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## Evolution: Speciation by Migratory Drop-Off in Flycatchers

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Identifying the isolating barriers that lead to species formation is challenging. New genomic, phylogenetic and life-history data in Tyrant flycatchers — the largest bird family — suggest long-distance migration contributes to reproductive isolation among closely related forms and to differential diversification across the family.

“The mechanisms that isolate one species reproductively from others are perhaps the most important set of attributes a species has, because they are, by definition, the species criteria”. This quote from Ernst Mayr’s “Animal Species and Evolution” [1] emphasizes the importance of the barriers to reproduction between closely related species, also known as ‘isolating barriers’. Then, as now, there remain questions as to which specific barriers — such as pollen compatibility among plants, or differences in plumage coloration or breeding location in birds — might contribute to reproductive isolation between a given pair of species [2]. Moreover, how might these specific isolating barriers scale-up to higher-order patterns of species formation and diversification within a clade of organisms? Take, for example, the elongated nectar spurs on the petals of columbine flowers: the spurs appear to promote pollinator specialization of closely related columbine species, and spur-containing columbine clades are more species-rich [3]. This suggests that divergence in spur morphology

itself might drive speciation in columbines. Studying these characters in plants is fairly tractable, yet connecting these threads — isolating barriers and diversification — in highly mobile animals has proven more challenging. This requires a careful examination of genetic, phenotypic and natural history variation to identify specific isolating barriers, while simultaneously testing whether those barriers contribute to higher diversification. In a new study in this issue of *Current Biology* [4], Valentina Gómez-Bahamón, Carlos Daniel Cadena and colleagues take precisely this kind of multifaceted approach to bear in their study of speciation in tyrant flycatchers.

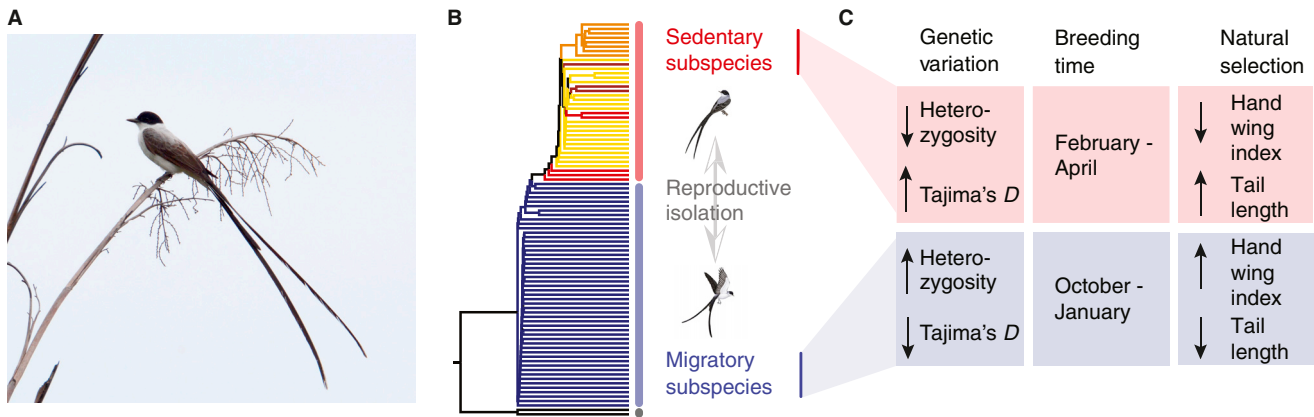
The isolating barrier that Gómez-Bahamón and colleagues [4] focus on is long-distance migratory behavior. Migration in this context describes the movement of individuals between distant breeding and non-breeding grounds. Migratory behavior is estimated to have evolved in birds approximately 80 million years ago, although it has been subsequently lost and regained many

times across the group [5]. There is debate about what drove the evolution of bird migration [6], although the conventional wisdom suggests it was favored as a way to escape competition for resources and breeding opportunities in tropical wintering grounds or to exploit seasonal availability of these resources on breeding grounds.

The role of long-distance migration in diversification can initially appear paradoxical. For example, migratory species are generally quite mobile, given their broad seasonal movements. If this mobility translates into high rates of gene flow among populations, by definition this should also slow the formation of new species. Yet, contrary to this expectation, higher rates of speciation have been estimated for migratory as compared to non-migratory (*i.e.* sedentary) bird lineages [5].

How might changes in migratory behavior drive the formation of new species [7,8]? The simplest way for this to happen is for there to be a gain or loss of migration in a population that results in reproductive isolation between migratory and sedentary groups. Consistent with





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**Figure 1. Migratory drop-off results in reproductive isolation in tyrant flycatchers.**

(A) The fork-tailed flycatcher (*T. savana*; photo: J. D. Curlis). (B) Sedentary subspecies are nested within migratory *T. s. savana*, suggesting the sedentary lineage arose via migratory drop-off. (C) Genetic, natural history, and morphological evidence for reproductive isolation between sedentary and migratory subspecies. In (C), 'hand wing index' refers to the shape of the wing, which is more pointed in migratory individuals — a pattern consistent across many species of migratory bird [12] (illustrations used with permission from [whatbird.com](http://whatbird.com)).

this, speciation events in birds tend to be accompanied more often by losses of migration than by its gain, and extinction rates are lower for migratory species [5]. Such migratory 'drop-off' populations are common across different groups of birds, as well as other migratory organisms, such as monarch butterflies [9]. Gómez-Bahamón and colleagues [4] sought to investigate whether this 'drop-off' signal was present across a single clade of birds — the largest avian family — the tyrant flycatchers (Tyrannidae). They get their name from their acrobatic mode of foraging for small insects in the air, and species in this group are highly variable in their migratory strategies.

Gómez-Bahamón and colleagues [4] reconstructed the evolutionary history of over 300 species of tyrant flycatcher, traced transitions in migratory behavior and estimated rates of speciation across the group. They found that within tyrant flycatchers, migratory drop-offs were more common than gains, and speciation rates were much higher for migratory lineages. Their results also suggest that partial migration — where some individuals migrate and others do not — is likely to mark the transition from a migratory to sedentary lifestyle.

Next, Gómez-Bahamón and colleagues [4] explored the evolution of reproductive isolation within the partially migratory fork-tailed flycatcher (*Tyrannus savana*). This species occurs throughout Central

and South America and is well-known for its exceptionally long, bifurcating tail, which can extend 23 cm in some males (Figure 1A) [10]. Previous studies have described at least four geographically separate subspecies, which show subtle differences in the shape of a notch at the tips of their flight feathers. Among these subspecies, only one (*T. s. savana*) is known to migrate seasonally whereas the others are sedentary [4]. Gómez-Bahamón and colleagues [4] found evidence for genetic differentiation between the subspecies, with the largest difference separating migrant *T. s. savana* from the sedentary subspecies. They next addressed an important question: do the sedentary subspecies represent migratory drop-offs? The most compelling evidence for this is that the sedentary subspecies are nested within the migratory subspecies (Figure 1B). Supporting this notion, they documented reduced genetic variation of the sedentary subspecies, consistent with the founding of several small drop-off populations from migratory ones (Figure 1C).

Finding a clear pattern of the evolution of sedentariness from a migratory ancestor is consistent with the findings of their comparative analyses, but does it coincide with the evolution of reproductive isolation? In other words, are there barriers to gene flow among the migrant and sedentary subspecies? Gómez-Bahamón and colleagues [4]

used two independent approaches to address this: genetics and natural history. The genetic data suggest there is little to no evidence of contemporary gene flow between the migrant and sedentary lineages. However, from these genetic data it can be difficult to distinguish gene flow from other evolutionary processes, so it is equally important to understand whether this finding is reflected in natural isolating barriers.

To test whether individuals of the migratory and sedentary subspecies interbreed, Gómez-Bahamón and colleagues [4] studied locations in eastern Colombia where the migratory *T. s. savana* and one of the sedentary subspecies, *T. s. monachus*, co-occur during part of the year. They found that while nearly all of the individuals from the sedentary subspecies were in breeding condition, none of the migratory individuals showed typical breeding traits, such as males actively tending nests and females expressing a brood patch (a reduction in belly feathers that facilitates heat transfer during egg incubation; Figure 1C). That the migrant and sedentary individuals do not appear to interbreed despite having opportunity to do so is consistent with strong reproductive isolation between the groups (*i.e.* allochronic speciation [11]). Finally, Gómez-Bahamón and colleagues [4] found morphological differences in wing shape and tail length between migratory

and sedentary individuals [12], suggesting that reproductive isolation has also facilitated differential selection for migratory traits in the independent lineages (Figure 1C).

Taken together, Gómez-Bahamón and colleagues [4] present an impressive combination of genetic, morphological and natural history data, which reveal how migratory behavior has influenced speciation across vast scales: from the specific isolating barriers between individuals of different subspecies of the fork-tailed flycatcher, to the differential diversification amongst migrant versus sedentary lineages within the largest family of birds. Yet, in the end, what triggers migratory drop-offs, and are the changes that spur sedentariness directly linked to reproductive isolation? It is clear in the fork-tailed flycatcher, the migratory form is genetically distinct from the sedentary forms, but which of these genetic differences contribute to the observed life history changes, and do any of them directly produce incompatibilities in hybrids between sedentary and migrant parents? What might be the role of behavioral plasticity in the establishment of sedentary lineages? Additional, detailed studies of the mechanisms underlying the

transition to a sedentary life-style are clearly needed to address these questions. However, we speculate that the multigenic architecture of the complex migratory program in birds [13,14], combined with strong natural and sexual selection on flight and plumage traits, makes genetic differences between migratory and sedentary lineages prone to involvement in hybrid incompatibilities. In the case of migration, given the large suite of genes and traits possibly involved in the behavior, there are many parts of this program that could diverge between independently evolving groups. Identifying which are most important to reproductive isolation will be central to future studies.

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## Meiosis: Location, Location, Location, How Crossovers Ensure Segregation

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The proper behavior of homologous chromosomes at the first meiotic division is usually ensured by crossing over. A new study shows that crossover position influences the successful completion of the chromatin remodeling processes that facilitate homologous segregation.

In most meiotic systems, the segregation of each pair of homologous chromosomes requires the production of crossovers (COs) that serve to lock

the paired chromosomes together until anaphase I. COs are created as one outcome of the repair of programmed double strand breaks (DSBs) that are

induced during early prophase. Those DSBs that are not repaired as COs become gene conversion events. Once created, CO-bearing pairs of

