.5038/2074-1235.54.2.1717

Age structure during migration can provide valuable insight into migration strategies and the potential role of social guidance by parents and adult conspecifics in shaping the migratory behavior of juveniles. I examined temporal changes in juvenile proportion during the onset of autumn migration of Lesser Black-backed Gulls *Larus fuscus graellsii* in southwest Iceland. Using age-ratio counts from seven sites (72 counts), juvenile proportion increased significantly with date, from 4.6% (95% confidence interval [CI]: 2.5–9.1) on 01 August to 89.3% (95% CI: 83.2–92.7) by 15 September. This pronounced seasonal shift indicates age-segregated migration and suggests that juveniles are capable of migrating independently of adults.

Key words: age-ratio, differential migration, endogenous migration program, *Larus fuscus*, migration strategy, social learning

INTRODUCTION

Bird migration strategies vary widely in the extent to which age structure and social guidance influence migration (Newton, 2024). In some species, juveniles migrate in family groups and rely on experienced adults for navigation, as documented in cranes, geese, and swans (Kölzsch et al., 2020; Mueller et al., 2013). In contrast, many wader species exhibit age-segregated migration, with juveniles departing later than adults. Consequently, some late-migrating individuals must complete their first migration without direct guidance from adults (Carneiro et al., 2024; Meltofte, 1996; Verhoeven et al., 2022). Understanding where species fall along this continuum provides insight into the mechanisms underlying avian navigation and the relative contributions of innate orientation and social information.

Large white-headed gulls (genus *Larus*) exhibit a range of migration patterns (Coulson, 2019), from dispersal over tens to hundreds of kilometers from nesting sites (e.g., Camphuysen et al., 2011; Spear et al., 1986; Spear, 1988) to regular long-distance migrations in which nesting and wintering grounds are separated by several thousand kilometers (e.g., Bustnes et al., 2013; Panagoda et al., 2025). Comparatively little is known about migration strategies in many *Larus* gull species during their first autumn migration. Most high-precision tracking studies of gull migration have focused on adults, whereas juveniles remain underrepresented (Borrman et al., 2021). Consequently, it is unclear whether young gulls depend on social guidance during migration or can migrate largely independently, as occurs in many wader species.

A GPS-tracking study of Lesser Black-backed Gulls *Larus fuscus graellsii* from Germany showed that juveniles had migration routes and timing broadly similar to those of adults (Borrman et al., 2021), suggesting that social guidance may play an important role in shaping juvenile migration and wintering strategies. Similarly, in Caspian Terns *Hydroprogne caspia*, young birds closely followed adults during their first migration, highlighting the potential for socially inherited information in long-distance migration within the family Laridae (Byholm et al., 2022). However, other studies of larid gulls suggest that juveniles migrate later and travel farther than adults (Wernham et al., 2002), hinting towards independent migration by young birds. Re-sightings of banded Lesser Black-backed Gulls from the Netherlands further show that juveniles migrate later than breeding adults and winter farther south (Camphuysen et al., 2024).

In Iceland, the breeding population of Lesser Black-backed Gulls consists of long-distance migrants that leave the country in autumn (Hallgrimsson et al., 2012; data retrieved from eBird, 2026). The core winter range of this population extends across the Iberian Peninsula and northwest Africa (Hallgrimsson et al., 2012), overlapping with the winter range of other breeding populations from northwest Europe (Galván et al., 2003; Helberg at al., 2009; Wernham et al., 2002). Iceland is topographically isolated and lies largely outside the main migration routes of other European populations. Furthermore, virtually all individuals in the population migrate, and the departure period is relatively short (Fig. 1). Consequently, changes in age ratios within groups of departing gulls likely reflect true age-related differences in migration timing, without the complications associated with partial migration or population mixing reported elsewhere in Europe (Marques et al., 2009). If juveniles in the Icelandic population migrate independently and later than adults, the proportion of juveniles is expected to increase over the course of the autumn migration period.

Here, I use age-ratio data collected at multiple sites in southwest Iceland during autumn to test whether the proportion of juveniles in Lesser Black-backed Gulls increases over the migration period.

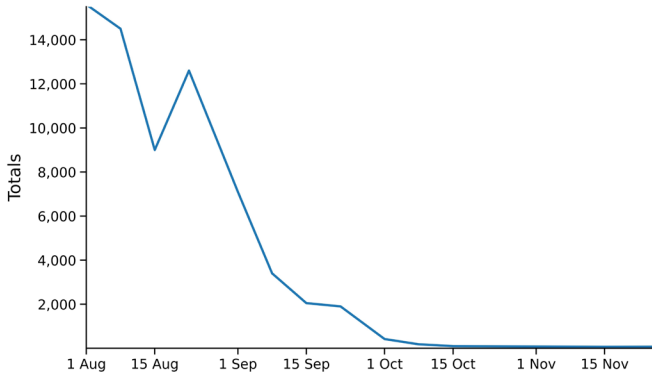

Fig. 1. Total counts of Lesser Black-backed Gulls *Larus fuscus graellsii* in Iceland submitted to eBird from August to November, 2000–2026.

By quantifying temporal changes in age structure and accounting for spatial heterogeneity among sites, I assess whether migration timing is age-segregated and discuss the implications for the potential role of social guidance in this species.

METHODS

Age-ratio counts were conducted at seven sites in southwest Iceland during autumn 2008 (Fig. 2). The majority of Lesser Black-backed Gulls in Iceland breed within the study area, although smaller, scattered colonies occur elsewhere in the country. The study sites were therefore considered representative of the Icelandic population. Each count recorded the number of juveniles and adults (fourth calendar year and older) based on plumage characteristics (Malling Olsen & Larsson, 2004). Immature birds (second–third calendar year) were excluded because these age classes occur in relatively low numbers in Iceland and were unlikely to influence overall age ratios (Hallgrimsson et al., 2012).

To reduce bias associated with small sample sizes, only groups consisting of ≥ 30 individuals (adults and juveniles combined) were included in the analyses (total = 72 groups). All sites were freshwater ponds that attracted gulls and were located within 2 km of breeding colonies but clearly outside colony boundaries. Sampling effort varied among sites; therefore, site was included as a categorical predictor to account for spatial heterogeneity.

To test whether the proportion of juveniles changed over time, the numbers of juveniles and adults were modelled as a binomial response using generalized linear models with a logit link. Date was treated as a continuous predictor. Initial models showed substantial overdispersion; therefore, quasibinomial models were used for inference. The primary model included date and site as fixed effects:

cbind(juveniles, adults) ~ date + site

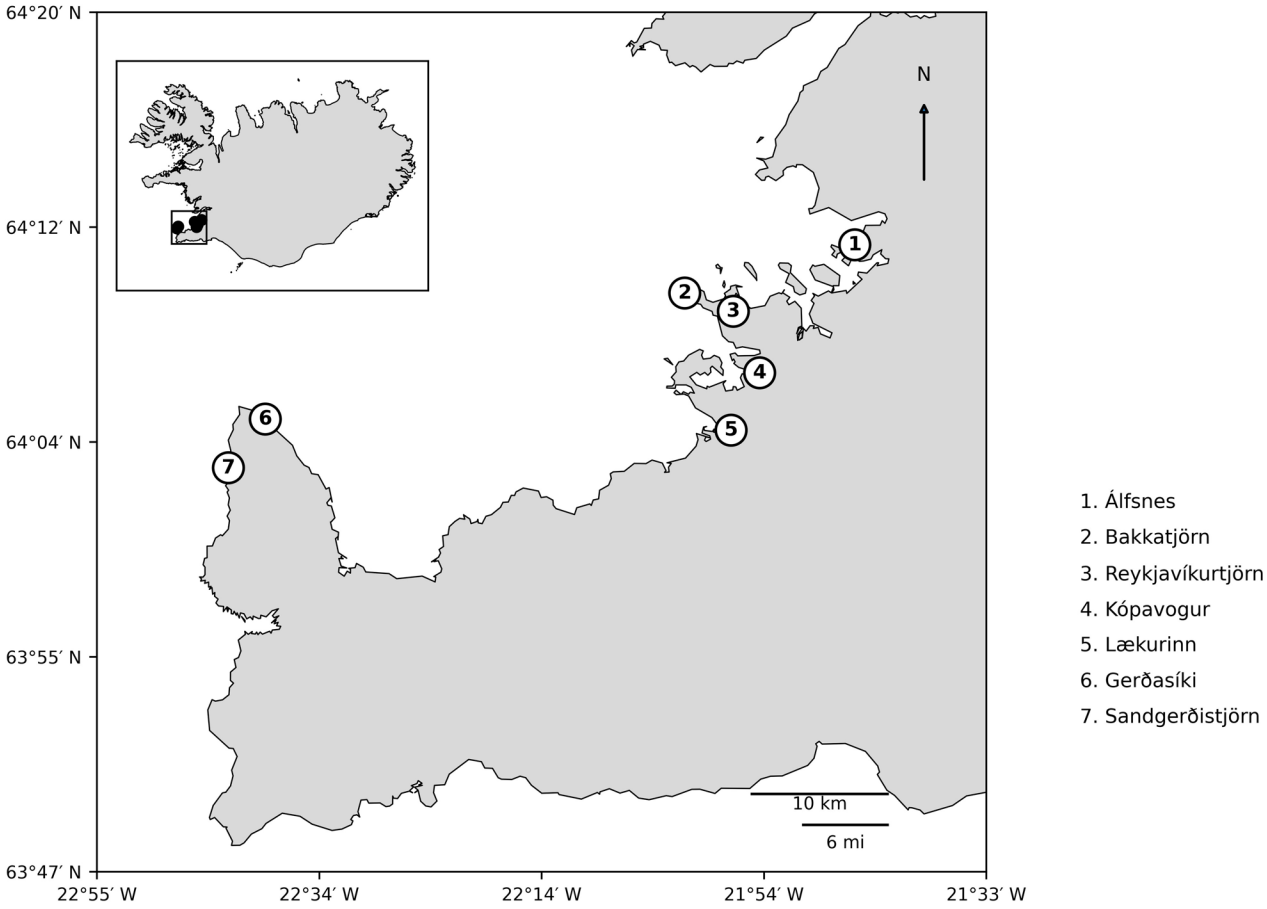

Fig. 2. Locations in southwest Iceland where age-ratio counts of Lesser Black-backed Gulls *Larus fuscus graellsii* were conducted. All sites were freshwater ponds situated outside breeding colony boundaries.

Model predictions and 95% confidence intervals (CI) were generated on the link scale and back-transformed to the response scale. All analyses were conducted in R (RStudio v.2025.05.1).

RESULTS

After accounting for spatial variation among sites, the proportion of juveniles increased significantly with date (Table 1). Site also influenced juvenile proportion, indicating differences in baseline age structure among locations; however, the positive temporal trend was consistent across sites (Fig. 3).

Model predictions averaged across sites indicated a pronounced seasonal shift in age composition. The predicted proportion of juveniles increased from 4.6% (95% CI: 2.5–9.1) on 01 August to 89.3% (95% CI: 83.2–92.7) on 15 September.

DISCUSSION

The proportion of juveniles increased markedly during the onset of autumn migration of Lesser Black-backed Gulls in southwest Iceland. This pattern suggests that juveniles are capable of independent migration. The trend remained robust after accounting for spatial heterogeneity among sites and correcting for overdispersion, indicating that the observed pattern reflects a genuine seasonal shift in the migratory population rather than local sampling effects. The magnitude of the change—from < 10% juveniles in early August to ~90% by mid-September—further indicates pronounced age segregation in migration timing. This result suggests that at least some juveniles migrate from Iceland to their wintering grounds in Iberia and West Africa without travelling with adult conspecifics. As in several wader species, these naive individuals therefore appear capable of completing their first migration without direct social guidance from adults, suggesting that mechanisms other than social guidance contribute to the development of migratory behaviour in this species.

TABLE 1
Results of a quasibinomial generalized linear model testing the effects of date and site on the proportion of juvenile Lesser Black-backed Gulls *Larus fuscus graellsii* during autumn migration in southwest Iceland[a]

Predictor	Estimate	Standard error	*t*	*p*
Intercept	−1,753.0	94.7	−18.52	< .001
Date	0.124	0.007	18.53	< .001
Bakkatjörn	−2.301	0.3	−7.67	< .001
Gerðasíki	−1.333	0.351	−3.80	< .001
Kópavogur	−0.257	0.81	−0.32	.752
Lækurinn	−0.650	0.278	−2.34	.022
Reykjavíkurtjörn	−0.474	0.266	−1.78	.080
Sandgerðistjörn	−0.209	0.274	−0.77	.447

[a] The response variable was specified as cbind(juveniles, adults) with a logit link. Estimates are presented on the logit scale, and the intercept represents the reference site (Álfsnes).

Although the results of this study do not provide clear evidence of social guidance during migration, both innate orientation programs and individual navigation abilities are known to guide inexperienced migrants (Berthold, 1996; Wiltschko & Wiltschko, 2003). In addition, young birds have been found to compensate for large-scale displacement and adjust their direction towards population-specific wintering areas in the absence of social guidance (Thorup et al., 2020).

As for potential sources of bias, failed breeders may depart earlier than successful breeders, potentially creating an apparent age-related pattern if early movements are driven primarily by failed adults while successful adults and juveniles migrate at similar times. However, re-sightings of color-banded Lesser Black-backed Gulls from Iceland show that adults initiate southward migration around mid-August, with the main passage extending to mid-September, whereas juveniles typically depart later, from mid-September through late October (Hallgrimsson et al., 2012). These patterns closely match the age-ratio trends observed in the present study and suggest that the observed increase in juvenile proportion cannot be explained solely by the early departure of failed breeders. The very high proportion of juveniles late in the season is consistent with successful breeding adults also departing earlier than juveniles.

Because virtually all individuals of the Icelandic Lesser Black-backed Gull population are migrants (Fig. 1), the observed age-ratio pattern cannot be explained by age-related differences in the propensity to migrate. Instead, it is consistent with the well-documented age-segregated migration observed in many wader species, in which juveniles depart later than adults and can complete their first migration without travelling in adult-led groups (Carneiro et al., 2024; Verhoeven et al., 2022). However, social information, either from the parent or other adults, may still influence some juveniles. Even a small number of experienced individuals can, in theory, have a disproportionate effect on group-level movement through social guidance (Couzin et al., 2005). Furthermore, social learning may influence stopover behavior or movements after arrival at wintering grounds, although a recent study found no clear evidence of social learning in movement or foraging during the first 20 days of migratory stopover (Morel et al., 2024).

A recent synthesis highlights the need to integrate altricial and precocial perspectives by explicitly linking the post-fledging period to life-history strategies and population dynamics (Jones et al., 2026). Variation in parental care and early independence shape how juveniles develop movement behavior, influencing migration timing and the degree of age-specific segregation.

Further research on Lesser Black-backed Gulls, combining age-ratio monitoring with high-precision tracking of parents and juveniles, will help clarify spatial associations among individuals, determine whether differences in timing reflect variation in stopover behavior, and assess the extent to which social interactions occur during migration. Such research could also quantify the proportion of Lesser Black-backed Gulls that migrate without social cues from conspecifics. Given the considerable individual variation in behavior documented in Lesser Black-backed Gulls and other larid species, some individuals may travel under parental guidance, whereas others may follow experienced conspecifics, migrate independently, or travel in juvenile associations. It would therefore be valuable to investigate whether these differences have implications for subsequent survival, habitat use, and other aspects of their life history.

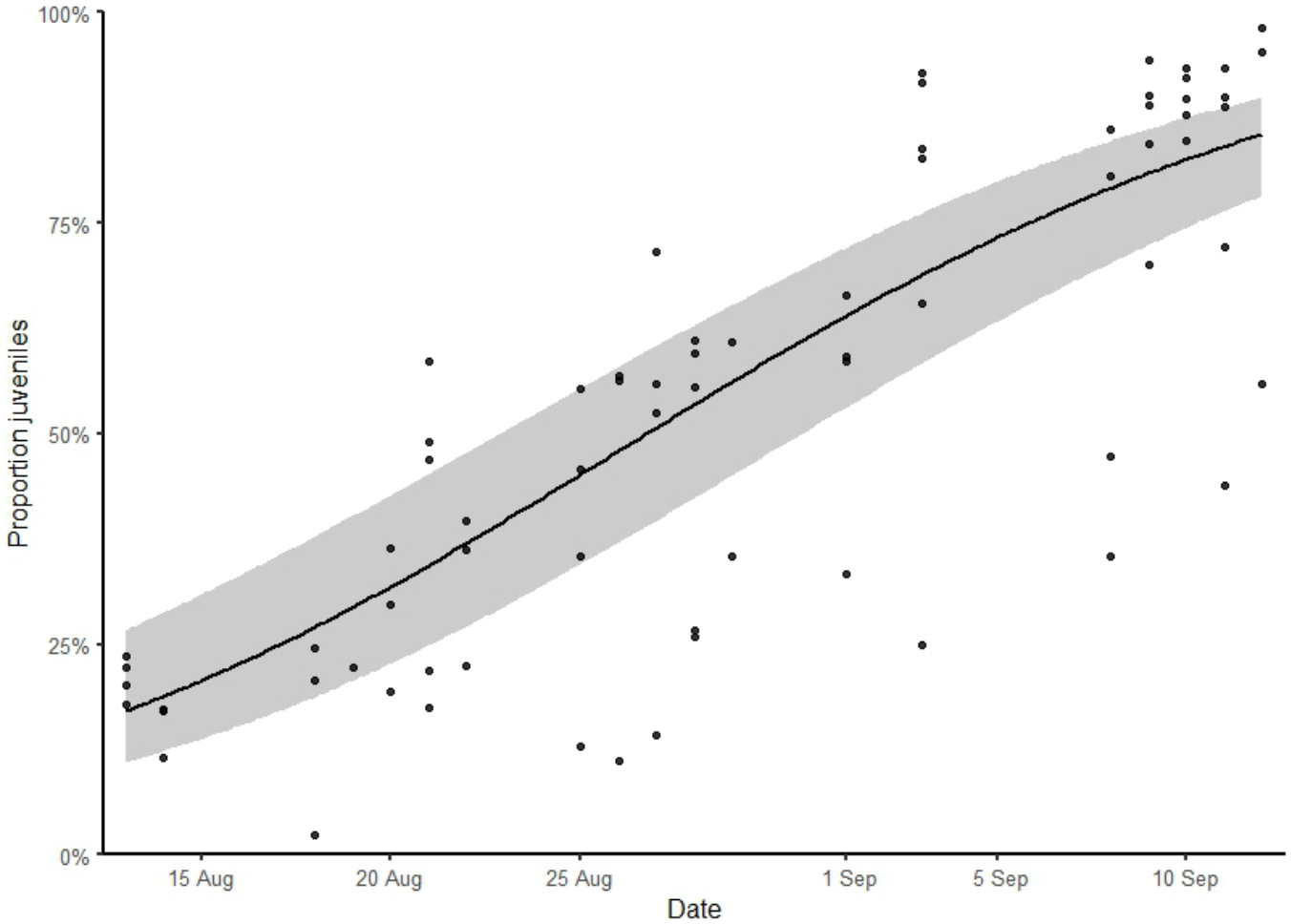

Fig. 3. Proportion of juvenile Lesser Black-backed Gulls *Larus fuscus graellsii* during autumn migration in southwest Iceland in 2008. Points represent observed juvenile proportions by date. The solid line shows the model-predicted mean proportion averaged across sites, and the shaded area indicates 95% confidence intervals from a quasibinomial generalized linear model.

CONCLUSION

The findings of this study suggest that juvenile Lesser Black-backed Gulls are capable of initiating migration independently of adults, consistent with largely endogenous control of migration and an early ability to further develop foraging skills independent of parental guidance.

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AUTHOR CONTRIBUTIONS

Conceptualization, investigation, methodology, formal analysis, writing—original draft, writing—review & editing: GTH.

REFERENCES

Berthold, P. (1996). *Control of bird migration*. Chapman and Hall.

Borrmann, R. M., Phillips, R. A., Clay, T. A., & Garthe, S. (2021). Post-fledging migration and wintering strategies of individual juvenile Lesser Black-Backed Gulls *Larus fuscus*. *Ibis*, *163*(3), 1017–1031. https://doi.org/10.1111/ibi.12917

Bustnes, J. O., Moe, B., Helberg, M., & Phillips, R. A. (2013). Rapid long-distance migration in Norwegian Lesser Black-backed Gulls *Larus fuscus fuscus* along their eastern flyway. *Ibis*, *155*(2), 402–406. https://doi.org/10.1111/ibi.12022

Byholm, P., Beal, M., Isaksson, M., Lötberg, U., & Åkesson, S. (2022). Paternal transmission of migration knowledge in a long-distance bird migrant. *Nature Communications*, *13*, Article 1566. https://doi.org/10.1038/s41467-022-29300-w

Camphuysen, C. J., van Donk, S. C., Shamoun-Baranes, J., & Kentie, R. (2024). The annual cycle, breeding biology and feeding ecology of the Lesser Black-backed Gull *Larus fuscus*. *Ardea*, *112*(1), 31–61. https://doi.org/10.5253/arde.2023.a7

Camphuysen, C. J., Vercruijsse, H. J .P., & Spaans, A. L. (2011). Colony- and age-specific seasonal dispersal of Herring Gulls *Larus argentatus* breeding in The Netherlands. *Journal of Ornithology*, *152*, 849–868. https://doi.org/10.1007/s10336-011-0664-7

Carneiro, C., Gunnarsson, T. G., Kaasiku, T., Piersma, T., & Alves, J. A. (2024). Icelandic Whimbrel first migration: Non-stop until West Africa, yet later departure and slower travel than adults. *Ibis*, *166*(2), 715–722. https://doi.org/10.1111/ibi.13282

Coulson, J. (2019). *Gulls*. HarperCollins.

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*, 513–516. https://doi.org/10.1038/nature03236

eBird. (2026). *eBird: An online database of bird distribution and abundance* [web application] Cornell Lab of Ornithology. Retrieved March 20, 2026, from https://ebird.org/barchart?byr=2000&eyr=2026&bmo=8&emo=11&r=IS&spp=lbbgul

Galván I., Marchamalo J., Bakken, V., & Traverso, J. M. (2003). The origin of Lesser Black-backed Gulls *Larus fuscus* in central Iberia. *Ringing & Migration*, *21*(4), 209–214. https://doi.org/10.1080/03078698.2003.9674295

Hallgrimsson, G. T., Gunnarsson, H. V., Torfason, O., Buijs, R.-J., & Camphuysen, K. C. J. (2012). Migration pattern of Icelandic Lesser Black-backed Gulls *Larus fuscus graellsii*: Indications of a leap-frog system. *Journal of Ornithology*, *153*, 603–609. https://doi.org/10.1007/s10336-012-0816-4

Jones, T. M., Kaiser, S. A., & Sillett, T. S. (2026). Post-fledging ecology of birds: Emergent patterns, knowledge gaps, and future frontiers. *Biological Reviews*, *101*(1), 237–267. https://doi.org/10.1111/brv.70080

Kölzsch, A., Flack, A., Müskens, G. J. D. M., Kruckenberg, H., Glazov, P., & Wikelski, M. (2020). Goose parents lead migration V. *Journal of Avian Biology*, *51*(3), Article e02392. https://doi.org/10.1111/jav.02392

Malling Olsen, K., & Hansson, L. (2004). *Gulls of Europe, Asia and North America*. Helm.

Marques, P. A. M., Costa, A. M., Rock, P., & Jorge, P. E. (2009). Age-related migration patterns *in Larus fuscus* spp. *Acta Ethologica*, *12*, 87–92. https://doi.org/10.1007/s10211-009-0060-y

Meltofte, H. (1996). Are African wintering waders really forced south by competition from northerly wintering conspecifics? Benefits and constraints of northern versus southern wintering and breeding in waders. *Ardea*, *84*(1), 31–44.

Morel, M., Allaert, R., Stienen, E., Fijn, R., Verbruggen, F., Müller, W., & Lens, L. (2024). Learning on the job? Foraging strategies of juvenile versus adult Lesser Black-backed Gulls at their first migratory stopover. *Royal Society Open Science*, *11*(12), Article 241224. https://doi.org/10.1098/rsos.241224

Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P., & Fagan, W. F. (2013). Social learning of migratory performance. *Science*, *341*(6149), 999–1002. https://www.science.org/doi/10.1126/science.1237139

Newton, I. (2024). *The migration ecology of birds* (2nd ed.). Academic Press. https://doi.org/10.1016/C2020-0-00573-6

Panagoda, G., Wijethunge, I. K., Zhang, B., Meng, F., Liu, Y., Kotagama, S., Mundkur, T., Balachandran, S., Cao, L., & Seneviratne, S. S. (2025). A transcontinental migratory passage linking the Indian Ocean with the Arctic Ocean: Migration of Heuglin's Gulls from tropics to Arctic. *Biotropica*, *57*(3), Article e70045. https://doi.org/10.1111/btp.70045

Spear, L. B. (1988). Dispersal patterns of Western Gulls from Southeast Farallon Island. *The Auk*, *105*(1), 128–141. https://doi.org/10.1093/auk/105.1.128

Spear, L. B., Ainley, D. G., & Henderson, R. P. (1986). Post-fledging parental care in the Western Gull. *The Condor*, *88*(2), 194–199. https://doi.org/10.2307/1368915

Thorup, K., Vega, M. L., Snell, K. R. S., Lubkovskaia, R., Willemoes, M., Sjöberg, S., Sokolov, L. V., & Bulyuk, V. (2020). Flying on their own wings: Young and adult cuckoos respond similarly to long-distance displacement during migration. *Scientific Reports*, *10*, Article 7698. https://doi.org/10.1038/s41598-020-64230-x

Verhoeven, M. A., Loonstra, A. H. J., McBride, A. D., Kaspersma, W., Hooijmeijer, J. C. E.W., Both, C., Senner, N. R., & Piersma, T. (2022). Age-dependent timing and routes demonstrate developmental plasticity in a long-distance migratory bird. *Journal of Animal Ecology*, *91*(3), 566–579. https://doi.org/10.1111/1365-2656.13641

Wernham, C. V., Toms, M. P., Marchant, J. H., Clark, J. A., Siriwardena, G. M., & Baillie, S. R. (Eds.). (2002). *The migration atlas: Movements of the birds of Britain and Ireland*. T. & A. D. Poyser.

Wiltschko, R., & Wiltschko, W. (2003). Avian navigation: From historical to modern concepts. *Animal Behaviour*, *65*(2), 257–272. https://doi.org/10.1006/anbe.2003.2054