Animal Behavior: Song Learning out of the Box

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Our understanding of songbird song learning is derived mainly from two approaches: observations in the field and experiments in the laboratory. A clever new study combines elements of both and highlights how exposure to song can catalyze imitative learning.

Like people, songbirds of many species learn to vocalize through imitation [1,2]. The evidence for vocal imitation in songbirds has been wonderfully robust, supported by both natural observations and laboratory experiments. Natural observations have included discoveries of geographical song dialects, of distinct vocal patterns in isolated populations such as on islands, and of specific vocal patterns holding faithfully across generations [3–5] — all parallel to what we see with learned human speech. Laboratory experiments have featured demonstrations of young, naïve songbirds reproducing song models with great precision [6,7] and, inversely, failing to sing normally when denied access to song models [8,9]. Despite their many triumphs, however, studies on songbird vocal imitation have remained vulnerable to some difficult critiques. On the one hand, descriptive field studies typically lack rigorous designs or controls that could help researchers weigh alternative mechanisms that might drive observed vocal patterns, such as population-level stability or divergence in genetic factors. It is also impossible to document the range of acoustic stimuli that wild birds experience. Laboratory studies, on the other hand, allow for a certain degree of control, yet cannot provide the rich social or ecological contexts birds enjoy in the field, thus raising questions about these studies' ultimate biological validity. A new study by Daniel Mennill and colleagues [10] tackles these criticisms in an original way, by applying a controlled song-learning design yet with wild birds in their natural habitat. The study confirms that, as expected, young birds in nature develop their songs through imitative learning, but more importantly offers new and surprising insights into how birds learn to sing.

Mennill and colleagues [10] study migratory Savannah Sparrows (*Passerculus sandwichensis*) on their breeding grounds, on Kent Island in Canada (Figure 1). Like other sparrows, breeding male Savannah Sparrows sing as they court prospective mates and interact with territorial rivals. Songs also serve incidentally as acoustic models for young males learning to sing. The Savannah Sparrows of Kent Island have been subject to extensive behavioral and ecological research since the 1960s, including focused attention on vocal behavior since the late 1980s. A comprehensive prior analysis [11] revealed that young males can copy their songs from a diversity of song tutors; some young males learn from tutors during their first summer, before their first southward migration, whereas others seem to imitate tutors encountered during their first spring, upon returning from their first migration cycle (see also [12]). In their study, Mennill and colleagues [10] deployed 40 loudspeakers across the island through which they played, to five bird cohorts over six years, distinct songs that included foreign elements recorded from distant populations. Young males in the study cohorts thus encountered an artificially rich buffet of potential song models from which to choose: live songs from territorial residents, as they would hear normally, plus the extra songs piped in over loudspeakers. The research team was banking on some birds learning piped-in models.

If asked beforehand, I probably would have said that the study was poised to fail. Prior research has shown time and again that young male sparrows are highly motivated to copy songs from live, socially-interactive tutors [13,14]. There have in fact been cases of young sparrows being swayed, through live-tutoring, to copy songs of other species [15,16]. Why then would birds ever choose to copy disembodied songs emanating from boxes, when they had direct access to live serenades of real flesh-blood-and-feather musicians? For those who recall the old advertisement, I would have guessed that birds would always choose live over Memorex®. Yet, the research team found that young birds did indeed copy loudspeaker song models, and not rarely but as a matter of course. Loudspeaker-only copies, as detected by the reproduction of the non-Kent Island song elements, were observed in a whopping 30 different individuals; moreover, the odds that a given bird would learn its song from a loudspeaker, as opposed to a live model, turned out to be substantial, estimated at 1:2.

Most broadly, this finding offers strong and surprising support for the biological validity of loudspeaker-only tutoring regimes. That birds in the wild are willing to imitate songs from loudspeakers reinforces the view, developed in laboratory work, that songs themselves are highly relevant and meaningful in the learning process — not just as stimuli to be copied but also as salient events that, by virtue of their acoustic structure alone, can activate young birds' innate song learning templates [2,6,9]. Likewise, it suggests that we may have been over-weighing the contribution of social interactions as guides and catalysts for song learning in the wild. As a caveat, loudspeaker-only and live songs were not equally effective as models; live models were in fact more effective. As mentioned above, birds in this study were twice as likely to copy a live tutor than a loudspeaker. Moreover, the study birds presumably heard many more songs through loudspeakers than they did from

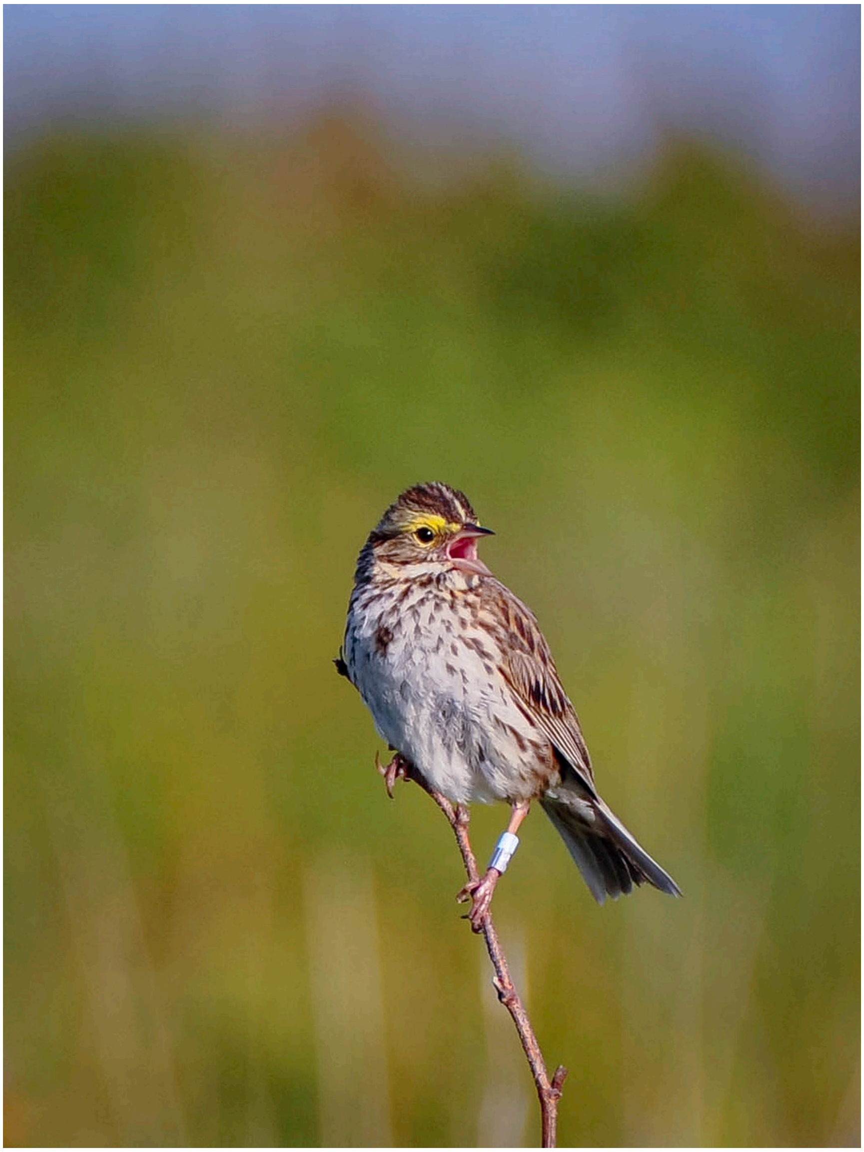

Figure 1. Savannah Sparrow on Kent Island, Canada.
Young male Savannah Sparrows in the wild will sometimes imitate songs played from loudspeakers, despite the ready availability of live song tutors (photo: Daniel Mennill).

live birds, because the research team opted to play loudspeaker songs at the upper end (90th percentile) of naturally observed song rates. That said, we are still left with the remarkable finding that birds opted on a regular basis to imitate sound-only models, in preference to live-tutor models.

The research team also presents evidence that the songs birds learned from loudspeakers functioned normally, on par with natural Kent Island songs. First, the team found that, in four cases, loudspeaker-learned songs were subsequently copied by birds in later cohorts, thus revealing these songs' suitability as learning models. It is worthwhile to pause a moment and contemplate the fact that the research team essentially implanted new acoustic memes into the Savannah Sparrow population — transduced from loudspeaker playback to learned songs and then to culturally-transmitted events and memories. It remains to be seen how long these memes will persist, and in what forms. Second, birds that learned to sing introduced songs — either directly or as new memes — suffered no detectable detriments in aspects of their lives related to singing. These birds matched others in their cohorts in their abilities to defend territories, attract mates, reproduce and survive.

A final notable outcome of this study was enabled by a creative tweak in experimental design, implemented for the final three cohorts. For these birds, distinct sets of song models were presented in three timing blocks: summer only (pre-migration), spring only (just before breeding), or during both summer and spring. By tracking which songs were copied, the research team could then weigh the relative importance of pre- versus post-migration learning. This aspect of the project was motivated by prior work showing that sparrows in the laboratory typically only memorize song models they hear during their first months of life, while, after a period of imprinting closes, potential song models are basically ignored [17]. Sparrows also typically memorize many more song types than they eventually sing as adults. Evidence for this emerges in birds' first spring, as they sing babble-like 'subsong' and 'plastic' renditions of multiple song models they heard the summer before — a process called 'overproduction' [7,18]. Still other research has asked how birds decide which previously-memorized songs they will retain, and which they will drop — a process called 'selective attrition' [18]. Sometimes birds will preferentially retain song types they share with territorial neighbors, an outcome that can later enable song-type matching [13,14,18]. Additionally, young birds in some species can fine-tune the structure of previously memorized models, in the final stages of song development, so as to more closely match the structure of territorial neighbors' songs [13], or to calibrate song structure to their own performance capacities [19,20].

Across the three timing cohorts, not a single Savannah Sparrow copied models from the 'spring only' block. This supports the general presumption that sparrows will only imitate song models heard early in life. For the other timing blocks, only two birds mimicked 'summer only' models, whereas 19 copies could be traced to 'summer plus spring' models. We might have expected a bias favoring the latter block given numbers alone: summer block songs were played for 91 days, whereas summer plus spring block songs were played for 135 days. Yet the observed copy ratio was skewed well beyond the null expectation. This implies that spring tutor copies in the prior study [11] might have been primed by exposure to those same song types during birds' first summers. More broadly, Mennill and colleagues [10] offer that mere "re-exposure" of previously-memorized summer models during spring blocks helps birds to cement their model choices, independent of other factors that favor specific learning outcomes. Given all of these new findings, the idea of training wild birds through loudspeakers no longer seems far-fetched; rather, it seems like the start of a new science meme, ready to be imitated.

REFERENCES

1. Doupe, A.J., and Kuhl, P.K. (1999). Birdsong and human speech: Common themes and mechanisms. Annu. Rev. Neurosci. *22*, 567–631.
2. Soha, J.A., and Peters, S. (2015). Vocal learning in songbirds and humans: a retrospective in honor of Peter Marler. Ethology *121*, 933–945.
3. Grant, B.R., and Grant, P.R. (1996). Cultural inheritance of song and its role in the evolution of Darwin's finches. Evolution *50*, 2471–2487.
4. Sung, H.C., and Handford, P. (2006). Songs of the Savannah Sparrow: structure and geographic variation. Can. J. Zool. Revue Canadienne De Zoologie *84*, 1637–1646.
5. Parker, K.A., Anderson, M.J., Jenkins, P.F., and Brunton, D.H. (2012). The effects of translocation-induced isolation and fragmentation on the cultural evolution of bird song. Ecol. Lett. *15*, 778–785.
6. Marler, P., and Peters, S. (1977). Selective vocal learning in a sparrow. Science *198*, 519–521.
7. Slater, P.J.B. (1989). Bird song learning: causes and consequences. Ethol. Ecol. Evol. *1*, 19–46.
8. Konishi, M. (1965). The role of auditory feedback in the control of vocalization in the white-crowned sparrow. Z. Tierpsychol. *22*, 770–783.
9. Marler, P., and Sherman, V. (1985). Innate differences in singing behavior of sparrows reared in isolation from adult conspecific song. Anim. Behav. *33*, 57–71.
10. Mennill, D.J., Doucet, S.M., Newman, A.E.M., Williams, H., Moran, I.G., Thomas, I.P., Woodworth, B.K., and Norris, D.R. (2018). Wild birds learn songs from experimental vocal tutors. Curr. Biol. *28*, 3273–3278.
11. Wheelwright, N.T., Swett, M.B., Levin, I.I., Kroodsma, D.E., Freeman-Gallant, C.R., and Williams, H. (2008). The influence of different tutor types on song learning in a natural bird population. Anim. Behav. *75*, 1479–1493.
12. Williams, H., Levin, I.I., Norris, D.R., Newman, A.E.M., and Wheelwright, N.T. (2013). Three decades of cultural evolution in Savannah sparrow songs. Anim. Behav. *85*, 213–223.
13. Liu, W.C., and Nottebohm, F. (2007). A learning program that ensures prompt and versatile vocal imitation. Proc. Natl. Acad. Sci. USA *104*, 20398–20403.
14. Templeton, C.N., Akcay, C., Campbell, S.E., and Beecher, M.D. (2010). Juvenile sparrows preferentially eavesdrop on adult song interactions. Proc. Biol. Sci. *277*, 447–453.
15. Baptista, L.F., and Petrinovich, L. (1984). Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow. Anim. Behav. *32*, 172–181.
16. Baptista, L.F., and Petrinovich, L. (1986). Song development in the white crowned sparrow: social factors and sex differences. Anim. Behav. *34*, 1359–1371.
17. Marler, P., and Peters, S. (1987). A sensitive period for song acquisition in the song sparrow, *Melospiza melodia*: a case of age-limited learning. Ethology *76*, 89–100.
18. Nelson, D.A., and Marler, P. (1994). Selection-based learning in bird song. Proc. Natl. Acad. Sci. USA *91*, 10498–10501.
19. Podos, J., Peters, S., and Nowicki, S. (2004). Calibration of song learning targets during vocal ontogeny in swamp sparrows, *Melospiza georgiana*. Anim. Behav. *68*, 929–940.
20. Lahti, D.C., Moseley, D.L., and Podos, J. (2011). A tradeoff between performance and accuracy in bird song learning. Ethology *117*, 802–811.

Epithelial Packing: Even the Best of Friends Must Part

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Textbooks commonly describe epithelia as tissues composed of regular arrays of prism-shaped cells. A recent study combining mathematical modeling with quantitative imaging has uncovered the scutoid, a new shape that is necessary for epithelial cells to pack into curved tissues.

Epithelial tissues are composed of cuboidal, columnar, or squamous cells that are packed together into sheets that line the surfaces of organs and organisms. Connections between epithelial cells can provide mechanical stability and serve as a barrier between compartments; consequently, the different surfaces of an epithelial cell contain distinct sets of proteins that serve both mechanical and signaling functions. Within a simple epithelium, the basal surface of the cell contacts the basement membrane and thus contains receptors for the extracellular matrix. On the opposite side of the cell, the apical surface is oriented toward an internal cavity (or the outside of the organism) and typically contacts air or liquid. The mechanical stability of the epithelium is provided by intercellular adhesions that form along the lateral surfaces and connect neighboring cells to each other. A new study by Gomez-Galvez *et al.* [1] now shows that, in order to form curved tissues, a subpopulation of epithelial cells must adopt a newly discovered shape in

