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Song pattern of black redstart populations in the Tibet Plateau: an intercontinental comparison

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Abstract. We analyzed the song pattern of the black redstart (*Phoenicurus ochruros*) from the Haibei area and compared it to three other recording sites on the Tibet Plateau using the Avisoft-SAS Lab program. Five extracted functions identified individuals from the Haibei population. By comparing populations from the Tibet Plateau (China), Slovakia (Central Europe), Germany and other sites in Europe, we established that the maximum song frequency was lowest in the Haibei population of the Tibet Plateau. On a large geographic scale, song differences increased with geographic distance. Black redstarts sing lengthy songs composed of two parts in both the Tibet Plateau and in Europe. However, while these two sections were totally or partly identical within the Tibet Plateau population, they were totally different in European populations. Redstart songs in the Tibet Plateau share a syllable of scrunching sound, while European individuals have a homologous section composed of repeat elements.

Key words: individual discrimination, homologous, song type, drift

Introduction

The significance of bird song has received much attention for many years (e.g. Darwin 1871, reviewed in Baker 2001). As one of the important secondary sexual characters, bird song has two main functions: mate attraction and territory defense, encoding a wide range of information about the singer (Catchpole & Slater 1995). Studies of bird song have revealed that vocalizations possess both species-specific characteristics and individually distinctive features (Becker 1982, Falls 1982, Marler 1960, Nelson 1989). Further observational and experimental evidence indicates that species can discriminate between conspecific and heterospecific song (e.g. Grant & Grant 1996, Marler 1960, reviewed in Ptacek 2000), which provides a basis for female preference and guarantees that female birds mate with high quality, conspecific males, hence increasing their fitness. At the population level in some species, such as the white-crowned sparrow, song dialects can prevent gene flow between different populations ensuring that offspring are well-adapted to the local habitat (Baker 1983, Tomback et al. 1984, MacDougall-Shackleton et al. 2002). On the other hand, species specificity and individual identity of songs are embodied as the commonness and variance among individuals within a bird species. Therefore, analysis of the song stereotype and variance can be an important first step for further study of mate choice. In addition, in order to optimize transmission, the frequency properties of songs reflect the sender's habitat characteristics (e.g. Hunter & Kreb 1979, Slabbekoorn & Smith 2002, Strote & Nowicki 1996).

Black redstarts (*Phoenicurus ochruros*) are sexually dimorphic and only males sing in breeding season and in the autumn (Weggler 2000, Andersson 2001). Plumage delay, regarding sexual dimorphism has been studied extensively in black redstarts (Landmann

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& Kollinsky 1995a,b, Kollinsky & Landmann 1996, Weggler 2001). As regards song, Nicolai (1992) revealed dialects and juveniles' song learning time of residents in Germany. Cucco & Malacarne (1999) concluded that song characteristics in this species could be an honest signal of their age status for mate choice in reproduction. Boehme & Boehme (1986) have explored the relationship of species of the genus *Phoenicurus* using acoustical signals. Additionally, a few studies have tried to elucidate the functions of black redstart's song in autumn (Weggler 2000, Andersson 2001).

However, studies of black redstart song in the extreme environments of the Tibet Plateau in China are lacking. In this paper, we analysed songs of this species for populations in Haibei, Heimahe, Wenquan, and Tuotuohe of the Tibet Plateau to examine: (1) temporal and frequency properties of song and song pattern of the Tibet Plateau population; (2) variability among individuals within the population; (3) differences in song between different parts of the Plateau; and (4) differences in song properties between populations of the Tibet Plateau and those other parts of this species' range.

Materials and Methods

Recording and analysis

We recorded black redstarts songs around the Haibei Alpine Meadow Ecosystem Research Station of the Chinese Academy of Sciences (37°29'N, 101°28'E, 3,200 m a.s.l.) from mid-April to late May, 2001, using an Uher tape recorder with a Sony directional microphone and Sony tapes. Songs in Heimahe (36°45'N, 99°46'E, 3,562 m a.s.l.), Wenquan (35°26'N, 99°26'E, 3,960 m a.s.l.), and Tuotuohe (34°06'N, 92°27'E, 4,700 m a.s.l.) (Qinghai Province, China) were recorded with a Sony MD Walkman Digital and Minidisk recorder MZ-R50 with a Sony ECR-598 directional microphone. Tapes used were Sony MDW-60 digital Audio MiniDisc. Songs of males in the Poľana Mts, Slovakia (1,200–1,400 m a.s.l.), were recorded with TASCAM DA-P1 in July 2004. Songs in Germany were obtained from previously recorded tapes (Die Vogelstimmen Europas). For sonogram quality comparison without quantitative analysis, we have also included previously published sonograms from the scientific literature or the World Wide Web. At the Haibei Alpine Meadow Ecosystem Research Station, we identified males on the basis of song site fidelity.

Analogue to digital conversion was 16 bit at a 22.05 kHz sampling rate. Songs were examined spectrographically using SAS-LAB PRO (Specht 1998). Sonograms were created with settings of 256 point transformation and a Hamming analysis window. The corresponding frequency resolution and band width are 86 and 112 Hz, respectively. Overlap is set at 50% with a temporal resolution of 5.8 ms and 1/band width equal to 9.4 ms.

In total, song samples of 10 male black redstarts were collected in the Tibet plateau, seven from the Haibei population, and one each from Heimahe, Wenquan, and Tuotuohe. Two males were recorded in Slovakia. All good quality samples were selected for parameter measurements.

Terminology and parameters

Song, Strophe and Syllable

Following Catchpole & Slater (1995), Cucco & Malancarne (1999), we defined the song, strophe and syllable of black redstarts in the Tibet Plateau as in Fig. 1. A strophe described in this paper is composed by syllables and defined as part of the song. Since we detected distinct song structures in black redstarts in Slovakia and Germany, we subdivided the songs from these two areas into two parts as in Cucco & Malancarne (1999).

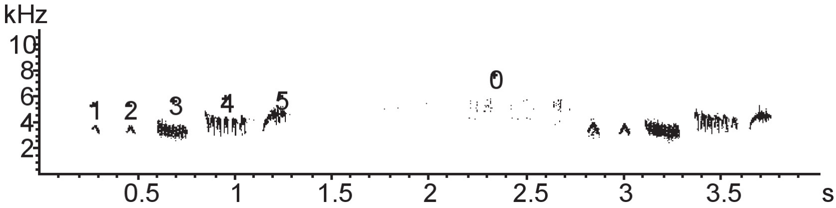


Fig. 1. A black redstart song from the Haibei population. Numbers 1 to 5 marked in the figure are the syllables that make up a typical strophe. The song is composed of two typical strophes plus syllable 0 between them.

Drift

Lambrechts & Dhondt (1987) termed the increase of the length of the pauses between strophes and the shortening of strophes as 'drift'. Black redstarts often reduce syllables from the end of the typical strophes. Here we define the syllable reducing within strophes as 'drift'; each strophe performances with a different syllable reduction one as 'drift type' and all the drift types of a given male as 'drift repertoire'.

Parameters are defined as follows:

D_i, the duration of syllable i, i = 1, 2, 3, 4, 5;

D_n, the length of one element of syllable 4;

I_i, the interval between syllable i and syllable i + 1, i = 1, 2, 3, 4;

N, the number of repeat elements in syllable 4;

L_i, the lowest frequency of syllable i, i = 1, 2, 3, 4, 5;

Ls, the lowest frequency of an entire typical strophe;

H_i, the highest frequency of syllable i, i = 1, 2, 3, 4, 5;

Hs, the highest frequency of an entire typical strophe;

MPF_i, frequency of highest amplitude of syllable i, i = 1, 2, 3, 4, 5;

MPFs, frequency of highest amplitude of an entire typical strophe;

t_1, the duration of the first part of songs in Slovakia and Germany (Fig.2);

t_2, the duration of the second part of songs in Slovakia and Germany (Fig.2);

f_1, the highest frequency of the first part of songs in Slovakia and Germany (Fig. 2);

f_2, the highest frequency of the second part of songs in Slovakia and Germany (Fig. 2);

t_n, the duration of repeat elements in the first part of songs in Slovakia and Germany (Fig. 2);

n, the number of repeat elements in the first part of songs in Slovakia and Germany.

Due to the difficulty in determining the temporal and frequency boundary of syllable 0, its duration and frequency were not measured.

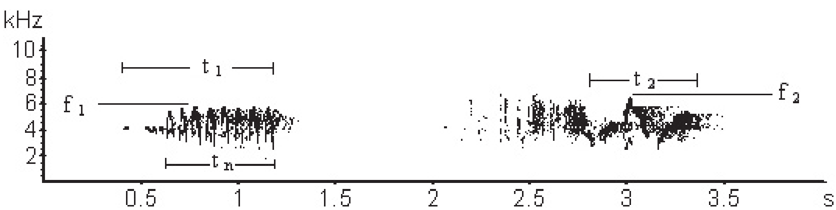


Fig. 2. A black redstart song from Slovakia (parameters – see chapter Material and Methods).

Statistics

The discriminating factors of males were abstracted from all parameters listed above by discriminate analysis. Cluster analysis for songs from different sites of the Tibet Plateau was performed using the average of the above parameters at the individual level. Discriminant analysis, NPar (Non parametric test) and Cluster analysis were all performed with SPSS 10.0 package for Windows.

Results

Sonogram stereotype within population and individuals in Haibei of the Tibet Plateau

Songs of males from the Haibei population share six basic syllable types in a common song syntax (Fig.1). Songs can be classified as two basic cases: (1) long songs, composing of two typical strophes often with syllable 0 between them, the two parts being totally or partly the same; (2) short songs, containing one strophe. Long songs accounted for different proportions of songs in different males. In male 1 (n = 53), 4 (n = 109), and 5 (n = 102) with large song samples, the proportion of long songs was 37%, 34.6%, and 46.0%, respectively. Black redstarts often modified the typical strophe by reducing syllables from the end in most cases. Songs showed high stability of spectrograms within an individual and no daily change was found.

As regards song rate, we were unable to determine whether the differences between individual males derive from actual song variation or sampling, since a single male black redstart can sing a different number of strophes per minute during separate song bouts, and occasionally song rate differs significantly between song bouts for the same individual. The males sampled in Haibei sang 6.6 to 12.9 strophes per minute.

Variance among individuals within Haibei population

Song durations varied significantly for the same individual. Long songs, such as song 1 in Fig. 1 lasted up to 4.23 s, but in ones composed of an incomplete strophe, sometimes of only one or two syllables, song length was shorter than 0.3 s.

Table 1. Standardized canonical discriminant function coefficients.

	Function				
	1	2	3	4	5
D_n	0.875	-0.138	0.234	-0.559	0.037
D_2	0.165	-1.093	0.098	-0.183	0.289
N	0.098	0.452	0.461	0.571	0.595
D_5	0.223	-0.735	0.677	0.373	-0.462
MPF_1	-0.707	0.200	-0.375	-0.584	-0.250
MPF_2	0.289	-0.559	-0.694	0.607	0.366
L_3	0.639	0.520	-0.485	0.455	-0.125
H_4	0.513	0.809	0.443	0.100	-0.371
MPF_4	0.031	0.623	-0.156	-0.474	0.313
L_5	0.525	0.661	-0.167	-0.202	-0.388

In the discriminate analysis, five discriminate functions were extracted for identifying individuals (Table 1). The success of classification of individuals was high: 92% songs were correctly assigned to individuals in the Haibei population.

Duration of syllable 4 and its element numbers in the Haibei population

Syllable 4 was composed of a series of repeat elements. The duration of the syllable (D_4) was highly correlated with the element numbers of a male ($R = 0.87876 \pm 0.01307$ for male 2; $R > 0.9$ for other males of this population). So was it in Heimahe male ($R = 0.96525$). But among individuals, D_4 differed significantly even though they have the same numbers of elements ($p < 0.001$), and the correlation between the duration and element numbers of D_4 is weak ($R = 0.63370 \pm 0.05289$).

Song drift in the Haibei population

Males of the Haibei population did not always sing normal songs composed of typical strophes throughout the time of the recordings. As described above, songs appeared to be shortened at random, i.e. songs 'drifted'. The drift song is thus shorter than the normal song. The drift type accumulation rates among individuals are different (Fig. 3). For example, the song types of male 5 increased faster than male 2, i.e., given consecutive songs in equal number, male 5 had more drift types than male 2 (Fig. 4). Precisely because of song drift, individuals displayed different singing performance heterogeneity, and the typical strophe accounted for 40% to 72.2% of total strophe types for different individuals.

We recorded individual 5's songs on three days (May 10th, 11th and 16th) for comparison and found that most song drift types were the same on each separate day. Of nine drift types out of 72 songs recorded consecutively on May 10th and eleven song drift types out of 72 songs recorded on May 11th, 8 song types were similar or even identical to each other. On May 16th, no new drift types were found in 25 sampled songs. The results indicate that the rate of increase in drift repertoire of one individual tends to decrease with sample size. This conclusion is also supported by results from other individuals with large song samples, e.g. males 1 and 4.

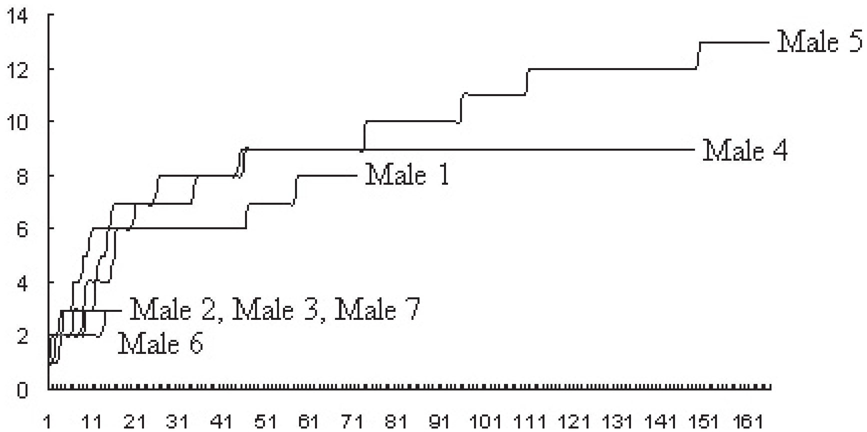


Fig. 3. Song drift type accumulation in the black redstart.

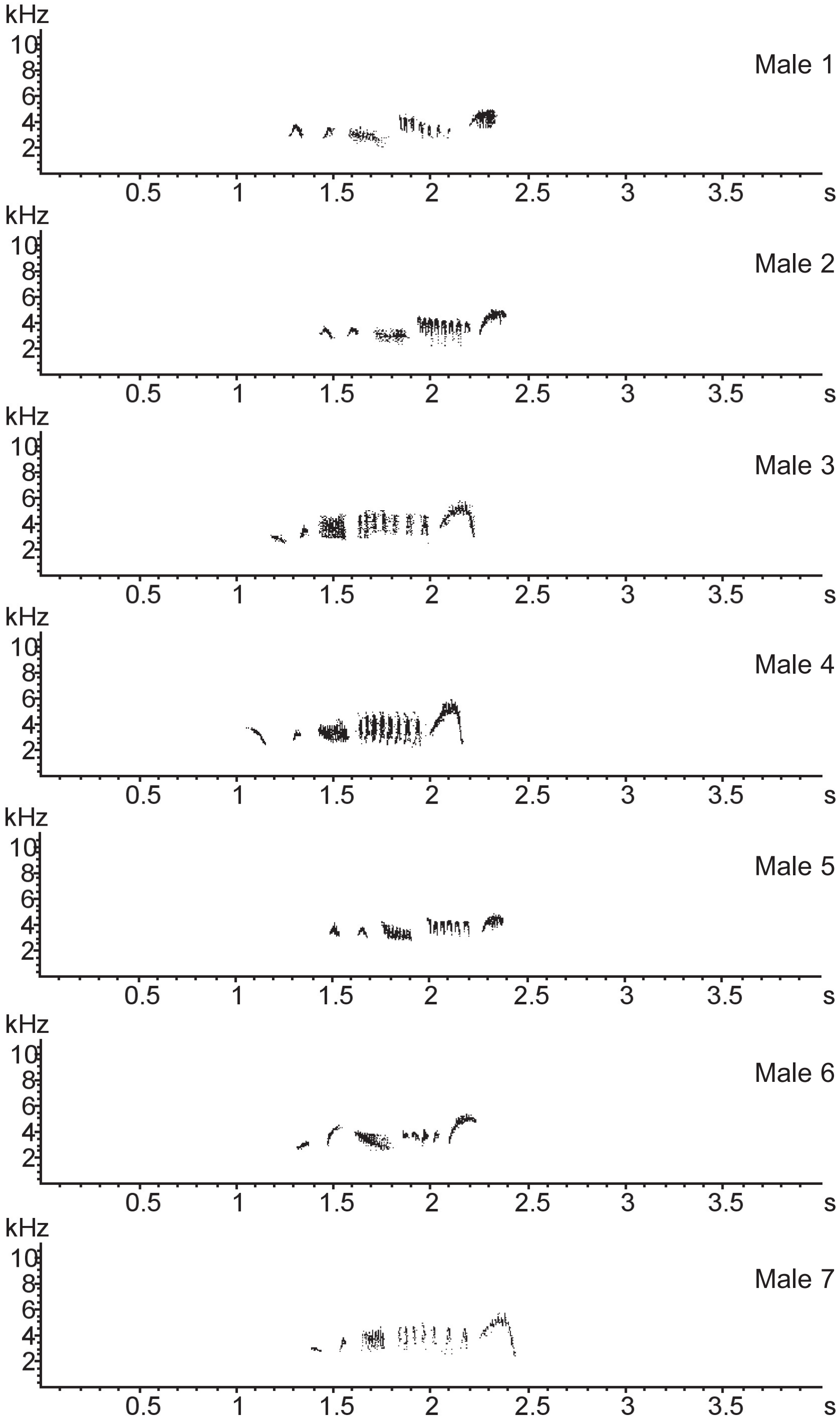


Fig. 4. Strophe sonograms of black redstarts from the Haibei population.

Song difference among three populations of the Tibet Plateau

Because of the high stability of song within a population, despite the small song sample size from other sites of the plateau, we can use the available spectrograms to illustrate

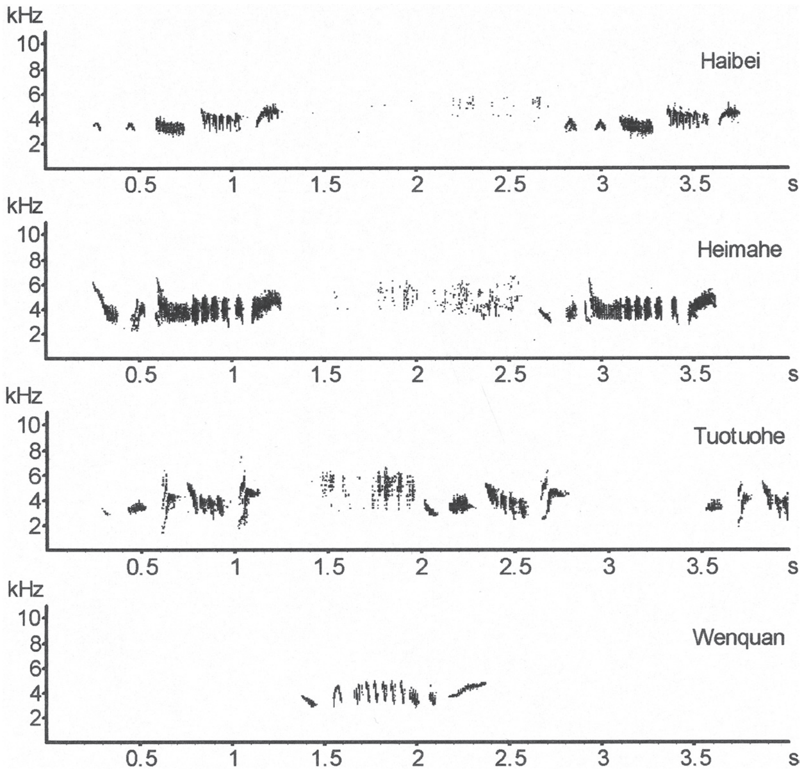


Fig. 5. Black redstart songs in different parts of the Tibet Plateau.

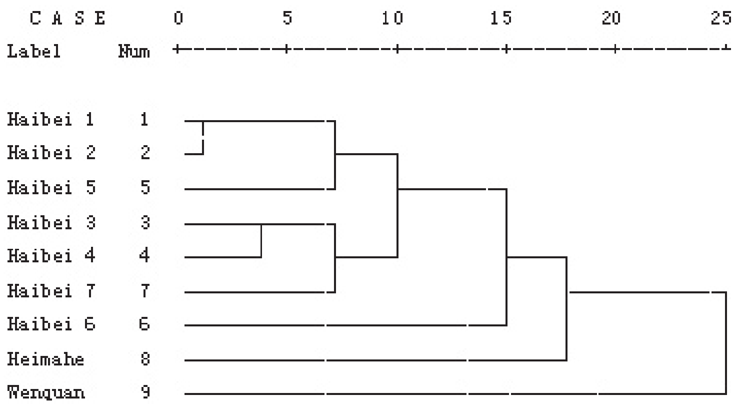
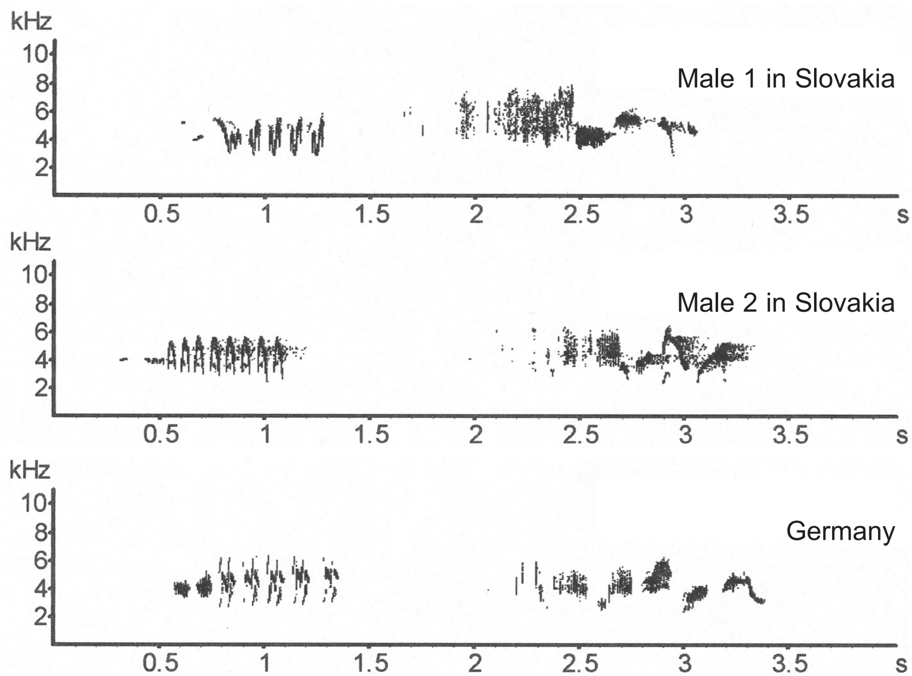
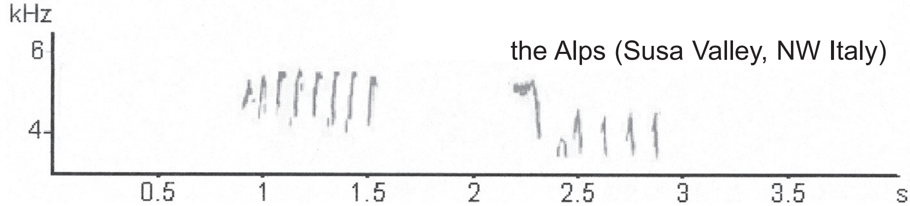


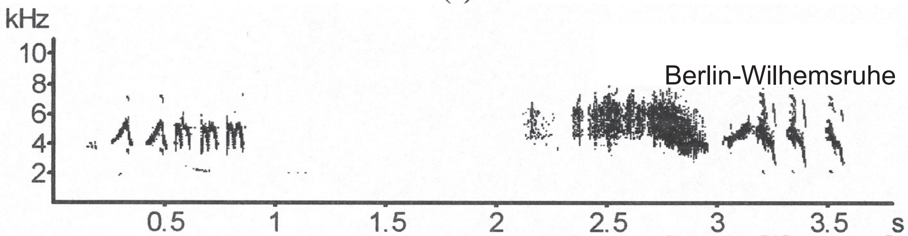
Fig. 6. Hierarchical cluster analysis of individuals from different areas of the Tibet Plateau. Dendrogram using average linkage (between groups).


kHz
10
8
6
4
2
Male 1 in Slovakia
0.5
1
1.5
2
2.5
3
3.5
s
Male 2 in Slovakia
Germany

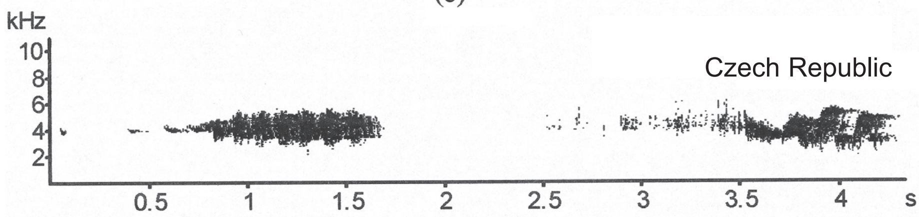
(a)


kHz
6
4
the Alps (Susa Valley, NW Italy)
0.5
1
1.5
2
2.5
3
3.5
s

(b)


kHz
10
8
6
4
2
Berlin-Wilhemsruhe
0.5
1
1.5
2
2.5
3
3.5
s

(c)


kHz
10
8
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4
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Czech Republic
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1
1.5
2
2.5
3
3.5
4
s

(d)

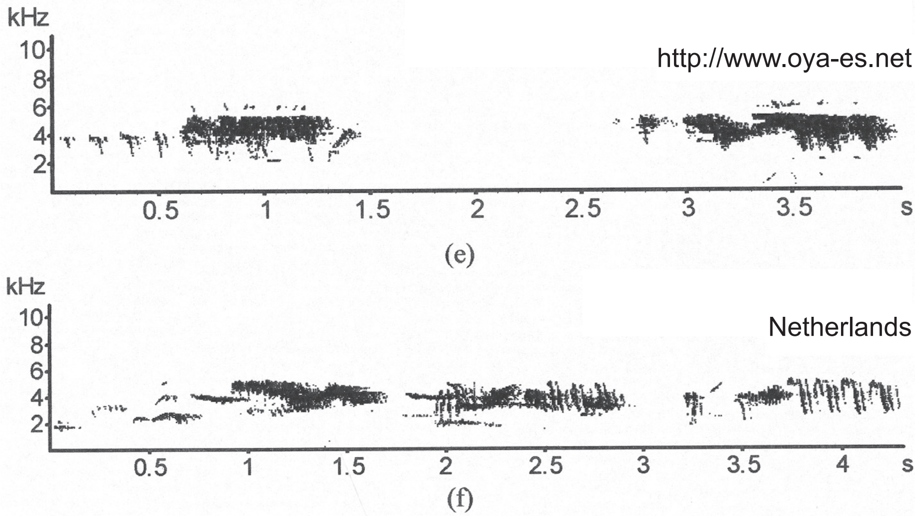

Fig. 7. Sonograms of the black redstart from different areas of Europe: (a) Slovakia and Germany; (b) the Alps (Susa Valley, NW Italy) (modified from Cucco & Malacarne 1999); (c) Berlin-Wilhelmsruhe (http://www.avisoft-saslab.com), f_1 = 5.94, f_2 = 7.57 kHz; (d) Czech Republic (Český rozhlas) (http://www.junglewalk.com), f_1=5.51; f_2 = 5.77 kHz; (e) downloaded from http://www.oya-es.net; (f) The Netherlands Club voor Natuurgeluiden Registratie (http://home.hccnet.nl/wim.rougoor/cnr/opnamen.htm).

the similarities and obvious differences existing between Haibei and Heimahe / Wenquan (Fig. 5). One of the conspicuous differences in sonograms between the sites was the duration of the interval between syllable 3 and syllable 4 (I_3). I_3 for males in the Haibei area (69.8 ± 6.5 ms, N = 129) was significantly longer than that in Heimahe (10.23 ± 1.88 ms, N = 12) and Wenquan (4.46 ± 0.65 ms, N = 3) ($p < 0.001$, NPar). Hierarchical Cluster analysis grouped nine individuals correctly into different areas. Individuals 1 to 7 in Haibei are grouped into one main branch, and individuals from Heimahe and Wenquan are grouped into two separate branches (Fig. 6). It was not possible to identify I_3 in songs of males from the Tuotuohe population, which instead possessed syllables of harmonics, so we did not analyse this population in the same manner.

D_4 in the Haibei population had more elements than in other three sites. The element numbers in Haibei were often six to eight (except for individual 6), while they were no more than five in males of other sites of the Tibet Plateau.

Song pattern of black redstart in Poľana Mts, Slovakia

As for the Tibet Plateau population, males of Poľana Mts population in Slovakia also sang long and short songs and song drift was detected in a few cases. However, in contrast to the Tibet population, long songs in Slovakia have two totally different parts (Fig. 2). Short songs could be further subdivided, being either similar to the first or the last part of long songs. Like D_4 in songs from the Tibet Plateau, part 1 of the Slovakian song contained a series of the same elements, and t_1 and t_n are highly correlated with the number of elements that t_n contained in a given male (e.g. in male 2: R = 0.9813 ± 0.0142 for t_1 and 0.9998 ± 0.0066 for t_n). The parameters defined in Fig. 2 are listed in Table 3.

Comparison of black redstart songs between Haibei, Poľana Mts and other European populations

Every sampled male sang songs containing syllable 0 as did most of the songs found on the World Wide Web, and this syllable was often set between two song parts. A few songs have no syllable 0 probably because small sample size or because the recording started later. Apparently, not all songs from the same individual have syllable 0 based on our findings in the Tibet plateau populations.

Figs 3 and 7 show the song form similarity and variability existing in several sites of the Tibet plateau as well as the differences between the Tibet Plateau and European sites. In long songs, the two parts in Europe were totally different in form while the two parts of songs from the Tibet Plateau area shared common syllables organized with the same syntax. As far as the highest frequency of songs is concerned, both f_2 ($p < 0.05$ NPar) and f_1 ($p < 0.05$ NPar) of songs in the two males from Slovakia were higher than the highest frequency H_5 of songs of the Haibei population. However, for the latter part of songs of male 2 in Slovakia, the frequencies are mainly distributed from 3 to 5.8 kHz, and the frequency of the terminal note was similar to that in Haibei ($H_5 = 5.32 \pm 0.34$, $N = 7$ males).

Discussion

Simple song type and song drift in the Haibei population

Previous studies of this species have primarily focused on repertoire size and the evolution of complex song. However, a simple song type still exits in some bird species such as sage sparrows (*Amphispiza belli*) (Wiens 1982) and black redstarts (this study). Wiens (1982) concludes that song type simplicity in sage sparrows reflects the fact that the song plays a simple role and that selection for a more complex song is lacking in this species. In this study, black redstarts were observed singing on conspicuous posts. For a species with a simple song type, song posts may be useful for individual discrimination. As regards repertoire size, it has been suggested that a small repertoire may facilitate individual recognition by reducing the complexity of an individual's song, thus rendering its identitification less ambiguous (Krebs & Kroodsma 1980). Small repertoires might also foster the development of sharp dialect boundaries among local populations, since it might be much easier to establish a dialect pattern among individuals sharing a single song type than among individuals that each sings a large number of song types (Kroodsma 1978). For example, in the willow warbler, which sings highly variable songs, there are no regional dialects across its large transpalearctic range. On the other hand, regional dialects are also unlikely to evolve from extremely repetitive songs; the coal tit (*Parus ater*) provides a good example (reviewed in Martens 1996). In contrast, this study shows that the similar basic song type in black redstarts on the Tibet plateau coupled with the variance between sites indicates the potential of this song type to form geographic differences and dialects.

Various drift types occur in black redstart song. Drift can be explained either by neuromuscular exhaustion or by a decline in motivation to sing, although the two hypotheses are not mutually exclusive (Lambrechts & Dhondt 1988, Weary et al. 1988, 1991). Anti-exhaustion hypothesis predicts that males that have a larger repertoire size should show less drift, because they can switch more frequently to another song types and thus avoid neuro-muscular exhaustion (Lambrechts & Dhondt 1988). This hypothesis was confirmed in interspecific level in some birds; for example, great tits (*Parus major*) have the smallest repertoires and the highest levels of drift, while coal tits (*P. ater*) have the largest repertoires and rarely drift (Poesel1 & Kempenaers 2000). Songs of the black redstart are stereotyped from our limited recordings, more recordings are needed to test whether the song drift is due to neuromuscular exhaustion. As to the relationship between song type simplicity and song drift, data of other relative species are needed to test the hypothesis in inter-specific level. Temporary respiratory activity, oxygen consumption, and energy constraints are alternative explanations for the syllable reduction. For example, in some zebra finch individuals, significant hyperventilation occurs during song, causing almost complete apnea. When motif duration is taken into account, there is only small inter-individual variability in oxygen consumption per motif (Franz & Goller 2003). If energy consumption is the key factor determining the length of a typical strophe in black redstart, we can expect that the duration reflects the individual's temporary condition and selection for song duration may occur.

Song homologous character and geographic variability

Black redstart songs of each sampling site except the Netherlands site, shared syllable 0, a scrunching sound. Long songs from all sites are organized into two parts and short songs are composed of one of the two parts. In European sites, part I has a series of repeat elements equivalent to D_4 in the Tibet Plateau songs. The length of the song syllable of the black redstart in the Tibet Plateau (D_4) is also correlated with the repeat numbers, as has been found in Alps (Cucco & Malacarne 1999). They are almost certainly homologous. Marler (1960) predicted that vocal features of bird song that are used to recognize species should differ from those that are used to recognize individuals within a species. The traditional view of mating signal evolution suggests that certain features of the mating signal serve for species recognition; stabilizing selection decreases variance in these properties making them reliable species indicators (Waage 1975, Barlow & Siri 1997, reviewed in Ptacek 2000). Konishi (1985) has listed four generalizations about species recognition derived from previous studies: (1) some (not necessarily all) song properties common to all members of a species serve in species recognition; (2) two to three song properties are usually sufficient for species recognition; (3) different cues may have similar or different effects; (4) different species may use different aspects of song for species recognition. For example, female song sparrows (*Melospiza melodia*) responded preferentially to songs containing their own species' syllables and to songs containing their own species' temporal patterns, while female swamp sparrows (*M. georgiana*) were also sensitive to both syllable type and temporal pattern, in contrast to male swamp sparrows, which show no preference for swamp sparrow temporal patterns (Searcy et al. 1981). In conclusion, syllable 0, the trill, and the organization reflected in a long song may have evolved under stabilizing selection for species recognition. Redstarts (*Phoenicurus phoenicurus*) also have repeat elements in their songs similar to those of D_4 of black redstarts in the Tibet Plateau and many areas of Europe (part I of the song), so this song section is homologous beyond the species level. However, syllable 0 was not found in redstart songs (Thimm 1973), and it may be that syllable 0 acts as the species-specific characteristic of the black redstart and serves for species recognition.

With regards song spectrum, it is no doubt that the difference between the Tibet plateau and Europe is greater than those within the Tibet plateau. On a large geographic scale, the similarity between black redstarts from different populations decreased with distance. Within the Tibet Plateau, cluster analysis revealed that song variations between individuals from different populations are greater than those between those from a same population. However, variation of songs is assumed to be inconsistent with increasing distance. Sonograms of Haibei, Heimahe, and Wenquan populations are similar in morph, but their parametric measurements are significantly different in quantity. Songs from the three areas have 6 identical syllable types and syntax. In contrast, one black redstart in Tuotuohe has different syllable types.

Nicolai (1992) found that black redstart juveniles learned song between about 80 and 120 days of age. They watch selected adult males (= tutor) and copy their complete song during the autumn song period. After dispersal in late summer and autumn, juveniles tend to reside in or near the territory that of song learning and this is also the preferred settlement area in the following breeding season. We also observed autumn singing of this bird species in Wenquan (Qinghai Province) and in the Haibei area: black redstarts are resident from April to October although they breed during early May to late July (Zhang 1982, Zhang & Deng 1986). So, for the Haibei population, although migration can influence the development of song dialects, juveniles still have the opportunity of learning the local songs. If all birds return to their birth place with the local song, it becomes simple to explain the similarity within populations. Rare immigrants may also modify their songs to match the local songs. Note that cluster analysis

Table 2. Parameters of songs of ten male black redstarts in four sites of the Tibet Plateau.

Parameter	Haibei (N^a = 7) mean ± SD	Heimahe (N^b =12) mean ± SD	Wenquan (N^b =1 or 2) mean ± SD	Tuotuohe (N^b =3) mean ± SD
D_1(ms)	68.58±13.27	114.2±36.35	77.82±11.67	59.89±19.64
D_2 (ms)	51.74±12.70	64.62±11.15	63.03±10.44	114.9±23.48
D_3 (ms)	157.6±17.87	180.6±10.22	29.73	73.23±2.50
D_4 (ms)	275.2±81.96	279.7±25.19	15.26	214.4±24.61
D_5 (ms)	147.3±18.83	160.8±8.97	21.90	128.0±16.97
D_n (ms)	52.25±15.75	58.41±6.43	104.74	44.94±4.39
D_s (ms)	992.40±55.83	1010.00±77.93	1010	724.27±33.55
H_1 (kHz)	3.43±0.23	5.58±0.52	3.79±0.12	3.68±0.60
H_2 (kHz)	3.81±0.32	4.58 ± 0.44	4.8±0.07	4.13±0.32
H_3 (kHz)	4.08±0.41	5.9±0.67	5.03	6.86±0.15*
H_4 (kHz)	4.58±0.32	5.13±0.12	4.86	5.42±0.08
H_5(kHz)	5.32±0.34	5.34±0.14	4.99	7.83*

N^a, sample size of males; N^b, sample size of songs of one male; * harmonic.

Table 3. Parameters of songs of three male black redstarts in Slovakia and Germany.

Parameter	Male 1 in Slovakia	Male 2 in Slovakia	Male in Germany
t_1 (ms)	925.8±65.38 (4)	838.4±69.61 (10)	844.0±108 (4)
t_n (ms)	509.0±55.70 (4)	610±7.04 (14)	577.0±86.51(4)
t_2 (ms)	455±36.77 (2)	520±19.8 (19)	570.3±32.59 (3)
f_1 (kHz)	5.53±0.040 (4)	5.75±0.094 (13)	6.05±0.48 (4)
f_2 (kHz)	6.84±0.063 (2)	6.26±0.110 (17)	6.37±0.09 (3)
n	5.50±0.58 (4)	8.64 ±0.929 (14)	5.75±1.50 (4)

The estimates of all parameters are presented as mean ± SD (sample size) places the sonogram of male 6 of the Haibei population, closer to an individual in Heimahe than to other Haibei individuals. This is probably because male 6 has fewer elements in syllable 4 than individuals from Heimahe and Wenquan. Further evidence is required to confirm that male 6 may be an immigrant to the Haibei population.

Of the factors considered, only habitat vegetation feature and elevation could not account for the song frequency difference among the recording sites. The highest frequency of songs (excluding syllable 0) of black redstarts in Haibei areas is lower than that in the Poľana Mts, Slovakia and Germany (Tables 2 and 3), but similar to that in the Alps (Susa valley, NW Italy 1,200 to 2,020 m elevation; 5.50 ± 0.12 kHz; $N = 20$) (Cucco & Malacarne 1999). The song frequency of black redstarts in Haibei (3,200 m a.s.l.) is lower than in Tuotuohe (4,700 m a.s.l.) and Poľana (1,200–1,400 m a.s.l.). Theoretically, however, the forest vegetation of Poľana decrease the transmission of a sound signal of high frequency and subsequently, the song frequency should be low. If the difference between Haibei and Poľana are the result of elevation, it is difficult to explain why the frequency in Tuotuohe is higher than in Haibei. Investigations to elucidate the reason for this peculiarity are ongoing.

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