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Animal behaviour

Open-ended song learning in a hummingbird

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Vocal learning in birds is typically restricted to a sensitive period early in life, with the few exceptions reported in songbirds and parrots. Here, we present evidence of open-ended vocal learning in a hummingbird, the third avian group with vocal learning. We studied vocalizations at four leks of the long-billed hermit *Phaethornis longirostris* during a four-year period. Individuals produce a single song repertoire, although several song-types can coexist at a single lek. We found that nine of 49 birds recorded on multiple days (18%) changed their song-type between consecutive recordings. Three of these birds replaced song-types twice. Moreover, the earliest estimated age when song replacement occurred ranged from 186 to 547 days (mean = 307 days) and all nine birds who replaced song-types produced a crystallized song before replacement. The findings indicate that song-type replacement is distinct from an initial early learning sensitive period. As half of lekking males do not survive past the first year of life in this species, song learning may well extend throughout the lifespan. This behaviour would be convergent to vocal learning programmes found in parrots and songbirds.

1. Introduction

Vocal learning is a rare ability found in a handful of mammalian taxa, including humans, and in three avian orders: songbirds, parrots and hummingbirds. Human and avian vocal development share characteristics at the neural, developmental and social level [1,2]. Both humans and birds have evolved specialized brain areas for vocal learning, require auditory feedback to improve their own vocalizations during a sensitive period early in development and are predisposed to species-specific vocalizations [1,2]. A few bird species also share with humans the ability to modify their vocalization late in life [3]. The striking resemblance between human and avian systems has contributed to our understanding of the ecological and social factors shaping the evolution of vocal learning [4].

Vocal learning generally occurs during a sensitive period in which juveniles memorize and develop species-specific vocalizations. In songbirds, this period can be identified by the production of subsong: imprecise copies of tutor songs with irregular timing and frequency, analogous to babbling in humans [3,5]. At the end of the sensitive period, birds are able to produce stereotyped songs that resemble those of adults, known as crystallized song [3]. The extent of the process varies markedly among species [5], ranging from closed-ended learners with a single sensitive period in the first year of life [6] to open-ended learners in which the ability to modify their repertoires remains open or reopens seasonally in adulthood [7].

Research in this area has focused on songbirds and parrots and the vocal ontogeny of hummingbirds remains largely unexplored. To our knowledge, there is a single study on the subject performed on the Anna's hummingbird *Calypte anna*; it found a developmental pattern analogous to closed-ended learning typical of many songbirds [8]. Some have proposed that hummingbirds have rudimentary song learning strategies [9], but the similarity of hummingbird

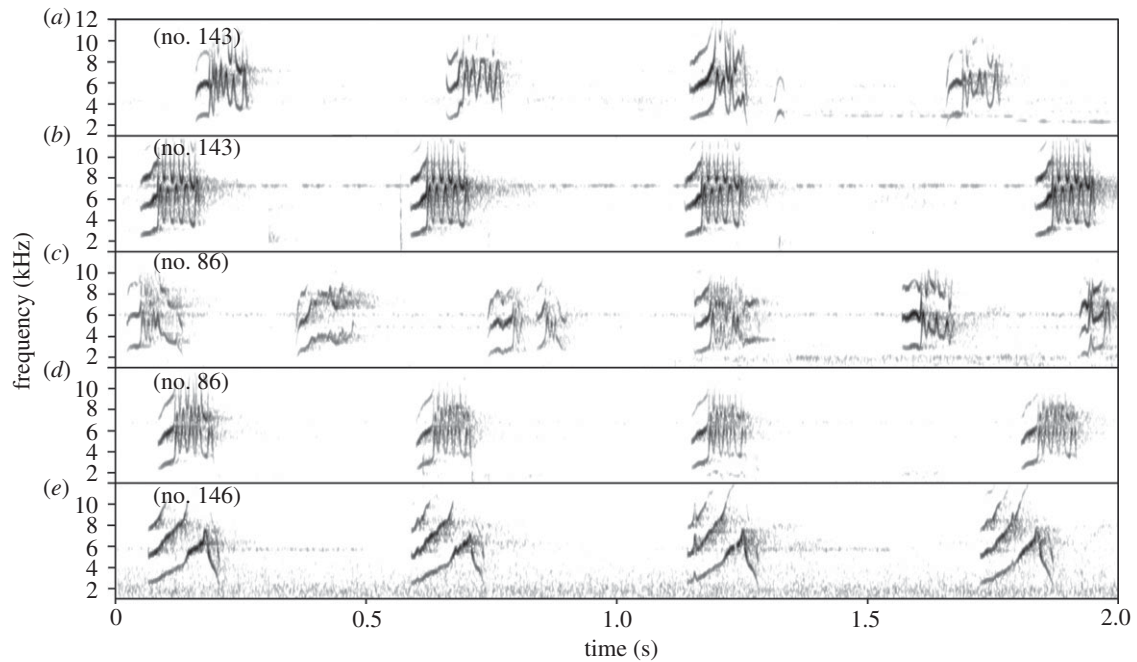


Figure 1. (a,c) Spectrogram of subsongs and (b,d) crystallized songs of individual long-billed hermits nos. 143 and 86. (e) Crystallized song that occurred at the earliest estimated age (151 days; no. 146).

neural mechanisms to those in parrots and songbirds [10,11] suggests that a comparable complexity and diversity in song learning programmes might be expected.

Here, we document the timing of vocal ontogeny in free-living, long-billed hermits *Phaethornis longirostris*. This hummingbird has a lek mating system in which males have repertoires of single song-types produced only on leks [12]. Interestingly, previous work has shown that several song-types can coexist in a single lek, song-types are not shared among leks and there is a high turnover rates of song-types within leks [12], suggesting social influences on the learning of songs and potentially open-ended learning.

2. Material and methods

Fieldwork was conducted during four breeding seasons (2010–2013) at La Selva Biological Station, Costa Rica (10°25' N; 84°00' W). Birds from four leks (SUR, Sendero Sura; CCL, Camino Circular Lejano; CC, Camino Central and LOC, Lindero Occidental) were mistnetted and marked with numbered bands plus a flag with unique colour combinations on the back and chest or attached to leg bands [13]. Behavioural observations and territory mapping were used to ensure that all males in a lek were sampled in a given period. We made observations on singing and territorial behaviour of marked individuals from 5.20 to 10.30 in the morning, when the peak of activity occurs. Perches of singing males were mapped using a 20 × 20 m grid system as reference. Then, a map of lek territories based on an initial observation period was used to identify areas for further intensive netting and observations to identify all territorial males. We recorded individuals on a Marantz PMD 660 and a Sennheiser ME 67 microphone or a Sennheiser ME62 microphone on a parabolic antenna (53 cm diameter). Birds at SUR and CCL were recorded in four breeding seasons, whereas birds at CC and LOC were recorded during three and two seasons, respectively.

We determined the developmental phase of songs (subsong versus crystallized) by visual inspection of spectrograms. Subsongs are identified by greater variability in timing and spectrographic structure (figure 1a,c) when compared with crystallized songs

(figure 1b,d,e). We further tested this assumption by comparing via cross-correlation the spectral similarity of five pairs of consecutive subsongs versus five pairs of crystallized songs from each of two individuals. Nested ANOVA was used with song phase nested within individual. Spectrograms and cross-correlations were done using Seewave [14] in the R environment [15].

We classified song-types produced in every recording at the four leks by visual inspection of spectrograms. This preliminary analysis identified apparent song-type replacement events at two leks (CCL and SUR). Song-types from these two leks were then independently classified by four observers; song-types of 114 songs from 34 individuals were classified in this manner. Inter-observer reliability of song-type discrimination within and across individuals was evaluated by comparing scores from observers, using κ statistic for categorical data [16]. When two or more song-types were identified within an individual with 100% observer agreement, that individual was identified as one who replaced songs.

Individuals' ages at the time of recording were estimated to infer the extent of the learning sensory period. These calculations were facilitated by two pieces of information: (i) juveniles (up to six months) can be distinguished by the extent of corrugations in the base of the maxilla that gradually disappear as the bird matures [17] and (ii) hatching occurs no earlier than 15 January and no later than 1 August in this population (M. Araya-Salas unpublished data; [13]). Hence, we conservatively estimated the date of birth for juveniles as exactly six months prior to date of capture. If this date fell within the non-breeding season (1 August to 15 January), we assumed the bird was born in 15 January of the year when first captured. Conversely, for birds that were already adults in their first capture, we assumed they were at least six months old. For individuals who replaced song-types, the last day when birds were recorded singing their first song-type was assumed to be when song replacement occurred. These calculations allowed a conservative estimation of the earliest age when song replacement occurred, as well as the latest age when juveniles acquired crystallized songs.

3. Results

We recorded 38,964 songs in 320 recordings from 98 adults at four leks (average: 11 males per lek yr⁻¹; range 4–21). Songs

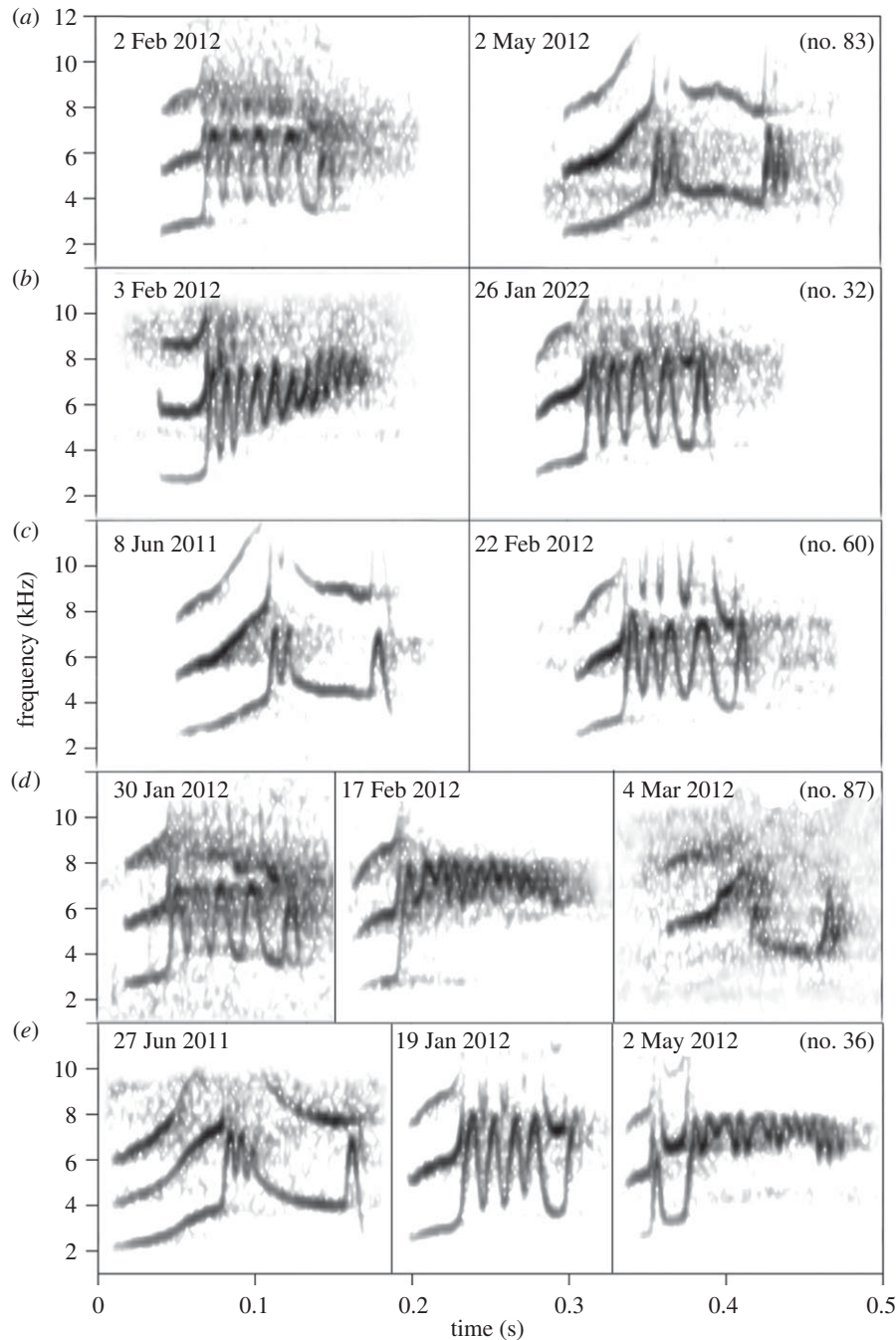


Figure 2. Songs from long-billed hermits that replaced song-types. Recording dates are in the upper left corner and bird ID numbers in parentheses.

were classified to type with strong inter-observer reliability both within ($\kappa = 0.92$; $p < 0.0001$) and across individuals ($\kappa = 0.77$; $p < 0.0001$). All adults produced only a single song-type per recording session in all 320 recordings (average songs recorded per session: 122; min: 12; max: 402). Fifteen additional birds were juveniles when first captured and were recorded subsequently in the same year. The average oldest age at which these birds presented a crystallized song was 151 days (min: 83; max: 192; figure 1e). Two of these birds were observed producing sub-songs (nos. 83 and 143; figure 1a–d). Spectral similarity was significantly higher in crystallized songs than in subsongs (Nested ANOVA: $F_{1,16} = 22.92$, $p < 0.001$, figure 1a–d) and the estimated ages at which subsongs were produced were 109 days (no. 143) and 174 days (no. 146).

We detected song-type replacement between recording sessions in nine out of the 49 birds (18%) recorded in at least two recording sessions (average 131 days apart; min: 3; max: 402; figure 2). Three of these birds replaced their song-type

twice (nos. 36, 83 and 87) for a total of 12 different replacements. All birds who replaced song-types produced a crystallized song before replacement. These birds belonged to the SUR lek except no. 18, who was recorded at CCL and found next year at SUR, where it adopted a local song-type. The average earliest estimated age that song-type replacement occurred was 307 days (min: 186; max: 547). The average time lapse between the first recording of crystallized song and the day of song-type replacement was 53 days (min: 1; max: 236; excluding birds in which the date when first recorded was used as the date of replacement). Two of these replacements occurred while the birds were in at least their second year (nos. 36 and 60: both 547 days old; figure 2c,d). No significant differences in time lapse between first and last recording (ANOVA, $F_{1,47} = 0.19$, $p = 0.66$), age at last recording (ANOVA, $F_{1,47} = 0.089$, $p = 0.76$) or number of recordings were found between replacing and non-replacing birds (ANOVA, $F_{1,47} = 0.70$, $p = 0.41$).

Three lines of evidence support the conclusion that these events represent true song-type replacement by males with a single-song repertoire and not sampling of different songs from a larger repertoire. First, we never found an individual producing more than one song-type in a given recording. Second, individuals typically used the same song-type across different sessions. From the 40 individuals recorded in at least two sessions that did not replace song-types, the average accumulated songs recorded was 711. We recorded 4365 songs in 25 different sessions during 4 years for one individual and 1850 songs in 11 sessions during 3 years for another. These birds produced only a single song-type across all recordings. Third, no individual who replaced song-types was later recorded singing its previous song-type after replacement.

There appear to be two sources for the new songs produced by birds that replaced songs. In 10 replacements, birds adopted a song-type already present on the lek. Individuals nos. 18 and 87 adopted a song-type that appeared at the lek after their hatch date, when the birds were already 275 and 186 days old, respectively. In two events, birds replaced their song-type with a novel song-type not previously found in the lek and presumably invented by these birds (nos. 36 and 95).

4. Discussion

We documented song-type replacement in a considerable fraction of lekking male hummingbirds over a wide range of ages (approx. 6–18 months old). Estimated dates when subsongs and the earliest crystallized songs occurred place song crystallization at the end of the fifth month of life. Given that all song replacements occurred after a crystallized song was already produced, the observed replacements appear to be distinct from an initial sensitive period. Moreover, the oldest ages at which song-type replacement were found were after the first year. By definition, the sensitive period of learning is limited to the first year of life for closed-ended song learners [3], including the only other hummingbird in which song development has been studied [8]. Taking into account our conservative approach for calculating age and date of song-type replacement, we expect that it occurs at even older ages in long-billed hermits. As half of lekking males do not survive past the first year [12], the ability to acquire new songs may remain open throughout the short lifespan of this species.

The appearance of new songs late in life could result from either an open-ended learning programme [3] or a closed-ended learning programme where birds learn multiple

songs early and later switch between already learned songs [18]. The latter would require learning of several songs at their own lek or neighbouring leks and production in subsequent seasons. Several lines of evidence suggest this is not the case. First, two birds replaced their initial song with a song-type that first appeared long after they produced a crystallized song and two others produced a song-type not previously found at any lek. Second, throughout this study and a previous four-year long study [12], song-types have never been observed at more than one lek, suggesting transfer of song-types between leks is rare or non-existent. Finally, only 4.1% of the birds observed at least twice were found in two different leks, and only one bird (approx. 0.6%) was observed singing at two leks. Hence, song re-expression is unlikely to explain the replacement of song-types seen in these hummingbirds.

Our study also provides insight into other aspects of song ontogeny in long-billed hermits. The absence of song exchange among leks [12] suggests that the two adopted song-types previously unheard at the lek were either created *de novo* or generated by modification of song-types present in the lek. This ability is also suggested by the appearance of three new song-types produced by newcomers who have not previously held territories elsewhere (M. Araya-Salas unpublished data). Hence, song learning seems to range from faithful copying to improvisation or invention of new variants. There is diversity in the complexity of song in hummingbirds, from the simple single-note songs produced by long-billed hermits to the phonologically and syntactically complex songs produced by the wedge-tailed sabrewing (*Campylopterus curvipennis*) [19]. This study indicates that vocal learning programmes in hummingbirds also are more diverse than previously thought. The occurrence of adult song learning in hummingbirds, an ability previously documented only in songbirds and parrots, suggests a parallel diversification of song learning strategies among independent evolutionary pathways.

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Data accessibility. Recordings were deposited in the Dryad repository doi:10.5061/dryad.vd61h.

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