Recent northward range expansion promotes song evolution in a passerine bird, the Light-vented Bulbul

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Abstract

In common with human speech, song is culturally inherited in oscine passerine birds ('songbirds'). Intraspecific divergence in birdsong, such as development of local dialects, might be an important early step in the speciation process. It is therefore vital to understand how songs diverge, especially in founding populations. The northward expansion of the Light-vented Bulbul *Pycnonotus sinensis* (J. F. Gmelin, 1789) into north China in the last 30 years provides an excellent opportunity to study birdsong evolution. We compared ~4400 songs from newly established northern populations with ~2900 songs from southern populations to evaluate song divergence after recent expansion. The total pool of syllables and especially song types was considerably smaller in the north than in the south, indicating 'founder effects' in the new population. The ancestral pattern of mosaic song dialects changed into a pattern of wide geographical sharing of a few song types and syllables, likely the result of fewer geographical barriers to 'meme flow', and the recent spread across a large area in the north. Our results suggest that song evolution and vocal trait shifts can arise rapidly after range expansion, and that in the Light-vented Bulbul 'founder effects', geographical isolation, and recent rapid expansions played important roles in the evolution of song dialects.

Introduction

Cultural evolution is the change in behavioural traits transmitted through social learning (Whiten *et al.*, 1999; Freeberg, 2000; Krutzen *et al.*, 2005; Bluff *et al.*, 2010; Cardoso & Atwell, 2011). Song in oscine passerines, parrots and hummingbirds is a classic example of a cultural trait (Baptista & Schuchmann, 1990; Pepperberg, 1994; Catchpole & Slater, 2008a). Selective pressures and stochastic factors are considered to be key drivers of song evolution, although the relative importance and interplay among these processes are poorly understood. For example, songs have been suggested to change in response to (i) environmental conditions affecting sound transmission (Morton, 1975; Wiley, 1991; Badyaev & Leaf, 1997; Slabbekoorn & Peet, 2003; Seddon, 2005); (ii) morphological adaptations influencing vocalizations, e.g. bill size/shape and overall body size (Podos, 2001; Laiolo & Rolando, 2003; Seddon, 2005; Huber & Podos, 2006); (iii) interspecific interactions, such as maladaptive hybridization ('reproductive character displacement') (Seddon, 2005) or competition for sound space (Grant & Grant, 2010); (iv) female choice based on various song attributes (Searcy & Andersson, 1986; Hasselquist *et al.*, 1996); (v) male-male competition, e.g. for efficient territorial defence (Beecher *et al.*, 2000; Cate *et al.*, 2002; Ellers & Slabbekoorn, 2003); (vi) stochastic factors, e.g. 'cultural mutation' caused by copying errors or improvisation, and 'cultural drift' (Lemon, 1975; Baker & Jenkins, 1987; Lynch & Baker, 1993; Lynch, 1996; Martens, 1996; Payne, 1996; Baker *et al.*, 2003; Lachlan &

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Feldman, 2003; Parker *et al.*, 2010; Cardoso & Atwell, 2011); or (vii) changes in the balance between natural and sexual selection (Irwin, 2000). Song divergence as a result of cultural evolution might cause reproductive isolation and hence promote speciation (Grant & Grant, 1996; Slabbekoorn & Smith, 2002; Brambilla *et al.*, 2008; Kirschel *et al.*, 2009), and it has been suggested that song learning might accelerate the rate of speciation (Lachlan & Servedio, 2004; Edwards *et al.*, 2005).

Comparing song variation over time and geographical space is one of the best methods to understand vocal cultural evolution (Podos & Warren, 2007). A rare opportunity is provided by recent range expansions. Some studies have focused on populations introduced by humans, such as North Island Saddlebacks *Philesturnus rufusater* in New Zealand (Parker *et al.*, 2012), House Finch *Carpodacus mexicanus* (Mundinger, 1975; Pytte, 1997) and Eurasian Tree Sparrow *Passer montanus* (Lang & Barlow, 1997) in eastern USA, and Common Chaffinch *Fringilla coelebs* in New Zealand (Jenkins & Baker, 1984), whereas others have examined natural range expansions, such as Common Chaffinch in Chatham Island (Baker & Jenkins, 1987), Dark-eyed Junco *Junco hyemalis* in California (Newman *et al.*, 2008), Western Gerygone *Gerygone fusca* on an Australian off-shore island (Baker *et al.*, 2003), and two species of Darwin's finches (latter in response to colonization of a third Darwin's finch species) (Grant & Grant, 2010).

Several of these studies, as well as comparisons of songs in island and mainland populations of unknown age, have found depauperate pools of syllables or song types in the isolated populations as a whole, and suggested 'founder effects' after colonization as a likely explanation for this pattern (Lack & Southern, 1949; Mundinger, 1975; Mirsky, 1976; Baptista & Johnson, 1982; Baker & Jenkins, 1987; Baker, 1996; Baker *et al.*, 2006). However, conversely, a few studies have reported high vocal diversity among newly established populations, and linked this to a relatively high number of founders, subsequent immigration, or high rates of 'cultural mutation' (Lynch & Baker, 1994; Lang & Barlow, 1997; Pytte, 1997; Kroodsma *et al.*, 1999; Hamao & Ueda, 2000; Baker *et al.*, 2003). Different results may arise at different levels of song structure, as has been shown in studies of Common Chaffinches in New Zealand vs. the UK (Jenkins & Baker, 1984) and Iberia vs. the Canary Islands (Lynch & Baker, 1993). In the former study, one part of the song was more complex whereas another part was simpler in the introduced population compared with the source population.

Geographical variation in vocalizations has long been classified into macro and micro, based on geographical scale. The former is the variation found among geographically widely separated populations that are unlikely to meet, whereas the latter refers to variation among neighbouring groups of birds that might interact with each other. Dialects are a type of micro-geographical

variation with sharp boundaries among populations within species (Catchpole & Slater, 2008b). Besides humans (Nettle, 1999), bats (Davidson & Wilkinson, 2002), primates (Mitani *et al.*, 1992; de la Torre & Snowdon, 2009), cetaceans (Weilgart & Whitehead, 1997) and a few sub-oscine passerine birds (Noad *et al.*, 2000; Saranathan *et al.*, 2007; Fitzsimmons *et al.*, 2008), vocal dialects have been widely documented in the groups of birds with learned vocalizations, i.e. oscine passerines (Kroodsma, 2004), hummingbirds (Gaunt *et al.*, 1994) and parrots (Baker, 2000). Many hypotheses have been proposed to explain how dialects are formed (Lemon, 1975; Baker & Cunningham, 1985; Podos, 2001) and maintained (Harbison *et al.*, 1999).

As song is believed to be an important reproductive isolating barrier in birds (Grant & Grant, 1997; Edwards *et al.*, 2005), it is relevant to understand how songs evolve, especially in newly established populations, which often represent the first step in the speciation process (Mayr, 1942; Grant & Grant, 2008a,b; Price, 2008). Few of the previous studies on bird song dialects uncovered how these changed after successful colonization of new areas. In this study, we compared song differentiation between founding and source populations in the Light-vented Bulbul *Pycnonotus sinensis*, with the aim to investigate if and how a recent range expansion has affected song evolution in this species.

Materials and methods

The light-vented bulbul

The Light-vented Bulbul is a medium-sized (19 cm) oscine passerine bird in the widespread Old World bulbul family (Pycnonotidae). It is near-endemic to China, where it was previously resident south of the Yangtze River, in the Oriental region. However, it began expanding northward in the 1930s, and now occupies the wide Palearctic ecozone of northeast China (Cheng, 1976; Zhang *et al.*, 2003; Fishpool & Tobias, 2005; Wang *et al.*, 2005; Fig. 1). The expansion has been rapid: in the 1980s and 1990s, numbers were small in northeast China (Williams *et al.*, 1992), but now it is locally common (Zhang *et al.*, 2003; Wang *et al.*, 2005). It occurs in open habitats with scrub and trees, including human-made environments, such as orchards, campuses and parks. It has various vocalizations, including several types of single-syllable call, and more musical, complex multiple-syllable songs (Fishpool & Tobias, 2005). Song dialects have been noted in its southern distribution area (Jiang *et al.*, 1996; Ding & Jiang, 2005; Yang & Lei, 2008).

Song recording

The Light-vented Bulbul is commonly distributed south of Yangtze River, China (red dotted line in Fig. 1; (Fishpool & Tobias, 2005)), which we defined as the
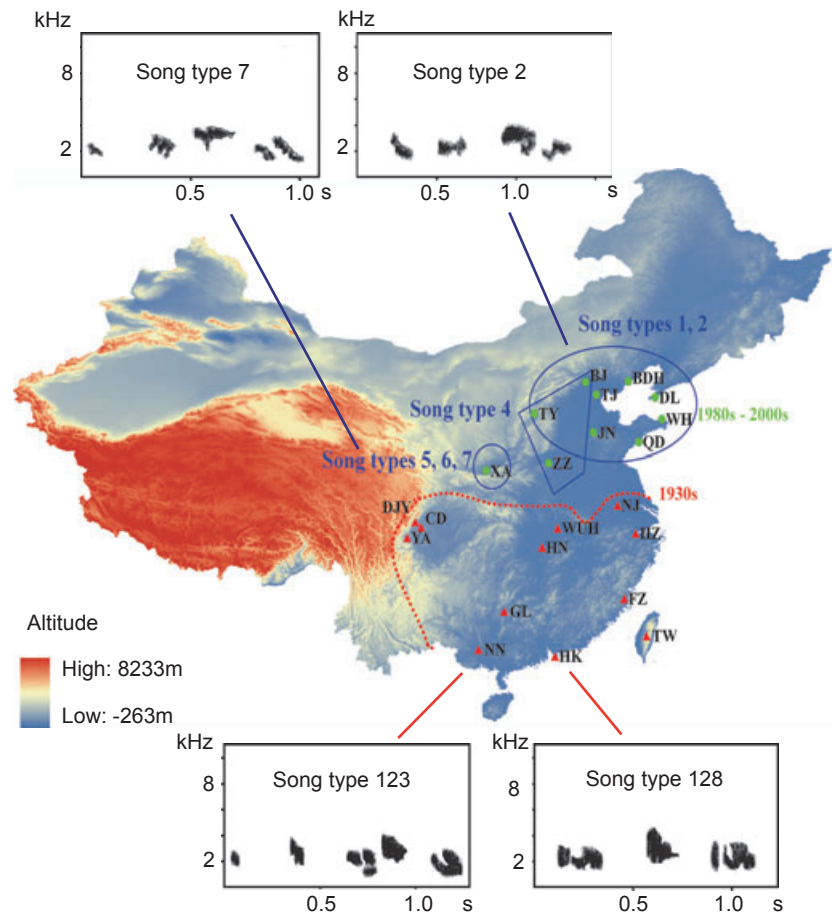
Fig. 1 Recording localities and distribution of song types in Light-vented Bulbul. Abbreviations of localities explained in Table S1. Northern and southern populations indicated by green dots and red triangles respectively. Years and red dotted line indicate the distribution boundary between northern and southern populations and time of colonization. Blue figures and letters indicate the seven song types sung by northern populations (cf. Fig. 3). Seven of the ten northern populations encircling Bohai Bay and TY sung song types 1 and 2 (DL also had a unique song type, 3); TY, ZZ and BJ sung song type 4 (ZZ sang only this song type; just few individuals of TY and BJ sung song type 4); and XA had three unique song types, 5, 6 and 7 (one individual also sang song type 1). Spectrograms show examples of different song types.

boundary between southern and northern populations, as that was previously its northern limit. We chose 12 cities south of the Yangtze River to represent 12 southern populations. Ten cities north of the Yangtze River were chosen to represent the recently established northern populations. Within each southern or northern city, we recorded bulbuls at several sites, such as parks, campuses etcetera. At each site, we recorded birds that were sufficiently widely spaced to be considered different individuals, and each site was visited only once to avoid the risk of recording the same individual more than once. In the south, two persons recorded in different places at the same time. To obtain a representative sample of each male's repertoire, we recorded each male for as long time as possible, usually until it stopped singing or flew away. For each northern individual, we recorded 27.2 ± 32.8 songs (range: 1–222; for only 3 of 162 northern individuals only one song was recorded; see Definitions of terms, below), and for each southern individual 18.6 ± 20.8 songs (range: 1–172; for only 12 of 167 southern individuals only one song was recorded). Songs were recorded during the breeding season (March–June) from 2005 to 2011,

from 6 AM to 9 AM, using a TASCAM DA-P1 portable tape recorder and Sennheiser MKH 416 directional microphone. Recordings from Taiwan were downloaded from the Macaulay Library, Cornell Lab of Ornithology and http://www.xeno-canto.org/.

Definitions of terms

See Fig. 2. *Song:* A series of syllables (see below) separated from other songs by distinct pauses (usually at least 2 s in the Light-vented Bulbul). *Syllable:* Smallest song unit used here. It may contain one or more elements (i.e. unbroken patterns in a sonogram) which appear together in a fixed sequence. There are obvious 'blank spaces' between different syllables in a sonogram. *Song type:* Contains specific syllable types given in a specific sequence. *Variant:* song types have one or more of these syllables deleted or repeated. Accordingly, differences between variants of the same song type are considerably smaller than differences between different song types. *Repertoire (song/variant/syllable):* Number of different types recorded in one individual.
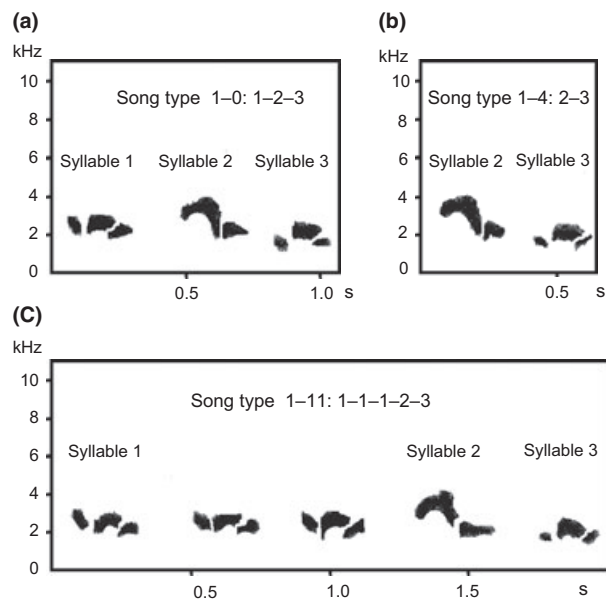
(a)

(b)

(C)

Fig. 2 Definitions of song type and syllable. Song type 1-0 (1-2-3) is the basic, commonest variant of song type 1 with a whole version of syllable types, and has three different syllable types arranged in a fixed order. Song type 1-4 is variant 4 of song type 1, which lacks syllable 1, and song type 1-11 is variant 11 of song type 1, which gives syllable 1 three times in a sequence.

Song analysis

Although our sampling was uneven across populations (Table 1), to some degree this reflected the population densities at different sites. The northern populations TY and TJ and the southern populations HN and NN (cf. Fig. 1) were excluded from the statistical analyses as only 1, 5, 1 and 2 individuals, respectively, were recorded at each of these sites. However, these small-sample populations were included in the qualitative (song type distribution) analyses, as they were considered to provide some useful information despite the small sample sizes. For example, although only one individual was recorded at TY, its 81 songs were classified into three song types, whereas the 437 songs recorded from 11 individuals in another northern population (ZZ) all belong to the same song type.

Using Avisoft-SAS Lab Pro 4.52 (Avisoft Bioacoustics, Berlin, Germany), we digitized song recordings with a sampling rate of 22 050 Hz, and made spectrograms with frequency resolution of 56 Hz and temporal resolution of 2.90 ms (spectrogram settings: Flat Top window, overlap 87.5%, FFT length 512 points). Syllable types and song types were classified by visual inspection of these spectrograms. Different syllable types and song types differed clearly in spectrograms (see examples in Figs. 1 and 2) and audibly. Although there were minor differences among individuals in the

Table 1 Sample sizes and numbers of song, variant and syllable types in the southern and northern populations; values per individual were based only on a sub-sample of 18 extensively recorded birds from each region.

	Southern populations	Northern populations
Total sampling		
No. of songs	2922	4406
No. of individuals	167	162
No. of populations	12	10
No. of song types	118	7
No. of variant types	508	273
No. of syllable types	131	36
Re-sampling		
No. of song types	23	4
No. of variant types	130	82
No. of syllable types	55	22
No. of song types per individual	1.8 ± 0.6 (range: 1–3)	1.7 ± 0.8 (range: 1–3)
No. of variant types per individual	7.6 ± 6.4 (range: 2–28)	7.8 ± 3.3 (range: 3–14)
No. of syllable types per individual	7.7 ± 3.0 (range: 4–14)	6.5 ± 3.0 (range: 2–13)

detailed appearance of syllables, classification was usually unambiguous after examination of a large sample of recordings. As there were many more syllables and song types in the south than in the north, two observers (X.Y.X. and X.J.Y.) classified the southern songs independently, whereas all of the northern songs were classified by one of these persons (X.Y.X.). Syllables and song types were assigned numbers. For example, syllable sequence 1-2-3 was denoted as song type 1-0, which means the basic, most common, variant of 'song type 1', in which the syllables are given in the order syllable 1, syllable 2, syllable 3; and syllable sequence 1-1-1-2-3 was denoted as song type 1-11, which is variant type number 11 of song type 1 in which syllable 1 is given three times, followed by syllable 2 and syllable 3 (Fig. 2). Each syllable and song type was coded to create a song library for all the 329 individuals from 22 populations.

We performed Bivariate Correlation Analysis and made a cumulative curve to evaluate whether the sampling of song, variant and syllable pools was sufficient in the north and south. The cumulative curve was plotted with the number of individuals recorded against the number of different song/variant/syllable types found. As more and more songs were recorded, fewer and fewer new ones were found, and eventually, the curve would become horizontal when all of the types have been recorded would be expected to plateau when repertoires were well sampled (Catchpole & Slater, 2008c; Baker, 2012).

To evaluate the similarity of the pools of song types across population, and relate it to geographical distances between these populations statistically, we did a Mantel test (Payne *et al.*, 2000; Slabbekoorn

et al., 2003; Peakall & Smouse, 2006), as implemented in GenALEx 6.5 based on 1000 permutations. Mantel test is a nonparametric test that assesses the relationship between the elements of any two matrices with matching entries (Peakall & Smouse, 2006, 2012). It uses multiple random permutations of the observed data to generate the chance expectation and produces an *r* value between −1 and +1 that can be interpreted like a correlation coefficient of the two matrices (Molles & Vehrencamp, 1999). Its null hypothesis is that the two matrixes have no significant correlation. The Mantel statistic was evaluated with the distribution of values permuted randomly and the probability that two matrices were more similar than expected by chance (Payne *et al.*, 2000). In this study, the first matrix of population song similarity was calculated using Jaccard's similarity coefficient, and the second matrix was produced using geographical distances (km) between each two populations. The test was procedured in northern and southern areas, respectively, both for song type and syllable type. Significant negative *r*-value means that the song similarity tended to decline with distance increase – nearby populations had more similar songs, whereas the positive *r*-value means oppositely. Jaccard's coefficient (S_j) was calculated as the number of song types common to both populations divided by the total number of song types across both populations (Podos *et al.*, 1992; Tracy & Baker, 1999).

Considering differences in individual sample sizes, and as the Bivariate Correlation Analysis and cumulative curve (Figure S1) indicated that southern sampling were not sufficiently well sampled, we re-sampled a subset of well-recorded individuals from the total dataset, to evaluate whether the number of song, variant and syllable types differ between northern and southern populations, both at the individual level and at the whole ancestral and colonial population level. Among 167 southern individuals, ≥ 40 songs were recorded for 18 individuals, and among 162 northern individuals, ≥ 40 songs were recorded for 33 individuals. These 18 southern individual and 18 of the northern ones (randomly chosen) were selected. For individuals with more than 40 songs, we picked up 40 songs randomly from song repertoire of each individual. *T*-test and Mann–Whitney *U* test were used to investigate differences at the individual level between north and south. Chi-Square test was used to compare differences between the whole northern and southern populations. All data were tested for normality by One-sample Kolmogorov-Smirnov test before *t*-tests were performed. These statistical analyses were conducted using SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

Results

According to the Bivariate Correlation Analysis (Table 2), in the north the number of song types and

syllable types were not correlated with the number of recorded songs or individuals (all *P* values > 0.05), whereas the number of variant song types was correlated with the number of songs ($r = 0.953$, $P < 0.01$) and individuals ($r = 0.868$, $P < 0.01$) recorded. In the south, the number of song types and syllable types were not correlated with the number of recorded songs or individuals too (all *P* values > 0.05), but the number of variant type was correlated significantly with the number of songs recorded ($r = 0.748$, $P < 0.05$). The cumulative curves of northern song and syllable types became approximately asymptotic with increasing number of individuals sampled, whereas the northern curve for number of variants and all three southern curves did not approach the asymptote (Figure S1). These two methods both suggested that northern populations were well sampled with respect to song and syllable types, whereas repertoire sizes for southern populations and northern variant song types were insufficiently sampled. For these reasons, a comparable subsample of extensively recorded individuals was selected from the total dataset for additional comparisons (see Materials and methods).

In the total dataset, the newly established northern populations had much smaller pools of song, variant or syllable types than the combined southern source populations (Tables 1 and 3 and Figure S1). In total, seven song types, 273 variant types and 36 syllable types were recorded in the north, whereas southern populations

Table 2 Results of bivariate correlation analysis.

	Correlations	No. of songs recorded	No. of individuals recorded
Northern populations			
No. of song type	*r*	0.295	0.183
	P	0.477	0.664
	N	8	8
No. of syllable type	*r*	0.635	0.527
	P	0.091	0.180
	N	8	8
No. of variant type	*r*	0.953*	0.868*
	P	< 0.001	0.005
	N	8	8
Southern populations			
No. of song type	*r*	0.403	0.188
	P	0.248	0.603
	N	10	10
No. of syllable type	*r*	0.534	0.561
	P	0.112	0.092
	N	10	10
No. of variant type	*r*	0.748†	0.33
	P	0.013	0.352
	N	10	10

N stands for the number of populations.
*Correlation is significant at the 0.01 level (2-tailed).
†Correlation is significant at the 0.05 level (2-tailed).

had a total of 118 song types, 508 variant types and 131 syllable types. For the re-sampled dataset comprising 18 northern individuals and 18 southern individuals, the numbers of song/variant/syllable types were 4/82/22 and 23/130/55 respectively. Despite more songs having been recorded in northern populations (Table 1), they had significantly smaller pools of song types, variants and syllable types (all $\chi^2 > 54$, all $P < 0.001$; Table 3). The same conclusion is reached using only the subsample of extensively recorded individuals (all $\chi^2 > 10$, all $P < 0.001$; Table 3). The numbers of song type, variant or syllable types sung per individual did not differ between northern and southern populations (subsample of extensively recorded individuals: t-tests, all $|t| < 1.2$, all d.f. = 17, all $P > 0.25$; Table 4).

In the north, a small number of song types and syllable types were widespread, and nearby localities showed a high degree of similarity in song and syllable type composition (Fig. 3). In contrast in the south, few song types and syllable types were recorded at more than one locality, even in geographically closely related populations (three populations in Sichuan Basin: DJY, CD, YA).The results of Mantel tests confirmed these differences (Fig. 4). In northern populations, there was a significant negative correlation between song/syllable type similarity and geographical distance (for song type, $r = -0.637$, $P < 0.05$; syllable type, $r = -0.653$, $P < 0.05$), meaning that song/syllable type similarity decreased significantly with increasing geographical distance, that is geographically closer populations had more similar song types and syllable types. But this

pattern was not observed in southern populations: there was no association between song/syllable type and geographical distance was apparent (for song type: $r = -0.218$, $P = 0.110$; syllable type: $r = 0.128$, $P = 0.842$). Accordingly, northern populations showed evidence of divergence by distance, whereas the low level of common song types among southern populations suggested a mosaic pattern of song dialects across the southern distribution.

On the basis of song type distributions (Figs. 1 and 3), we divided the 10 northern populations into three dialect regions (Fig. 1): (i) seven populations around Bohai Bay and another population (TY, $n_{\text{individuals}} = 1$) sung song types 1 and 2; the most northeastern population (DL) had a unique song type, number 3; (ii) ZZ had only one song type, number 4, which was also sung by a few individuals in BJ and TY; (iii) XA had three unique song types, numbers 5, 6 and 7, and one individual also sang the variant type 1-7.

Only three song types (2.4%) were sung both in the north and in the south. The northern common song types 1 and 2 were recorded in only one individual in one southern population (GL). The third shared song type, 3, was recorded in northern population DL (in 14 of 52 individuals) and in southern population DJY (in 6 of 12 individuals). Twenty-three syllable types were sung both in the north and south, representing 63.9% in the north ($n = 36$) and 17.6% in the south ($n = 131$) of the total syllable types respectively.

Discussion

Very few song types were common to northern and southern populations of bulbuls. In contrast, 63.9% ($n = 36$) of the northern syllable types were also found in the south. This suggests that the syllable is a more conservative unit than song type in the vocal evolution
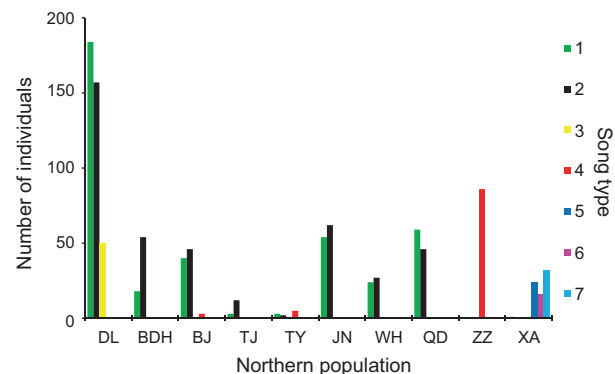
Table 3 Song comparisons between the whole north and the whole south.

	Chi-Square test		
	χ^2	d.f.	P
Total sampling			
No. of song types	98.568	1	0.000
No. of variant types	70.711	1	0.000
No. of syllable types	54.042	1	0.000
Re-sampling			
No. of song types	13.370	1	0.000
No. of variant types	10.868	1	0.001
No. of syllable types	14.143	1	0.000

Table 4 Song comparisons of southern and northern individuals.

	t-test		
	t	d.f.	P
No. of song types	$Z = -0.609$	17	0.542
No. of variant types	0.13	17	0.897
No. of syllable types	-1.166	17	0.252

Fig. 3 Song types in ten northern populations (arranged from north to south on x axis). Song types 1 and 2 are widespread in the seven populations encircling Bohai Bay (DL, BDH, BJ, TJ, JN, WH and QD) and TY (latter just one individual with three song types). See Fig. 1 and Table S1 for explanation of locality codes.
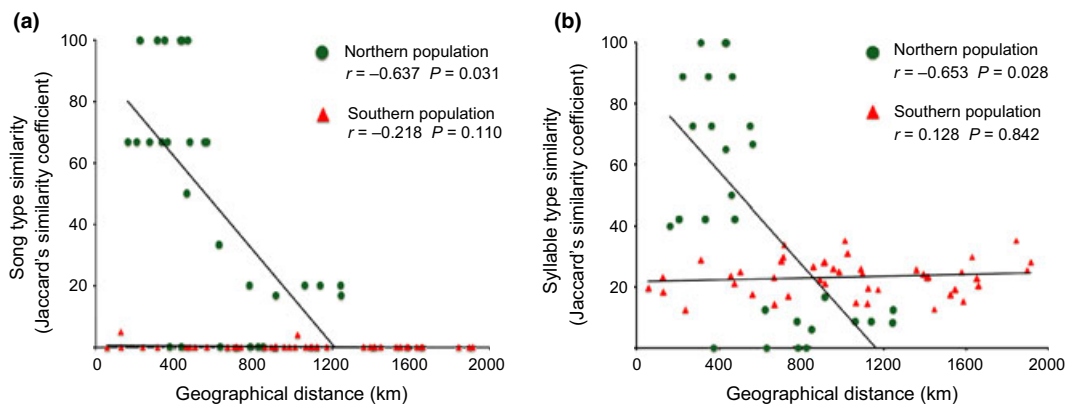
Fig. 4 Plot of the similarities among populations in the pool of (a) song types or (b) syllable types in relation to geographical distances. Each dot represents a pairwise comparison between the Jaccard's similarity coefficient for pool of (a) song types or (b) syllable types against the geographical distances (km) between these populations both in north and south respectively. The results (regression lines, r and P values) indicate that both the similarities of song and syllable types correlated negatively with geographical distances in north, but not correlated with geographical distances in south.

of the Light-vented Bulbul, in agreement with some studies on other birds (Lynch *et al.*, 1989; Burnell, 1998; Nelson *et al.*, 2004).

Newly established northern populations only retained a small subset of the total syllable pool of the ancestral southern populations. In the north, we did not hear any other song types in addition to the seven types that we classified. Although we cannot be sure that we covered each individual male's full repertoire (in some cases we almost certainly did not do that), we are confident that our sampling is sufficient to broadly represent the northern populations. Despite the cumulative curve for the south (Figure S1) was still growing which suggested the south not being sampled as exhaustively as the north, the results still show higher diversity in the south. So the interpretation of results is unaffected.

According to founder effect/cultural drift theory in birdsong studies (Baker & Jenkins, 1987; Lachlan & Slater, 2003; Huber & Podos, 2006), founders would only sing a small subset of source populations' song types and syllables, thereby decreasing the total variation. This has previously been found in some founding populations of birds (Bitterbaum & Baptista, 1979; Baker & Jenkins, 1987; Baker *et al.*, 2001; White, 2012). In addition, the low density of pioneers and the concomitant small number of learning models would probably further decrease the vocal diversity and increase stereotypy (Bitterbaum & Baptista, 1979; Pytte, 1997; Matthysen *et al.*, 2002). Our results agree with these predictions. However, as there was hardly any song type sung both in northern and southern bulbuls, it is uncertain to what degree original southern song types were retained in the newly colonized populations. Alternatively, the song types might have diverged quickly after the new colonization, as has been suggested for some other birds (Jenkins & Baker, 1984;

Baker *et al.*, 2003; Förschler & Kalko, 2007; Parker *et al.*, 2012).

The wider geographical distribution of a few song types in the north could have at least two, nonexclusive explanations. One of these is that it might result from the fewer geographical barriers and hence, more 'meme flow' than in the south. Several of the southern populations are isolated by topographical barriers, such as mountainous areas or water bodies (Fig. 1), whereas the northern Bohai Bay populations inhabit a topographically rather homogeneous region. The northern ZZ and especially, XA populations, which are the most isolated ones of the northern populations, also have the most distinct (divergent) songs. Moreover, the northern DL population, which is the most remote of the seven Bohai populations, is the only one of these in which a unique song type was recorded. The differences between the southern CD, DJY and YA, which are in close proximity and not separated by any apparent geographical barriers, are more difficult to explain. Similar microdialects have been observed in other species (Leader *et al.*, 2000; Baker, 2003; Slabbekoorn *et al.*, 2003; Podos & Warren, 2007). It is possible that the southern populations are more resident than the northern ones, which would further contribute to the observed differences. This has been noted in the White-crowned Sparrow, in which northern, migratory, populations have been found to have more widely distributed dialects than southern populations (Baptista, 1977; Kroodsma *et al.*, 1984; Austen & Handford, 1991; Chilton *et al.*, 2002). However, the statement that northern populations of the Light-vented Bulbul are migratory, unlike southern ones (Fishpool & Tobias, 2005), is not correct, as good numbers winter in the north (personal observations; P. Holt and J. Hornskov in litt.).

Another plausible explanation for the wider geographical distribution of song types in the north is that the recent spread across a large area might have contributed to the homogenization of the northern songs. As a result of the rapid expansion, local song types may not have had sufficient time to form. In agreement with this is the observation that the XA population, which is the southernmost and hence, possibly the oldest one, had the most unique song of the northern populations.

Conclusions

We found that compared with southern source populations, the northern, recently established populations (i) had depauperate song type and syllable type pools, but did not differ in repertoire size of individual birds; and (ii) had altered the geographical distribution of song types from mosaic to a few wide-spread song types. A combination of 'founder effect', fewer geographical barriers to 'meme flow' and the recent spread across a large area in the north are likely explanations for these differences. Our results show that founding populations can change their pools of acoustic signals rapidly after range expansion.

Acknowledgments

Conflict of Interests

The authors have declared that no competing interests exist.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Cumulative curves of song/variant/syllable types for northern and southern populations. The trend of curve showing how the number of new types found rises as the number of individuals recorded increased, indicating finite pools of northern song and syllable types, but the other four seemed like not.

Table S1 Song sampling information for Light-vented Bulbuls.