



A live Iberá Seedeater male (left) challenges a painted male model that is delivering a song playback (right), whom he sees as a threat in his territory.

EVOLUTION

At the beginning of speciation

Appearance and song are sexually selected factors to maintain a new bird species

By **Erich D. Jarvis**

Understanding how one population of individuals can split into two species has remained a challenge, especially when the newly emerging species lives inside the geographic area of the older one (1). One possible answer is offered by Turbek *et al.* (2) on page 1337 of this issue. They studied two songbird species belonging to the Southern capuchino seedeater lineage, where the Iberá Seedeater (*Sporophila iberensis*) lives entirely within the territory of the Tawny-bellied Seedeater (*S. hypoxantha*) in Iberá National Park, Argentina. Despite having similar genomes and the ability to form viable hybrids, the two species maintain mating isolation from each other, based on male plumage and learned song. These pre-mating barriers are proposed as the mechanism that maintains the beginning of speciation within the past million years, and which is expected to eventually lead to post-mating barriers where their genomes will sufficiently diverge to prevent viable offspring.

The authors found that the two species differ in only three genomic regions, each no more than 50,000 base pairs in length, out of their 1.2 billion-base pair genomes. Two of these regions contain mutations in regulatory regions of plumage coloration genes, which could explain the male plumage differences. One of these two was on the Z sex chromosome, indicating a link to sexual selection. In birds, sex chromosome organiza-

tion is the inverse of that in mammals, where females have ZW chromosomes (instead of XX) and males have ZZ (instead of XY).

To show that sexual selection was driving speciation, Turbek *et al.* used an ingenious experimental setup. Model birds were painted to look like real male birds (Iberá models with an off-white belly and chest; tawny-bellied models with an orange chest), mounted on branches in the wild in a male's territory, in the presence of a female. A male's song was played through a speaker placed beneath the model. Iberá males responded with a high-intensity territorial response to the Iberá model playing the Iberá song, but they largely ignored tawny-bellied males with tawny-bellied song. The opposite result occurred when the models and songs were switched. Hybrid mixes of plumage and song received territorial responses of intermediate intensity.

For the females, using a genetic test, Turbek *et al.* found (like for some other songbird species) that there was a high degree of secret extra-pair mating, where ~52% of the offspring were fathered by another male. But extra-pair mating occurred entirely within each species. Thus, despite a <0.1% difference in their genomes, males and females of each species mostly stay with their own species (based on appearance and song). This finding was determined from genotyping DNA sequencing of parents and their offspring and analysis of single-nucleotide polymorphisms that can distinguish genetic parentage and species.

Some unanswered questions include whether species selection for song is cultural only, or cultural and genetic. Songbirds are one of the rare groups of species that have

vocal learning, the ability to imitate sounds and culturally pass them on from one generation to another (3, 4). The other vocal learning lineages (apart from humans) are parrots and hummingbirds among birds, and cetaceans (whales/dolphins), pinnipeds (e.g., seals), elephants, and bats among mammals. Theoretically it should be possible for a young Iberá male to learn to imitate the song of a tawny-bellied male and vice versa. If given the choice, with all factors being equal, would isolated young Iberá males have a preference for which song they imitate? If they show no preference, it would indicate that selection for how they “talk” has been purely cultural. But if a preference exists, it would indicate a genetic predisposition, perhaps controlled by genes potentially involved in vocal learning in one of the three genomic regions with differences. Another potential issue is that these are draft genomes generated with short reads, which have difficulty sequencing through regions rich in guanine-cytosine (GC) base pairs (which include many regulatory regions), as well as difficulty resolving repetitive regions (which could also include regulatory regions and recent gene duplications). High-quality de novo genome assemblies, as done with the Vertebrate Genomes Project (5), could reveal additional genomic regions as candidates contributing to recent speciation.

The findings of Turbek *et al.* prompt the question of how widespread this pre-mating mechanism of speciation might be. Perhaps it can give rise to local population differences within a species. Humans are vocal learners, which is necessary for spoken language (3). People take for granted that their apparent mate preferences are for others of the same culture who speak the same language. But perhaps these choices could be part of a broader, genetically determined recognition mechanism that influences mate selection and speciation. Answers to these questions can be gained in future studies in genomics, behavior, and ecology, following the model of Turbek *et al.*, to assess the beginning of population divergence and speciation. ■

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