

Rattling cisticola song features and variability across sub-Saharan Africa

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Abstract

1. Rattling cisticolas are a group of small, insectivorous birds found in sub-Saharan Africa. They are known for their distinctive rattling song, which is a series of rapid, repetitive notes. This study examines the variability of these songs across different regions of sub-Saharan Africa.

Introduction

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song features are markedly more divergent than morphology and may therefore be better indicators of species affiliation (Lynes, 1930; Erard *et al.*, 1997). The rattling cisticola is

structure, we distinguished introductory syllables from end phrases and counted the number of syllable types used by each bird during each part of the song. Some end phrases contained brief breaks between sounds, but we treated them as single units because all were given as fixed units with the component parts never re-shuffled.

We measured frequency and timing characteristics for 221 songs from the 61 recordings. Sound files were visualized in RAVEN sound analysis software v. 1.2 (Cornell Laboratory of Ornithology, NY, USA). All measurements were made from Hanning-type spectrograms with a grid size of 10.8 Hz and a discrete Fourier transform size of 4096 samples. Whenever possible we measured the first song on each track, the middle song on each track and the last song on each track for two introductory note types. Because tracks contained variable numbers of songs and because some included only one introductory note type, we measured between one and six songs per track. If songs were obscured by other sounds, we measured the closest song with good recording quality. For each song, we measured the first introductory syllable, the end phrase and the entire song. We recorded the following variables: (1) low frequency; (2) high frequency; (3) frequency with maximum power; (4) frequency range; (5) temporal duration. We calculated average song parameter values for each individual and then averaged those to obtain species-wide estimates of song parameters. Unless otherwise stated, results are reported as means \pm standard deviations.

We used the five acoustic measures detailed earlier to generate principal components describing the variation in three syllable categories: the two most common introductory notes (sweeps, buzzes) and all end phrases. We did not include a third introductory note type because it was relatively rare and geographically restricted. To test for clinal variation over large geographic scales, we ran three standard least squares linear mixed models with maximum likelihood estimation. For the first principal component describing each of the three song features (sweep, buzz and end phrase), we ran a linear mixed model on all measured songs with a geographic factor (definition below) as a fixed effect, site as a random factor and

individual as a random factor nested within site. This accounts for greater sampling of songs at some sites relative to others



quency characteristics of the three introductory note types, end phrases and whole songs are detailed in Table 1.

In total, we identified 179 song types from the 61 recorded birds. The largest recorded repertoire of an individual included 16 song types and 15 syllable types. Individuals typically sang with eventual variety. Longer recordings contained more song types (Appendix S1), and all recorded birds continued to produce new song and end-phrase types up to the end of each recording. Thus, we expect that more extensive sampling would discover more song types from every individual. Song bouts may include a wide variety of song forms generated by altering (1) the type of introductory note; (2) the number of repetitions of the introductory note; (3) the type of

end phrase; (4) the number of repetitions of the end phrase; (5) the addition of a third note type (Fig. 4).

Geographic variation

On a local scale, songs were highly varied: multiple tracks ($n=2-4$) from nine common locations did not show evidence of song sharing by neighbours. This is because (perhaps surprisingly) we found no end-phrase types shared among different birds in the same location, even from recordings made within the same year (15 recordings from six sites).

At a larger geographic scale, similar end phrases were recorded at very distant sites. For example, multiple birds

Fig. 1. *C. icola chiniana*

	Loadings on PC1	Loadings on PC2	Loadings on PC3	End phrases	Weighted
Low frequency (Hz)	2 400 ± 785	1 261 ± 357	1 539 ± 791	1 408 ± 336	1 267 ± 264
High frequency (Hz)	6 684 ± 948	10 351 ± 1 902	12 759 ± 2 068	5 683 ± 1 174	8 483 ± 2 024
Frequency range (Hz)	4 284 ± 1 285	9 090 ± 2 109	11 220 ± 2 072	4 275 ± 1 204	7 216 ± 2 141
Frequency with maximum power (Hz)	4 677 ± 702	4 715 ± 1 355	5 195 ± 714	3 532 ± 707	4 170 ± 835
Diversity	0.201 ± 0.031	0.167 ± 0.039	0.207 ± 0.046	0.422 ± 0.103	1.27 ± 0.282

Fig. 2

	Low frequency (Hz)	High frequency (Hz)	Frequency range (Hz)	Frequency with maximum power (Hz)	Diversity	% of individuals
Score on PC1	-0.700	0.762	-0.202	0.994	0.042	42
Score on PC2	0.506	0.508	0.701	0.081	0.640	28
Score on PC1	-0.645	0.931	0.434	0.976	0.175	49
Score on PC2	-0.050	0.040	-0.606	0.046	0.846	22
End phrases PC1	-0.244	0.938	0.601	0.961	0.271	46
End phrases PC2	0.927	0.141	0.369	-0.103	-0.106	21

Fig. 3

Fixed effect	Variable	Beta ± SE	d.f.	F	P
Low diversity	Loadings on PC1	0.0078 ± 0.19	1, 29.43	0.0017	0.97
End phrases	Loadings on PC1	-0.00041 ± 0.00043	1, 16.27	0.90	0.36
Low diversity	Loadings on PC2	-0.41 ± 0.27	1, 23.47	2.40	0.13
End phrases	Loadings on PC2	-0.00043 ± 0.000086	1, 8.39	0.25	0.63
Low diversity	End phrases	0.34 ± 0.12	1, 39.80	8.43	0.006*
End phrases	End phrases	0.0000083 ± 0.00036	1, 23.68	0.0005	0.9818

* Significant at $P < 0.05$.

produced a repeated chevron-shaped note (Fig. 3a) and a simple trill (Fig. 3b). The chevron-shaped note was recorded from birds representing six subspecies in Botswana, Kenya, Tanzania and South Africa. The trill was recorded from birds representing seven subspecies in Botswana, Kenya, Tanzania, South Africa and Zambia. Both notes were produced slightly differently by different individuals, for example, one bird produced a trill with a frequency range of 2.9 kHz, whereas another had a range of 3.7 kHz. Thus, a more stringent syllable differentiation scheme may have classified them separately and our estimate of syllable-type diversity is relatively conservative.

Introductory note types were much less numerous than end phrases and showed different patterns of geographic variation. We observed frequency sweeps and buzzes across the range of the species. Many birds were recorded singing both note types, and it is likely that with expanded sampling most birds would be found to produce sweep and buzz syllables. Harmonic stacks, in contrast, were only recorded from five individuals in Botswana and Namibia of subspecies *smithersi* and *frater*. This represents all of our samples recorded west of 26° longitude. Two of these individuals also produced intro-

ductory sweep notes, and one of them produced all three introductory note types (interestingly, this bird was recorded in central Botswana, approximately 750-km east of the other birds using harmonic stacks and 300-km west of all other sampling locations).

Our principal component analyses of song features tended to produce first principal components that were influenced most by the high frequencies and frequency ranges of song components (Table 2). When we looked for clinal patterns of song variation across the geographic range of the species, we found that the first principal component describing end phrases varied significantly with location (Table 3). This pattern is mainly driven by an increase in high frequency, frequency ranges and frequency with maximum power as you move north-east across the species' range. We found no significant geographic directional change in the first principal component of introductory sweeps or buzzes (Table 3). Analyzed songs were recorded at sites ranging from 64 to 1975 m in elevation. None of the three syllable types showed a significant effect of elevation (Table 3). A Bonferroni correction for the six tests sets the significant P -value at 0.0083 (Miller, 1991), under which we

continue to support significant geographic variation in end phrases only.

Discussion

Rattling cisticola songs showed high variability, with individual birds singing at least 16 different song types that include a diverse array of end-phrase elements. Because we obtained these songs from libraries and because we are covering such large geographic distances, our sampling in any one location is not extensive. Therefore, the observation of 16 song types is merely a minimum estimate of repertoire size. Similarly, across the species' range, birds likely sing many more than the 179 identified song types. Our initial analysis suggests that individual syllable and song-type variety is

result of multiple evolutionary pressures, including stabilizing selection on some elements for species identification and selection for diversity on the form and frequency characteristics of other elements. In a previous study (Benedict & Bowie, 2009), we found that a congener, the red-faced cisticola, also showed diverse song forms with some species-specific elements, supporting the idea that song form is generated by multiple evolutionary pressures (Seddon, 2005). In both cisticola species, song structure and a few characteristic syllable forms are fixed, but birds of the two species generate song diversity differently. Red-faced cisticolas mix up the ordering of syllables and vary song duration, whereas rattling cisticolas have relatively fixed song durations and ordering, but generate highly variable end-phrase forms (Benedict & Bowie, 2009). These two data points illustrate the potential for song variation to arise through many different avenues. Fixed features can take many forms, potentially allowing all 40 plus species of the morphologically conserved cisticola warblers to signal species identity with song. These studies illustrate the importance of phenotypic features beyond morphology for species identification. They also emphasize the value of library resources for evaluating phenotypic features of problematic groups. Many forms of information, including sound archives with wide geographic sampling, are available to researchers wishing to examine current patterns of diversity and the resulting indicators of evolutionary processes.

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