

6-2014

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Early song discrimination by nestling sparrows in the wild

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Abstract

Songs play an important role in premating isolation in birds. However, when songs are learned, experience with both conspecific and heterospecific songs in early life could lead to the development of both mixed songs and mixed preferences. One way that such learning errors can be prevented is if birds can discriminate between songs of different species prior to learning and preferentially memorize conspecific songs. Prior captive studies have shown that white-crowned sparrows, *Zonotrichia leucophrys*, are able to discriminate songs early in the process of song memorization, after about 10 days since hatching. I studied early song discrimination in wild golden-crowned sparrows, *Zonotrichia atricapilla*, the sister species of white-crowned sparrow. The two species occur syntopically in the study population, and therefore sparrows were expected to selectively learn conspecific songs. Playbacks of songs elicited vocal responses from nestlings as young as 6 days old, and nestlings responded more to conspecific songs than to songs of the sympatric white-crowned sparrow subspecies. These results suggest that conspecific song templates exist at the onset of song memorization, and this could allow golden-crowned sparrows to learn the songs of their own species correctly despite syntopy with their sister species. I suggest that studying species recognition prior to learning could provide fresh insights into the evolution of reproductive isolation and song divergence.

Keywords: auditory template, birdsong, predisposition, species recognition, *Zonotrichia*

The production and recognition of species-specific signals is critical to the evolution of reproductive isolation (Coyne and Orr, 2004; Price, 2008). In many birds and other species, prior experiences affect both mating preferences and sexual display traits. Thus, learning plays an important role in the evolution and maintenance of divergent populations (Irwin and Price, 1999; Servedio et al., 2009; Verzijden et al., 2012). Critically, the influence of learning on evolution (e.g. whether learning promotes or inhibits speciation) depends on whether mechanisms exist to ensure that learning is restricted to conspecific cues (Lachlan and Feldman, 2003; Lachlan and Servedio, 2004; Laland, 1994; Olofsson et al., 2011; Servedio et al., 2009). In the absence of mechanisms that restrict learning to conspecific cues, learning could lead to the breakdown of assortative mating through the acceptance of heterospecific mates (Grant & Grant, 1997) or convergence in courtship traits due to heterospecific copying (Sorjonen, 1986).

Selective learning has been intensively studied in the context of song learning in birds. In many species, the ability of birds to memorize songs is heightened during the period after fledging (i.e. the “sensitive period”), although the duration of this sensitive period can vary across species, populations and experimental protocols (Catchpole & Slater, 2008). During

this period, young birds will typically hear the songs of many species that share the habitat. Thus, in order to produce species-typical songs later in life, young songbirds must avoid learning heterospecific songs. Because songs are often used for territoriality and courtship, birds learning mixed-species songs may be less successful in gaining mates, or may attract heterospecific mates (reviewed in Slabbekoorn & Smith, 2002). Females that do not sing in courtship also learn songs (Casey and Baker, 1992; Riebel, 2003), and selective learning may also be important for mate choice: those with mixed preferences may be more likely to choose heterospecific mates (e.g. Grant & Grant, 1997). Thus, overly permissive learning (i.e. learning both conspecific and heterospecific song) may be maladaptive because of sexual selection or selection against hybrids, and mechanisms to restrict learning to conspecific song elements are expected to evolve. Consistent with this prediction, laboratory studies have repeatedly shown that songbirds preferentially learn the songs of their own species over those of sympatric species (Braaten and Reynolds, 1999; Marler, 1970, 1990; Marler and Peters, 1977; Thorpe, 1958).

There are a few potential mechanisms that could promote selective song learning. Selective learning could be guided by song templates that allow naïve individuals to identify con-

specific songs prior to learning (Marler, 1990); these song templates could be genetically inherited ("innate template": Marler, 1990) or acquired from fathers early on in life through sexual imprinting (ten Cate, Vos, & Mann, 1993). In addition, naïve individuals may be able to learn from conspecific tutors reliably through predictable patterns of social interactions (Baptista & Petrinovich, 1984). These general mechanisms are not mutually exclusive, and there is experimental evidence for the roles of both song templates and social interactions (Baptista and Petrinovich, 1984; Marler and Peters, 1977). A critical test for the song template model (either innate or acquired very early in life) is to show that young birds are able to discriminate between conspecific and heterospecific songs by the time they begin song memorization. In white-crowned sparrows, *Zonotrichia leucophrys*, experiments in captivity have shown that young fledglings (11–20 days old) preferentially respond to songs of conspecifics over those of sympatric heterospecifics (Nelson and Marler, 1993; Soha and Marler, 2001; Whaling et al., 1997). Because the sensitive period for song learning in this species is thought to occur after the young leave the nest around 10 days posthatch (Marler, 1970; Marler and Tamura, 1964; Nelson et al., 1995), these results suggest that song templates exist prior to song memorization. Here, I adapt this behavioral assay for the field to investigate song discrimination prior to song memorization in the sister species of the white-crowned sparrow: the golden-crowned sparrow, *Zonotrichia atricapilla*.

Golden-crowned sparrows and white-crowned sparrows are sister species (Carson and Spicer, 2003; Weckstein et al., 2001; Zink and Blackwell, 1996) that share sympatric breeding ranges in western North America. While there are occasional reports of hybrids (Miller, 1940), the two species are not known to maintain any hybrid zones. These two species sing distinct songs, but they share some key features that are known to be important in song learning of white-crowned sparrows. For example, white-crowned sparrows preferentially learn songs that contain a whistle (Soha & Marler, 2000), a feature that is shared across the two species (Figure 1). However, there is no evidence that individuals in sympatry sing mixed songs. The lack of mixed or heterospecific song as well as the establishment of reproductive isolation between these closely related species could be driven by the evolution of mechanisms to ensure selective learning. Here, I test the hypothesis that a song template exists before the period of song memorization in golden-crowned sparrows by determining whether they can discriminate between songs of conspecifics and songs of sympatric white-crowned sparrows during the nestling stage.

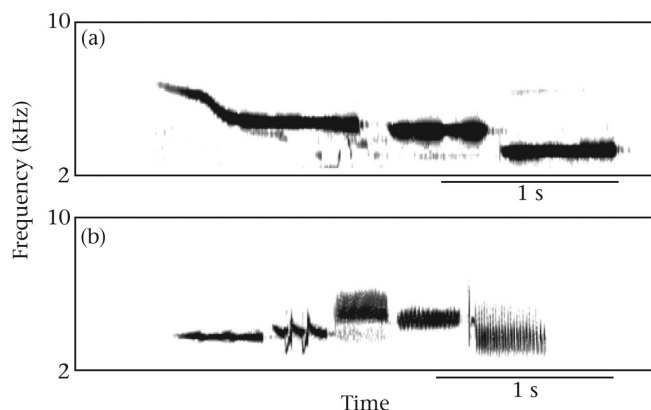


Figure 1. Spectrogram of songs of (a) golden-crowned sparrow and (b) Gambel's white-crowned sparrow.

Methods

Study System

I studied golden-crowned sparrows at Hatcher Pass, Alaska, U.S.A. (61°46'N, 149°13'W) in June–July 2012. At this site, golden-crowned sparrows are syntopic (i.e. they co-occur in the same habitat) with the Gambel's subspecies of white-crowned sparrows (*Z. leucophrys gambelii*). Golden-crowned sparrows defend territories against conspecifics, but interspecific aggression is rare (Shizuka & Hudson, n.d.). The territories of the two species overlap considerably, and nestlings are likely to hear the songs of both conspecific and heterospecific neighbors. No mixed-species pairs have been detected at this population ($N = 60$ golden-crowned sparrow nests in 2012–2013).

Nests ($N = 11$ nests used for this study) were found during the incubation or nestling stages. Nests found during incubation were checked daily to determine the hatching date for each individual. Hatch date (day 0) was the first day that an individual was seen to have completely emerged from the egg (due to hatching asynchrony, some eggs hatched on the second day). For nests found during the nestling stage, I estimated hatching day using feather length (see below). Individual chicks were marked using nontoxic markers until day 6, at which point they were banded with U.S. Fish and Wildlife-issued leg bands.

Playback Stimuli

Song recordings were collected in the field using a solid state recorder (Marantz PMD-660, 16-bit depth, 48 kHz sampling rate) with a shotgun microphone (Sennheiser ME67). Playback stimuli were constructed using Raven Pro 1.3 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.), saved as a .wav file, and played back using an iPod Touch. Each 2 min track consisted of a single song repeated 12 times at 10 s intervals. Each track was high-pass filtered above 1 kHz and standardized for root-mean-squared amplitude. I prepared six playback tracks for each treatment, each consisting of a song from a different individual (see Supplementary Figure S1). The conspecific and heterospecific playback tracks were presented as paired sets (e.g. stimulus "a" was always matched with stimulus "b" in Figure S1), and each chick from the same brood listened to a different stimulus set. I used a balanced design so that each stimulus set was used roughly an equal number of times. All playback songs were recorded away from the experimental site. For white-crowned sparrows, songs were recorded from the Gambel's subspecies throughout its range in Alberta, British Columbia, Canada, and Alaska in 2011. For golden-crowned sparrows, all songs were the typical dialect in Alaska, recorded more than 100 km away from the study site in 2011.

Nestling Playback Protocol

Playback experiments were conducted on day 6 ($N = 4$), day 7 ($N = 8$) or day 8 ($N = 17$) after hatching. For the five nestlings with unknown hatch day, experiments were conducted when the length of the longest exposed primary feather corresponded with the average of chicks at 7 or 8 days old. Each nestling was placed individually in a portable pet carrier outside of the focal territory, and song stimuli were broadcast at standardized volume (~60 dB at 1 m) from a speaker (iHome Audio, iHM60) set directly outside the pet carrier. The speaker and pet carrier were partially covered with a tarp to reduce the volume of playback sound that could be heard by other birds, and I aborted the experiment if any adult sparrows approached the experimental set-up. The aborted trials are not

included in the sample sizes given here. Between trials, chicks were kept in separate bird bags and held by an assistant out of earshot from the playback. After all trials were completed, the chicks were returned to the nest.

Each nestling received two treatments in separate trials: a golden-crowned sparrow (conspecific) treatment and a white-crowned sparrow (heterospecific) treatment. Each trial consisted of 1 min of preplayback white noise, 2 min of playback and 2 min of postplayback white noise. Trials were separated by at least 5 min. Eighteen of 34 nestlings (53%) listened to the golden-crowned sparrow track first. The number of chirps that the nestlings produced during each time period was noted during the experiment. For all analyses, I calculated the response as the total number of chirps produced during the playback and postplayback periods.

Statistical Analysis

For all analyses, I used generalized linear mixed model (GLMM) approach with the function “glmer” in the R package “lme4” (Bates, Maechler, & Bolker, 2012). I first tested for the effect of presentation order on nestling responses to songs by using the number of chirps as the dependent variable, treatment type and presentation order as fixed effects (there was no interaction effect between treatment type and presentation order). I included the stimulus set and individual nested within nest as random effects. Having found a significant effect of presentation order (see Results), I restricted subsequent analyses to the first trial for each individual. To test for the response to conspecific and heterospecific playbacks, I used either the number of chirps or a binary response (1 if chirped, 0 if no chirp) as the dependent variable, treatment type and feather length as fixed effects and stimulus set and nest as the random effects. For all analyses, I tested the fixed effects using a likelihood ratio test. The model used Gaussian or binomial error depending on the response variable used (i.e. number of chirps or binary response, respectively). Because the residuals of the model did not conform to the normality assumption when using the number of chirps as the response variable, I further confirmed these results using a Mann-Whitney *U* test.

Ethical Note

The study was conducted under a U.S. Federal Bird Banding Permit (number 23759) and a Special Use Permit from Alaska State Parks. The experimental protocol was approved by the Institutional Animal Care and Use Committee of the University of Chicago (ACUP number 71393). Because the experiment caused disturbance to the nest, my assistants and I minimized nest visits by taking all nestlings from the nest in a single visit and conducting multiple trials simultaneously in separate locations at least 200 m apart. While outside the nest, each chick was kept in a separate bird bag and kept warm using human body heat. No pairs abandoned the nest during our trials, and we visited the focal territories over the next 1–5 days to confirm that adults were feeding nestlings or fledglings.

Results

Effect of Presentation Order

There was a significant effect of presentation order on nestling chirp responses (likelihood ratio test, LR: $\chi^2_1 = 11.0$, $P < 0.001$): nestlings were more likely to respond in the second trial (Figure 2). The presentation order effect was likely due to a carryover of their response during the first trial. Supporting this claim, nestlings that responded to conspecific songs in the





<u>First trial</u>			<u>Second trial</u>		
Conspecific			Heterospecific		
Response	No. nestlings		Response	No. nestlings	
Yes	7		Yes	6	
			No	1	
No	11		Yes	3	
			No	8	
<hr/>					
Heterospecific			Conspecific		
Response	No. nestlings		Response	No. nestlings	
Yes	1		Yes	1	
			No	0	
No	15		Yes	12	
			No	3	

Figure 2. Numbers of nestlings responding to different treatments in two sequential trials. Of those that responded to the conspecific song in the first trial (7 of 18), most (6 of 7) also responded in the second trial with heterospecific song. Most nestlings (15 of 16) failed to respond to the heterospecific song in the first trial, but most of those (12 of 15) responded to the conspecific song in the second trial. The statistical analyses presented in the Results take into account the intensity of response (number of chirps) and include random effects (individual nested within nest).

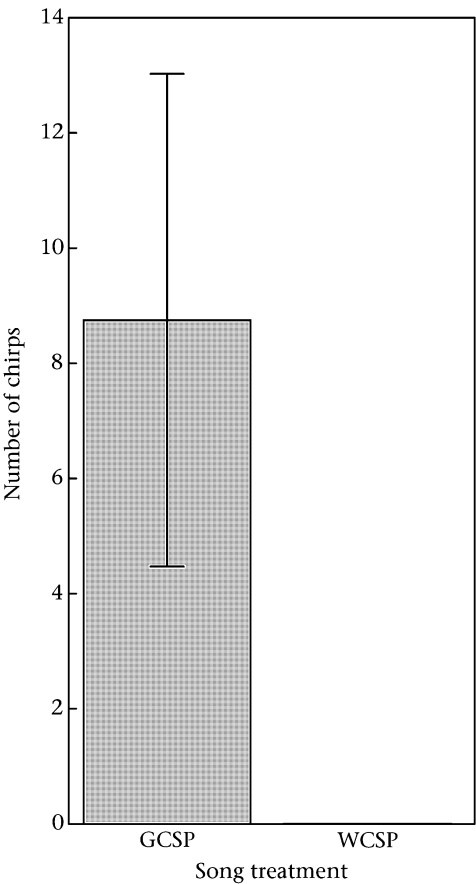


Figure 3. Number of chirps given by golden-crowned sparrow nestlings in response to songs of their own species (GCSP) and to songs of the sympatric subspecies of white-crowned sparrows (WCSP).

first trial (7 of 18 nestlings) responded more to heterospecific songs in the second trial than those that did not respond to conspecific song in the first trial (LR: $\chi^2 = 11.5$, $P < 0.001$). I could not make the same comparison for nestlings that heard the heterospecific songs in the first trial (16 nestlings) because only one individual responded during this first trial. Because of the strong carryover effect across trials, I restricted subsequent analyses to the first trial for each chick. I also excluded trials in which the nestling chirped during the preplayback period ($N = 4$), as this could also cause a carryover effect into the playback period. However, the main results were the same regardless of whether these trials were excluded.

Responses to Conspecific and Heterospecific Songs

Golden-crowned sparrow nestlings chirped more to conspecific songs than to songs of white-crowned sparrows (Mann-Whitney U test: $U = 154$, $N_1 = 18$, $N_2 = 16$, $P = 0.014$; Figure 3). However, only nestlings past a certain developmental stage (measured as the length of the longest primary feather) produced chirps, even to conspecific songs. Overall, there was a significant interaction between playback treatment and feather length on the number of chirps produced by the nestling (LR: $\chi^2 = 4.8$, $P = 0.03$). Using a binary response index (chirp response versus no chirp), golden-crowned sparrow nestlings with longer feathers (i.e. more developed) were more likely to respond to conspecific song (LR: $\chi^2 = 9.2$, $P = 0.002$; Figure 4), but they were no more likely to respond to white-crowned sparrow songs ($\chi^2 = 0$, $P = 1$; Figure 4).

Discussion

This study provides experimental evidence that golden-crowned sparrow nestlings respond to the songs of conspecifics more than to the songs of their sympatric sister species, the white-crowned sparrow. Nestling responses can be induced before the nestlings fledge, between 6 and 8 days after hatching. These results suggest that the ability to discriminate songs precedes the period of sensitivity for song learning, which generally begins around the time of fledging (about 10 days posthatch) in white-crowned sparrows (Marler, 1970; Petrinovich, 1985). The timing of fledging is the same in golden-crowned sparrows, and I make the assumption here that the timing of the sensitive period is similar to that of white-crowned sparrows. Moreover, I found that the probability of response to playbacks was a function of developmental stage (i.e. feather length). This result may reflect the development of the physiological mechanisms of the chirp response rather

than the cognitive capacity for song recognition: nestlings may be capable of song discrimination much earlier than this behavioral assay could detect. Methods to measure physiological responses (e.g. heart rate, metabolic rate: see Dooling & Searcy, 1980) rather than behavioral responses could help identify the precise function of early song discrimination by decoupling the cognitive process from the physiological constraints on the production of behavioral responses.

Song discrimination at the beginning of song memorization has been shown in laboratory settings for two species: white-crowned sparrows (Nelson and Marler, 1993; Soha and Marler, 2001; Whaling et al., 1997) and swamp sparrows, *Melospiza georgiana* (Dooling & Searcy, 1980). (The idea was tested in a third species, the song sparrow, but the results were inconclusive.) These experiments targeted birds that had been taken from the wild as nestlings and kept in isolation until 11–20 days old. The present study shows that such song discrimination can be detected even earlier, while the birds are still in the nest, and that such experiments can be conducted in the wild. This experimental procedure is minimally invasive because the playback experiments can be conducted in less than 15 min per nestling and does not require nestlings to be held for longer periods. Thus, this experiment could be replicated easily across populations and species, providing new insights into the evolution of song templates.

Behavioral assays for early song discrimination in the wild could also provide new avenues for the study of species recognition. To date, most studies of species recognition in birds have used territorial responses of adult males or copulation solicitation displays in females as measures of discrimination. However, these responses are potentially confounded by ecological context and the effects of prior experiences. For example, relative abundance of conspecifics and heterospecifics in a population may affect the benefits of excluding heterospecifics in a territorial setting or courting heterospecific mates (Ord et al., 2011; Reeve, 1989). Similarly, prior experience with conspecific or heterospecific individuals of the opposite sex can affect mate recognition (Dukas, 2008; Hebets, 2003; Kozak and Boughman, 2009; Kozak et al., 2011; Svensson et al., 2010; Verzijden and ten Cate, 2007). Playback experiments to naïve juveniles allow us to study species recognition in a different context: recognition of conspecific tutors for learning. Thus, comparing responses by nestlings and adults could help provide new insights into the current debate over what species recognition is and how it evolves (Mendelson & Shaw, 2012).

Song learning involves both innate and learned components (Marler, 1997), and a major challenge is to determine whether early song discrimination represents a purely innate component, or whether birds learn to recognize songs during the first week of life. Previous studies have argued that early song discrimination and learning predispositions are based on an innate template for song learning (Marler, 1990; Nelson and Marler, 1993). This study does not provide definitive evidence for innate or learned song discrimination: although nestlings were only 1 week old, they could have learned to differentiate conspecific and heterospecific songs during this first week of life. A true test of an innate song template requires cross-fostering or acoustically isolating birds beginning at the egg stage; otherwise, very early experience could be used to form an early song template. This requirement is rarely met in song tutoring experiments in sparrows: in most cases, birds are taken as nestlings from the wild. However, in a few studies, offspring taken from the nest as eggs showed learning predispositions (Konishi, 1985; Marler and Peters, 1977). In a particularly compelling case for innate recognition of species-specific vocalizations, brood parasitic brown-headed cowbirds, *Molothrus ater*, are able to discriminate “chatter” calls of their own

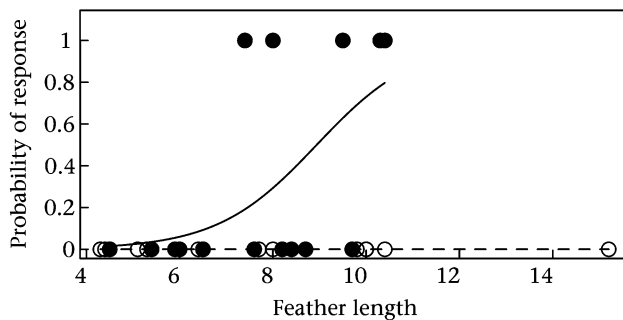


Figure 4. Relation between feather development in golden-crowned sparrow nestlings and their likelihood of response to conspecific song (black circles, solid line) and to white-crowned sparrow song (white circles, dotted line). Lines are logistic regression fits.

species from other heterospecific vocalizations despite being reared by a foster species (Hauber, Russo, & Sherman, 2001). Evidence suggests that the innately recognized species-specific calls allow cowbirds to then identify appropriate tutors for song learning. Thus, there is at least some evidence for innate song templates in certain songbird species, and it may be a general component of song learning.

There are also some arguments against the importance of innate song templates. Most prominently, social interactions have been shown to be critical in facilitating song learning in white-crowned sparrows: access to live heterospecific tutors can override pre-existing song templates and promote heterospecific learning (Baptista and Petrinovich, 1984, 1986). Such social influence could potentially begin in the nestling stage. While some experimental data show that altricial nestlings have reduced sensory capabilities (Khayutin, 1985), more recent evidence suggests that nestling birds are sensitive to various acoustic cues early on. For example, nestlings can differentiate between alarm calls of different species (Davies et al., 2004; Madden et al., 2005) or even different types of alarm calls of their parents (Suzuki, 2011). Altricial birds can even learn components of vocalizations from mothers while still in the egg (Colombelli-Négrel et al., 2012). This growing evidence for discrimination and learning in the nestling stage in altricial birds leaves open the possibility that some cues heard during the nestling stage could influence the selectivity of song learning. Thus, it remains unclear whether song discrimination in older nestlings is evidence for innate song recognition or the influence of very early social experience. Further study involving cross-fostering design could potentially elucidate the role of innate components of song learning.

The results of this study have important implications for the maintenance of divergent songs between sympatric sister species. When closely related species come into contact, courtship signals could diverge as a consequence of reproductive character displacement (Grant and Grant, 2010; Kirschel et al., 2009; Seddon, 2005), or converge when there is no selection against heterospecific copying (Haavie et al., 2004; Laiolo, 2012; Secondi et al., 2003; Sorjonen, 1986; Tobias and Seddon, 2009; Vokurková et al., 2013). We currently lack a mechanistic explanation for these contrasting patterns of song divergence versus convergence; the presence or absence of early song discrimination could be one such mechanism that determines whether cultural traits diverge or converge. For some populations of white-crowned sparrows, the species-specific cue responsible for preferential learning (the introductory whistle), a song feature shared across all members of the species, is used as a cue for selective learning (Soha & Marler, 2000). There are several key song features that reliably differ between white-crowned and golden-crowned sparrows (e.g. frequency modulation in introductory whistles, the presence of complex notes), and it would be interesting to determine whether song features that consistently differ among species are important for early discrimination. Similarly, it would be of interest to determine whether white-crowned sparrow nestlings in populations that are sympatric with golden-crowned sparrows show elevated levels of early song discrimination compared to allopatric populations.

Early song discrimination also has important implications for the maintenance of reproductive isolation between these two sympatric sister species. In birds, early experience affects future mate choice in a process termed sexual imprinting (Grant and Grant, 1997; Immelmann, 1972; ten Cate and Vos, 1999). Importantly, the time window of learning during sexual imprinting continues long after the young bird leaves the nest (Casey & Baker, 1992; Clayton, 1989; ten Cate et al., 1993). Thus, the development of discrimination prior to fledg-

ing could reduce learning errors in species recognition, particularly in sympatric populations of sister species. An important question is whether such mechanisms to reduce learning errors evolve as a consequence of reinforcement (Servodio et al., 2009). While there are no currently recognized hybrid zones between golden-crowned sparrows and white-crowned sparrows, patterns of mitochondrial introgression suggest that hybridization may have occurred in the recent past (Weckstein et al., 2001). The evolution of early song discrimination and subsequent bias in learning could have been a consequence of reinforcement during this period of past hybridization. While these scenarios remain speculative at this time, further work on phylogeography and gene flow through time, coupled with careful work on species recognition in early life, could elucidate how cognitive processes evolve and in turn, how cognitive processes influence evolution.

Acknowledgments — I thank Jack Andreasen, Dylan Carter and Melissa Kardish for valuable assistance in the field. I thank T. Price, D. Wheatcroft, D. Hooper, E. Scordato, N. Bloch, E. Hudson and E. Greig for comments and discussions during the early phase of this work. This work was supported by the Chicago Fellows Postdoctoral Program and approved by the Institutional Animal Care and Use Committee of the University of Chicago. There are no conflicts of interest to be declared.

Supplementary Material is given following the References.

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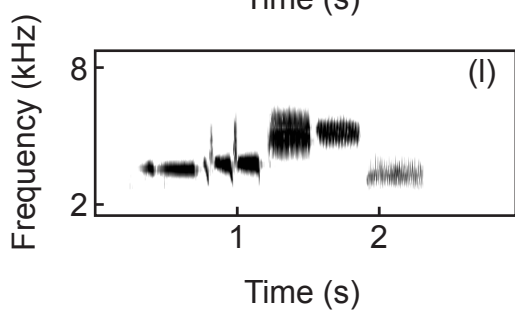
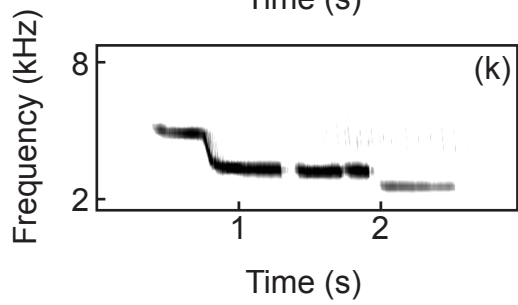
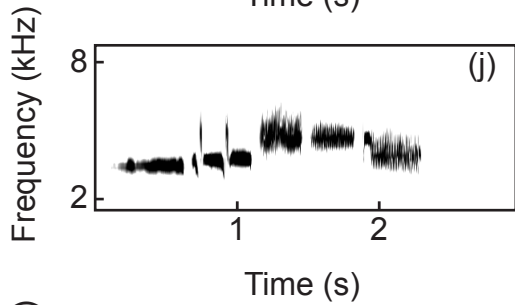
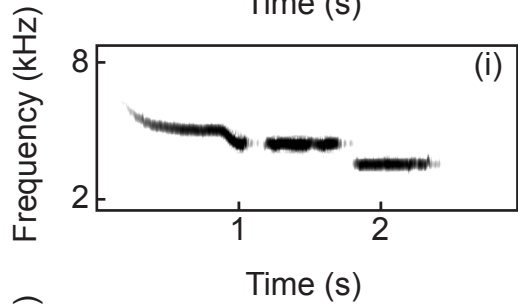
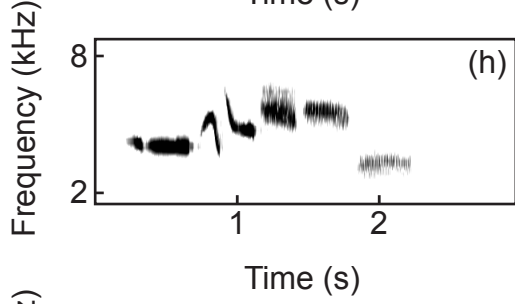
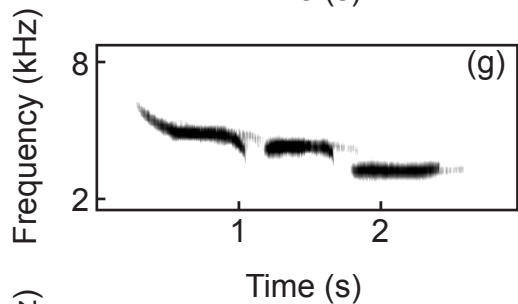
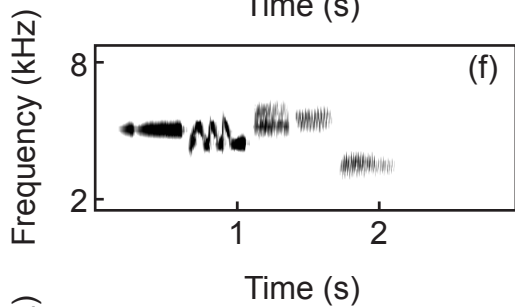
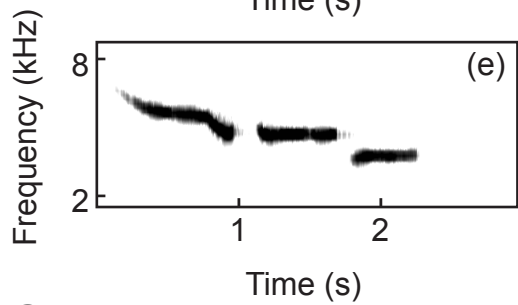
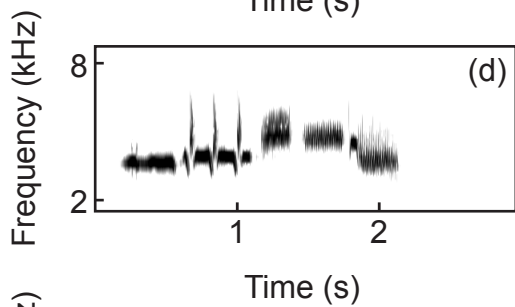
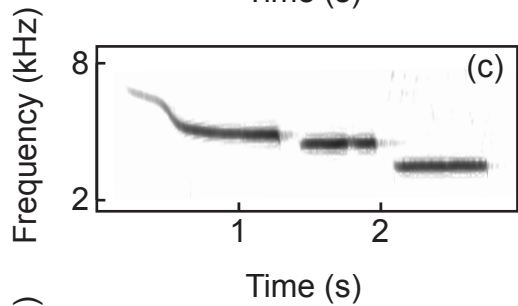
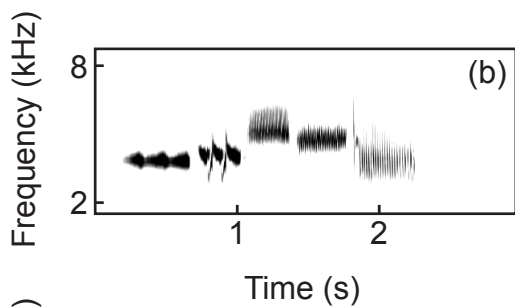
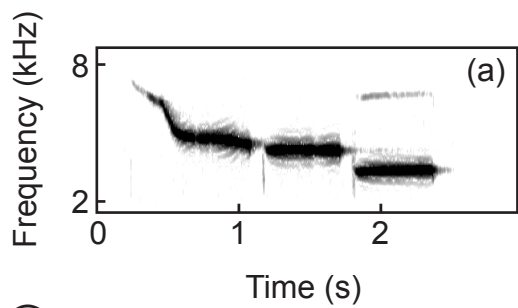


Figure S1. Sonagrams of (a, c, e, g, i, k) golden-crowned sparrow and (b, d, f, h, j, l) white-crowned sparrow songs used for playback stimuli.