

## Synergy between assortative mating and allopatry favor speciation in endemic Galapagos birds

Klaus Jaffe\* and Carlos Bosque Universidad Simon Bolivar, Caracas, Venezuela \* Corresponding author

## **Abstract**

Integrating new data with older reports on the behavior of small land-birds in the Galapagos archipelago reveal that geographic isolation of population together with behavioral segregation of populations produce a synergy that is more likely to produce speciation than any of those factors on its own. This result expands our understanding of assortative mating, based on computer experiments of biological evolution, showing that assortation favors speciation in both sympatric and allopatric populations.

Empirical feed-back for theoretical studies in evolution is hard to get. Here an exceptional case of empirical evidence for evolutionary from the Galapagos Archipelago, wich was also the starting point for evolutionary thinking.

Sexual imprinting is the mechanism by which animals learn early in life to recognize the opposite sex and to imprint the preferred characteristics of future mates. The pioneering studies of sexual imprinting in geese (Lorenz 1935) opened the way for ethological studies of mate preferences. Recently, the role of sexual imprinting in assortative mating and premating isolation in Darwin's finches has been studied in detail (Grant & Grant 2018). These studies, among others, present details of how sexual imprinting modulates assortative mating: mate preferences develop from sexual imprinting. This mechanism favors reproductive isolation as demonstrated in *Geospiza* finches (Grant & Grant 2018), where learning of parental morphology and song early in life binds individuals into breeding collectives favoring assortative mating.

Theoretical studies show that allopatry is the most probable mechanism for speciation but that assortative mating may also promotes speciation. Specifically, assortative mating allows speciation in sympatric populations (Dieckmann & Doebeli 1999, Kondrashov & Shpak 1998 for example). The Galapagos archipelago is probably the most studied natural laboratory for speciation. The recent work on Galapagos *Geospiza* birds suggest that assortative mating plays a role also in allopatric speciation. This can be guessed from the fact that In the Galapagos archipelago, only endemics species of songbirds (oscines), mockingbirds and finches, that practice assortative mating have speciated allopatrically (Table 1). Endemic birds with a wide foraging range or those that



prosper on oceanic habitats, have not speciated in the Galapagos archipelago. In contrast, small land-birds belonging to the genera *Certhidea, Camarhynchus and Geospiza,* mate assortatively and are species rich in the archipelago. Revealingly, similar small land-birds that do not mate assortatively, belonging to the genera *Laterallus* and *Myiarchus*, are monotypic.

Extensive experiments simulating biological evolution point to an important roles in biological evolution of assortation in sexual reproduction. The main route to assortation in biological populations is assortative mating. Assortation, besides favoring speciation, accelerates adaptation, reduces the error threshold of mutations, and produces less misadapation in the evolution of complex genomes, compared to random mating or mating's where selection is based on good genes (Jaffe 1999, 2002). The data from Galapagos birds presented here adds a novel effect for assortative mating: it produces synergies with allopatry in promoting speciation. That is, geographic isolation of population together with behavioral segregation of populations are more likely to produce speciation than any of those factors on its own. This result expands our understanding of assortative mating showing that it may have a role in favoring speciation in both sympatric and allopatric populations.

This conclusion is based on the fact that only genera with a synergistic interaction between allopatry and assortation became species rich in the Galapagos archipelago. An absence of assortative mating does not produce speciation even among allopatrically distributed population, as the case of *Laterallus* and *Myiarchus* show. Unveiling the mating systems of species from the genera *Platyspiza* and *Mimus* can help complete Table 1, allowing to falsify or corroborate this hypothesis. But acknowledgment of the strong benefits for speciation produced by assortment raises the question: Why evolution has produced monotypic land birds in Galapagos that do not mate assortatively? Or if they do assort, why they do not speciate?



## Table 1: Assortative mating and allopatric speciation in endemic Galapagos birds

	Assortative mating
Monotypic species	
Butorides sundevalli	_
Phalocrocorax harrisi	_
Buteo galapagoensis	_
Platyspiza crassirostris &	_
Laterallus spilonota &	No[1]+
Myiarchus magnirostris &	No[ <mark>2</mark> ]+
•	
Species with incipient allopatric speciation	
Zenaida galapagensis (2 subspecies) &	_
Species with allopatric speciation	
Certhidea (olivácea, fusca) &	Yes[ <mark>3</mark> ]*
Mimus (parvulus, trifasciatus, macdonaldi, melanotis) &	-
Camarhynchus (psittacula, pauper, parvulus, pallidus, heliobat	tes) & Yes[4]
Geospiza (magnirostris, fortis, fuliginosa, difficilis, scandens, co	onirostris) & Yes[ <mark>5-6</mark> ]
Zenaida galapagensis (2 subspecies) &  Species with allopatric speciation Certhidea (olivácea, fusca) & Mimus (parvulus, trifasciatus, macdonaldi, melanotis) & Camarhynchus (psittacula, pauper, parvulus, pallidus, heliobat	- tes) & Yes[ <mark>4</mark> ]

& small land birds, - No data found, \* Habitat selection favors assortative mating,

- + Studies from congeneric species not from Galapagos
- 1- Hall, Schmidt & Beissinger 2018
- 2- Rising 1983
- 3- Tonnis et al. 2005
- 4- Peters et al. 2017
- 5- Huber et al. 2007
- 6- Grant & Grant 2018



## References:

- Dieckmann U, Doebeli M (1999). On the origin of species by sympatric speciation. *Nature*, *400*(6742), 354.
- Grant PR, Grant BR (2018). Role of sexual imprinting in assortative mating and premating isolation in Darwin's finches. PNAS 115 (46)
- Hall L A, Van Schmidt ND, Beissinger SR (2018). Validating dispersal distances inferred from autoregressive occupancy models with genetic parentage assignments. J Anim Ecol, 87(3), 691–702
- Huber SK, De Léon LF, Hendry AP, Bermingham E, Podos J (2007) Reproductive isolation of sympatric morphs in a population of Darwin's finches. Proc Biol Sci 274: 1709–1714.
- Jaffe K (1999). On the adaptive value of some mate selection strategies. *Acta Biotheoretica*, *47*(1), 29-40
- Jaffe K (2002). On sex, mate selection, and evolution: An exploration. *Comments® on Theoretical Biology*, 7(2), 91-107.
- Kondrashov A S, Shpak M (1998). On the origin of species by means of assortative mating. *Proc. R. Soc. B: Biological Sciences*, 265(1412), 2273-2278.
- Peters KJ, Myers SA, Dudaniec RY, O'Connor JA, Kleindorfer S (2017) Females drive asymmetrical introgression from rare to common species in Darwin's tree finches. J Evol Biol 30:1940–1952
- Rising J D (1983). The great plains hybrid zones. In *Current ornithology* (pp. 131-157). Springer, Boston, MA.
- Tonnis B, Grant PR, Grant B R, Petren K (2005). Habitat selection and ecological speciation in Galapagos warbler finches (Certhidea olivacea and Certhidea fusca). Proc. R. Soc. B 272, 819–826
- Lorenz K (1935) Der Kumpan in der Umwelt des Vogels. Journal für Ornithologie 83 (3), 289-413.