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Introductory whistle is sufficient for early song recognition by golden-crowned sparrow nestlings

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Many songbird species have a predisposition to learn conspecific songs, suggesting song learning may be guided by an innate auditory template. Evidence for such a template includes preferential response to conspecific song in early life, even before song learning begins. A prime example of an innate cue for selective song learning is the introductory whistle of white-crowned sparrows, *Zonotrichia leucophrys*. The songs of its sister species, the golden-crowned sparrow, *Zonotrichia atricapilla*, also contain an introductory whistle, which differs in structure from that of white-crowned sparrows. Here we tested the ability of nestling golden-crowned sparrows in a sympatric population to discriminate between conspecific and heterospecific songs based on introductory whistles alone, prior to the onset of song learning. Golden-crowned sparrow nestlings responded with more chirps to playbacks of conspecific whistles than to heterospecific (white-crowned sparrow) whistles, and they responded similarly to full conspecific songs and conspecific whistles alone. We suggest that the introductory whistle alone is sufficient for song recognition in the golden-crowned sparrow. We discuss similarities and differences in the role of the introductory whistle between these sister taxa, and how this divergent song phrase may share a role in species recognition in both sister species. Identifying the cues underlying song recognition prior to song learning could be key to understanding the evolution of behavioural isolation between closely related songbird species.

Organisms across many taxa must learn species-appropriate behaviours based on experience with conspecifics. Learning is involved in the development of mate preferences in a wide array of organisms, including spiders, damselflies, guppies and many bird species (reviewed in Verzijden et al., 2012). When behaviour relating to mate attraction is learned, however, organisms may mistakenly learn to produce or prefer heterospecific signals in lieu of conspecific signals (Baptista & Morton, 1981; Slagsvold, Hansen, Johannessen, & Lifjeld, 2002). Thus, selection should favour learning strategies that minimize heterospecific learning when there are fitness costs to learning the wrong species' signals. For example, selection to minimize learning errors may explain the time constraints (Nottebohm, 1969) and innate conspecific preferences (Marler & Peters, 1977; Slagsvold et al., 2002) that often characterize song learning in oscine songbirds. This suggests that there are heritable mechanisms that direct cognitive processes at the earliest stages of song learning.

The auditory template model (Marler, 1990) posits that an innate, crude template exists in newly hatched songbirds, against which learners compare songs of potential tutors. Such a template should constrain the learning process and increase the probability that only conspecific song elements are learned, even when juveniles are exposed to both conspecific and heterospecific tutors. Prior studies on several songbird species have demonstrated species discrimination abilities in fledglings based on their behavioural and physiological responses to song playbacks (Dooling & Searcy, 1980; Nelson & Marler, 1993), and even in nestlings prior to the onset of song learning (McFarlane, Söderberg, Wheatcroft, & Qvarnström, 2016; Shizuka, 2014). These studies suggest that songbirds are already able to recognize conspecific song before learning begins, as the auditory template hypothesis predicts.

What song elements might young songbirds use to recognize conspecific songs prior to song learning and how might the use of particular song elements evolve? In general, an ideal auditory cue for species recognition might consist of a simple acoustic element that is invariant within species and absent in other sympatric species (Nelson, 1989). Existing evidence suggests that specific notes or phrases, or the relative frequency between song phrases that fit these criteria are used for species recognition (Becker, 1982;

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Colombelli-Négrel et al., 2012; Hauber, Russo, & Sherman, 2001; Hurly, Ratcliffe, & Weisman, 1990). In the case of a song learning cue, an additional criterion is that the cue must be discriminable to young birds before the song learning process begins. During the initial stages of population divergence, the cues involved in species recognition are likely to be shared in recently diverged taxa. If selection against hybridization favours species recognition, then evolution may proceed in two ways. First, one species may shift to using a new feature for species recognition (e.g. the feature that is most divergent between the taxa). Alternatively, the divergent taxa may use the same feature for recognition, but the feature itself may diverge. Testing these hypotheses requires a system in which the specific features involved in song recognition are already known and there is evidence of reproductive isolation between recently diverged taxa.

The New World sparrow genus *Zonotrichia* is exceptionally well studied and presents an ideal opportunity to explore the evolution of song recognition. The white-crowned sparrow, *Zonotrichia leucophrys*, has been the subject of particularly intensive research and many details of its song learning and recognition programme have been resolved (reviewed in Soha, 2017). In this species, the introductory whistle of its song has been implicated to play a critical role in song learning. The flat introductory whistle is species-universal: white-crowned sparrows show geographical variation in song, but all subspecies and regional dialects begin with a pure-tone whistle (Soha & Marler, 2000). This whistle is an innately encoded component of song: young male white-crowned sparrows raised in isolation produce simple songs consisting primarily of whistles (Marler, 1970). Moreover, the introductory whistle serves as a cue to memorize syllables that follow it; Soha and Marler (2000) showed that young male white-crowned sparrows preferentially memorized heterospecific syllables following a conspecific whistle, rather than conspecific syllables without an introductory whistle. Finally, recent genetic and behavioural evidence from two subspecies suggests that there is fine-scale variation in the duration of this introductory whistle between subspecies, and that individuals respond more strongly to songs of their own subspecies (Lipshutz, Overcast, Hickerson, Brumfield, & Derryberry, 2016).

The white-crowned sparrow shares its range with its sister species, the golden-crowned sparrow, *Zonotrichia atricapilla*, and the two species are commonly found in the same breeding habitat near tree-line in parts of Alaska and northwestern Canada. The two species are reciprocally monophyletic in all existing phylogenies (Weckstein, Zink, Blackwell-Rago, & Nelson, 2001; Zink, 1982). The scant record of hybrid individuals (Miller, 1940; Morton & Mewaldt, 1960) and presence of fixed nuclear genetic differences (Weckstein et al., 2001) suggest that there is strong reproductive isolation between these two species. Shared mitochondrial haplotypes between at least some populations of golden-crowned and white-crowned sparrows indicates that they may have experienced gene flow in the past, but the subspecies of white-crowned sparrow, *Z. l. gambelii,* that is sympatric with golden-crowned sparrows in the breeding season does not show this pattern (Weckstein et al., 2001). Thus, the existing evidence suggests that these are sister species, with little to no ongoing hybridization in areas of sympatry.

Like white-crowned sparrows, golden-crowned sparrows show considerable geographical variation in song across their ranges, but all begin their song with a species-characteristic introductory whistle (Shizuka, Lein, & Chilton, 2016). However, whereas white-crowned sparrow introductory whistles have no frequency modulation, the golden-crowned sparrow introductory whistle always contains descending frequency modulation in all dialects (Fig. 1; Shizuka et al., 2016). Moreover, golden-crowned sparrows can distinguish between conspecific song and the songs of sympatric white-crowned sparrows at 6–8 days of age (Shizuka, 2014). Thus, both white-crowned and golden-crowned sparrows seem to share two features: a species-universal introductory whistle and the ability to recognize conspecific songs at the onset of song learning. This raises the question: is the introductory whistle sufficient for song recognition at the earliest stages of life? We addressed this question by conducting a series of playback experiments of conspecific and heterospecific songs and whistles to golden-crowned sparrow nestlings.

METHODS

We conducted this study at Hatcher Pass Management Area, Alaska in June and July, 2015. This golden-crowned sparrow population is sympatric with white-crowned sparrows, and nestlings are exposed to both species' songs in the nest. We found golden-crowned sparrow nests by following females during nest building, incubation or feeding of nestlings.

Whistle stimuli were prepared using Raven Pro 1.4 (Cornell Lab of Ornithology, 2011) by extracting a single whistle from the full songs of each of five unique male white-crowned sparrows (heterospecific treatment) and five golden-crowned sparrows (conspecific treatment), as shown in Fig. 1. All golden-crowned sparrow songs were recorded in another population within the local dialect region, but more than 100 km away and thus the recorded individuals were unfamiliar to the subjects. White-crowned sparrow songs were from the local subspecies, *Z. l. gambelii*, and likewise recorded away from the study site. The extracted whistles were standardized for root mean squared amplitude. All stimuli files were sampled at 48 kHz and 16 bits per sample. Whistles were repeated every 10 s for 2 min, and 1 min of white noise was added before and after the 2 min of whistles.

Based on results of a prior study (Shizuka, 2014), we conducted experiments when approximately 6 mm of the longest primary feather was exposed in all nestlings, which corresponded to 7–8 days after hatching. All chicks from a nest were removed at once and held in an insulated cloth lunchbox when not being tested or measured. Nestlings were placed individually in a portable pet carrier (26 × 27 × 48 cm) and randomly assigned to either a heterospecific whistle treatment ($N = 7$), conspecific whistle treatment ($N = 7$), heterospecific full song treatment ($N = 13$), or conspecific full song treatment ($N = 16$). Songs were played back from iPod Nano mp3 players (Apple) using iHome model IM60 and IM70 (SDI Technologies, Inc., Rahway, NJ, U.S.A.) speakers placed outside of the pet carrier. Playback volume was standardized to 60 dB SPL at 1 m from the speaker. If a chick was chirping during trial set-up, we waited until it stopped chirping to begin the trial; if the chick then resumed chirping during the pre-track period of white noise at the start of the trial, this was recorded as the pre-track response.

We measured the behavioural response as the number of chirps during the 2 min whistle presentation period, and measured the pre-track response as the number of chirps during the 1 min pre-playback period of white noise. Chicks assigned to either the conspecific or heterospecific whistle treatment or the full heterospecific song treatment that showed no response to their treatment playback subsequently received a full local conspecific song treatment as a positive control. Chicks that showed no response to the positive control ($N = 8$) were excluded from the analysis (raw data provided as Supplementary Material).

Data were analysed with a linear mixed model using the function lmer in the package lme4 (Bates, Maechler, Bolker, & Walker et al., 2015) implemented in R v.3.2.4 (R Core Team, 2016). We first generated a global model including chirp response as the response variable, with pre-track response, exposed primary feather length (a proxy for developmental stage) and two levels of

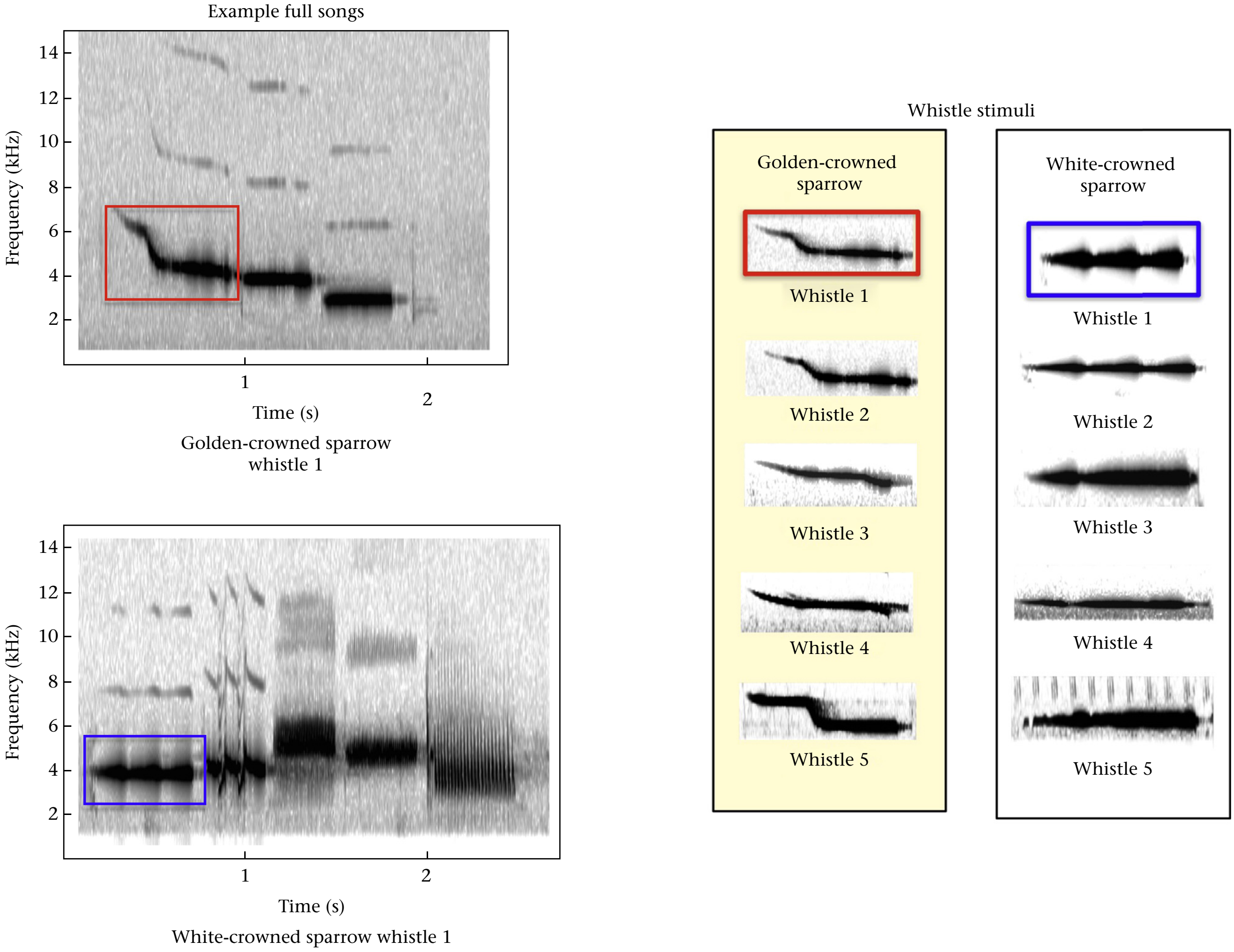

Figure 1. Whistle stimuli were created by highlighting the first note (introductory whistle) of golden-crowned and white-crowned sparrow song, then copying and pasting the whistle into a separate song file in Raven Pro 1.4. See Methods for full details. Whistle stimuli were created from the songs of five different individuals for each species.

treatment (species (conspecific or heterospecific); whistle versus full song) as fixed effects, and nest of origin and the identity of the playback stimulus as random effects. We initially included an interaction term between the two treatment types, but this term was not significant and was dropped from subsequent analysis. We then used model selection with Akaike's information criterion corrected for small samples (AICc) to determine the top models with ΔAICc <4. We used model averaging with these top-ranked models to determine the effects of fixed terms from our global model using the MuMIn package (Bartoń, 2016).

We conducted post hoc tests to further confirm our findings. To do this, we compared the effect of species recognition in the full song treatments and the whistle treatments independently. For the whistle-only treatments, we did not include the playback stimulus as a random effect, as only one track was used more than once. In each case (full song comparison and whistle-only comparison) we fitted the full model and then used likelihood ratio tests to assess the significance of a model while excluding the species treatment effect.

Given our statistical results showing song recognition by whistle alone (see Results), we measured two basic spectral and temporal features of the whistles used for playback stimuli in order to quantify the most prominent species difference in each of these features. We measured the duration of the whistle as well as the difference in peak frequency between the first 100 ms and the last 100 ms of this note using Raven Pro 1.4 (Cornell Lab of Ornithology, 2011).

Ethical Note

This work was conducted under a U.S. Geological Survey banding permit (no. 23759) and an Alaska State Parks Special Park Use Permit, and with the approval of the Institutional Animal Care and Use Committee of the University of Nebraska – Lincoln (IACUC project no. 1277). Chicks were returned to the nest immediately after testing for that nest concluded. No nests were abandoned after our trials.

RESULTS

All three of our top models using AICc model selection retained both the pre-track response and species as fixed terms (Table 1), and these variables were the most important in explaining variation in chick responses (Table 2). In contrast, chicks' responses to playbacks of full songs and playbacks of only the introductory whistle did not differ significantly (Table 2). The length of the exposed feather, used as a proxy of developmental stage, had little effect on chick responses (Table 2).

In this study, we included the chirping rate of the nestling prior to the playback to capture the potential effect of variation in

Table 1
Top models (ΔAICc <4) from model selection procedure

Terms	*df*	Log likelihood	AICc	ΔAICc	Weight
Intercept + pre-track + species	6	−177.55	369.4	0.00	0.52
Intercept + pre-track + whistle/fullsong + species	7	−177.12	371.4	2.00	0.19
Intercept + feather + pre-track + species	7	−177.55	372.3	2.87	0.12

Table 2
Estimates of effects of fixed terms using model averaging (including models with AICc <4)

Term	Estimate	SE	*Z*	*P*	Importance
Intercept	15.57	5.12	2.94	0.003	N/A
Pre-track response	1.11	0.32	3.31	<0.001	1
Species	−11.01	3.64	2.93	0.003	1
Whistle vs full song	−5.48	5.83	0.91	0.36	0.23
Feather	0.04	0.95	0.04	0.97	0.15

nestling condition, motivation or environmental factors that may influence response level. This is because a prior study with this species showed that nestlings that chirped in response to a playback were much more likely to respond to a subsequent playback trial >5 min later, suggesting that nestling behaviour prior to the trial may affect response levels (Shizuka, 2014). As suspected, the chirp rate prior to the playback was an important predictor of nestling responses to playback, and our statistical analysis accounts for this effect. In contrast to Shizuka (2014), we did not detect an effect of developmental stage (using feather length as a proxy) on nestling responses. This is likely due to the fact that we used these prior results to intentionally conduct the playback experiment at a slightly later developmental stage when we had increased likelihood of eliciting responses.

To examine our specific hypothesis that species differences in whistles are sufficient for species recognition, we conducted post hoc tests using likelihood ratio tests. Golden-crowned sparrow nestlings receiving conspecific whistles chirped more than chicks receiving heterospecific whistles (likelihood ratio test: $\chi^2_1 = 4.69$, $P = 0.03$; see Fig. 2) and chirped more to full conspecific song than to full heterospecific song ($\chi^2_1 = 4.22$, $P = 0.04$).

In the playback stimuli we used, the introductory whistle of the two species consistently differed in at least two major features that do not overlap between species: whistle duration and frequency modulation. The golden-crowned sparrow whistles were longer in duration (mean = 0.96 s, range 0.82–1.16 s; white-crowned sparrow: mean = 0.48 s, range 0.40–0.54 s) and contained greater frequency modulation (mean = 1171.8 Hz, range 1171.8–2411.7 Hz; white-crowned sparrow: mean = 46.2 Hz, range 0–187.5 Hz) than the white-crowned sparrow whistles used in this experiment.

DISCUSSION

We found that golden-crowned sparrow nestlings respond differently to songs of conspecifics and their sympatric sister species, the white-crowned sparrow, confirming the results of a previous study (Shizuka, 2014). Moreover, we found that nestlings respond differently to playbacks of just the introductory whistles of these two species' songs, and their responses to whistle-only stimuli did not differ significantly from their responses to full songs. Our findings suggest that the golden-crowned sparrow introductory whistle, which is one of the features that reliably distinguishes golden-crowned sparrow song from that of its closest relative, is sufficient for nestling birds to perform song recognition. In white-crowned sparrows, male nestlings at this age (<10 days old) have not yet begun to learn their adult song (Marler, 1970). If these two species follow the same song-learning timeline, our results suggest that introductory whistles could act as an innately recognized cue that guides later song learning in golden-crowned sparrows.

We focused on the role of the introductory whistle in early song recognition for two reasons. First, the introductory whistle is

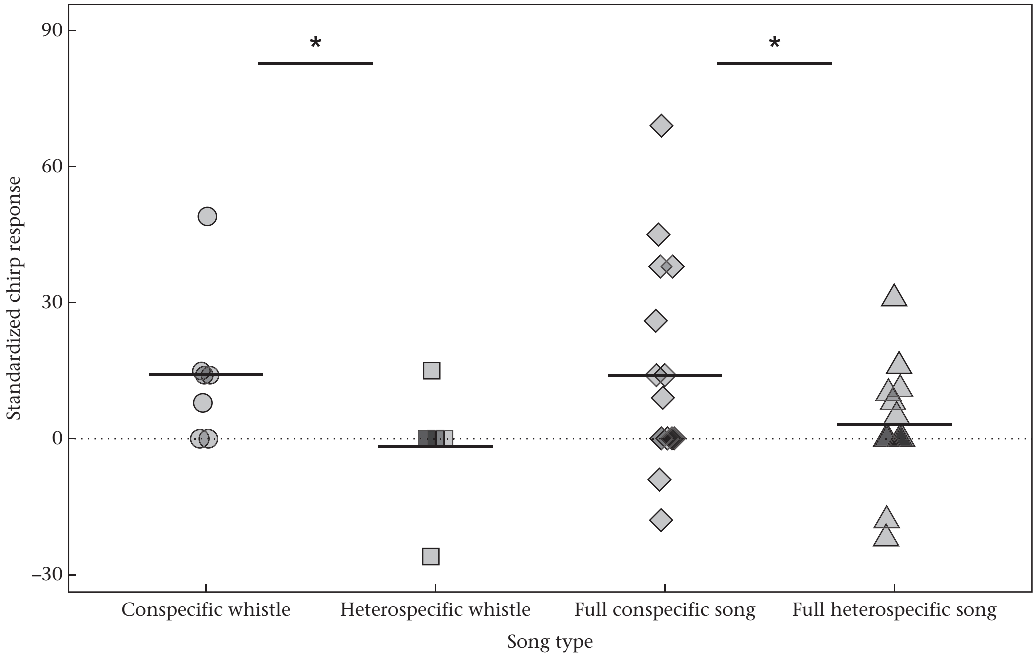

Figure 2. Standardized chirp response (number of chirps during the 2 min playback period, minus twice the number of chirps during the 1 min pre-playback period) of golden-crowned sparrows to each playback treatment. Darker colour indicates overlapping data points. Horizontal bars within each column represent the mean response for each treatment. Asterisks indicate significant ($P < 0.05$) differences due to treatment, as determined by likelihood ratio tests.

known to play a critical role in song learning in white-crowned sparrows: juvenile white-crowned sparrows are more likely to learn phrases of songs that begin with an introductory whistle (Soha & Marler, 2000). We discuss the relevance of our study in this context later. Second, while both species' songs vary geographically, the two species songs can be reliably distinguished by features of the introductory whistle alone, and thus this phrase could play a key role in species recognition. Moreover, Soha and Marler (2000) suggested that whistles may be particularly resistant to cultural evolution because they can be described with fewer parameters than other song elements, such as trills and note complexes, which may result in fewer opportunities for copying errors and slower cultural evolution. This could make the introductory whistle of golden-crowned and white-crowned sparrows particularly reliable as a means for species recognition. One prominent species difference is the spectral property of the introductory whistle: white-crowned sparrow whistles have constant frequency, while golden-crowned sparrow whistles always contain a descending frequency sweep (Fig. 1). This feature seems to be species-universal in each species, and reliably distinguishes the two species regardless of dialect (Shizuka et al., 2016). Moreover, the spectral features of the introductory whistle seem to be resilient to cultural evolution: Harbison, Nelson, and Hahn (1999) demonstrated that the introductory whistles in white-crowned sparrows remain stable over two decades while other song features changed, and Shizuka et al. (2016) likewise found no changes in golden-crowned sparrow introductory whistle forms over 15 years. In our playback stimulus set, the two species' songs differed in both the frequency modulation and the duration of the introductory whistle. We do not have quantitative data on whistle duration across all song dialects for both species at this time, so we could not determine whether this feature reliably distinguishes between species across all populations. However, a recent study showed that whistle duration alone could distinguish between subspecific songs in white-crowned sparrows (Lipshutz et al., 2016), suggesting that this feature may also play a key role in species recognition.

Although other song elements (e.g. the presence/absence of complex notes, buzzes and trills, number of syllables; see Fig. 1) could be used to distinguish between golden-crowned and white-crowned sparrows in our study population, many of these features vary across populations (e.g. some golden-sparrow dialects contain buzzes and trills; Shizuka et al., 2016). In this experiment, we did not test whether other acoustic elements could also be used for species recognition. Thus, while we can conclude that the introductory whistle alone is sufficient for species recognition, we cannot determine whether it is, in fact, the only cue used for species recognition at this early stage of life. Prior studies have shown that naïve fledgling white-crowned sparrows still recognize and respond strongly to all conspecific phrase types, not just whistles (Soha & Marler, 2001; Whaling, Solis, Doupe, Soha, & Marler, 1997), even though, without tutoring, they will not produce these additional elements themselves. Our results show that nestling golden-crowned sparrows, like fledgling white-crowned sparrows, are capable of distinguishing heterospecific from conspecific song based on whistles, but further study is needed to determine whether, like fledgling white-crowned sparrows, they are equally receptive to all conspecific song elements.

When comparing our results to previous studies in *Zonotrichia*, it is also important to note that our experiment was conducted on nestlings reared in the wild, where they were exposed to both conspecific and heterospecific songs, rather than raised in acoustic isolation. This issue of prior exposure is important to consider in light of the possibility that acoustic templates can be composed of both preactive templates, which are not affected by experience, and latent templates, which require exposure to be expressed (Marler, 1997; Soha, 2017). Moreover, although song learning is not thought to occur during the nestling period (Marler & Peters, 1987; Marler, 1970), it is possible that the amount of early exposure to conspecific versus heterospecific song plays a role in species discrimination in nestlings. If different nests are exposed to different amounts of heterospecific song at sympatric sites, it should be possible to determine whether this factor influences nestlings' ability to perform species recognition based on song.

Species discrimination using cues that are learned (e.g. the songs of oscine songbirds) can either facilitate or inhibit reproductive isolation, and predicting the effect of learning on speciation has been an active topic of research (Servedio, Sæther, & Sætre, 2009; Verzijden et al., 2012). The use of simple cues for early song recognition, such as the introductory whistle in *Zonotrichia* species, may be one mechanism that facilitates the evolution of behavioural isolation in songbirds through preferential learning of conspecific songs. Multiple lines of evidence suggest that reproductive isolation between white-crowned and golden-crowned sparrows is relatively well established, as there are very few reported instances of hybridization between the two species (e.g. Miller, 1940; Morton & Mewaldt, 1960) and phylogenetic studies support two distinct lineages with high confidence (e.g. Klicka et al., 2014). However, there is also evidence of mitochondrial haplotype sharing between the species despite clear divergence at nuclear loci (Weckstein et al., 2001). This pattern of mito–nuclear discordance suggests a potential history of hybridization and introgression following initial divergence of the two lineages (Weckstein et al., 2001). Combined with detailed knowledge of the song recognition and learning programmes in this system, the *Zonotrichia* sparrows offer an opportunity to investigate the evolution of song learning as it relates to species interactions.

White-crowned and golden-crowned sparrow nestlings both pay attention to the introductory whistle during early development, and the divergence in the acoustic features of the whistle seems to be sufficient to allow golden-crowned sparrow nestlings to distinguish species. Thus, the divergence of the acoustic feature, rather than divergence in the cognitive process of song recognition (e.g. using a different song feature) can maintain preferential learning of songs in this sympatric population. These results point to key questions about the cause and effect of trait divergence and reproductive isolation between golden-crowned and white-crowned sparrows. Did the introductory whistle form diverge between species due to selection against hybridization (due to reinforcement or reproductive character displacement), or did divergence in this key acoustic feature in allopatry (e.g. by cultural drift) facilitate isolation upon secondary contact? Moreover, did the importance of the introductory whistle in the song learning programme evolve as a consequence of selection against hybridization between these two species? One way to address these questions is by comparing the extent of introgression in different populations of golden-crowned and white-crowned sparrows. If the importance of the introductory whistle as a learning template is due to reinforcement and populations of golden-crowned sparrows have different histories of hybridization, we would expect greater discrimination against heterospecifics (based on whistles alone) in populations that have experienced gene flow. Clarifying the evolutionary history underlying the behaviour described here will allow us to begin to disentangle whether innate recognition templates are a prerequisite for, or an outcome of, sympatry between related species. More generally, continued studies of song recognition at the earliest life stages in passerines (Dooling & Searcy, 1980; McFarlane et al., 2016) may provide a clearer picture of the evolutionary causes and consequences of mechanisms underlying song learning.

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Supplementary Material

Supplementary data related to this article can be found at https://doi.org/10.1016/j.anbehav.2017.09.018.

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