

Divergent island hybrids mixing waves of ancient gene flow

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Abstract

In this issue of Molecular Ecology, Salter et al. (2023) discovered that the Cuban Northern Bobwhite subspecies, *Colinus virginianus cubanensis* (Gould, 1850), is an ancient hybrid population formed due to historical hybridization between lineages from divergent spatiotemporal origins. Slater et al. sequenced genomes extracted from contemporary samples of Northern Bobwhites, as well as historical museum specimens with the oldest specimens dated in 1859. With this data, they reconstructed the evolutionary origin and history of *C.v. cubanensis* by combining historical literature with demographic modeling. The demographic model revealed the hybrid origin of the *C.v. cubanensis* from hybridization between divergent lineages. The Bobwhite first arrived in Cuba between the 12th and 16th centuries from Southern Mexico. Then the secondary gene flow from the Southeastern USA occurred between the 18th and 20th centuries (Figure 1). *C.v. cubanensis* are hybrids with mixed ancestries while possessing unique genetic variants, which confirm the subspecies status. Hybridization can be a creative process generating and maintaining genetic diversity over space and time.

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Figure 1 A Brief History of Northern Bobwhites . Left: illustration (Pope, 1878) of a Northern Bobwhite (*Colinus virginianus*) breeding pair and the fledglings. Right: the reconstruction of historical gene flows that gave rise to *C. v. cubanensis* based on Slater et al. (2023). Map illustration by Wang S. with the reference of *C. virginianus* range map from BirdLife International (2016).

A complex evolutionary history

Salter et al. (2023) carefully combined historical literature with demographic modeling to reconstruct the backbone of the evolutionary history of the Cuban Northern Bobwhites. Despite that there was uncertainty in the timing and frequencies of the earlier colonization events, the model confidently showed: (1) the divergence among Southeastern U.S., Northern and Southern Mexican populations occurred around 300 Kya; and (2) that the initial Cuban colonization was from Southern Mexico and the secondary gene flow was from Southeastern USA.

The timing of the initial arrival provides clues for whether the founding event was human-mediate or not. The initial migration from Southern Mexico to Cuba could be aided by the lower sea level without human mediation 5 kya. However, if the initial colonization date is much more recent (<0.5 Kya) when the sea level has become much higher, human mediation would be more necessary. Unfortunately, the demographic models could not discern these two possibilities. I wonder if a model with two gene flow pulses from Southern Mexico would fit the data better after controlling for the extra migration parameter.

Reconstructing ancient gene flow events is generally challenging when evaluating demographic models with limited subsamples from contemporary populations, which might not sufficiently represent the target populations. Moreover, small, isolated populations that are subject to a greater extent of gene drift might rapidly lose many ancestral variants that had contributed to the initial admixture. The Southern Mexico source population is also isolated from other Bobwhite populations by the Gulf of Mexico and the Transvolcanic Belt. Therefore, both the source and the island population could be subject to rapid loss of ancestral variants due to drifts after the ancient gene flow. Luckily, this study had historical samples that contributed resolution closer to the ancient gene flow event(s), empowering its reconstruction. This allows the model to confidently estimate the historical gene flow from the Southeastern USA. However, the date of the initial arrival to Cuba from Southern Mexico was still uncertain. The ancient evolutionary history is apparently beyond the limit of the demographic models.

Asymmetry of Introgression

The asymmetric admixture in *C. v. cubanensis* is remarkable. The Southeastern USA ancestry is four times more prevalent than the Southern Mexican ancestry in *C. v. cubanensis* . Introgression sustains and rescues populations from drift load by masking the deleterious alleles (MacPherson et al. 2023). This asymmetry indicates the relatively greater genetic load in the Cuba versus Southeastern USA populations at the time of

hybridization. The isolated Cuban island population could have been susceptible to receiving foreign alleles from recent gene flow. This Cuban population that received historical introgression but still harbors its unique alleles could provide valuable insight for assisted gene flow programs for wildlife conservation.

Divergent hybrids in the changing world

Divergent ecoclimatic adaptation may drive the divergence of hybrid populations from the parental populations if divergently adapted parental lineages hybridized and recombined in a novel ecoclimatic environment. The Cuban bobwhites reside in a distinct ecoregion (the West Indies) than its parental lineages (Tropical Wet Forest and Eastern Temperate Forest). This resembles the ancient hybrid *Setophagawarbblers* in coastal North America that contain locally adapted genetic variants and reside in a climatic condition distinct from the parental ranges (Wang et al. 2021). We might be only seeing the tip of the iceberg of the divergent ancient hybrid populations due to the prehistoric shifts in population ranges driven by the changing ecoclimatic conditions. Future studies could investigate whether the unique variants and/or the unique combinations of parental variants are selected for ecoclimatic adaptation.

Naturalized anthropogenic hybrid populations

Should *C. v. cubanensis* lose its conservation attention because of its hybrid origin? I would argue not. *C. v. cubanensis* harbors an equivalent amount of unique genetic variants as the Southern Mexican population and thus contributes to the valuable genetic diversity of the nearly threatened species. Since the initial arrival to Cuba 0.5-5 Kya, the Cuban ecological community has been coevolving with this terrestrial bird. The absence of this species might perturb the ecosystem. *C. v. cubanensis* is thus a naturalized anthropogenic hybrid population that contributes to local biodiversity. This study shed light on historical human migration in shaping the biodiversity around the world.

Reference

- BirdLife International. 2016. *Colinus virginianus*. The IUCN Red List of Threatened Species 2016: e.T22728956A95000808. <https://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22728956A95000808.en>. Downloaded on 27 June 2018.CC BY-SA 4.0
- Gould, J. (1850). A monograph of the Odontophorinæ, or, Partridges of America. John Gould, F. R. S. Preface [a monograph of the Odontophorinæ, or, partridges of America].
- MacPherson A., Wang S., Rieseberg L., Yamaguchi R., Otto S. 2022. Parental population range expansion before secondary contact promotes heterosis. *American Naturalist*. 200: E1-E15.
- Pope., A. Jr. 1878. Part third, plate V, in: Upland game birds and waterfowl of the United States. Charles Scribner's Sons, New York, United States.
- Slater J.F., Brumfield, R.T., Faircloth, B.C. 2023. An island 'endemic' born out of hybridization between introduced lineages. *Mol. Ecol.* 00:1-15.
- Wang S., Ore M., Mikkelsen E., Lee-Yaw, J., Rohwer S., Irwin DE. 2021. Signatures of mito-nuclear climate adaptation in a warbler species complex. *Nature Communications*. 12:4279.

