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# Digest: Exploring the interplay between migration and speciation in the barn swallow\*

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**When members of the same population follow distinct migration routes, a migratory divide can arise. Could differences in migratory strategies contribute to genetic differentiation and possibly speciation? In this study, Turbek et al. combine genomic data, stable isotopes, and geolocators to characterize a migratory divide between two subspecies of the barn swallow (*Hirundo rustica*). Their findings set the stage for further analyses into the genetic basis of migratory behavior.**

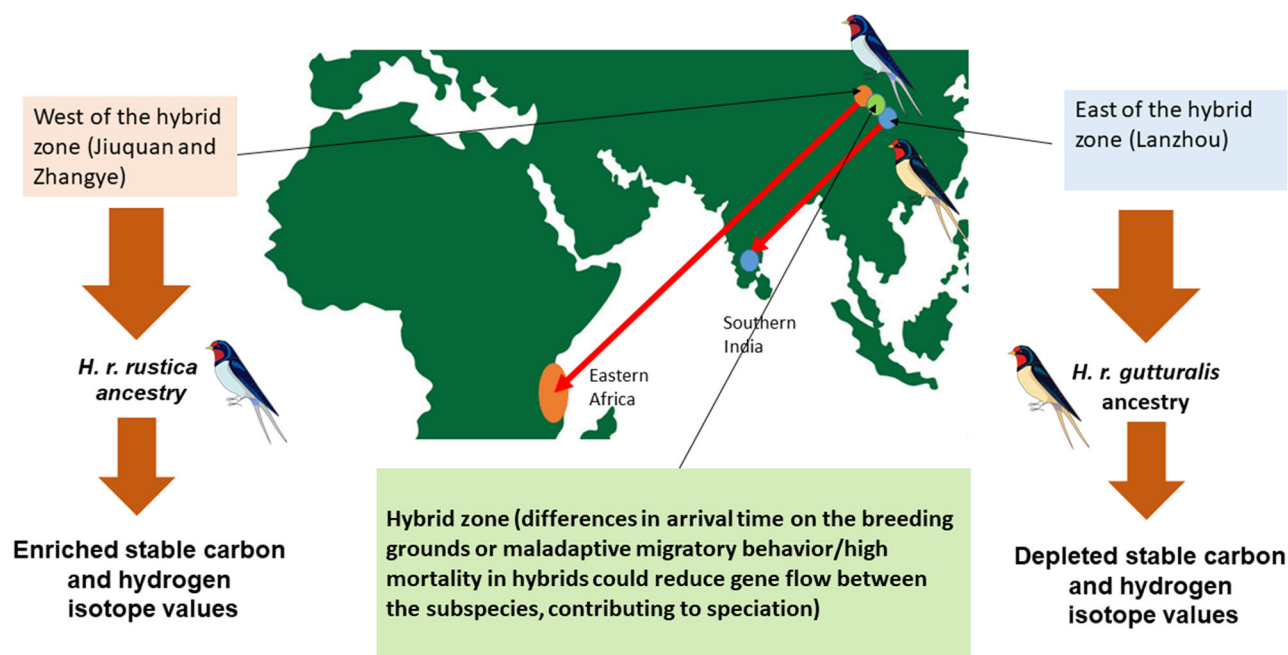
Each year, countless fish, mammals, insects, and birds embark on epic migratory voyages to follow periodic variations in resource availability, taking them thousands of miles away from their breeding sites (Dingle 2014). These seasonal journeys between breeding and nonbreeding environments require a comprehensive set of anatomical, metabolic, perceptual, and behavioral adaptations allowing for lengthy travel, as well as survival and reproduction in different settings. A geographic barrier between neighboring populations can result in a migratory divide, with one population traveling in one direction and a neighboring population in another (Irwin and Irwin 2005). Despite having a zone of interaction at their breeding grounds, these populations will have divergent migratory tactics during the nonbreeding season.

Different migratory strategies can promote and maintain genetic differentiation between populations, potentially culminat-

ing in the origin of distinct species (Turbek et al. 2018). The complex interplay between migration and speciation can be studied first-hand at migratory divides. In Asia, there is a potential migratory divide between two subspecies of the barn swallow (*Hirundo rustica rustica* and *Hirundo rustica gutturalis*). Genomic analyses suggest limited gene flow between these subspecies, which also showed strong differentiation in stable isotope values for  $\delta^{13}\text{C}$  (Scordato et al. 2020). Although these patterns are in line with a migratory divide, other mechanisms could explain the findings. For example, variation in  $\delta^{13}\text{C}$  values can also be due to divergent habitat selection on a smaller scale or different diets. Hence, the existence of this migratory divide remained to be confirmed with more direct methods, such as geolocators.

In this study, Turbek et al. (2022) combined data from genomics, stable isotopes, and geolocators to study the possibility of a migratory divide between the barn swallow subspecies. The geolocators provided direct evidence for two distinct migratory routes and overwintering locations, which were associated with the genetic ancestry of the birds. Individuals traveling to eastern Africa had mainly *H. r. rustica* ancestry, whereas individual

\*This article corresponds to Turbek, S. P., D. R. Schield, E. S. Scordato, A. Contina, X. W. Da, Y. Liu, Y. Liu, E. Pagani-Núñez, Q.-M. Ren, C. C. R. Smith, et al. (2022). A migratory divide spanning two continents is associated with genomic and ecological divergence. *Evolution* 76:722–736. <https://doi.org/10.1111/evo.14448>.



**Figure 1.** How migratory divides between two subspecies of barn swallow differing in migratory routes influence diversification and potentially speciation. Created with Biorender.

migrating to southern India had mostly *H. r. gutturalis* ancestry (Fig. 1). These results were corroborated by the stable isotope analyses, showing that birds with *H. r. rustica* ancestry had higher values for  $\delta^{13}\text{C}$  and  $\delta^2\text{H}$  compared to birds with *H. r. gutturalis* ancestry. Taken together, these patterns confirm the existence of a migratory divide between two subspecies of the barn swallow.

The geolocators revealed that the two subspecies follow separate migratory routes over the high-altitude Karakoram Range, arriving at their breeding grounds 3 weeks apart from one another. These findings suggest that reproductive isolation might be related to assortative mating based on arrival time and/or selection against hybrids, such as developmental defects leading to mortality (Rohwer and Irwin 2011). In addition, intermediate migratory behavior of hybrids may contribute to reproductive isolation between the subspecies. The evolution and maintenance of distinct migratory routes might have been shaped by uninhabitable geographic locations. There is also the possibility that some degree of social learning is involved, and hence direct tracking data from juveniles could shed more light on the contribution of postmating isolation to the maintenance of subspecies boundaries.

Finally, this migratory divide can be used to pinpoint potential “migration genes.” This approach has been successful in

the willow warbler (*Phylloscopus trochilus*) where three genomic regions—on chromosomes 1, 3, and 5—were highly differentiated between birds with distinct migration routes (Lundberg et al. 2017). Similarly, genomic analyses of the golden-winged (*Vermivora chrysoptera*) and the blue-winged Warbler (*Vermivora cyanoptera*) converged upon the gene *VPS13A*, which might be associated with more efficient mitochondrial activity to cope with longer migration routes (Toews et al. 2019). The migratory divide described in the present study provides another exciting opportunity to determine the genomic basis of migration in the barn swallow. Exploring the genomic landscape of differentiation can help researchers understand how birds move across geographical landscapes.

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