

# Rattling cisticola song features and variability across sub-Saharan Africa

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## Keywords

birdsong; geographic variation; species recognition; Africa; Cisticolidae; Passeriformes.

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## Abstract

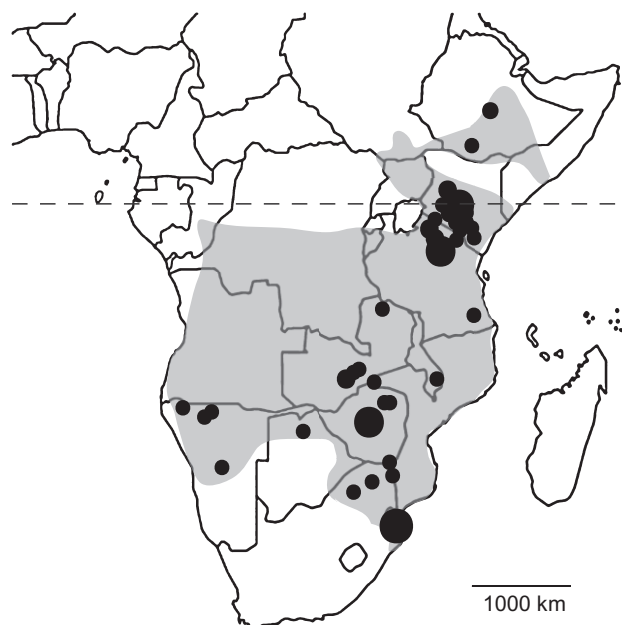
Quantifying bird song variation can be an important tool for ensuring accurate species identification and can provide a significant basis for understanding the evolutionary processes that shape phenotypic diversity. This study describes variation in the songs of rattling cisticolas *Cisticola chiniana* across sub-Saharan Africa. For many cisticola species, learned songs are the most obvious phenotypic indicators of species affiliation and may also function to indicate individual quality. We examined 957 songs recorded from 61 individuals and archived in sound libraries. To assess the diversity of syllable and song types, we examined patterns of syllable use. We also measured vocalization frequency and time parameters and assessed how they vary through space. Results indicated that rattling cisticola songs are highly variable, but also have features that are species-specific. Examined songs had a relatively fixed structure containing one of three characteristic introductory note types, followed by an end phrase. Two of the introductory note types were sung across the species' range (some 4500 km), whereas the third was only recorded in south-western Africa. End phrases generated most of the diversity in songs and appeared to have an unlimited number of forms. End-phrase characteristics showed a strong geographic variation, but did not vary with elevation. Song features varied individually and geographically in ways that are consistent with evolution due to multiple selective pressures, including stabilizing selection for species recognition on the introductory notes and diversifying selection on the end phrases. This pattern of lability in some song features coupled with stability in others may be a common feature of cisticola songs as it has also been found in *Cisticola erythrops*, a congener with a similarly broad range.

## Introduction

The songs of birds vary spatially and temporally in a multitude of different ways (Podos & Warren, 2007; Catchpole & Slater, 2008). Songs are often used as a species-identifying characteristic, but may not be effective if the range of song features for any one species is not well-described. A thorough understanding of within-species song diversity is particularly important for birds with wide geographic ranges that occur in a variety of habitats. As a practical consideration, such species are likely to be sympatric with many other species, creating abundant opportunities for mis-identification. Simultaneously, they are likely to show diversity in song characteristics due to multiple selective pressures on song form (Seddon, 2005; Podos & Warren, 2007). Evolutionarily, a large geographic range allows for greater diversification due to drift (cultural or genetic) and local adaptation (Edwards *et al.*, 2005; Price, 2007; Benedict & Bowie, 2009). Widely distrib-

uted birds will necessarily occur at a range of geographic locations with varying climates, elevations and habitats, all of which have been shown to influence bird song properties (Ryan & Brenowitz, 1985; Bertelli & Tubaro, 2002; Kirschel *et al.*, 2009). Ecologically, varied habitat features may cause diversifying selection on acoustic traits due to differing sound transmission properties of the habitat (Morton, 1975; Wiley & Richards, 1982; Slabbekoorn & Smith, 2002a). Variation in the strength and outcomes of local sexual selection can also generate diversity (Andersson, 1994). Among song-learning birds, like cisticola warblers, song form can be shaped by both genetic and cultural evolution (Slater, 1989).

Rattling cisticolas *Cisticola chiniana* belong to a genus including 40 plus species of drab brown birds, which have long confounded recreational birders and ornithologists alike (Lynes, 1930; Ryan, 2006; Nguembock *et al.*, 2007). Individuals in the field and museum study skins are regularly mis-identified (R. C. K. Bowie, unpubl. data). Within this genus,



**Figure 1** Recording locations for rattling cisticola *Cisticola chiniana* songs included in this study. The species' geographic range is indicated in grey. Dots mark recording locations and are scaled to reflect the number (1–8) of recordings made in each area.

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 widely distributed across sub-Saharan Africa with a range that begins at a longitude  $10^{\circ}$  north of the equator and extends to  $30^{\circ}$  south (Fig. 1) (Sinclair & Ryan, 2003; Ryan, 2006). Rattling cisticolas are found in woodland, savannah and scrub habitats where they are often the most abundant or obvious cisticola species (Sinclair & Ryan, 2003; Ryan, 2006). These traits eliminate location and habitat preference as important clues to species identity when birds are encountered in the field. Existing descriptions indicate that rattling cisticola songs are extremely variable but have a stereotyped structure consisting of two parts: several introductory notes, followed by a more rapidly paced end phrase that may form a trill. Building on this simple description of song structure, there is a need for better description of song form, including quantification of the diversity of syllable structures and geographic variation (Erard *et al.*, 1997).

Bird songs may vary across many parameters, including the shape and frequency of syllables, the timing of syllable or song delivery and the sequence of different syllable or song types (Williams, 2006; Catchpole & Slater, 2008). Different song forms may be generated by different selective regimes (Edwards *et al.*, 2005). For example, a closely related species, the red-faced cisticola *Cisticola erythrops*, shows a pattern of song variability, which results from changes in syllable use and delivery order (Benedict & Bowie, 2009). In the red-faced cisticola, song form has apparently been shaped by multiple

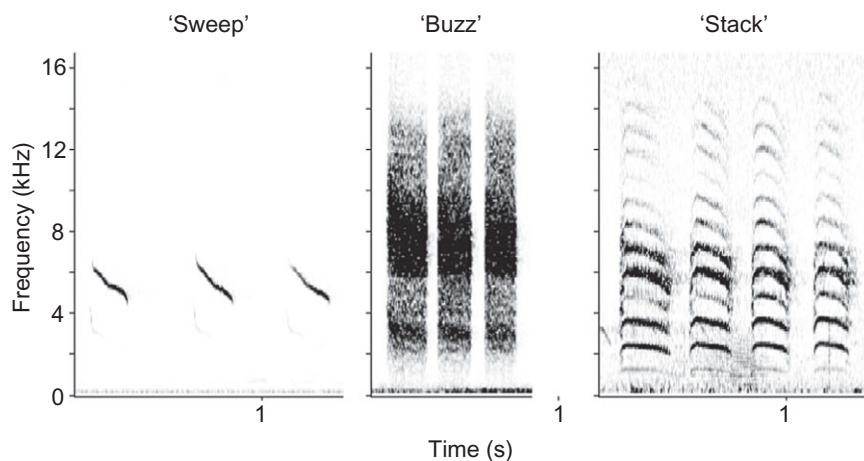
evolutionary forces, including diversifying cultural drift and stabilizing selection on syllable delivery rate that may help delimit species boundaries (Benedict & Bowie, 2009).

With the data presented here, we quantify song variation across the geographic range of the rattling cisticola, we look for song features that are useful for species identification, and we discuss evolutionary processes that may have generated the observed patterns. Rattling cisticolas are expected to experience stabilizing selection on songs as indicators of species identity, so we predict that some elements of song will be stable across the geographic range. At a local scale, rattling cisticolas live in social groups where males sing to defend territories of varying quality (Carlson, 1986). We therefore predict that sexual selection will select for diversity of some song elements as signals of individual identity and quality (Catchpole, 1987; Andersson, 1994). Finally, we predict that patterns of syllable use and other song features are likely to vary across the large geographic range of this species.

## Methods

We analyzed 61 recordings (957 songs) of rattling cisticolas obtained from the British Library, the Macaulay Library of Natural Sounds and the Ditsong National Museum of Natural History (Transvaal Museum) (Appendix S1). The use of archived songs allowed access to many sites widely distributed across sub-Saharan Africa. We assessed all sound files to confirm that the songs were from a rattling cisticola and found that every song matched the general species description of having several introductory notes followed by a trill-like end phrase. Closely related species of cisticolas that are found sympatrically with rattling cisticolas have very different song structures, making us confident in our identifications (L. Benedict, unpubl. data). Tracks varied in length from 5 to 404 s (mean =  $71.1 \pm 73.4$  s) and included from 1 to 81 songs (mean =  $15.7 \pm 16.3$ ). Recordings came from 38 different sites. Based on statements and notes from the recordists, we eliminated sound files from our analysis that were duplicates of a single bird. We did include tracks that were recorded at similar locations and/or dates but were distinct in time or specific location as they are likely to represent different birds. Analyzed recordings represented 12 of 17 subspecies and covered most of the species' geographic range (Fig. 1). We assigned subspecies identity following Erard *et al.* (1997). We used Google Earth (<http://www.google.com/earth/index.html>) to obtain elevation, latitude and longitude (Appendix S1).

We examined song diversity in two ways. First, we created a library of song and syllable types to assess syllable diversity. Second, we measured frequency and timing characteristics of whole songs and individual syllables or phrases. Song- and syllable-type diversity was assessed for all 957 songs. We counted the number of song types produced by each bird. Songs of the same type all contained the same syllable types arranged in a fixed pattern. We identified syllable types by eye based on frequency and timing characteristics. Our observations confirmed that rattling cisticola songs always have introductory notes followed by variable end phrases – we never saw other song structures. Because of the typical two-part song



**Figure 2** Typical examples of the three introductory note types used at the start of rattling cisticola *Cisticola chiniana* songs.

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

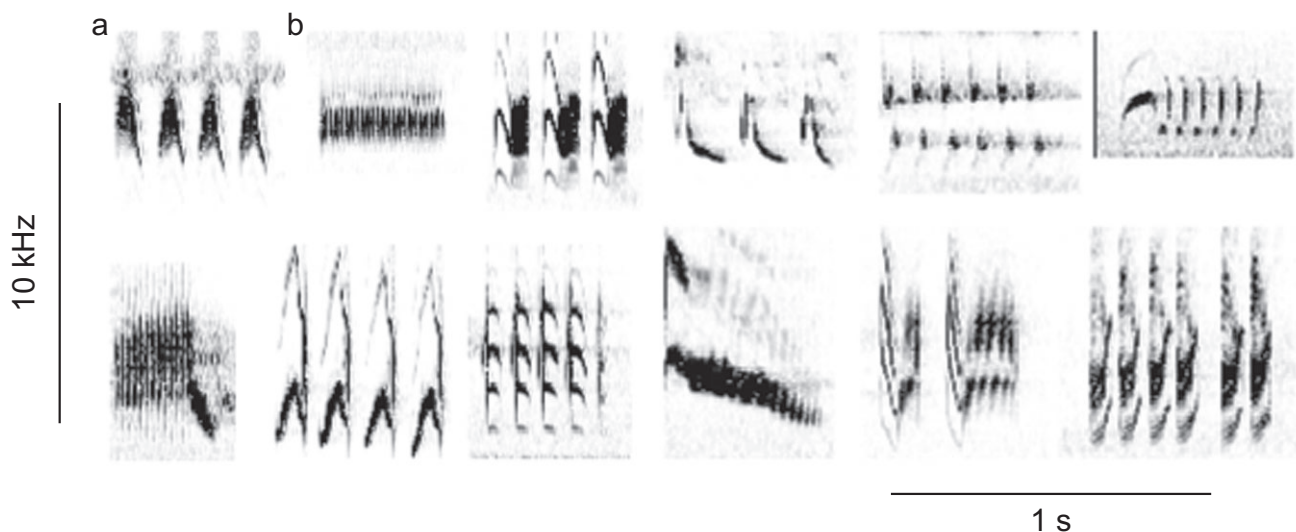
individual as a random factor nested within site. This accounts for greater sampling of songs at some sites relative to others and for unequal numbers of measurements taken from each bird. Latitude and longitude were correlated, so to avoid multicollinearity we used the first principal component of these two variables as our geographic factor. This principal component explained 84% of the variance in latitude and longitude. We used the same model to test for elevation effects on each of the three song features by removing the geographic factor and replacing it with elevation values for the site of each recording. We ran these three tests separately from the previous three because the geographic factor was correlated with elevation. All statistics were performed in JMP version 9.0 (SAS Institute Inc., Cary, NC, USA, 2010).

## Results

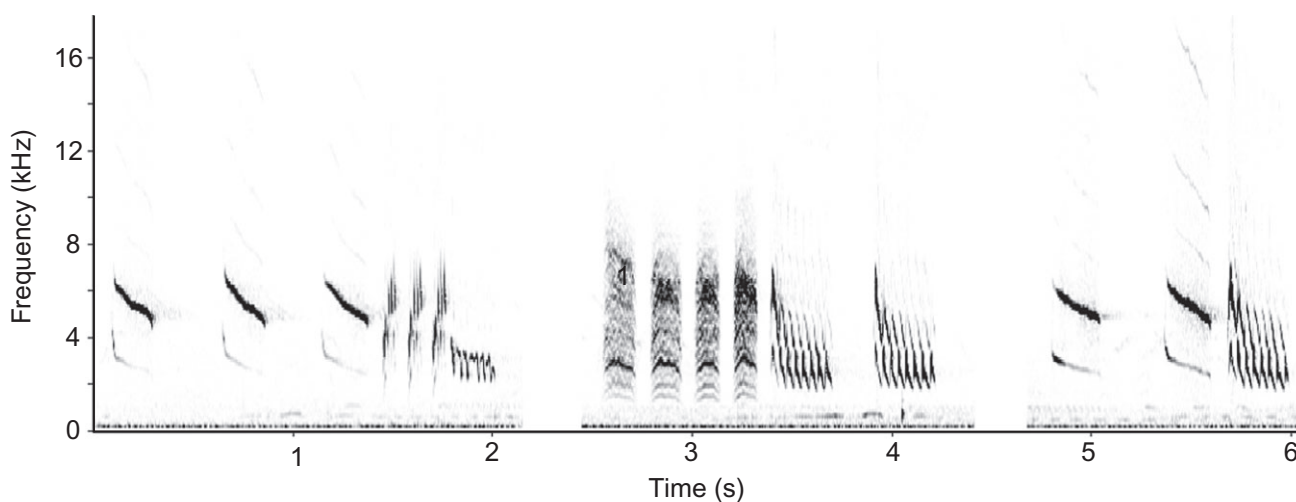
### Song description

All measured songs were discrete and brief with breaks between songs lasting at least 1 s. All birds sang songs that included one or two introductory note types, followed by a more complex end phrase that often ran into a trill (Figs 2–4). Songs with two different introductory note types were rare, and 87% of songs included only two syllable types: an introductory note repeated up to six times, followed by an end phrase that was sometimes repeated more than once. We observed three general introductory note types: (1) a descending frequency sweep (46 birds); (2) a broadband buzz (32 birds); (3) a harmonic stack (5 birds) (Fig. 2). Nineteen birds sang multiple introductory note types, with one singing all three introductory notes. Acoustically, these notes were not all identical among individuals, but were clearly identifiable to type.

Song end phrases showed much more diversity in form than introductory notes (Fig. 3). We identified 77 end-phrase types. Of these, 42 were unique to single birds; the remaining 35 end phrases were shared by two to seven individuals each. Fre-



**Figure 3** Twelve examples of end phrases used at the end of rattling cisticola *Cisticola chiniana* songs.



**Figure 4** Three song types sung by one rattling cisticola *Cisticola chiniana* in a song bout, illustrating how different song types are formed through recombination and repetition of syllables in the repertoire.

frequency 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

**Table 1** Frequency characteristics and duration of three song introductory note types, end phrases and whole songs produced by rattling cisticolas *Cisticola chiniana*

	Introductory sweep	Introductory buzz	Introductory stack	End phrase	Whole song
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
Duration (s)	0.201 ± 0.031	0.167 ± 0.039	0.207 ± 0.046	0.422 ± 0.103	1.27 ± 0.282

**Table 2** Loading factors for principal component analysis of three song features

	Low frequency (Hz)	High frequency (Hz)	Frequency with max power (Hz)	Frequency range (Hz)	Duration (s)	% of the variance explained
Sweep PC1	-0.700	0.762	-0.202	0.994	0.042	42
Sweep PC2	0.506	0.508	0.701	0.081	0.640	28
Buzz PC1	-0.645	0.931	0.434	0.976	0.175	49
Buzz PC2	-0.050	0.040	-0.606	0.046	0.846	22
End phrase PC1	-0.244	0.938	0.601	0.961	0.271	46
End phrase PC2	0.927	0.141	0.369	-0.103	-0.106	21

**Table 3** Results of linear mixed models testing the effects of location and elevation on the first principal components describing three song features

Fixed effect	Y variable	Beta ± SE	d.f.	F	P
Location	Introductory sweep	0.0078 ± 0.19	1, 29.43	0.0017	0.97
Elevation	Introductory sweep	-0.00041 ± 0.00043	1, 16.27	0.90	0.36
Location	Introductory buzz	-0.41 ± 0.27	1, 23.47	2.40	0.13
Elevation	Introductory buzz	-0.00043 ± 0.000086	1, 8.39	0.25	0.63
Location	End phrase	0.34 ± 0.12	1, 39.80	8.43	0.006*
Elevation	End phrase	0.0000083 ± 0.00036	1, 23.68	0.0005	0.9818

\*indicates a significant *P*-value.

d.f., degrees of freedom.

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 potentially infinite. In conjunction with their high individual variability, rattling cisticola songs have fixed features that are consistent at the continental scale. Songs are brief in duration with a structure that always includes repeated introductory notes, followed by a more complex end phrase. Across the species range, we found only three introductory note types. This fixed structure and limited number of introductory note types may facilitate species recognition, both for humans and for other cisticola warblers.

Because rattling cisticolas are sympatric with many congeners, we expect that their songs are under stabilizing selection to maintain species-specific elements that ensure correct mate-choice (Price, 2007; Benedict & Bowie, 2009). Simultaneously, however, rattling cisticolas must compete intra-specifically for territories, creating selection pressures for trait elaboration as an indicator of quality (Carlson, 1986; Andersson, 1994). Tests in controlled and natural environments indicate that other bird species use the introductory phrases of songs to indicate species affiliation and then use the remainder of the song to encode information about identity (Baptista & Morton, 1981; Mathevon *et al.*, 2008). It is not surprising that cues to species identity should come at the beginning of a communication signal as this information is fundamental in determining receiver response to any signal content that follows (Bradbury & Vehrencamp, 1998). For example, although white-crowned sparrow *Zonotrichia leucophrys* songs differ greatly across the geographic range of the species, they all begin with a stereotyped introductory syllable which young birds use as a cue to species identity when learning songs (Marler & Tamura, 1964; Baptista & Morton, 1981; Soha & Marler, 2000). Thus, evolution can occur via stabilizing selection for species-specific introductory elements in conjunction with diversifying selection on the following elements that encode individual identity or quality (Milligan, 1966; Baker *et al.*, 1987). In such cases, the resultant song is predicted to have a structure like that of the rattling cisticola's song, with introductory elements that are relatively fixed across all members of the species, followed by elements that show a wide range of forms.

We found that although rattling cisticolas across all of sub-Saharan Africa sing songs with only three introductory syllable types, they sing at least 77 distinct end-phrase types. Furthermore, the acoustic properties of the end phrases were

more likely to vary across geographic gradients, a pattern consistent with a lack of stabilizing selection on these phrases. Potential causes of this clinal variation include localized sexual selection, climate variation, ecological adaptation and drift. Some authors have also suggested that social complexity facilitates the evolution of large repertoires (Byers & Kroodsma, 2009). Rattling cisticolas are known to live in groups and to compete for territories using song as a sexually selected intra-specific signal (Carlson, 1986). In at least one other species, sexual selection is thought to drive clinal variation in bird song properties across large geographic distances (Irwin, 2000).

Clinal variation in rattling cisticola song features could result from sexual selection but could also be driven by large-scale geographic variation in morphology and/or ecology. Other studies of African birds have found increases in body size and associated decreases in song frequencies with elevation (Kirschel *et al.*, 2009). Our results do not support this pattern, as we did not find birds singing lower frequency songs at higher elevations. We did find that birds located farther south-west, away from the equator, sang songs with lower high frequencies and smaller frequency ranges. This pattern is consistent with Bergmann's rule of increasing body size and resultant decreasing song frequencies in cooler climates (Wallschläger, 1980; Ryan & Brenowitz, 1985; Ashton, 2002; Meiri & Dayan, 2003). Ecological variables, including tree cover, forest type and ambient noise, have been shown to influence song structure in African birds and may create geographic gradients in song features (Slabbekoorn & Smith, 2002b; Kirschel *et al.*, 2009, 2011). As rattling cisticolas are known to be habitat generalists, we expect that local adaptation to specific habitat characteristics might be lower in this species than in habitat specialists (Sinclair & Ryan, 2003). Nevertheless, habitat gradients across Africa may contribute to the variation that we observed and could work in concert with sexual selection and morphological evolution.

It is likely that the acoustic properties of the introductory and end phrases sung by rattling cisticolas have evolved in response to differential costs of degradation through all habitat types (Morton, 1975; Wiley & Richards, 1982). Many bird songs consist of introductory notes that have little frequency modulation and propagate well through all environments, followed by rapidly modulated trills that degrade rapidly, but may indicate individual quality (Wiley & Richards, 1982; Podos, 1997; Naguib *et al.*, 2008). In such cases, the introductory notes may serve an alerting function, preparing receivers for the message to follow in the end phrases (Richards, 1981; Soha & Marler, 2000). The introductory notes of rattling cisticola songs tend not to include rapid frequency modulations and thus may broadcast species identity to a wide range of receivers, both conspecific and heterospecific. Complex, trilled rattling cisticola end phrases are well suited for use in signalling to an intended receiver over relatively short distances, such as a bird might do when defending his territory from an intruder (Carlson, 1986).

Despite their striking diversity, the songs of rattling cisticolas have traits that are a characteristic of the species across a wide geographic range. Song form has likely evolved as a

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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## Supporting information

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

**Appendix S1.** List of analyzed sound files with source, location data, and some song features.

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