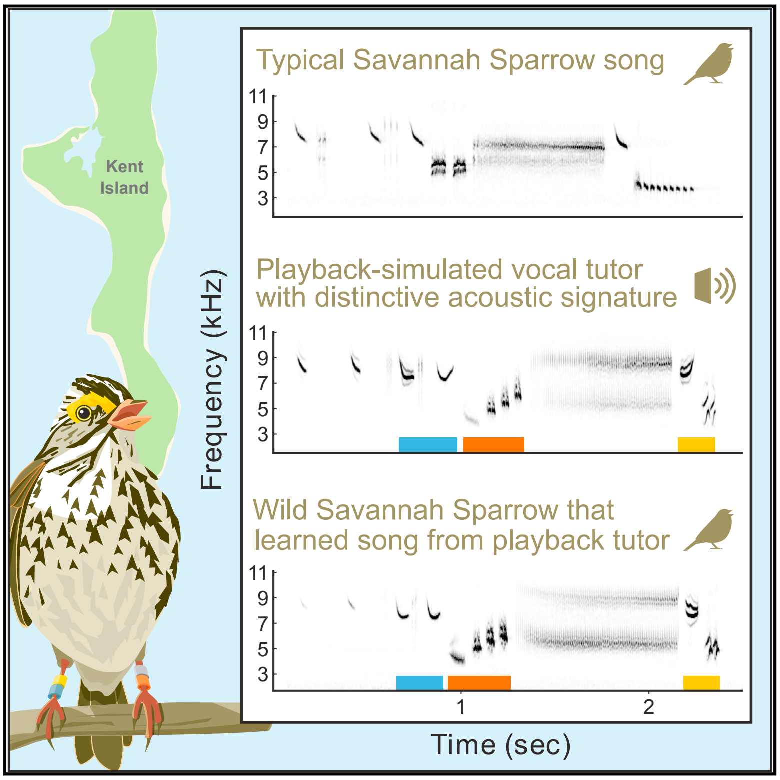
Report

Current Biology

Wild Birds Learn Songs from Experimental Vocal Tutors

Graphical Abstract



Highlights

- Wild Savannah Sparrows learn songs from playback-simulated vocal tutors
- Birds preferentially learn songs heard in both their natal summer and first spring
- Birds pass experimentally introduced songs on to subsequent generations

Authors

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In Brief

Using playback to broadcast novel songs, Mennill et al. show that wild Savannah Sparrows learn songs by listening to adult tutors. Birds preferentially learn songs heard during both their natal summer and the outset of their first breeding season. Birds that learn from simulated vocal tutors also pass these songs on to subsequent generations.

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Report

Wild Birds Learn Songs from Experimental Vocal Tutors

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SUMMARY

In eight groups of animals, including humans and songbirds, juveniles are understood to learn vocalizations by listening to adults [1–4]. Experimental studies of laboratory-reared animals support this hypothesis for vocal learning [5–7], yet we lack experimental evidence of vocal learning in wild animals. We developed an innovative playback technology involving automated loudspeakers that broadcast songs with distinctive acoustic signatures. We used this technology to simulate vocal tutors in the wild and conducted year-long tutoring sessions to five cohorts of free-living migratory Savannah Sparrows in eastern Canada. We confirm that wild birds learn songs by listening to adult conspecific animals, and we show that they pass these songs on to subsequent generations. Further, we provide the first experimental evidence in the wild that the timing of exposure to tutor song influences vocal learning: wild Savannah Sparrows preferentially learn songs heard during both their natal summer and at the outset of their first breeding season. This research provides direct experimental evidence of song learning by wild animals and shows that wild birds learn songs during two critical stages of development early in life.

RESULTS AND DISCUSSION

Vocal learning occurs when animals develop vocalizations by listening to sounds produced by conspecific individuals, often during a sensitive period early in life [1]. Eight groups of animals are thought to have evolved this behavior including songbirds, hummingbirds, parrots, bats, cetaceans, pinnipeds, elephants, and humans [2–4]. Experimental studies of laboratory animals provide convincing support for the hypothesis that young animals learn to vocalize by listening to conspecific individuals (i.e., the vocal learning hypothesis). Young songbirds, for example, fail to develop normal song if they are experimentally deafened or if they are reared in acoustic isolation of adult songs [5]. These findings parallel patterns of vocal development in deaf human children and in rare cases of human children isolated from exposure to adult language [1]. In the laboratory, young songbirds develop normal song when exposed to conspecific tutors or even tutors simulated through playback [5, 6]. Through decades of study of captive animals, laboratory-reared songbirds have become the model system for testing hypotheses about vocal learning in humans and other animals [7].

Outside the laboratory, observational evidence of wild animals suggests that similar processes are at play. For example, many wild animals produce vocalizations with features similar to their parents or other nearby animals; these similarities have been used to infer the presence of vocal learning [8–12]. Furthermore, many wild animals exhibit vocal dialects, where individuals in one region produce vocalizations that differ from vocalizations in distant regions; this pattern is thought to arise from vocal learning coupled with limited dispersal [13, 14]. Vocal learning in wild animals, however, is subject to many complex pressures that are absent from the laboratory [8, 15], including the social interactions that are commonplace in free-living animal populations [16] and the environmental processes that influence sound transmission through natural habitats [17, 18]. To date, there has been no direct experimental tests of whether patterns of vocal learning observed in the laboratory hold true in the wild. Experimental studies of wild animals are important because they offer the potential to reveal more precisely how social and environmental factors interact to shape animal evolution, ecology, and behavior.

We used an innovative playback experiment to study vocal learning in wild migratory Savannah Sparrows, *Passerculus sandwichensis*, on Kent Island, New Brunswick, Canada. We simulated vocal tutors using sound playback: we deployed 40 loudspeakers that broadcast Savannah Sparrow songs modified to contain distinctive acoustic signatures (Figure S1). Birds in this island population exhibit high natal site philopatry [19], presenting us with the opportunity to experimentally manipulate the early acoustic environment of juveniles and then study the vocalizations of these same individuals when they return from migration to their breeding grounds. This population has been studied for many decades [20], providing a background library of population-typical songs (Figure S2) to contrast against the population-atypical experimental stimuli. Over a 6-year period between 2013 and 2018, we experimentally tutored five cohorts of sparrows, from birth to adulthood,

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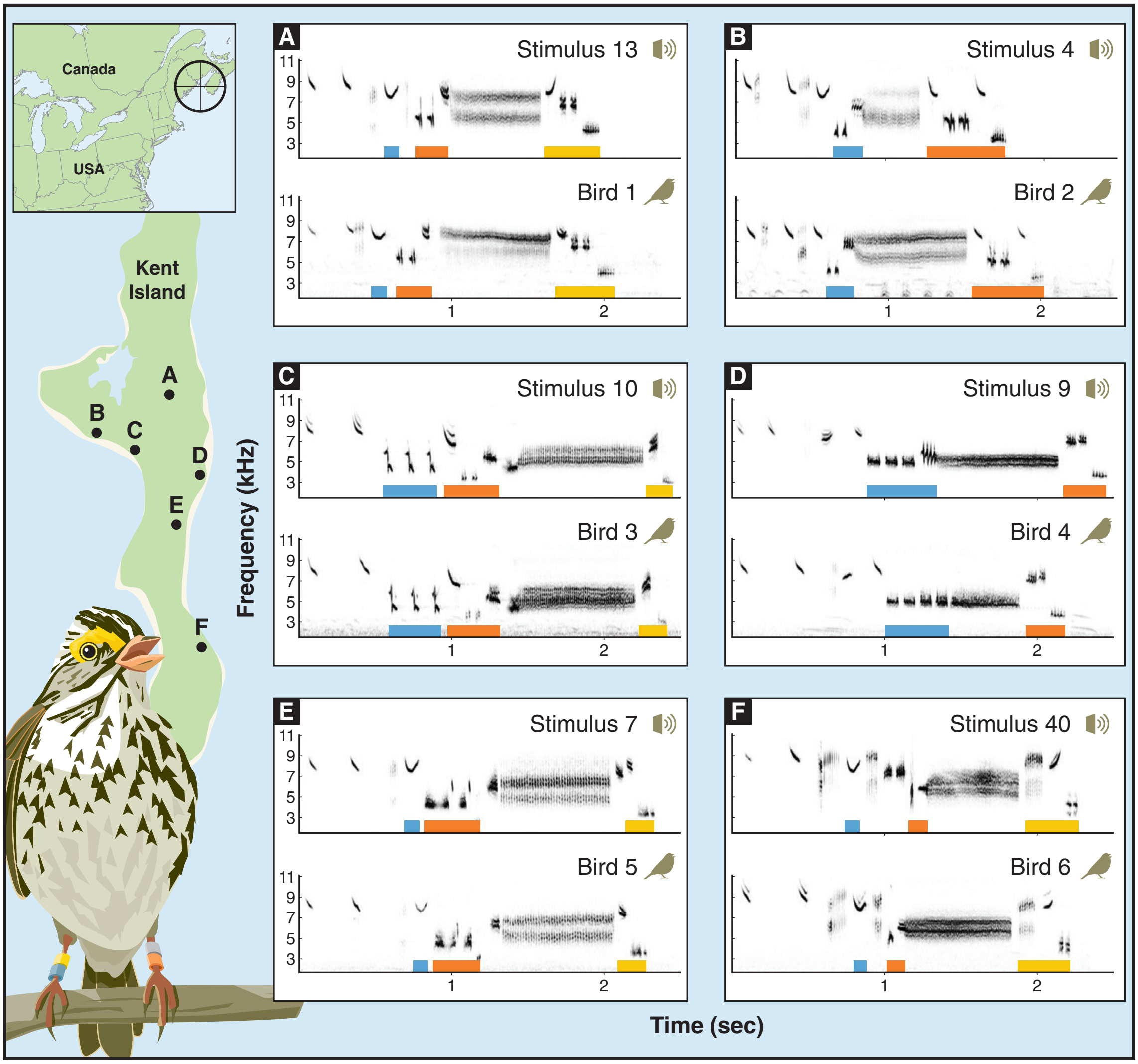

Figure 1. Wild Songbirds Learned Songs from Experimental Vocal Tutors

(A–F) Map of Kent Island, Canada, showing six pairs of sound spectrograms that reveal a high degree of similarity between experimental playback stimuli and the songs of Savannah Sparrows. In total, 30 birds learned songs from speakers that broadcast songs with distinctive elements originally recorded from distant locations (24 additional examples are shown in Figure S3). Colored bars show distinctive phrases that match between playback-simulated vocal tutors and subjects; these phrases were absent from the study site prior to their introduction through playback. Inset map shows location of study site in the Bay of Fundy in eastern North America. See also Figures S1–S4 and Table S1.

using loudspeakers to broadcast adult conspecific songs with distinctive acoustic signatures.

Song Learning in Wild Birds

Wild Savannah Sparrows learned experimentally manipulated songs from playback-simulated vocal tutors (Figure 1). Across five annual cohorts, 30 birds produced songs that matched the experimental stimuli but did not match population-typical songs (Figure S3). In all 30 cases, the birds produced songs containing phrases that had not been recorded at our study site during 3 decades of field recordings of hundreds of animals across many generations [20]. These results provide unambiguous support for the vocal learning hypothesis: wild birds learn songs based on sounds heard in the first year of life.

In addition to the 30 birds that learned experimentally modified songs from the playback-simulated vocal tutors, 4 birds learned to sing from experimental subjects that had been tutored previously, demonstrating two generations of vocal learning (Figure 2). Each second-generation tutee learned one or more distinctive phrases from the first-generation tutee's song. In all four cases, the distinctive phrases had not been broadcast through the loudspeakers since long before the egg containing the second-generation tutee was laid; the sole opportunity for the second-generation tutee to hear these distinctive phrases was from the first-generation tutee.

Of the 34 birds that learned experimental songs, 18 were originally banded as nestlings. This represented exactly one-third of the 54 males that were banded as nestlings and returned to

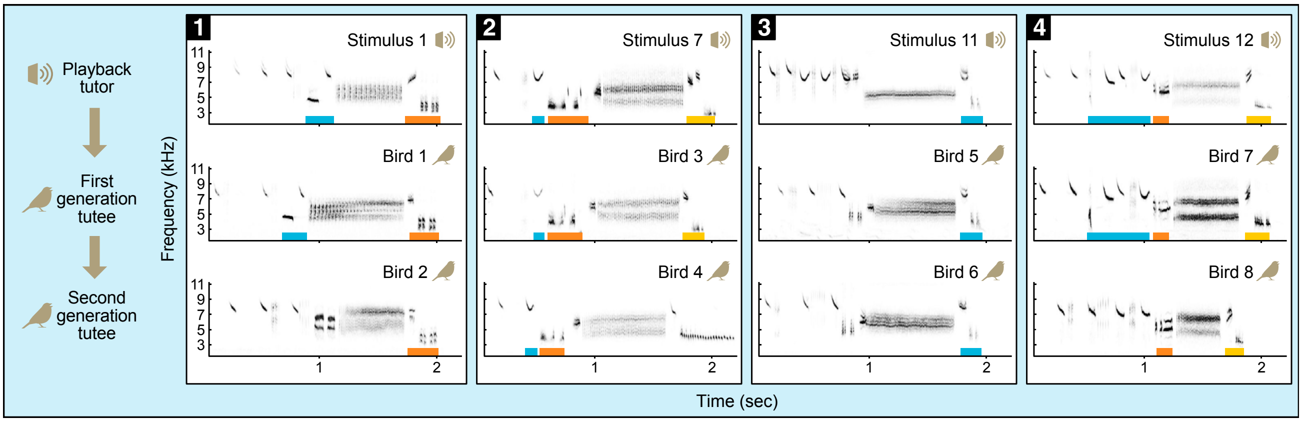

Figure 2. Wild Songbirds Learned Songs from Experimental Vocal Tutors and then Passed Those Songs On to Second-Generation Tutees

Sound spectrograms depict four lineages of song learning in Savannah Sparrows, starting with a playback-simulated tutor song (top), a first-generation tutee that learned from the playback tutor in his first year of life (middle), and a second-generation tutee that learned the stimulus from the first-generation tutee in a later year (bottom). Colored bars show distinctive phrases that match between the stimuli and the birds; these phrases were not present in the population prior to introduction by the playback-simulated tutors.

breed in the study population (2 of 4 in 2014; 1 of 8 in 2015; 3 of 10 in 2016; 7 of 21 in 2017; 5 of 11 in 2018). Banded nestlings that learned experimental songs were born slightly, but non-significantly, later in the year than banded nestlings that learned population-typical songs (ordinal hatch day: 176.4 ± 13.6 versus 168.5 ± 14.9; U = 1.9, p = 0.06, n = 54). Birds that learned experimental songs were distributed across the island, and no aspect of their distance to loudspeakers varied between these two groups of banded nestlings; birds that learned experimental songs were equidistant from loudspeakers in terms of their natal nest (47.3 ± 7.6 versus 41.9 ± 25.1 m; U = 0.35, p = 0.73, n = 54) and their first-year breeding territory (44.4 ± 30.4 versus 42.5 ± 28.7 m; U = 0.18, p = 0.85, n = 54). The banded nestlings that learned experimental songs exhibited similar longevity to birds that learned population-typical songs (2.6 ± 1.0 versus 2.4 ± 0.7 years, respectively; U = 0.8, p = 0.88, n = 54; Table S1). There was also no evidence that experimental songs had negative consequences on reproductive performance or survival of the birds that learned them. All birds that learned experimental songs successfully defended breeding territories, all but one individual attracted a mate, and most were observed to successfully reproduce (Table S1).

Interestingly, among the banded nestlings there were six cases where brothers returned to breed in the study population. In four cases, one brother learned population-typical song, and one or two brothers learned experimental song (Table S1). This demonstrates that divergent learning outcomes can arise within a common rearing environment, as in the laboratory [21].

Experimental songs were broadcast at high rates that often exceeded song rates of live tutors, and yet Savannah Sparrows were not more likely to learn experimental songs than local songs. Birds learned experimental songs significantly less often than we would expect if they learned songs in proportion to the frequency with which they were heard; the ratio of birds that learned experimental songs to those that learned local songs was 18:36, but the expected ratio based on the average daily output of experimental tutors versus live tutors was 234:202, or higher (Chi-square: 9.3, p < 0.002, n = 54, see STAR Methods). Evidently, factors beyond tutor song rate must influence which songs are learned by wild birds.

Timing of Song Learning

Laboratory experiments reveal that many songbirds are maximally sensitive to learning adult sounds during a short time period early in development (these animals are called “closed-ended learners” or “age-limited learners”) [22, 23]. Other vocal-learning animals show parallel patterns, including humans for whom language acquisition must occur in early life to develop normally [1]. Meanwhile, several lab-based experiments and field-based observations support the idea that, along with the critical sensitive phase early in life, songbirds also have a second phase of vocal learning immediately prior to their first breeding period [24, 25]. This situation may arise when young birds memorize many different songs as juveniles and later assess which songs are most important within the social environment of their breeding population. Songs heard within an animal’s breeding population are expected to have special importance given that they define the currency of mate choice decisions and territorial counter-singing exchanges [24]. Based on these ideas, we propose the re-exposure hypothesis: animals learn vocalizations that they have heard both early in life and then again, as adults, prior to the first breeding attempt. This hypothesis may explain the process of selective attrition, whereby young animals learn multiple songs early in life and ultimately reduce their repertoire based on experiences in early adulthood [26].

We tested the re-exposure hypothesis by varying the playback period for our experimental stimuli during the final three cohorts in this study. For each cohort, one-third of the stimuli were broadcast only during the first 3 months of life of the young animals (“summer-only playback”), another third were broadcast only when the animals returned from migration (“spring-only playback”), and the final third were broadcast during both periods (“summer-and-spring playback”; Figure 3A). Based on the re-exposure hypothesis, we predicted that birds would

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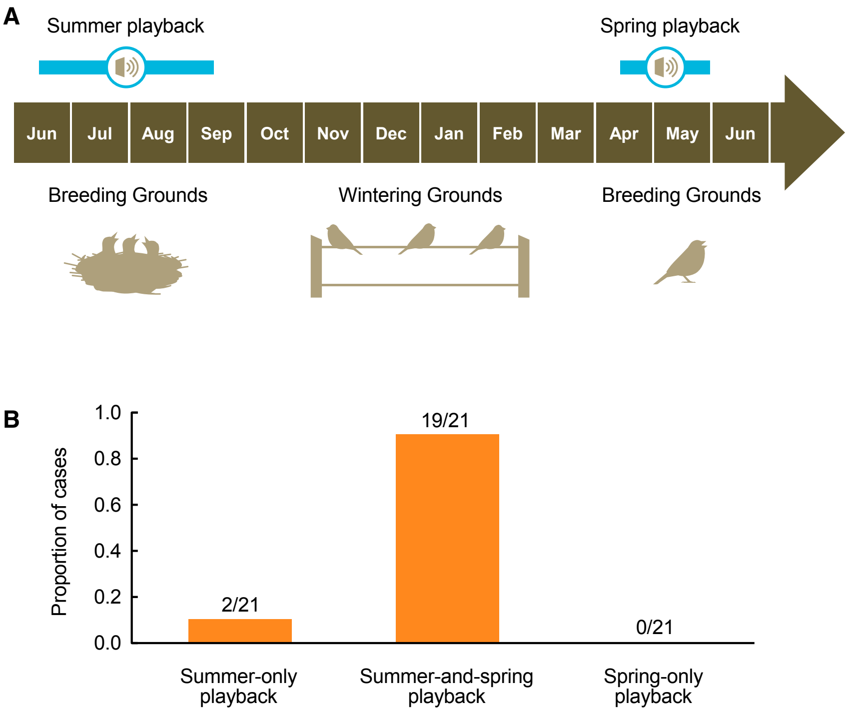

Figure 3. Wild Songbirds Preferentially Learned Songs Heard during Both Their Natal Summer and Their First Breeding Spring

(A) Savannah Sparrows were exposed to experimental playback stimuli that were broadcast only during their natal summer, only during the early spring upon their arrival from migration to the breeding grounds, or during both periods.

(B) Birds were significantly more likely to learn songs that were heard during both their natal summer and during the subsequent spring compared to songs heard only during one of these periods.

preferentially learn songs heard during summer-and-spring playback. In contrast, if the learning period early in life is the most important, we predicted that birds would be equally likely to learn songs heard during summer-only and summer-and-spring playback.

21 birds learned experimental songs during our test of the re-exposure hypothesis. 19 of 21 birds (90.5%) learned songs broadcast during both their natal summer and their first breeding spring, whereas only 2 birds (9.5%) learned songs broadcast only during their natal summer, and no birds learned songs broadcast only during their first breeding spring (Figure 3B). This was significantly different from expected frequencies calculated based on the total number of days of broadcast for each of the three categories of playback stimuli (summer-only: 91 days; summer-and-spring: 135 days; spring-only: 44 days; chi-square test: $X^2 = 13.9$, $p = 0.0009$, $n = 21$). These results provide strong support for the re-exposure hypothesis, revealing that birds almost exclusively learn songs that are heard during both their natal summer and the following spring. The fact that no birds ever produced spring-only playback stimuli supports the previously proposed idea that early exposure to sounds is critical for vocal learning [23].

We followed the activities of all the experimental subjects across their lifetimes (Table S1). Repeated annual recordings of all experimental subjects confirm that once birds crystallized their song during their first breeding season, they did not change their song even after playback of those stimuli had ceased and even when they were exposed to new stimuli (Figure S4). Several birds produced multiple song types in the initial weeks of their first breeding season but rejected all-but-one of these songs within 2 weeks and sang a single song for the remainder of their lives. This is a process known as ‘‘overproduction’’ and is known from other songbirds [26]. Four Savannah Sparrows sang an experimental song during the overproduction stage but rejected the experimental song and crystallized population-typical song (Figure S4).

Conclusions

Observational and correlational data support the idea of vocal learning in eight groups of animals [2–4], and decades of investigation of a handful of species provide compelling demonstrations of vocal learning in laboratory-reared songbirds [23], but direct experimental evidence of vocal learning by wild animals has been absent until now. Our findings that young songbirds learn to sing by listening to playback of conspecific adult tutors represents direct experimental evidence of vocal learning in free-living animals. These results provide confirmation that behaviors observed during decades of laboratory study hold true in the wild. Our research also introduces a new methodology that may be used broadly to study vocal learning in wild animals.

The experimental introduction of novel song types into our study population raises an exciting opportunity to track cultural evolution of these phenotypes, which will be the focus of our studies in the years ahead. It also raises ethical questions concerning when it is appropriate to introduce new phenotypes into a wild animal population. We felt our approach was appropriate for several reasons: Savannah Sparrows are a common and widespread species [27], our introduced songs were based on recordings of the same species modified in only subtle ways, and our study population is restricted to an oceanic island where the possibility of songs spreading to other populations is unlikely. Our observations of breeding activities of the experimental subjects (Table S1) reveal that the introduced phenotypes did not hamper survival or reproductive activities, and recordings of the two nearest islands confirm no spread of experimental songs beyond Kent Island during the study. We urge future researchers to carefully consider the ethics of this methodology, particularly when studying animals with small population sizes or when using artificial stimuli.

Our experimental study of wild birds corroborates longstanding ideas that arose from carefully controlled laboratory studies. (1) Sparrows that learned experimentally introduced songs continued to sing those songs throughout their lives, far beyond the conclusion of playback (Table S1; Figure S4). This confirms the idea that, for closed-ended learners like Savannah Sparrows and many other songbirds, vocal learning in the wild occurs early in development and that song subsequently remains fixed throughout an animal's adult life [5]. (2) Sparrows learned to sing playback stimuli heard in the absence of a live tutor and without social interaction with a live tutor, even in spite of the availability of live-tutor songs. This reveals that social interactions between young animals and tutors are not required for vocal learning in the wild, a surprising finding given that social interaction is important for learning in the laboratory [15]. (3) Upon arrival from migration on the breeding grounds, several sparrows produced multiple song types and then quickly reduced their repertoire to the species-typical repertoire size of one. This confirms the idea that wild birds learn more songs than they eventually sing as adults [26] and creates possibilities for future research on the social factors that influence song attrition. The behaviors we observed for Savannah Sparrows are consistent with the learning program described for other songbirds [28], suggesting that song overproduction early in the first breeding season is an important part of the vocal behavior of wild animals. (4) Finally, sparrows almost exclusively learned songs heard both early in life and immediately prior to breeding, demonstrating that two life-history stages are critical for shaping an adult's song: a critical window of exposure early in life and re-exposure as a reproductive adult.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- QUANTIFICATION AND STATISTICAL ANALYSIS
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SUPPLEMENTAL INFORMATION

Supplemental information includes four figures and one table and can be found with this article online at https://doi.org/10.1016/j.cub.2018.08.011.

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AUTHOR CONTRIBUTIONS

D.J.M., S.M.D., A.E.M.N., H.W., and D.R.N. designed the experiment. All authors shared in field research, analysis, and writing the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and Algorithms		
Audition 3.0	Adobe Systems	https://www.adobe.com/ca/products/audition.html
AviSoft SASLab Pro	Avisoft	https://www.avisoft.com/

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Dan Mennill (dmennill@uwindsor.ca).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Our study population of Savannah Sparrows (*Passerculus sandwichensis*) breeds in the meadows on Kent Island, New Brunswick, Canada at the Bowdoin Scientific Station (44°35’N, 66°46’W). This population has been studied since the 1960’s [29]. The peak nesting period occurs between late May and early July. Birds depart from the breeding population on southward migration from mid-September through mid-October; they return to breed beginning in late April and early May [30, 31]. Annually, we band all breeding adults in the central study area of the island, giving each animal a unique combination of numbered and colored leg bands. We record their songs and map their territories, locate and monitor their nests, and band all offspring [32]. Recordings of male song from this population have been collected annually since the 1980s, with previous studies focused on acoustic similarity between parents and offspring [9] and cultural changes in song [20]. Evidence suggests that birds sing only on the breeding grounds but not on their wintering grounds [27]. Decades of recordings reveal that each adult male has a single song that remains consistent throughout an individual’s life (i.e., they are closed-ended learners) [9, 20]. Field observations suggest that song plays a role in mate attraction and territory defense.

Animal procedures were approved by the University of Windsor Animal Care Committee (project AUPP 13-15).

METHOD DETAILS

Playback apparatus

Our playback system consisted of 40 custom-designed loudspeakers (modified Scorpion loudspeakers from FoxPro Inc., Lewiston PA; loudspeaker power rating: 7W). The speakers were housed in weather-proof plastic cases and mounted on wooden stakes at a height of 1 m, the typical height of a song post for a Savannah Sparrow. Weather-proofing was enhanced by covering each speaker in a cloth bag made from waterproof fabric depicting a camouflage pattern (Figure S1). Stimuli were stored on flash cards inside the speakers (stimulus details below). Speakers were arranged in pairs separated by a 20 m stereo sound cable; one speaker broadcast the left channel of a stereo sound file and the other speaker broadcast the right channel. This arrangement allowed us to simulate two different tutors using a single power source.

For the first two annual cycles in this experiment (i.e., June 2013 – May 2014 and June 2014 –May 2015), each pair of speakers was powered by eight rechargeable D-cell batteries that were changed every seven days. For the final three annual cycles (i.e., June 2015 – May 2016, June 2016 – May 2017, and June 2017 – May 2018) each pair of speakers was powered by a solar charging system (25 W solar panel, a solar charge controller, and a 12 V 24 Ah sealed lead-acid battery). To ensure that stimuli were broadcast only during daylight hours, power was regulated by a custom-built light sensor that turned the speakers on at the first light of dawn and off at the last light of dusk.

We set the amplitude of the loudspeakers at 85 dB measured at a distance of 1.0 m (Caselli sound level meter; model: CEL-24X; setting: fast; weighting: C). This amplitude matched the amplitude of songs produced by Savannah Sparrows based on aural assessment in the field, as well as the amplitude of songs in playback studies of other sparrow species [33, 34].

We placed speakers at the edge of the birds’ territories, simulating adult males singing at the territory boundaries of established resident birds. We positioned speakers with an approximate density of four speakers per hectare of Savannah Sparrow habitat (Figure S1). From most locations in our study site, it was possible to hear two to four loudspeakers (although no speakers within earshot played the same stimulus at the same time). In some cases, territorial animals responded very aggressively to a loudspeaker at the annual start of the playback, perching on top of the speaker and singing at an elevated rate. After we moved the loudspeaker's position several meters along the boundary with the neighboring male's territory, these aggressive responses declined. The speakers did not appear to influence territory settlement in spring; there were many cases where birds settled immediately adjacent to loudspeakers even with unoccupied habitat available nearby.

Playback stimuli

We created playback stimuli with distinctive acoustic signatures by modifying archival recordings of Savannah Sparrows from the Macaulay Library of Natural Sounds and the Borror Laboratory of Bioacoustics. We selected recordings collected from the western half of North America, at locations $\geq$ 2000 km away from our study site, focusing on songs that had unique elements that did not match any song recorded over the last three decades in our study population [20]. This approach allowed us to use naturally-occurring Savannah Sparrow song elements already known to occur in Savannah Sparrow vocal repertoires elsewhere in North America. We selected a single exemplar song from each archival recording, choosing a song with a high signal-to-noise ratio and minimal background noise. We then modified the songs in several ways. We removed unwanted background noise using the lasso selection tool and then reduced the amplitude to background levels with the "amplify" tool in Audition (Adobe Systems Inc., v. 3.0). We standardized the amplitude to -1 dB using the "normalize" tool in Audition. In cases where the stimulus did not have a sufficient number of unique elements, we duplicated a song element using the "copy" and "paste" tools of Audition; we added in an element from another Savannah Sparrow song from the Macaulay or Borror Libraries; or, rarely, we flipped the time axis of an individual song element using the "reverse" tool in Audition, or made subtle transpositions in frequency of repeated elements using the "transpose" tool in Audition. All 46 playback stimuli used in the experiment are shown in Figure S1. For many stimuli, we inserted a distinctive U-shaped introductory syllable in the first part of the song (this syllable is relatively common in west coast populations but historically absent from our study population); we did this because it made the experimental stimuli easy to recognize in our field recordings.

Using Audition, we pasted the individual playback stimuli into longer playback tracks for broadcast in the field. Each playback track was one hour in length. We varied the duty cycle of playback with time of day because Savannah Sparrows vary their song output with time of day: they show heightened vocal activity at dawn and dusk [35]. During the first hour of the day, and the final 1-2 hours of the day, each simulated tutor produced songs for 30 min per hour (sounds were broadcast in three blocks of 10 min, every 20 min); across the remaining daylight hours each simulated male produced songs for 12 min per hour (sounds were broadcast in blocks of 4 min, every 20 min; at the end of each day, the final period of higher duty cycle varied from 1-2 hours because of variation in day length; playback ended when the light sensors detected sunset).

During periods of playback by the simulated tutors, songs were repeated at a rate of one song every 10 s, resulting in 180 songs per hour during dawn and dusk, and 72 songs per hour between dawn and dusk. We chose these song rates to fall within the normal range of song output for breeding Savannah Sparrows in our population, but at the upper end of this range: the 90th percentile of song output for the first hour of the day is 180-311 songs per hour; the 90th percentile of song output at noon is 53-246 songs per hour; and the 90th percentile in the last hour of the day is 120-330 songs per hour (N = 34 males recorded twice per month between May and August [35]). Sparrows have higher song output in spring than summer [35], but we maintained the same song rate throughout the season to maximize the opportunity for young birds to hear the tutor songs. As a result, the playback stimuli were heard as commonly as the highest-song-rate sparrows during the breeding period (spring), and were much more common than local songs after the breeding period (summer to fall). To minimize habituation and simulate realistic singing behavior, we introduced variation into the pace of songs by randomly inserting or deleting short silent intervals of variable length between subsequent songs while still achieving an overall song rate of one song every 10 s.

Stimuli 1-10 were broadcast in the 2013-2014 and 2014-2015 playback periods; stimuli 11-28 were broadcast in the 2015-2016 playback period; stimuli 29-46 were broadcast in the 2016-2017 playback period; and stimuli 4, 6, 8-10, 14-18, 21-28 were broadcast in the 2017-2018 period (these stimuli were chosen for 2017-2018 because songs with novel elements became difficult to find and therefore we re-used previous stimuli providing that the stimuli hadn't been played for at least one year, and providing that any birds who had previously learned this song had been dead for at least one year). The simulated tutors were not restricted to a specific loudspeaker, but instead the stimuli were designed so that the experimental stimuli were broadcast across all of the 40 loudspeakers distributed across the study site; every hour after playback, a different simulated tutor was broadcast through each loudspeaker. We ensured that the same stimuli could not be heard from more than one loudspeaker at any position on the study site at any one time. We ensured that all stimuli were heard the same number of times per day across the entire island.

Re-exposure experiment

We tested the re-exposure hypothesis in the final three annual cycles of the study (i.e., June to May of 2015-2016, 2016-2017, and 2017-2018). One third of the stimuli were broadcast only during the first three months of nestlings' lives (the "summer-only treatment": 91 days, on average, between mid-June and mid-September); one third of the stimuli were broadcast only in the spring when these birds returned from migration (the "spring-only treatment": 44 days, on average, between mid-April and late-May); and the remaining third were played during both periods (the "summer-and-spring treatment"; Figure 3). We used a random number generator to determine whether a particular stimulus was used in summer-only, spring-only, or summer-and-spring treatments. In the first two cohorts of this experiment (i.e., those that hatched in the summers of 2013 and 2014) all stimuli (i.e., stimuli 1-12) were broadcast in both summer and spring, and therefore these data cannot be used to test the re-exposure hypothesis.

Detecting song learners

To detect birds that had learned the songs broadcast from the simulated vocal tutors, a team of recordists collected songs from all birds on Kent Island and the two adjacent islands (Hay Island and Sheep Island), and then compared their songs to other birds recorded in their natal year, to other birds recorded in their first breeding year, and to the playback stimuli. We collected recordings using two techniques: (1) In the central part of the island where all birds are banded as part of our long-term investigation, we collected focal recordings by standing in the adjacent breeding territory and recording birds during spontaneous bouts of song. Focal recordings were collected with a Sennheiser ME62/K6 microphone mounted in a Telinga parabola connected to a Marantz PMD660 or PMD661 digital recorder (monaural recordings; 44.1 kHz sampling rate; 16-bit accuracy; WAV format). (2) In outlying parts of the island, where Herring Gulls (*Larus argentatus*) dominate the landscape and produce a loud ruckus whenever a recordist is in the area, we used automated digital recorders. Automated recordings were collected with Wildlife Acoustics SM2 Song Meters (stereo recordings; 44.1 kHz sampling rate; 16-bit accuracy; WAC format). A recordist would enter an area to deploy the recorder, and recorders were left in place for 24 to 48 hours to sample Savannah Sparrow songs when the gulls grew quiet. Because male Savannah Sparrows produce only one type of song and songs usually differ substantially between individuals, we could detect each of the individual birds on the island in these automated recordings, even though some of the birds were unbanded. The age and natal location of the birds in these cases was unknown.

To assign songs to vocal tutors we applied the visual-comparison-of-spectrograms approach that has been used previously in this population [9]. This approach has been shown to produce equivalent results to computation of similarity scores with sound analysis software [9]. The songs of Savannah Sparrows have four sections (the introduction, the middle section, the buzz, and the terminal section [20]), and given the general consistency in structure of introductions and buzzes of Savannah Sparrow songs across their geographic range, we focused particularly on the middle sections and terminal sections. Comparisons of songs from our experimental stimuli (Figure S1) and non-experimental songs from our study population (Figure S2) make it clear that most of the bioacoustic differences occurred in these two sections, and prior research confirms that these two sections are the most individually distinctive components of song in this population [20]. Visual comparison of the spectrograms of young males' songs with those of either our experimental stimuli or population-typical song gave rise to clear matches in spectro-temporal similarity between 34 birds and our playback stimuli (see Figures 1, 2, S4). Initial comparisons were made by IGM, IPT, and other researchers in the laboratory of DJM; final comparisons were made by DJM (who has two decades of experience studying bird songs and sound spectrograms) and confirmed by the remaining coauthors. Buzz sections show high similarity between animals [20], therefore we applied a quantitative approach to compare buzzes. For the 30 first-generation tutees, we compared the spectral features of the buzz sections of the tutor songs to the tutee songs we had assigned on the basis of the middle and terminal sections. We used AviSoft SASLab Pro (R. Sprecht, Berlin) to measure the minimum frequency, peak frequency, and maximum frequency at 10 points distributed equidistantly across the buzz and calculated the average of each measure for each bird. The frequency characteristics of the buzz section of their songs showed significant correlations between tutors and tutees for minimum frequency of the buzz (Pearson correlation: $r = 0.87$, $p < 0.0001$, $n = 30$), peak frequency of the buzz ($r = 0.66$, $p < 0.0001$, $n = 30$), and maximum frequency of the buzz ($r = 0.69$, $p < 0.0001$, $n = 30$ first-generation tutees).

The vast majority of male Savannah Sparrows produce one song type as an adult, but rarely they produce two song types throughout their adult lives (this occurs in less than 2% of males [20]). In our dataset we had a single bird that produced two different songs as an adult: both of this male's songs matched experimental stimuli (bird L.RS from Figure S3). With respect to our test of the re-exposure hypothesis, both of the songs that this male learned were summer-and-spring songs.

QUANTIFICATION AND STATISTICAL ANALYSIS

Focusing on male Savannah Sparrows that were banded as nestlings and then returned to breed in the study population ($n = 54$), we compared the observed ratio of birds that learned experimental songs versus population-typical songs (18 and 36 respectively) to the expected ratio if birds learned songs relative to the frequency with which they were heard. In spring, when song output of live tutors was highest, the median number of songs per day from live tutors was 202 (calculated from day-long recordings of 30 males in mid-April to mid-May), and the median number of songs per day from each of the playback-simulated tutors was 234 (note: the songs of different tutors "moved" among the 40 loudspeakers on the island, as explained above, and this calculation is based on our estimate that each potential tutee was within earshot of four loudspeakers broadcasting experimental tutor songs). Therefore, we compared the observed ratio of 18:36 (banded nestlings that learned experimental songs versus banded nestlings that learned population-typical songs) to the expected ratio of 234:202 (song output per day from the average experimental tutor versus song output per day from the average live tutor) using a Chi-squared analysis. Output of simulated tutors was relatively constant

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across the breeding season (output varied only with day length), whereas output of live tutors declined as the breeding season progressed [35]; a Chi-squared comparison of our observed ratio to expected ratios larger than 234:202 only increased the strength of the comparison.

To test the re-exposure hypothesis, we compared the observed proportion of birds that learned summer-only playback stimuli, summer-and-spring playback stimuli, and spring-only playback stimuli (2:19:0) to the expected ratio of birds that would learn these three categories of stimuli based on the number of days they were broadcast (91:135:44) using a Chi-squared analysis.

DATA AND SOFTWARE AVAILABILITY

All sound files in this paper are available by contacting the first author, Dan Mennill (dmennill@uwindsor.ca), or by visiting: http://web2.uwindsor.ca/courses/biology/dmennill/CBSounds/.

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Supplemental Information

Wild Birds Learn Songs
from Experimental Vocal Tutors

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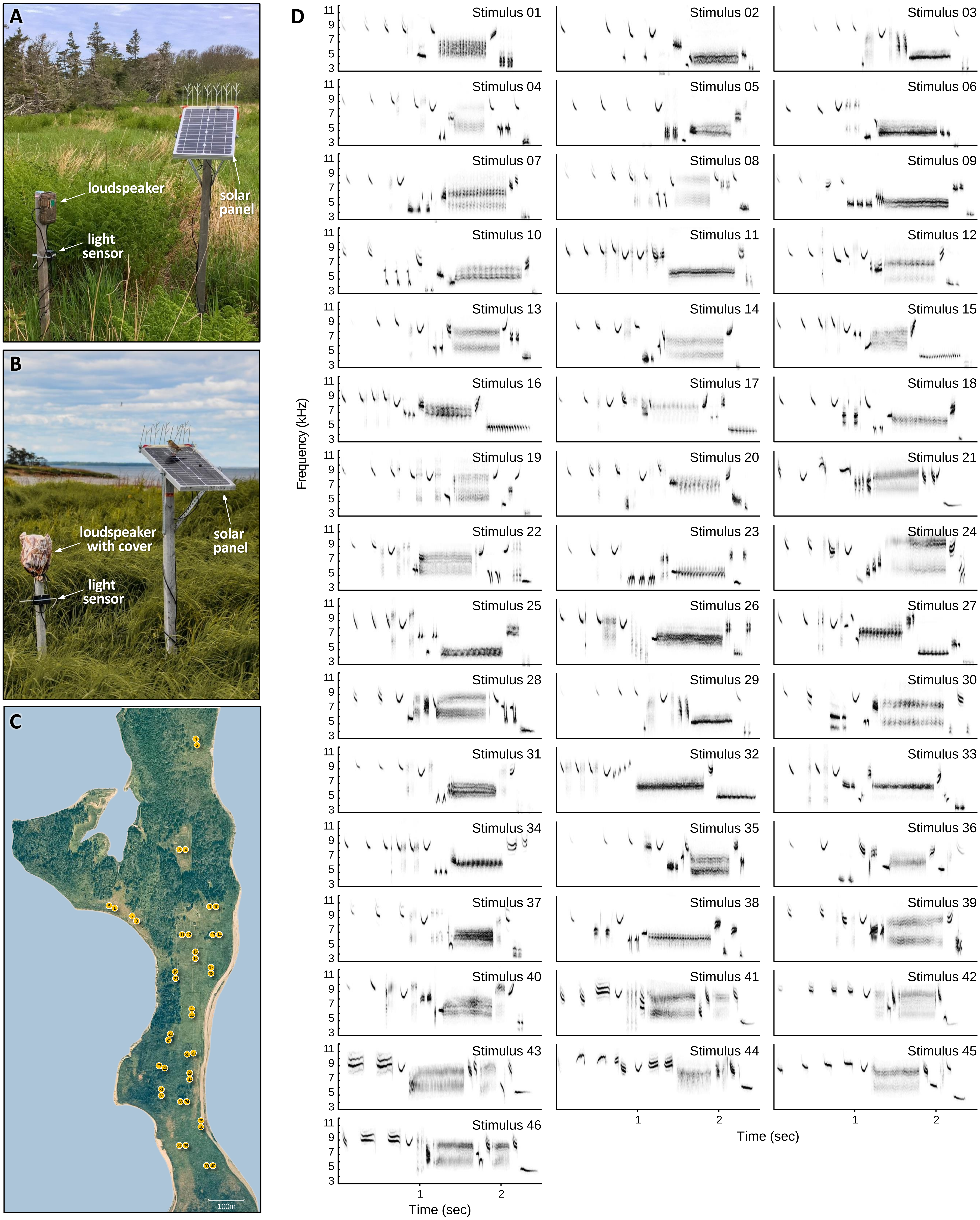

Figure S1. Photographs of playback devices, map of playback locations, and sound spectrograms of experimental playback songs used to simulate Savannah Sparrow vocal tutors on Kent Island, New Brunswick, Canada. Related to Figure 1.

(A-B) Photographs of the playback apparatus used to broadcast acoustically distinctive experimental songs of Savannah Sparrows, thereby simulating vocal tutors. The apparatus included weatherproof, programmable

FIGURE S1 CAPTION CONTINUES ON NEXT PAGE→

FIGURE S1 CAPTION CONTINUED FROM PREVIOUS PAGE→

loudspeakers, light sensors to deactivate the speaker at night, and solar panels to provide power. To enhance weather-proofing, loudspeakers were outfitted with a waterproof cloth cover (B). Each solar panel provided power to two loudspeakers separated by 20 m.

(C) Map of the study site showing the location of the 40 loudspeakers used to simulate vocal tutors to Savannah Sparrows in the meadows at the Bowdoin Scientific Station on Kent Island, New Brunswick, Canada. The loudspeakers were arranged in pairs separated by 20m. The position of each pair of speakers changed subtly over time based on the territory locations of the subjects (see Star Methods), but conformed to these general locations.

(D) Sound spectrograms of 46 experimental stimuli created for the vocal learning experiment with Savannah Sparrows. The stimuli were created from recordings of Savannah Sparrows in western North America, and were chosen because they contained distinctive acoustic elements that were absent historically from the study population. Some songs were modified in subtle ways, as explained in the Star Methods, to enhance their distinctive features. Stimuli 1-10 were broadcast in 2013-2015; stimuli 11-28 were broadcast in 2015-2016; stimuli 29-46 were broadcast in 2016-2017; and stimuli 4, 6, 8, 9, 10, 14-18, 21-28 were broadcast in 2017-2018.

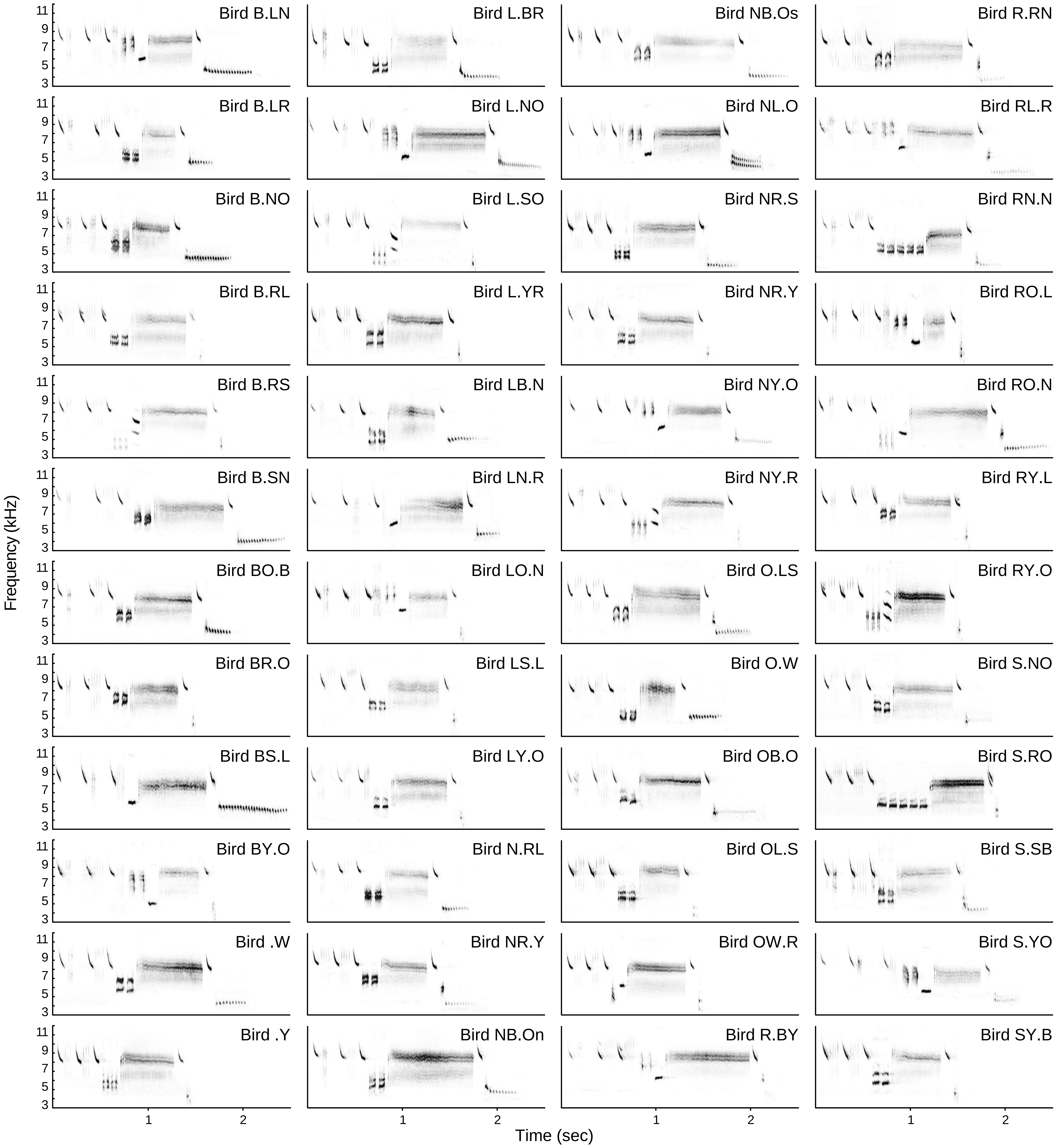

Figure S2. Sound spectrograms of typical Savannah Sparrow songs recorded in 2013 before the experimental manipulation began, showing population-typical songs from the island where we conducted playback. Related to Figure 1.

Together with the three decades of recordings described in Williams et al. [20], these recordings provide the acoustic backdrop against which we compare the experimental stimuli shown in Figure S1. Birds are named for the combination of colored bands on their legs.

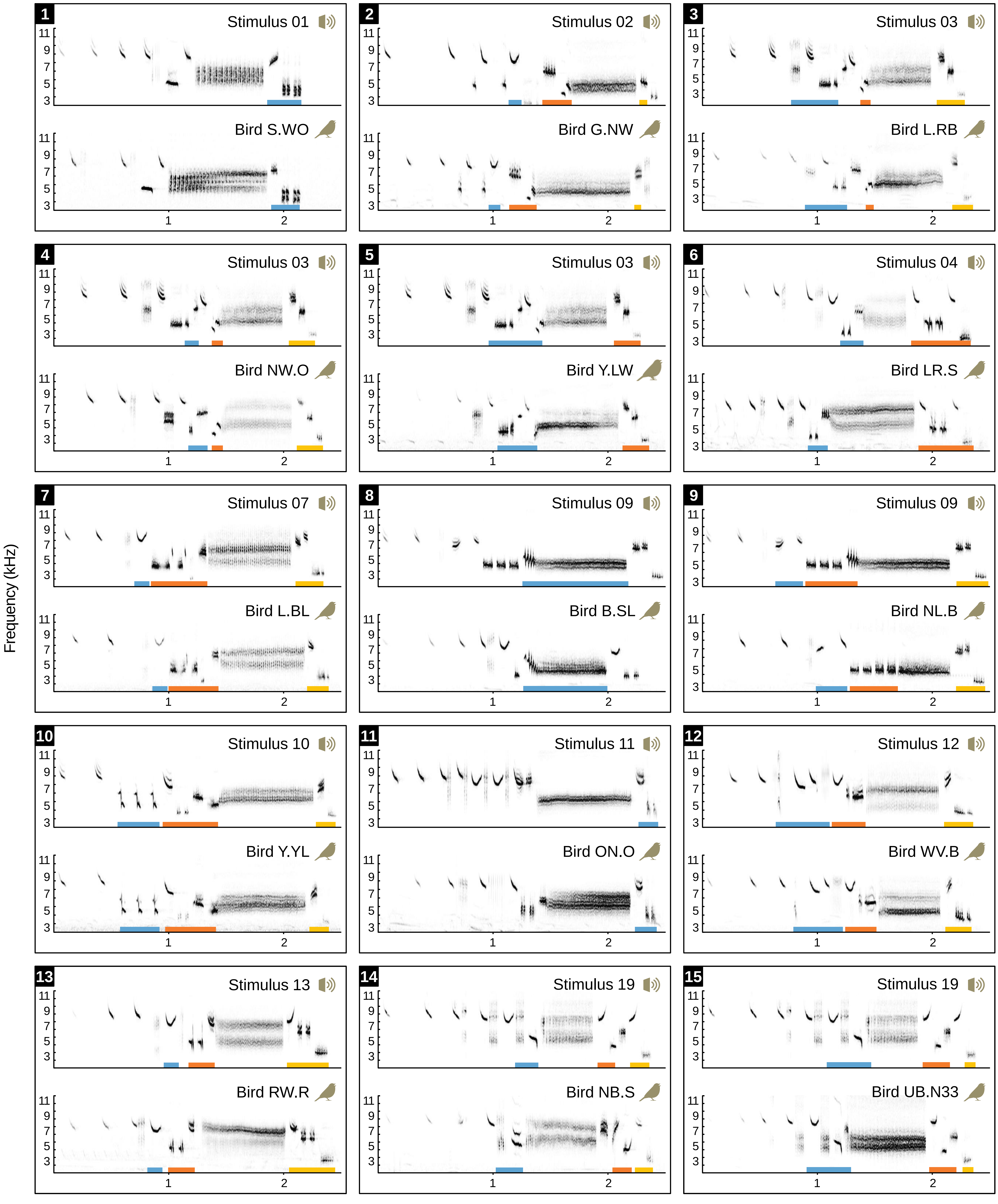

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Figure S3. Figure continues on next page.

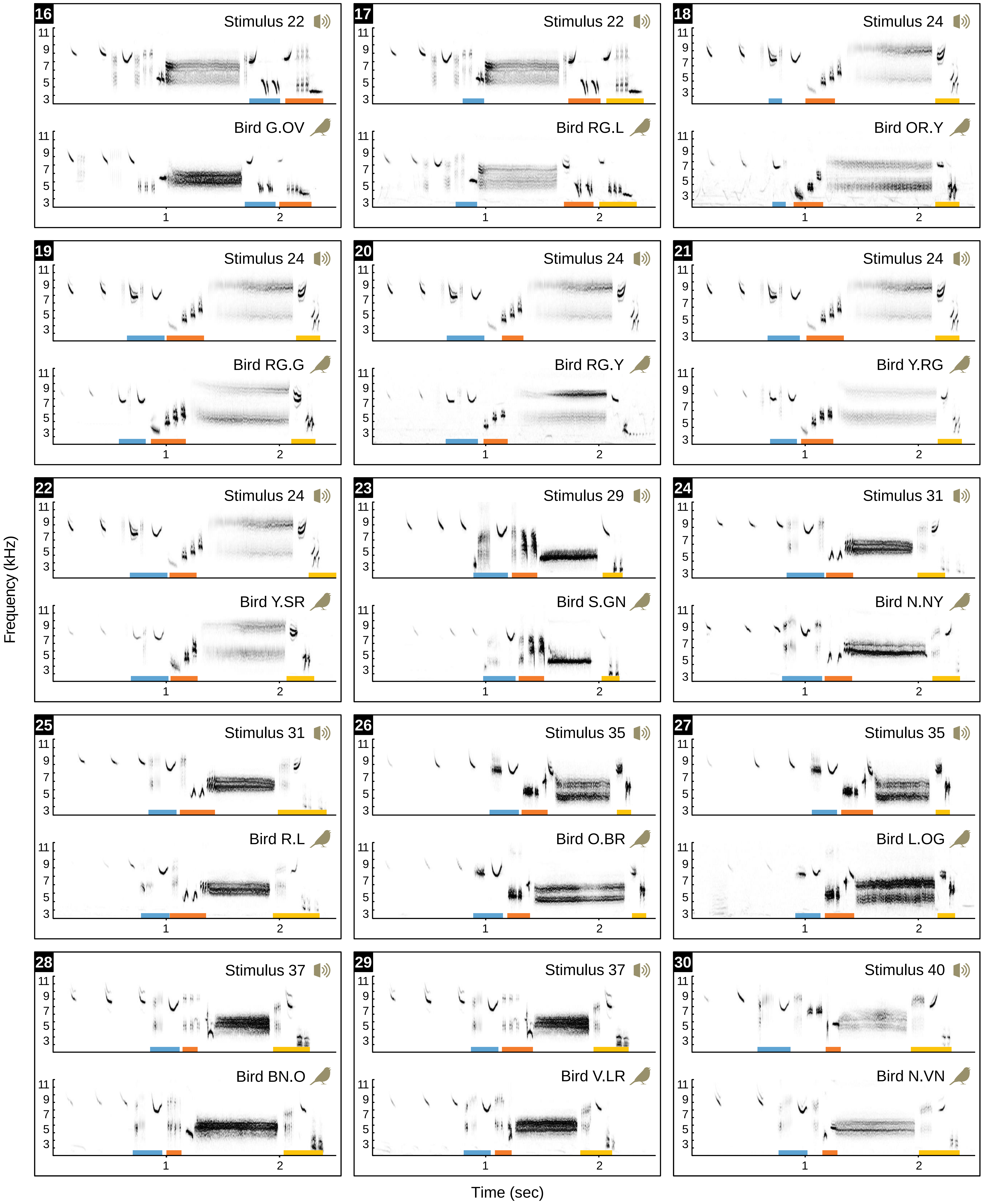

Figure S3. Thirty pairs of sound spectrograms showing songs of Savannah Sparrows that learned songs from experimentally simulated vocal tutors. Note: Figure spans two pages. Related to Figure 1.

Colored bars show distinctive phrases that match between the playback-simulated vocal tutors and the birds that learned those songs. Birds are named for the combination of colored bands on their legs.

Most male Savannah Sparrows produce a single song type as an adult, but approximately 2% of males produce two song types as adults [20]. Male LR.S (spectrogram pair 6, above) produced two songs that both matched experimental stimuli: stimulus 04 (shown) and stimulus 07 (not shown).

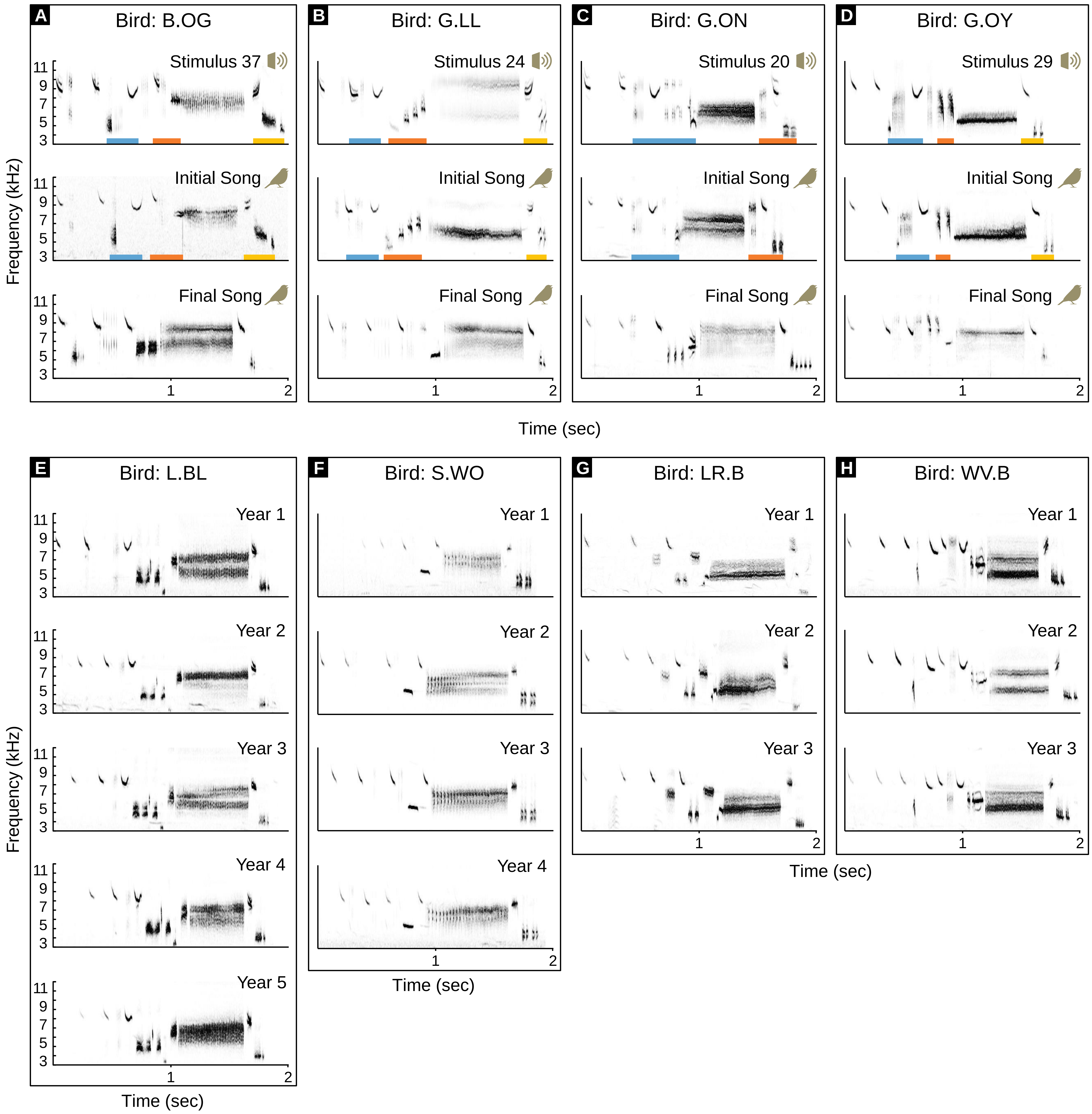

Figure S4. Sound spectrograms of Savannah Sparrow songs recorded over time, revealing overproduction and attrition in the first breeding spring of some birds, and consistency thereafter. Related to Figure 1.

(A-D) Sound spectrograms of the songs of four birds that produced experimental songs only briefly. Early in their first breeding spring (middle row) these four birds produced songs that matched experimental stimuli (top row), but within two weeks of arrival from migration they rejected the experimental songs in favor of population-typical songs (bottom row), which they produced for the remainder of their lives. Colored bars show distinctive phrases that match between the birds' initial songs and playback-simulated vocal tutors. With respect to our test of the Re-exposure Hypothesis, three of these birds briefly sang summer-and-spring experimental songs, and one of these birds briefly sang a summer-only experimental song.

(E-H) Sound spectrograms of annual recordings of four of the longest-lived experimental subjects, showing that all components of songs remained consistent throughout birds' lives. Bird L.BL was recorded in 2014-2018; bird SW.O was recorded in 2015-2018; bird LR.B was recorded in 2015-2017; and bird WV.B was recorded in 2016-2018.

Table S1. Notes on longevity, changes in song, breeding behaviour, and sibling relationships for 34 Savannah Sparrows, revealing that all experimental birds maintained their song throughout their adult life and that most held territories, attracted mates, and reproduced. Related to Figure 1.

Bird [a]	Born	Died	Changes in song [d]	Notes on breeding behaviour	Notes on brothers [e]
First-generation tutees					
LB.L	2013	2018 [c]	Same song for 5 years	Held territory and reproduced for 4 years; died in breeding season 5	
NL.B	2013	2014	Same song for 1 year	Held territory and reproduced for 1 year	
Y.YL	2013	2014	Same song for 1 year	Held territory and reproduced for 1 year	
LR.S	2013	2014	Same song for 1 year	Held territory and reproduced for 1 year	
G.NW	2014	2016	Same song for 2 years	Held territory and reproduced for 2 years	
S.WO	2014	*Still alive*	Same song for 4+ years	Held territory and reproduced for 4+ years	
Y.LW	2014	2015	Same song for 1 year	Held territory and reproduced for 1 year	
NW.O	2014	2016	Same song for 2 years	Held territory and reproduced for 2 years	
L.RB	2014	2017	Same song for 3 years	Held territory and had a mate in 2015-2017; no data on breeding	
NB.S	2015	2016	Same song for 1 year	Held territory and reproduced for 1 year	
WV.B	2015	*Still alive*	Same song for 3+ years	Held territory and reproduced for 3+ years	
RW.R	2015	*Still alive*	Same song for 3+ years	Held territory and reproduced for 3+ years	One brother: YW.O sang population-typical song
ON.O	2015	2017 [c]	Same song for 2 years	Held territory and reproduced for 2 years; died in breeding season 2	
UB.N33 [b]	2015	2016 [c]	Same song for 1 year	Held territory for 1 month; died in breeding season 1	
N.NY	2016	2017	Same song for 1 years	Held territory and reproduced for 1 year	Two brothers: R.L sang experimental song; B.OG sang population-typical song [f]
N.VN	2016	2017	Same song for 1 years	Held territory in 2017; no data on mate or breeding	Two brothers: N.NY sang experimental song; B.OG sang population-typical song [f]
O.BR	2016	*Still alive*	Same song for 2+ years	Held territory and reproduced for 2+ years	
R.L	2016	2017	Same song for 1+ years	Held territory and reproduced for 1 year	
S.GN	2016	*Still alive*	Same song for 2+ years	Held territory and reproduced for 2+ years	
V.LR	2016	2017	Same song for 1 year	Held territory and reproduced for 1 year	
BN.O	2016	2017	Same song for 1 year	Held territory and had a mate in 2017; no data on breeding	
.O	2016	*Still alive*	Same song for 2+ years	Held territory and reproduced for 2+ years	
B.SL	2017	*Still alive*	Same song for 1+ years	Held territory and reproduced for 1+ years	
G.OV	2017	*Still alive*	Same song for 1+ years	Held territory and reproduced for 1+ years	
O.	2017	*Still alive*	Same song for 1+ years	Held territory and reproduced for 1+ years	
R.GL	2017	*Still alive*	Same song for 1+ years	Held territory and reproduced for 1+ years	Two brothers: RG.G sang experimental song; SO.L sang typical song [f]
RG.G	2017	*Still alive*	Same song for 1+ years	Held territory and reproduced for 1+ years	Two brothers: RG.L sang experimental song; SO.L sang typical song [f]
RG.Y	2017	*Still alive*	Same song for 1+ years	Held territory and reproduced for 1+ years	
Y.RG	2017	*Still alive*	Same song for 1+ years	Held territory and reproduced for 1+ years	One brother: WG.L sang typical song
Y.SR	2017	*Still alive*	Same song for 1+ years	Held territory and reproduced for 1+ years	
Second-generation tutees					
B.LO	2016	2017	Same song for 1 year	Held territory and reproduced for 1 year	
UB.S19 [b]	2016	2017	Same song for 1 year	Held territory and reproduced for 1 year; died in breeding season 1	
Y.NW	2016	2017	Same song for 1 year	Held territory and reproduced for 1 year	
Y.OV	2017	*Still alive*	Same song for 1+ year	Held territory for 2+ months; no breeding partner as of July 2018	

[a] Birds are named for the combination of colored bands on their legs.

[b] Two birds were not banded (UB.N33 and UB.SP19). These birds were followed through time based on their individually distinctive song and their territory position.

[c] Whereas most birds died between breeding seasons (year of death is shown as the last year the bird was detected on the breeding grounds based on final observations in July 2018), three birds died during the breeding season: LB.L disappeared one month into his fifth breeding season (2018); ON.O disappeared two months into his second breeding season (2017); UB.N33 disappeared one month into his first breeding season (2016).

[d] Notes on changes in song are based on repeated recordings collected on a monthly and annual basis, indicating whether birds maintained experimentally-introduced songs throughout their lives.

[e] Among the 54 male banded nestlings that returned to breed in the study population between 2013 and 2018, there were 6 sets of brothers. In two cases both brothers sang population-typical song (not included in this table). In the remaining cases, one brother sang population-typical song and the remaining one or two brothers sang experimental song, as indicated. Note that bird B.OG learned a population-typical song after producing an experimental song for a brief period early in his first breeding season (see Figure S4).

[f] In the two cases of three brothers that were banded nestlings born to the same father, the fathers were themselves experimental subjects, an anecdotal result that raises the possibility that the propensity to learn non-local song might have a heritable basis: the father to brothers N.NY, R.L, and B.OG (born in 2016) was L.BL (born in 2013); the father to brothers RG.G, RG.L, and SO.L (born in 2017) was RW.R (born in 2015).