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Interspecific song imitation by a Prairie Warbler

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ABSTRACT. Song development in oscine songbirds relies on imitation of adult singers and thus leaves developing birds vulnerable to potentially costly errors caused by imitation of inappropriate models, such as the songs of other species. In May and June 2012, we recorded the songs of a bird that made such an error: a male Prairie Warbler (*Setophaga discolor*) in western Massachusetts that sang songs seemingly acquired by imitating the songs of a Field Sparrow (*Spizella pusilla*). Another song type in the bird's repertoire was a near-normal Group A Prairie Warbler song, but the bird used this song in contexts normally reserved for Group B songs. Despite its abnormal singing behavior, the aberrant bird successfully defended a territory and attracted a mate that laid two clutches of eggs. Results of playbacks of the focal bird's heterospecific song suggested that neighboring conspecific males learned to associate the Field Sparrow-like song with the focal male, and responded to the song as if it were a Prairie Warbler song. Our evidence suggests that the focal bird's aberrant singing evoked normal responses from potential mates and rivals. If such responses are widespread among songbirds, the general failure of heterospecific songs, once acquired, to spread through populations by cultural transmission is probably not attributable to a lack of recognition by conspecifics of the songs of heterospecific singers.

RESUMEN. **Imitación interespecífica de canto en *Setophaga discolor***
El desarrollo del canto en aves canoras depende de la imitación del repertorio de los adultos y esto causa vulnerabilidad al desarrollo de errores costosos, causados por la imitación de modelos inapropiados, como la canción de otras especies. En mayo y junio de 2012, grabamos la canción de un ave que incorporó uno de estos errores: un macho de *Setophaga discolor*, en la parte oeste de Massachusetts, cuyo canto lo obtuvo imitando la canción de un individuo de *Spizella pusilla*. Otro tipo de canto, en el repertorio del ave, lo fue una canción más o menos normal en lo clasificado como para el grupo A, de su propia especie, pero el ave utilizaba este canto en el contexto normalmente reservado para lo clasificado como el canto de los grupos B. Pese a su canto anormal, el ave con la aberración defendió exitosamente su territorio y atrajo una hembra que produjo dos camadas de huevos. El resultado de exponer con grabaciones del canto de esta ave, a vecinos, sugiere que estos aprendieron a asociar, el canto parecido al de *Spizella pusilla*, con el del ave y respondieron a esta como si fuera la canción de un individuo de su propia especie. Nuestra evidencia sugiere, que el canto aberrado, provocó respuestas normales tanto de rivales potenciales como de parejas prospectivas. Si estas respuestas están ampliamente distribuidas entre aves canoras, el fallo en general de canciones heteroespecíficas, una vez adquiridas, para que estas se diseminen entre la población por transmisión cultural, probablemente no es atribuible a que estos cantos (de otras especies) no puedan ser reconocidos por conespecificos.

Key words: birdsong, Field Sparrow, *Setophaga discolor*, *Spizella pusilla*, vocal learning

Among the costs of learning as a means of behavioral development is the risk of learning unsuitable or ineffective behaviors, should a learner encounter and assimilate inappropriate inputs (Johnston 1982, Boyd and Richerson 1989). If, for example, normal development of a behavior requires imitating the behavior of a normal conspecific adult, an individual that instead imitated the behavior of an abnormal adult or one of a different species might suffer consequences that would adversely affect its fitness. This potentially adverse consequence of learning-based developmental programs is sometimes observed in songbirds (i.e., oscine passerines).

Development of singing behavior by songbirds generally depends on imitation of adult songs (Hultsch and Todt 2004). Much of this imitation takes place in an acoustic environment that includes songs of multiple species, but

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developing birds (except for the few species whose singing features extensive interspecific mimicry) seem to filter out heterospecific sounds and memorize only conspecific songs. This stimulus filtering might be attributable to hard-wired learning preferences (Marler 1990) or to processes related to social interactions with conspecifics (Beecher and Burt 2004). Whatever the mechanism, the resulting canalization of development is generally effective, and songbirds typically sing only species-typical songs. Nonetheless, observers have occasionally reported instances of songbirds singing songs of other species (e.g., Borror 1977, Payne et al. 1984, Baptista 1988, Murray et al. 2004).

The relative rarity of heterospecific singing suggests not only that developmental errors leading to interspecific song imitation are infrequent, but also that the resulting abnormal song phenotypes do not spread through populations by subsequent cultural transmission. This lack of transmission might arise because heterospecific singers are not recognized by conspecifics as suitable models for imitation. If such recognition is indeed absent, one might predict that heterospecific singers would be unable to communicate effectively or, given the key role played by song in territory defense and mate attraction, reproduce successfully.

We report an instance of heterospecific singing, along with accompanying observations that might help to determine if the focal bird's apparent interspecific song imitation had negative effects on signal efficacy or reproduction. We discovered a free-living Prairie Warbler (*Setophaga discolor*) that sang songs resembling those of Field Sparrows (*Spizella pusilla*), and gathered information on the bird's nesting success and the responses of conspecific males to playback of the aberrant songs.

METHODS

We encountered the focal Prairie Warbler at Montague Plains Wildlife Management Area (42°33′N, 72°31′W) in Franklin County, Massachusetts. Most male Prairie Warblers in our study area, including the focal bird, were banded with a USGS aluminum band and a unique combination of color bands. When we banded the focal bird in 2012, we aged him as after second year (ASY) based on plumage characteristics. We monitored the focal male's nesting success via frequent observational visits and nest checks.

Prairie Warbler songs, like those of many wood-warbler species (*Parulidae*), fall into two categories (Spector 1992). First Category songs predominate in the singing of unmated males and the daytime singing of mated males, whereas Second Category songs are used in dawn bouts that begin before sunrise and during aggressive encounters between males. Nolan (1978) described the First Category songs of Prairie Warblers as Group A songs and Second Category songs as Group B songs. The song repertoire of a male Prairie Warbler typically includes a single Group A song type and a single Group B song type (Figs. 1s and b), though some males sing more than one type per category (Houlihan 2000).

On 7 May 2012, B. Kramer observed a male Prairie Warbler singing songs that lacked the buzzy notes that characterize normal Prairie Warbler songs. We subsequently recorded this male's singing on 28 May, 3 June, 9 June, and 12 June. Overall, we recorded 203 songs over 16 samples at various times between 04:30 and 09:30. The samples included two dawn bouts. Songs were recorded with a solid-state recorder (Nagra LB, Audio Technology Switzerland S. A., Romanel-sur-Lausanne, Switzerland; 48 kHz sample rate, 16 bit sample depth) and a microphone (MKH62, Sennheiser, Old Lyme, CT) in a parabolic reflector (Telinga, Tobo, Sweden).

Several colleagues listened to our recordings and viewed spectrographs of the aberrant songs and, based on their assessments and our own evaluation, we concluded that the aberrant songs were probably imitations of either a Prothonotary Warbler (*Protonotaria citrea*) song or, more likely, a phrase from a Field Sparrow complex song (complex songs form a class of multiphrase songs that Field Sparrows sing mainly at dawn; see Nelson and Croner 1991). To distinguish between these alternatives, we reviewed 59 Prothonotary Warbler and 71 Field Sparrow song recordings available via websites of the Cornell Lab of Ornithology Macaulay Library and Ohio State University Borror Laboratory of Bioacoustics. In addition, we asked four naïve observers to compare playbacks of the aberrant songs to playbacks of our candidate songs, and made automated pairwise comparisons using the sound similarity algorithm in Sound Analysis Pro (Tchernichovski et al. 2000). In the automated

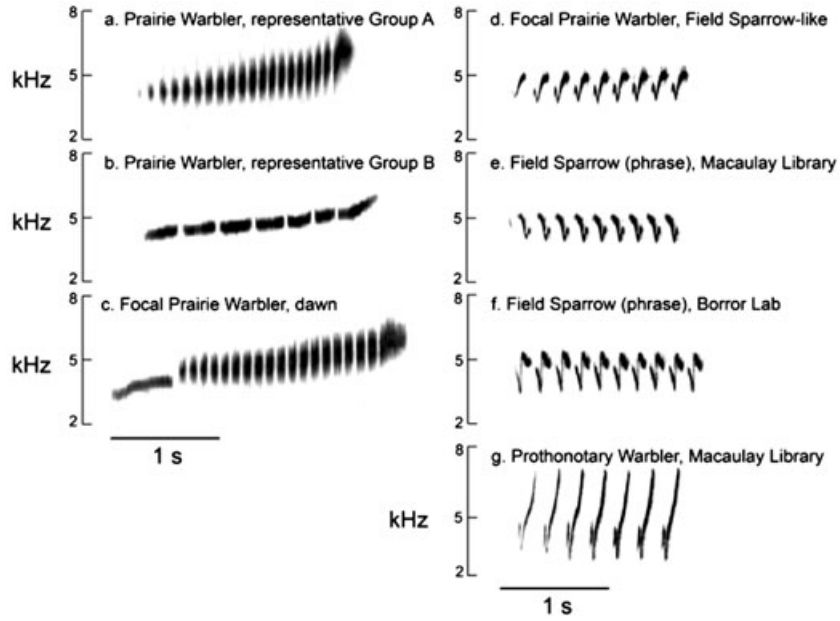

Fig. 1. Spectrographs of songs of normal and aberrant male Prairie Warblers from our study population in Massachusetts, plus spectrographs of two complex song phrases of Field Sparrows and a song of a Prothonotary Warbler for comparison. (a and b) Spectrographs illustrating typical Group A and Group B songs, respectively. Elements in the Group B song have longer duration and smaller bandwidth than do the elements in the Group A song. (c) Spectrograph of the song type that our focal bird sang during dawn bouts; it appears to be a Group A song, but with a Group B-style element at its beginning. (d) Spectrograph of the Field Sparrow-like song of our focal male. (e and f) Spectrographs of phrases from complex songs of Field Sparrows (Macaulay Library catalog #140055, Borror Lab catalog #28775, recorded in New York in 2009 and 1996, respectively). (g) Spectrograph of a Prothonotary Warbler song (Macaulay Library catalog #85157, recorded in Maryland in 1997). All spectrographs were generated with a 256-point fast Fourier transform.

comparisons, three elements from different renditions of the aberrant Prairie Warbler song were compared to four elements from different renditions of the Field Sparrow song phrases pictured in Figure 1 and to three elements from different renditions of the Prothonatory Warbler song type shown in the figure.

We also performed song playbacks to determine if conspecific males ($N = 8$) would respond to the aberrant songs. In each trial, the same 2.5-min segment of singing, transferred to a compact disk and containing 13 aberrant songs, was played from an SME-AFS speaker (Saul Mineroff Electronics, Elmont, NY) placed on the ground ~15 m from a singing male. The speaker's volume control was set at a level previously determined to yield a peak amplitude of 85 dB SPL measured at 0.5 m from the speaker (an amplitude typical of normal Prairie Warbler singing). We observed focal males from the beginning of playback until 1 min after playback ended, and noted their vocalizations, movements, and distance from the speaker. We conducted four trials in territories near the focal male (adjacent territory or one territory removed) and four trials in more distant territories (two ~1 km from the focal bird and two ~25 km away).

RESULTS

Like Prothonotary Warbler songs and many Field Sparrow complex song phrases, the aberrant Prairie Warbler song consisted of repetitions of a single element (Fig. 1d). The aberrant songs ($N = 106$) consisted of 7–10 (median = 9) elements per song, and had a mean duration of 1.54 ± 0.10 s, a mean bandwidth of 1500 ± 83 Hz, and a mean maximum frequency of 5132 ± 65 Hz. The repeated element had the same

basic form (i.e., the shape of its spectrograph trace) as the Prothonotary Warbler song element identified as type 17 by Bryan et al. (1987), but the bandwidth of that element is greater and the maximum frequency higher than those in the song of our focal Prairie Warbler (Fig. 1g). In contrast, the frequency ranges and bandwidths of many complex song phrases of Field Sparrows are similar to those in the aberrant Prairie Warbler song (Figs. 1e and f). However, despite this similarity, we found no song elements in the archived Field Sparrow recordings that precisely matched that of the aberrant Prairie Warbler song element.

Our more formal comparisons supported the conclusion that a Field Sparrow song was the most likely model for the aberrant Prairie Warbler song. The good match between the frequency profiles of the aberrant songs and Field Sparrow song phrases was apparent in listening comparisons; all four naïve observers judged the aberrant Prairie Warbler songs to be more similar to Field Sparrow phrases than to Prothonotary Warbler songs. In our automated pairwise comparisons, elements from the aberrant song were more similar to those from Field Sparrow complex song phrases (mean similarity score = 81.6%) than to those from a Prothonotary Warbler song (mean similarity score = 60.3%).

During dawn singing, the focal bird interspersed its songs with distinctive chip notes characteristic of Prairie Warbler dawn bouts, but did not sing its Field Sparrow-like song. Instead, it sang what appeared to be a typical Prairie Warbler Group A song, but with a single Group B element at the beginning (Fig. 1c). Given the context, this singing behavior was unusual; Prairie Warbler dawn bouts normally include only Group B songs. In 137 dawn bout samples recorded from 46 other male Prairie Warblers over two breeding seasons, we found no Group A songs. Thus, our focal Prairie Warbler's singing was doubly aberrant. It used a (slightly modified) Group A song in a context normally reserved for Group B songs, and used a Field Sparrow song in contexts that normally feature Group A songs. The bird's repertoire also included a more typical Group B song that we heard on three occasions (none during a dawn bout), but did not record.

Despite its seemingly gross violations of the rules of Prairie Warbler song use, our focal bird seemed to lead a normal breeding season social life. By 14 May, the bird had established a territory in an area occupied in prior years by other ASY males. We observed a female on the territory on 14 May and found a nest on 22 May. The nest had two eggs on 24 May, but was empty on 28 May. We located a second nest on 30 May. Four 1-d-old nestlings were present on 15 June, but the nest was empty on 19 June. This chronology was within the normal range for our study population, as was the nesting outcome (~40% of territorial males in our study population failed to fledge any offspring).

In our playbacks of the focal bird's sparrow-like songs, the four subjects with territories close to the focal bird (adjacent or one territory removed) changed their behavior during and immediately after playback. In contrast, the four more distant subjects did not alter their behavior in response to playback. All eight subjects were singing Group A songs when trials began. In the two trials in territories adjacent to that of the focal bird, one male immediately approached to within a few meters of the speaker and remained there, chipping repeatedly, for the duration of the playback period; the other adjacent male stopped singing and disappeared from view shortly after playback began. In the two trials in territories one territory removed from the focal male, one male closely approached the speaker and remained silent, moving away ~15 s after playback ended. The other male flew to a perch ~10 m from the speaker and sang Group B songs for the duration of the playback period. Overall, the behavior of three of the four nearby birds was similar to the behavior we typically observed when playing conspecific songs on Prairie Warbler territories to attract males to mist nets. Unlike nearby birds, the subjects of the four trials with males at more distant locations (1–25 km away) did not appear to respond to playback; all four continued singing Group A songs and did not change their locations during playback.

DISCUSSION

Our focal bird's aberrant singing behavior presumably resulted from a failure of the mechanisms that normally constrain vocal development so that it results in the acquisition of species-typical songs and singing behavior. This failure was likely fostered by interactions between the young Prairie Warbler and a singing Field Sparrow. These species have overlapping breeding ranges and nest in similar habitats

(Nolan et al. 1999, Carey et al. 2008). Field Sparrows are abundant breeders in our study area and their nests are often near those of Prairie Warblers. Thus, our focal bird likely had ample opportunity to hear and potentially interact with singing Field Sparrows during its period of song development.

In addition to its heterospecific song, our focal bird also acquired a near-normal song of its own species, but seemingly used the song in inappropriate contexts. Similarly, Harper et al. (2010) observed a Golden-winged Warbler (*Vermivora chrysoptera*) using its First Category song during the dawn chorus and its Second Category song later in the day, in reverse of the normal pattern. There is some evidence that context-appropriate use of wood-warbler song categories is a learned behavior (Spector et al. 1989), so our focal bird's apparent Group B-style use of a song with Group A structure may represent a further distortion of normal vocal learning. The manner in which the focal bird used its heterospecific song may signify an additional instance of mislearned context because the bird used its Field Sparrow song type as a Group A song, even though Field Sparrows only use complex songs in contexts corresponding to those normally reserved for Group B songs in Prairie Warblers (Nelson and Croner 1991).

Despite its aberrant singing behavior, our focal bird, like a normal Prairie Warbler, had different stereotyped song types that it used in different contexts. Potentially similar patterns of aberrant, but not completely discordant, wood-warbler singing that includes both heterospecific and conspecific songs have been described previously. A Cerulean Warbler (*Setophaga cerulea*) that sang Hooded Warbler (*Setophaga citrina*) songs also sang songs of its own species (Boves et al. 2010), as did a Prairie Warbler that sang Black-throated Green Warbler (*Setophaga virens*) songs (Martin et al. 1995). These investigators did not report whether the aberrant singers used their different song types in typical wood-warbler context-dependent fashion.

It is striking that a Prairie Warbler with singing behavior as unorthodox as that of our focal bird was able to nest successfully. Furthermore, our playback results suggest that neighboring males learned that the sparrow-like song was a signal belonging to a conspecific and responded accordingly. Perhaps prospecting females were able to make the same accommodation after observing the territorial behavior and visual displays of the focal male.

Our results suggest that conspecific birds did recognize and respond to our focal bird's aberrant singing, so lack of recognition by conspecifics must not be the factor responsible for the seeming failure of heterospecific-specific singing Prairie Warblers to transmit their songs to other birds and thereby increase the songs' frequency of occurrence. The nesting success of our focal aberrant singer is also inconsistent with the hypothesis that song learning facilitates rapid speciation (Lachlan and Servedio 2004; reviewed in Box 1 of Wilkins et al. 2013). If even extreme vocal divergence from the species norm does not necessarily prevent effective communication with rival males and potential mates, one would not expect that rapid vocal divergence in learned songs would accelerate reproductive isolation.

It would be useful to know if the apparent lack of serious adverse consequences for our aberrant singer represents a more general phenomenon. Each instance of interspecific song imitation constitutes a small natural experiment on the effects of rapid vocal divergence, so accumulating additional documented observations of heterospecific singing would be valuable, especially if the observations also document the communicative and reproductive consequences of aberrant vocal development.

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