

Song variation of a native songbird in a modified habitat by invasive plant

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Abstract

Habitat structure has been considered as an important factor affecting the acoustic evolution of birds, and bird songs are increasingly affected by artificial environmental variation. Invasive plants sometimes can dramatically alter native habitats, but the song variation of native songbirds migrating into invaded habitats has received little attention. The invasion of smooth cordgrass *Spartina alterniflora* in the coastal wetlands of eastern China has drastically altered the vegetation structure and some small passerines have begun to use invaded habitats to breed. In this study, we compared the song type prevalence and the song characteristics of male plain prinia *Prinia inornata* to identify differences in vocal behavior between native and invaded habitats. We also tested for differences in vocal behavior in relation to singing perch and wind speed variation between different habitats. The results indicated that males of plain prinia in invaded habitats sang shorter songs than those in native habitats and had a lower song diversity. The homogeneous vegetation structure and higher wind speed in invaded habitats likely leads to males changing the traditional perched singing style. The song variation may be related to the founder effect, the alteration of vegetation structure and microclimate in invaded habitats. This finding highlights the need for better understanding the behavioral evolution of native species in the process of adapting to the invaded habitat. In the future, experimental manipulation is needed to ascertain how the invasive plant drove these vocal behavior changes of native songbirds.

Key words: behavioral evolution, biological invasion, plain prinia, smooth cordgrass, song diversity

INTRODUCTION

Divergence of bird song is the outcome of gene-environment interactions, likely related to sexual selection, geographical distance, and environmental influences (Brumm 2004; Scordato 2018; Yandell *et al.* 2018). As proposed in the acoustic adaptation hypothesis, bird songs

may have evolved in response to habitat variations determined by climate conditions, background noise, and vegetation structure (Morton 1975; Brumm & Naguib 2009). The relationship between bird song structure and background environment has been confirmed in many species, and the acoustic properties of distinct habitats can affect song variation (Slabbekoorn & Smith 2002a; Seddon 2005). Due to vegetation structure scattering and atmospheric absorption, there are attenuation and reverberation in song transmission in natural habitats and increase as vegetation becomes denser (Naguib 2003; Catchpole & Slater 2008). Many studies demonstrate that bird songs

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are with lower frequencies, narrower frequency ranges and longer inter-element intervals which species settling in closed compared with open habitats (Boncoraglio & Saino 2007). Slowly repeating notes and low frequencies are less affected by reverberation and attenuation, and the species belonging to closed habitats often exhibit similar song characteristics (Baker 2006; van Dongen & Mulder 2006). Song diversity sometimes is limited by patch area and habitat continuity; for example, song repertoires of birds settling in smaller patches are significantly poorer (Laiolo 2008), birds in fragmented forests share fewer songs with populations in neighboring habitats (Rivera-Gutierrez *et al.* 2010).

Human-driven environment transformations are changing the acoustic properties in many habitats and affecting the communication signals of wild birds (Kight *et al.* 2012; Slabbekoorn & Den Boer-Visser 2006). A well-known example is the effect of anthropogenic noise on bird songs, for example, great tits (*Parus major*) sing at a higher frequency to reduce the masking effect of urban noise (Slabbekoorn & Peet 2003). In addition to noise, structural changes caused by human activities in natural habitats (e.g. urbanization, intensive farming, and deforestation) also alter the acoustic properties, thus affecting song transmission due to changes in vegetation structure and microclimate (Kopuchian *et al.* 2004; Nicholls & Goldizen 2006). Birds have shown a strong behavioral plasticity to adapt to the changing habitats; some species would alter the frequency, length, syllable rate and complexity of their songs in response to the remodeling of habitat structure (Bueno-Enciso *et al.* 2016; Hill *et al.* 2018).

Invasive plants often rapidly alter native vegetation structure and negatively affect many native taxa, including birds (Ortega *et al.* 2006; Skorka *et al.* 2010). However, some studies also suggest that invasive plants sometimes can give rise to novel habitat formation for native birds (Skorka *et al.* 2010; Nelson & Poesel 2013). Little attention has been paid to their song variation when native songbirds emigrate into new invaded habitats. Ortega *et al.* (2014a) indicated that the lower prevalence of older birds in habitats invaded by spotted knapweed (*Centaurea stoebe*) might lead to a decrease in local songs diversity of chipping sparrows (*Spizella passerine*). However, few studies have been reported on the effects of habitat changes caused by other invasive plants on bird song variation.

Smooth cordgrass (*Spartina alterniflora*), which is native to the Atlantic and Gulf coasts of North America, is a notable invasive plant (Nishijima *et al.* 2016). Smooth cordgrass was deliberately introduced into Chinese tidal

flats in 1979 to aid erosion control, dike protection, and soil amelioration (Gao *et al.* 2012; Zuo *et al.* 2012). However, extensive smooth cordgrass invasion has led to a series of deleterious ecological effects on native plants, benthic macrofauna, and birds (Li *et al.* 2009). Most previous studies have suggested that smooth cordgrass invasions have significant negative effects on bird habitat, foraging, community structure and reproduction as a result of the high density and the monocultural vegetation structure (Li *et al.* 2009; Gan *et al.* 2010). Although most breeding birds avoid habitats invaded by smooth cordgrass, some studies have found that some small passerine birds have begun to enter invaded habitats and over time will rely on exotic plants for perching and reproduction; this change may be related to the amount of time smooth cordgrass has been invading native habitats (Nordby *et al.* 2009; Lampert *et al.* 2014; Ma *et al.* 2014). Invaded habitats may provide empty niches for some species, especially birds that are highly territorial and face intense intraspecific- and interspecific-competition for resources, such as food or nesting sites (Ma *et al.* 2014). The shrinkage of native habitats due to smooth cordgrass invasion may drive more birds that rely on native vegetation (common reed *Phragmites australis*) for nesting to attempt nesting in invaded habitats. Obviously, the background of bird singing also changed accordingly for the alteration of vegetation structure. Whether the vocal behavior of songbirds differs between native and invasive habitats has not been studied.

Plain prinia (*Prinia inornata*) is widely distributed in Asia and adapts to multiple ecosystems from terrestrial systems to coastal marshes, and a common songbird in the coastal wetlands of eastern China (BirdLife International 2016). They breed in native reed habitats, and tend to produce simple territorial songs consisting of repeated syllables on a fixed perch; the syllable structure is often very stereotyped within individual males (Zhu *et al.* 2008). In recent years, we found that some individuals began to nest in the smooth cordgrass habitat. This made it possible for us to explore the song differences of plain prinia between native and invaded habitats. Native reeds have a greater plant height, while smooth cordgrass has a greater stem density and softer stems (Chen *et al.* 2019), resulting in 2 completely different habitat vegetation structures. The invasion areas of smooth cordgrass are closer to the coast, while the native reeds grow at relatively higher elevations, which leads to differences in microclimate, for example, wind speed, and then may affect the energetic cost of bird singing (Ward & Slater 2005). In this study, we investigated the song type prevalence and the song characteristics of plain prinia to identify the differences between

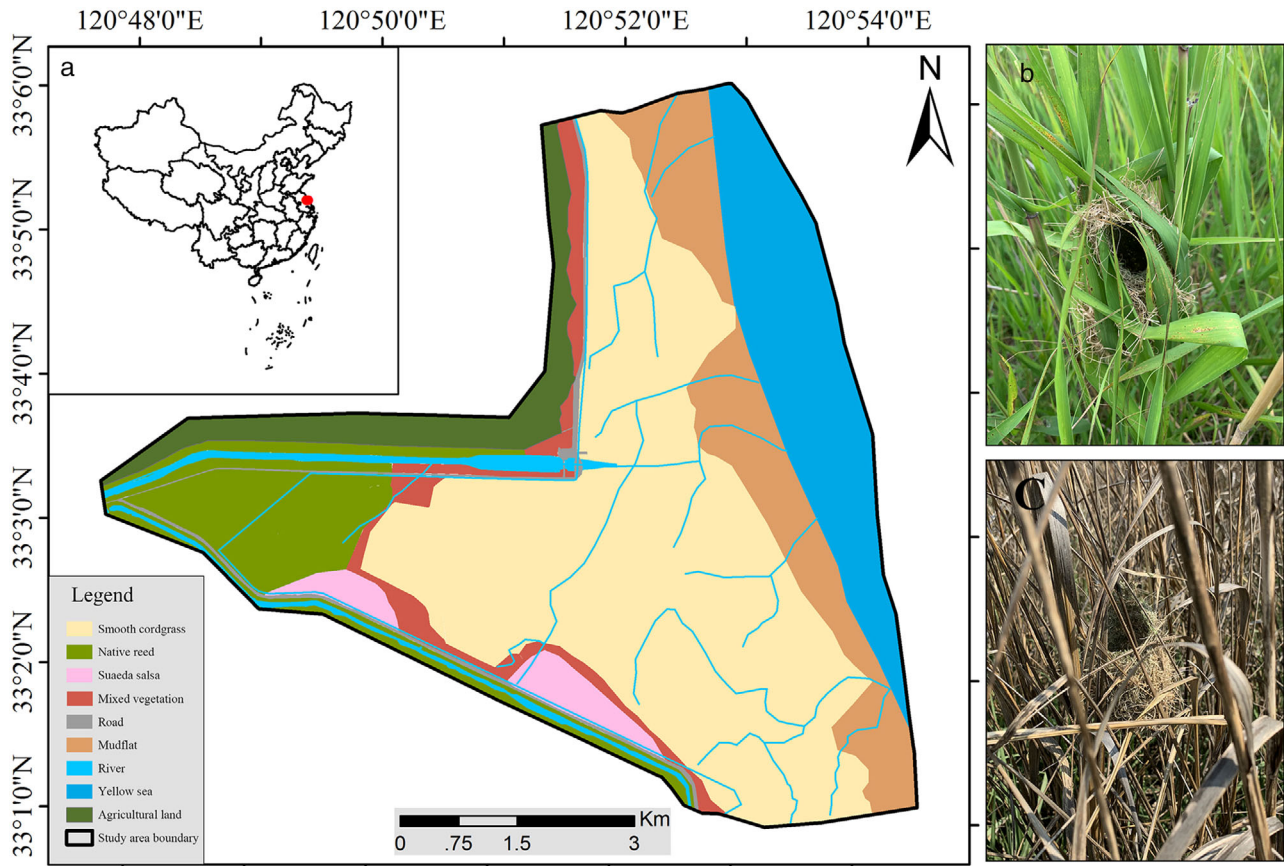


Figure 1 Habitat types in the study area at YNNR (a) and nests of plain prinia in native (b) and invaded (c) habitats.

native and invaded habitats. We also examined the differences of singing behavior and wind speed between different sampling sites. Our study may provide a new insight for better understanding the song variation and behavioral evolution of native songbirds in the process of adapting to the invaded habitats.

MATERIAL AND METHODS

Study site

Field work was performed in the core area of Yancheng National Nature Reserve (YNNR) (32°59'N–33°03'N, 120°47'E–120°53'E) in Jiangsu Province, China, which is located along the coast of the Yellow Sea (Fig. 1a). YNNR, is a typical original intertidal wetland, has high biodiversity and serves as a suitable habitat for many wetland birds (Melville *et al.* 2016). Historically, the vegetation of the reserve mainly consisted of common reed and *Suaeda salsa*. After smooth cordgrass invaded, its area

began to steadily expand, rapidly replacing native plants, and forming a band of monoculture vegetation along the shoreline (Chen *et al.* 2019), and resulting in a gradual decline in the native habitat of birds. At present, there are stable breeding populations of plain prinia in both native reed and invasive smooth cordgrass habitats (Fig. 1b,c). During the breeding season in 2019, our investigation found that the population density of plain prinia in native habitats was higher than that in invaded habitats (98.1 ± 6.3 vs 68.6 ± 6.7 ind./km²; $F_{1,5} = 5.71$, $P < 0.05$), and the nest density was extremely higher than that in invaded habitats (42.1 ± 6.0 vs 7.0 ± 1.9 num./km²; $F_{1,5} = 23.40$, $P < 0.01$).

Data collection

For this study, we selected 3 sites that were heavily invaded by smooth cordgrass, while 3 sites were dominated by native vegetation (common reed). The area of each site was approximately 0.5 km × 2 km, and sites were

separated by at least 0.5 km. Then we divided each site into several line transects and searched for the target individuals using behavioral observations of the adult birds. We recorded mating songs of plain prinia on ten rainless days (during the peak of courtship, April 20 to May 18, 2019), and sampling was scattered during 0600–1000 (morning) and 1500–1800 (afternoon). We recorded only mating songs, not other vocalizations such as alarm calls or flight calls. Although the males were not individually marked, we assumed we did not record the same individual twice. Because we visited each line transect only once and the locations of recorded birds were spaced at least 100 m apart. According to our field observation, the typical plain prinia territories were circular, <50 m in radius. Songs were recorded with a digital recorder (Marantz, PMD661) and a directional microphone (Sennheiser, ME66) pointed directly towards the singing individual. Recordings were sampled at 44.1 kHz, 16-bit resolution, mono, WAV format. To reduce human interference, all song recordings were collected from a distance of 10 m approximately. We also recorded the average wind speed at the time of individual recording by fixing an anemograph to the recording rod, and the singing state (perched or in flight) of each male.

Song analysis

Overall, we recorded songs from 44 males, 19 of which were in native habitats and 25 of which were in invaded habitats. Each male plain prinia usually sings a single song type consisting of repeated syllables (Zhu *et al.* 2008), which are themselves a combination of different notes (usually a pair of high- and low-frequency notes). Different song types can be distinguished depending on the syllable structure by the spectrogram, for example, direction of nonlinear frequency change and number of notes (Fig. 2). We generated the spectrogram and sonogram of each song using Raven Pro (versions 1.6, The Raven Team, NY, USA), with a 1024-point fast Fourier transform (FFT) and a Hamming window with 50% overlap (providing a resolution of 47 Hz and 10.7 ms). After visually examining the sonogram, we used a high-pass filter to remove the low-frequency background noise (below 1.0 kHz) without removing any components of the song (the lowest frequency of song was about 3.5 kHz, no overlap with noise) (Mockford & Marshall 2009). We selected the 3 highest quality recordings for each male for further analysis, distinguished the song type and measured the following temporal and frequency variables from the selected spectrogram: song length (s), syllable length (ms), syllable number per song, maximum fre-

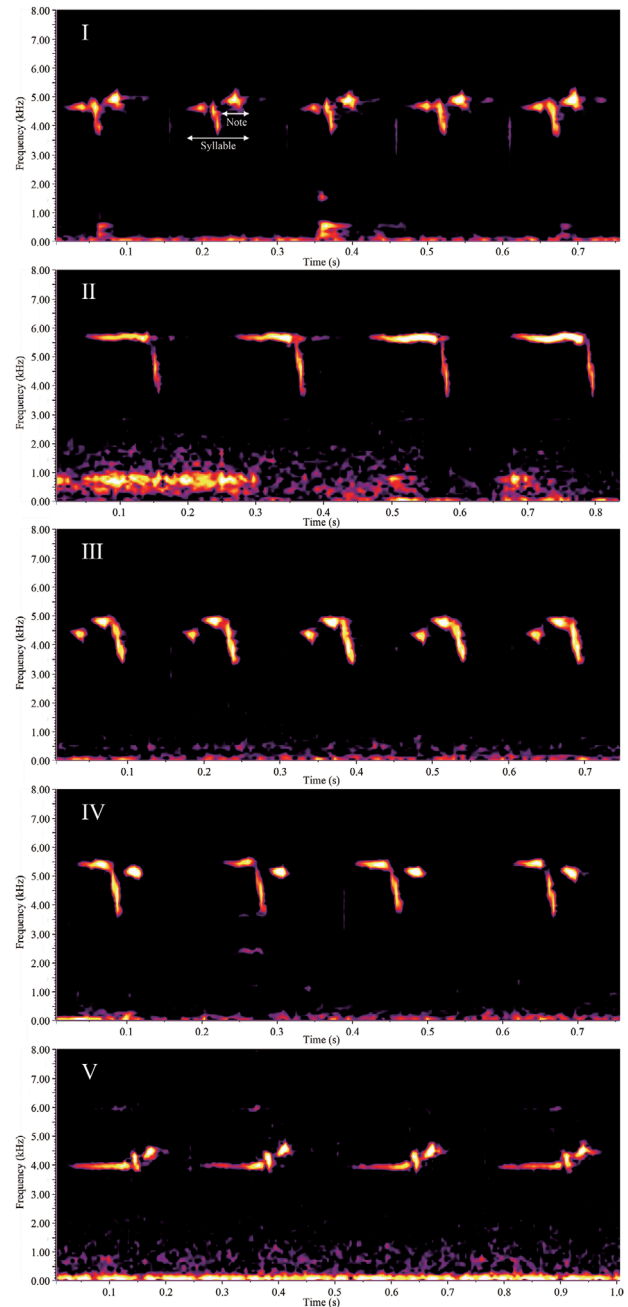


Figure 2 Five typical mating song types of male plain prinia as seen in Raven Pro spectrograms.

quency (Hz), minimum frequency (Hz), and frequency bandwidth (Hz). Variables of each song were measured manually by using the precise placement of the selection boxes in the spectrogram view (Fig. 3), and based on a cut-off amplitude threshold (−60 dBFS). Then these

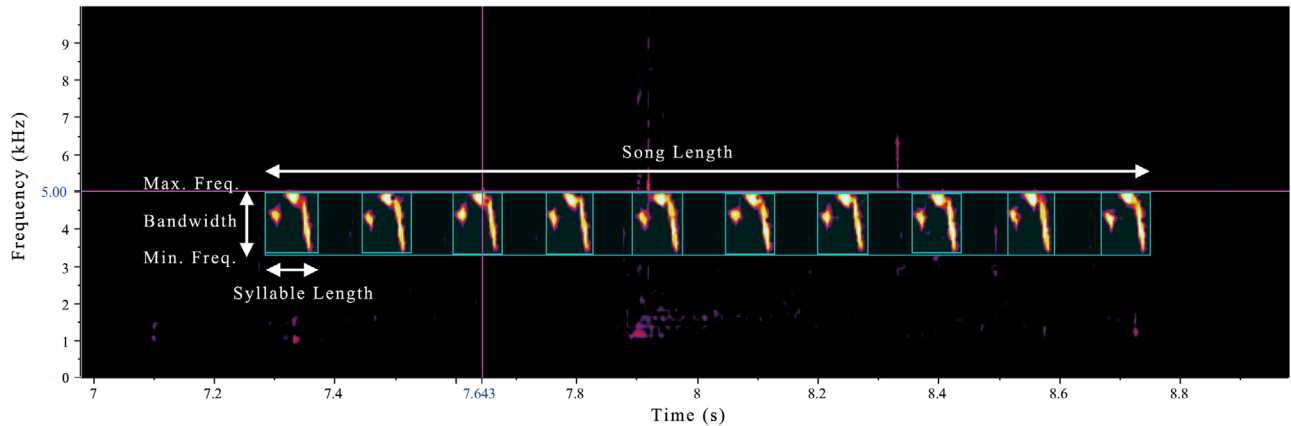


Figure 3 An example of measurement of song variables in the spectrogram.

variables data were automatically extracted and recorded by Raven.

Statistical analysis

We tested for the differences in the song type prevalence between the 2 habitat types using the chi-square test. We conducted generalized linear mixed models (GLMM) to test the differences in song characteristics between native and invaded habitats, with “habitat type” as a fixed factor and “male ID”, “site” as random factors. We further analyzed the differences between different song types in native habitats and the differences of the same song type between native and invaded habitats. To meet assumptions of normality and homogeneity of variance, the numerical data were transformed prior to statistical analyses, if necessary. We used principal component analysis (PCA) to assess the similarity among the third type of songs (the most common type) in different habitats, which incorporated temporal and frequency variables (as mentioned above). Each song was plotted as a point in space created by the first 2 principal components. We also used line regression to assess the relationship between the song length of male individual and the average wind speed at the time of recording. All statistical analyses and graphs were performed with R statistical software (R Core Team 2018) and the ggplot2 package of R (Wickham 2016).

RESULTS

We analyzed a total of 132 songs from 44 males; 57 songs belonged to 19 males in native habitats, while 75 songs belonged to 25 males in invaded habitats. We found that in native habitats, males of plain prinia produced

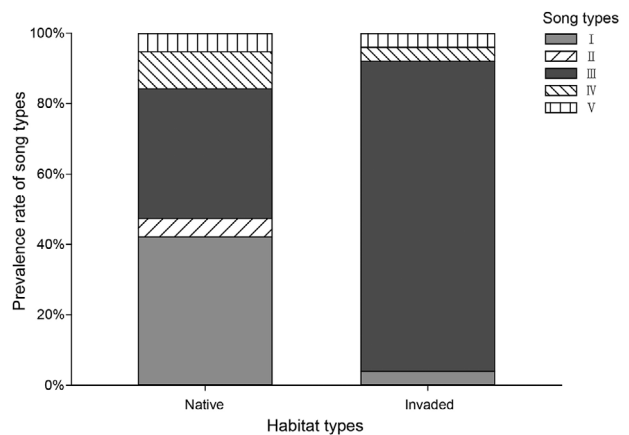


Figure 4 Prevalence rate of 5 song types compared between native and invaded habitats.

songs with a greater song and syllable length, a higher syllable number, and a lower frequency bandwidth than those in invaded habitats (Table 1).

Then, we divided songs into 5 types depending on the difference in syllable structures (Fig. 2). Each male only sang a single song type according to our records. We found that there were significant differences in the prevalence of song types between native and invaded habitats ($\chi^2 = 13.98$, $P < 0.001$). In native habitats, the individuals singing the first type of song accounted for 42.1% (8 of total 19 individuals), the third type of song accounted for 36.8% (7 individuals), and the fourth type of song accounted for 10.5% (2 individuals); however, in invaded habitats, the third type of song accounted for 88% (22 of total 25 individuals), and other types of songs were rare (Fig. 4). The third type of song is the only type common

Table 1 Song characteristics (song length, syllable length, syllable number, min. frequency, max. frequency, bandwidth) analyzed between native and invaded habitats

Song characteristics	Habitat types		df	F	P
	Native (<i>n</i> = 19)	Invaded (<i>n</i> = 25)			
Song length (s)	14.37 ± 3.10	4.72 ± 0.72	1, 42	11.03	< 0.01
Syllable length (ms)	93.30 ± 3.17	73.10 ± 1.66	1, 42	12.19	< 0.01
Syllable number	68.64 ± 13.03	26.06 ± 3.61	1, 42	11.73	< 0.01
Min. freq. (Hz)	3750.14 ± 59.54	3560.88 ± 36.56	1, 42	3.63	0.06
Max. freq. (Hz)	6136.60 ± 100.89	6269.29 ± 57.84	1, 42	0.75	0.39
Bandwidth (Hz)	2386.47 ± 79.15	2708.40 ± 53.96	1, 42	5.17	< 0.05

Shown are the mean ± SE.

in both habitats. We further analyzed the differences between the first and third types of songs in native habitats and the differences in the third type of song between native and invaded habitats (Tables S1 and S2, Supporting Information). We found that the first type of song had a longer syllable length and higher minimum frequency, while the third type of song had a higher frequency bandwidth in native habitats, with no differences in the other parameters (Fig. 5). The third type of song in native habitats had a longer song length, longer syllable length and higher syllable number than songs in invaded habitats, with no difference in frequency parameters (Fig. 5).

As shown in the PCA results based on the third type of songs, the first 2 principal components accounted for a total of 74.7% of the song variation between habitats; specifically, PC1 explained 43.2% of the variation, and PC2 explained 31.5% of the variation (Fig. 6; see variable loadings in Table S3, Supporting Information). The points representing the songs in native habitats were more widely scattered and covered a larger area of the coordinate axis, while the points representing those in invaded habitats were more concentrated and covered a smaller area of the coordinate axis. This result indicated that males of plain prinia in native habitats had a higher diversity of songs, even if the same song type, while birds in invaded habitats had a higher similarity of songs.

Most males of plain prinia chose a fixed perch (the top of a reed, shrub, or deadwood) to sing (Fig. 7a–d); only 12.7% of males added display flights when singing in native habitats, while 31.2% of males added display flights to sing in invaded habitats (Fig. 7e,g). We also found that the average wind speed in invaded habitats was significantly higher than that in native habitats because the areas of smooth cordgrass invasion were closer to the coastline (Fig. 7h). While no significant relationship in native habi-

tats ($df = 19$, $R^2 = 0.053$, $P = 0.341$; Fig. 8a), regression analysis showed that the song length of male was significantly shorter when the wind speed was higher in invaded habitats ($df = 24$, $R^2 = 0.196$, $P = 0.027$; Fig. 8b).

DISCUSSION

The divergence of bird songs due to environmental variation has received much attention (Slabbekoorn & Peet 2003; Brumm & Naguib 2009). Many studies have suggested that background differences lead to variations in bird song amplitude, frequency, length, and diversity (Brumm 2004; Bueno-Enciso *et al.* 2016; Lee & Park 2019). According to our results, the songs of male plain prinia in native habitats have longer song lengths, longer syllable lengths, higher syllable numbers, higher minimum frequencies, and lower frequency bandwidths than those in invaded habitats. These differences are primarily due to the different prevalence of each song type between native and invaded habitats. We found that males in native habitats had more diverse song types, while most birds in invaded habitats always sang the same song type (the third type of song). The first type of song had a longer syllable length and higher minimum frequency, while the third type of song had a higher frequency bandwidth. In songbirds, island or small populations sometimes tend to have lower song diversity than mainland or large populations for founder effects (Baker 1996; Hamao & Ueda 2000; Baker *et al.* 2006). When a few colonists to new habitat carry a small fraction of the native song diversity, this can lead to a cultural-genetic bottleneck (Hill *et al.* 2019). The population density of plain prinia in invaded habitats was significantly lower than that in native habitats, which may limit the song diversity. Considering the short history of smooth cordgrass invasion and the colonization of plain

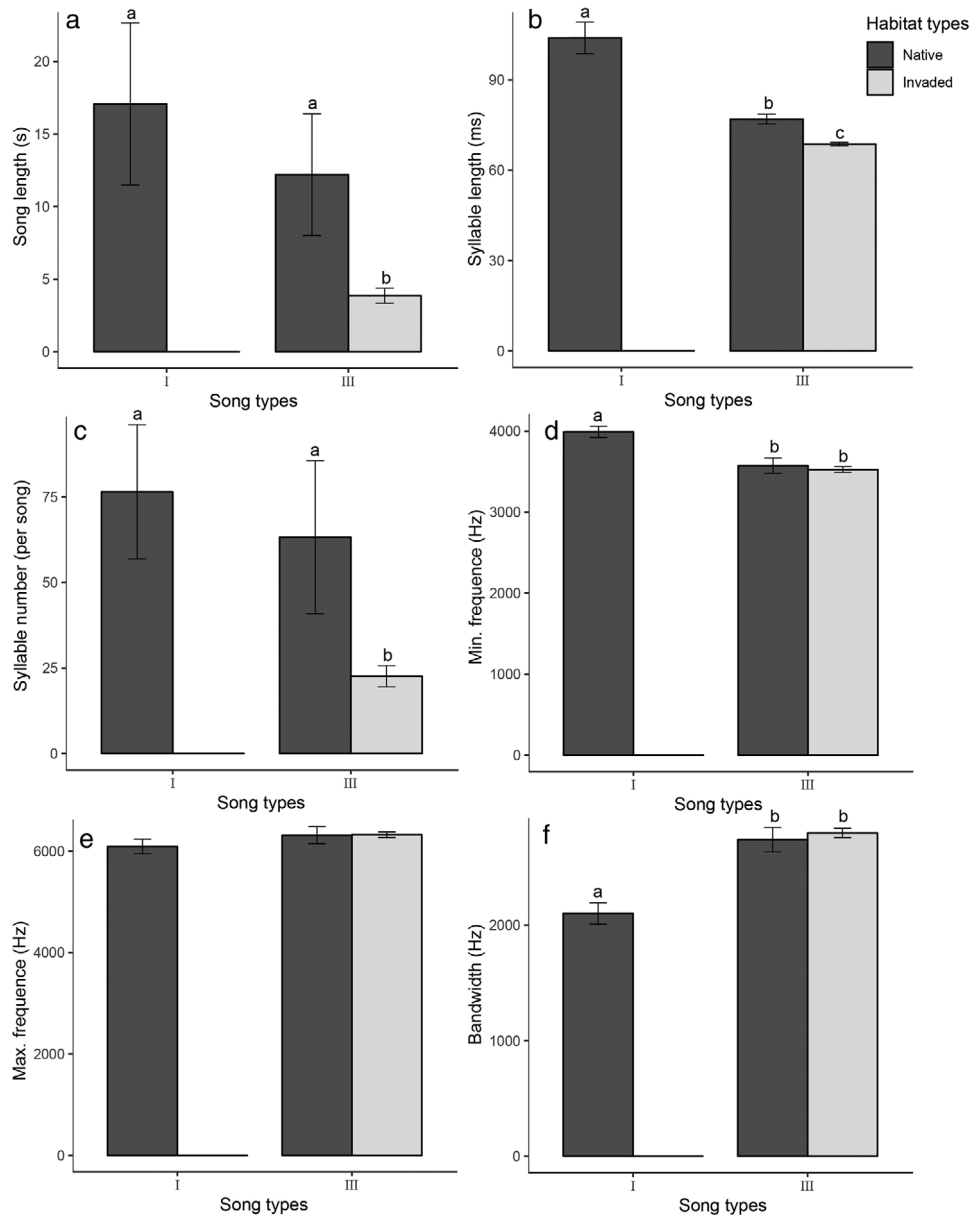


Figure 5 Differences of song characteristics between the first and third type of songs in native habitats and differences of song characteristics of the third type of song between native and invaded habitats. Different letters (a–c) indicate significant differences ($P < 0.05$).

prinia was only recently recorded, we speculate that most pioneer birds that emigrated into invaded habitats probably sang the third type of song and led to the commonality of song. However, the low song diversity in invaded habitats may be temporary for males with other song types have not colonized those areas.

After excluding the influence of song type, we found that the third type of song in native habitats had a

longer song length, longer syllable length, and higher syllable number than the same songs in invaded habitats (based on small sample sizes). The acoustic properties of distinct habitats often affect bird song variation (Slabbekoorn & Smith 2002a; Seddon 2005). Although the plant density is higher, smooth cordgrass habitat with lower plant height and monocultural vegetation structure is actually more open than native reed habitat with diverse

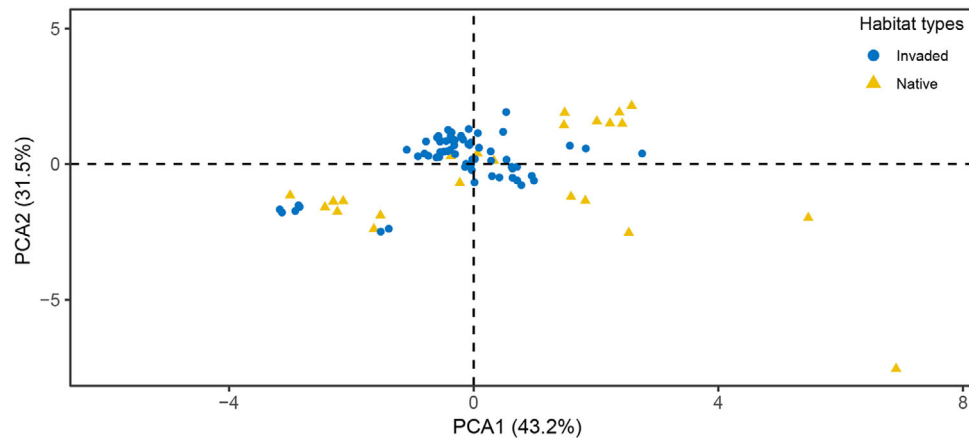


Figure 6 Plot of the PCA of song similarity between native and invaded habitats by the first 2 PCA axes (based on the third type of song).

vegetation. Shorter song and syllable length may be more suitable for transmission in invaded habitats, and this needs to be verified in further study by testing the effects of different songs in the 2 habitats. The PCA results also have shown that males in native habitats had a higher diversity of songs, even if the same song type. Although we recorded many singing individuals in invaded habitats, nests were rarely found. This suggests that most of those emigrated into invaded habitats might be young individuals with little reproductive experience. Compared with native habitats, invaded habitats may be suboptimal in terms of vegetation structure suitability, food resources, and other aspects; as a result, invaded habitats are not the first choice of old birds, but these habitats may provide more empty niches for young birds (Simberloff 2006; Ma *et al.* 2014). For songbird song characteristics, the developmental age of the founders may be an important factor, because young founders may not have completed song learning before migrating from the source population (Baker 1996). Young birds in invaded habitats may lack a good tutor song (Vaytina & Shitikov 2019), and the neighbor effect may cause the song types tend to be unitary because songs of neighbors are often similar (Nelson & Poesel 2013; Snijders *et al.* 2015).

Behavioral plasticity may be used to understand how native species respond to plant invasions. Individuals with a greater degree of flexibility may adapt more readily to invaded habitats (Ortega *et al.* 2014b). Males of plain prinia usually choose a fixed perch to sing in native habitats. Considering the especially soft stem of smooth cordgrass and the higher wind speed closer to the coastline in invaded habitats, it should be very difficult for birds to choose a permanent perch to sing for a long

time. As shown in the results, the song length of male was significantly negatively related to the wind speed in invaded habitats. These adverse conditions would lead to higher energy expenditure of singing, which explains the shorter songs of males in invaded habitats in another aspect. We also found that only 12.7% of males added display flight when singing in native habitats, while 31.2% of males added display flight in invaded habitats. This addition may be a behavioral compensation mechanism in response to habitat changes used to increase their exposure rate to attract females. The monoculture and overly dense vegetation structure in invaded habitats make it difficult for males to stand out (Fig. 7f); thus, the traditional perched singing style may not be suitable in new habitats, but given the more open habitat structure in the invaded areas, an alternative interpretation could be that there is more opportunity for males to visually display. We plan to further test these speculations by providing solid singing posts in invaded habitats and seeing the behavior variation of males in visual displays.

Evidence suggests the structure and diversity of bird song may rapidly evolve in isolated or fragmented habitats (Parker *et al.* 2012). Compared with the hypotheses of long-term genetic selection or long-term onto genetic changes (Slabbekoorn & Smith 2002b; Slabbekoorn & Den Boer-Visser 2006), short-term adaptation by plain prinia to locally-altered habitats may be a proper explanation to our results for we lack long-term data and a large sampling area. However, this accumulation of short-term behavioral adaptation may have unpredictable consequences for the long-term genetics of the population. Males of plain prinia in invaded habitats seem to lose song

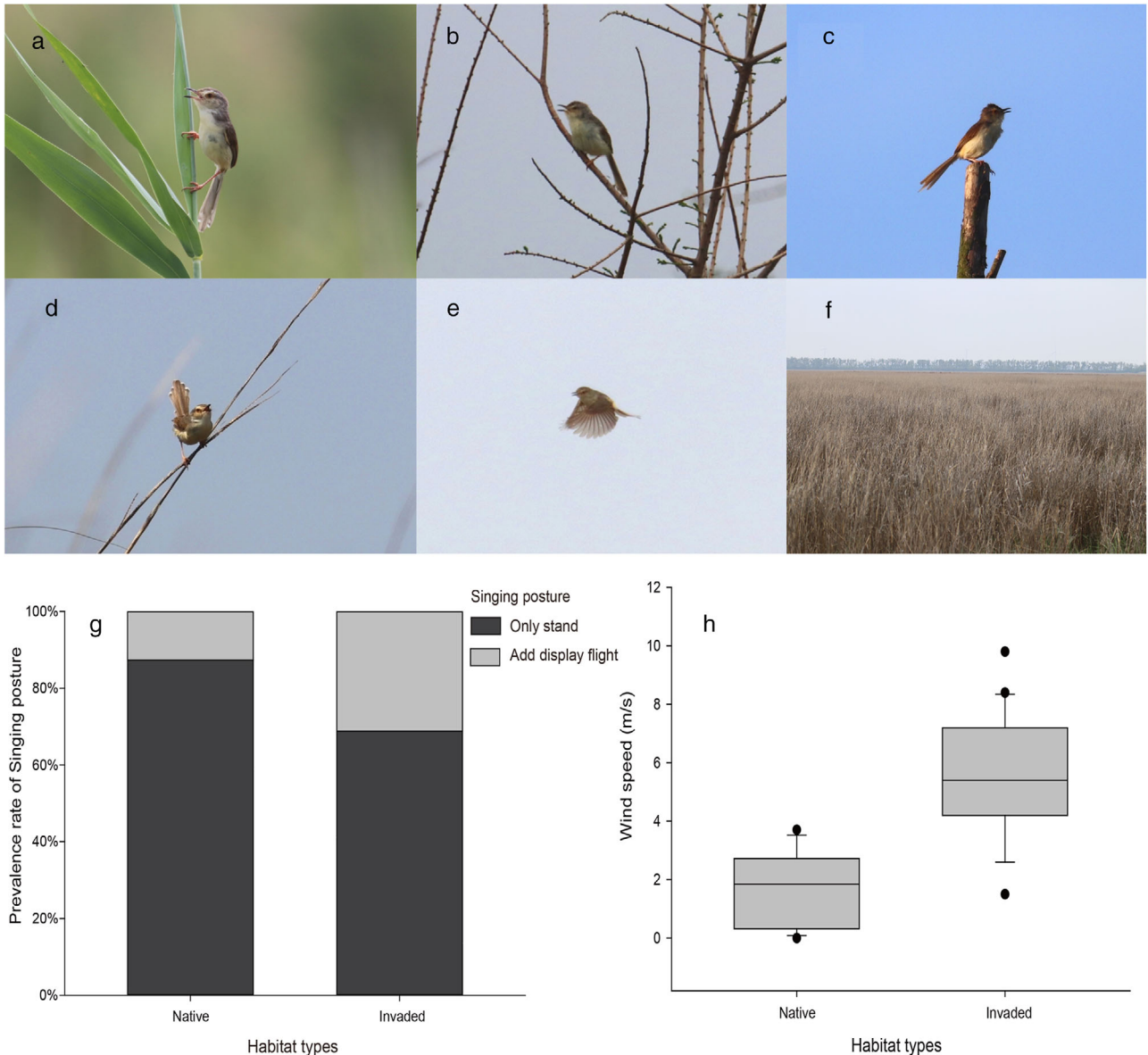


Figure 7 Singing postures of male plain prinia compared between native and invaded habitats. (a–c) Males of plain prinia sing on the fixed perches (the top of reed, shrub, or deadwood) in native habitats. (d) A male of plain prinia sings on a soft stem of smooth cordgrass. (e) With typical display flight when a male singing in invaded habitats. (f) Monoculture and overdense vegetation structure in invaded habitats. (g) Prevalence rate of singing postures between native and invaded habitats. (h) Difference of wind speed compared between native and invaded habitats.

diversity and have a higher similarity of songs; additionally, the song types tend to be unitary.

In future studies, we will need to better understand the demographic information (sex ratio, age ratio, etc.) of plain prinia, and the differences of acoustic transmission feature between native and invaded habitat structures. At the same time, we should also to understand the territorial

overlap and genetic relationship of populations between native and invaded habitats. These may help us better understand the role of invasive smooth cordgrass in the song variation of native birds. We recommend expansive ongoing studies to help ascertain the effects of modified habitats by invasive smooth cordgrass on the behavioral and molecular ecology of native species.

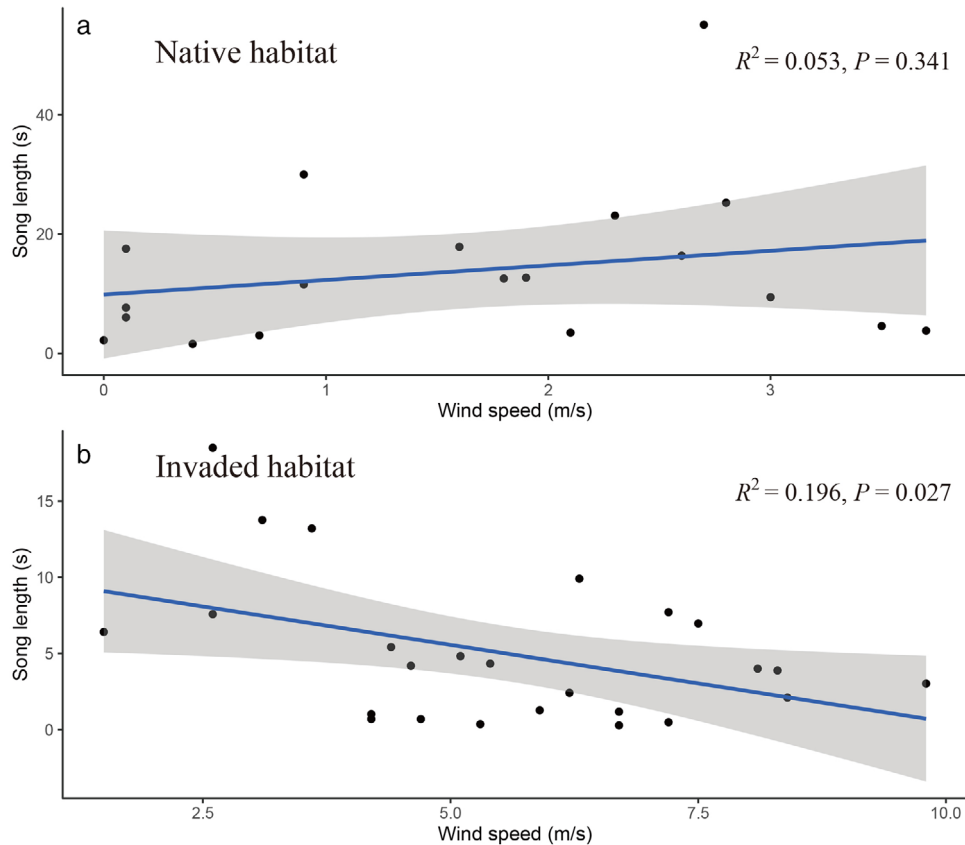


Figure 8 Correlation between the song length of male individual and the average wind speed at the time of recording based on simple linear regression: (a) Native habitat; (b) Invaded habitat. The grey areas represent the 95% confidence intervals.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Song characteristics (song length, syllable length, syllable number, min. frequency, max. frequency, bandwidth) analyzed between the first and third types of song in native habitats

Table S2 Song characteristics (song length, syllable length, syllable number, min. frequency, max. frequency, bandwidth) of the third type of song analyzed between native and invaded habitats

Table S3 Variable loadings of the PCA on the song characteristics (based on the third type of song)

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