



Disjunct resident population of Melodious Lark *Mirafra cheniana* discovered in East Africa

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Abstract

We describe the discovery of a previously unknown population of Melodious Lark *Mirafra cheniana* from northern Tanzania and southern Kenya, some 2000 km north of what was previously thought to be its northern limit in central Zimbabwe. The identification of this population as *M. cheniana* is based primarily on analyses of mitochondrial DNA and song. We also clarify relationships within this genus by sequencing material of White-tailed Lark *Mirafra albicauda* for the first time; although its relationships with other species in the group remain unclear, our analyses clearly show it to be different from *M. cheniana* in the newly discovered population. The discovery of a population of *M. cheniana* in East Africa conforms to a known pattern for closely related lark species to have disjunct distributions in southern and eastern Africa.

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Brian W. Finch and R. Stratton Hatfield have contributed equally to this work and share first authorship.

[†]Joe Grosel: Deceased. Sadly, our friend and colleague Joe Grosel died during the preparation of this article. We dedicate it to his memory.

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Zusammenfassung

Neu entdeckte disjunkte residente Population der Spottlerche *Mirafra cheniana* in Ost-Afrika

Wir beschreiben die Entdeckung einer bislang unbekannten Population der Spottlerche *Mirafra cheniana* in einem Gebiet von Nord-Tansania bis Süd-Kenia, ca. 2000 km nördlich von der bisher bekannten Verbreitungsgrenze in Zentral-Simbabwe. Die Bestimmung dieser Population als *M. cheniana* zugehörig basiert primär auf Analysen mitochondrialer DNA und des Gesangs. Darüber hinaus klären wir Beziehungen innerhalb der Gattung *Mirafra* durch die erstmalige Sequenzierung der Weißschwanzlerche *M. albicauda*. Obwohl die Beziehung von *M. albicauda* zu den anderen Arten der Gruppe ungeklärt bleibt, zeigt unsere Analyse ihre Unterschiedlichkeit von der neu entdeckten *M. cheniana* Population deutlich. Die Entdeckung einer Population von *M. cheniana* in Ost-Afrika stimmt mit bekannten Mustern nahe verwandter Lerchen-Arten mit disjunkter Verbreitung in Süd- und Ostafrika überein.

Introduction

The family Alaudidae (larks) comprises c. 100 species, which occur widely across Eurasia and Africa, with one species each reaching Australia and North America plus Colombia (de Juana et al. 2004; Fjeldså et al. 2020; Gill et al. 2022). Larks are found in various open habitats, such as different types of grasslands, open scrubland, and deserts. The phylogeny has been reconstructed for c. 80% of lark species, revealing a striking lack of agreement between traditional morphology-based taxonomy and phylogeny (Alström et al. 2013). Many of the species are renowned for having extremely similar appearances (de Juana et al. 2004) and therefore being difficult to identify in the field.

The Eurasian species are fairly well studied with respect to taxonomy, and several species complexes have been analysed using different approaches, often including morphological, vocal, other behavioural, genetic, ecological, and other data. These studies have resulted in a substantial increase in the number of recognized species (Alström 1998; Guillaumet et al. 2005, 2006, 2008; Drovetski et al. 2014; Ghorbani et al. 2020a, 2020b; Alström and Gombobaatar 2021; Alström and Sundev 2021; Alström et al. 2021). The African species are much less well studied, despite the fact that 60% of the species of larks occur exclusively in Africa. The southern African Karoo Lark *Calendulauda albescens* and Long-billed Lark *Certhilauda curvirostris* (sensu lato) complexes are nowadays often treated as three instead of two species and five instead of one species, respectively (Clements et al. 2021; Gill et al. 2022), based mainly on mitochondrial DNA (mtDNA) data (Ryan et al. 1998; Ryan and Bloomer 1999). The circumscriptions of Blandford's Lark *Calandrella blanfordi* and Rufous-capped Lark *Calandrella eremica* from the Horn of Africa and southern Arabian Peninsula are fundamentally different following the publication of a molecular phylogeny by Stervander et al. (2016), and Stervander et al. (2020) described a new

subspecies of Red-capped Lark *Calandrella cinerea* from Nigeria. Both Alström et al. (2013), Stervander et al. (2016), and Stervander et al. (2020) discovered unexpectedly deep mtDNA divergences within several species of larks, and suggested that further studies based on independent data were warranted. In contrast, Spottiswoode et al. (2013) provided morphological, vocal, and molecular evidence that the Horn of Africa Sidamo Lark *Heteromirafra sidamoensis* is synonymous with Archer's Lark *Heteromirafra archeri*.

East and northeast Africa are home to 12 species of larks in the genus *Mirafra* (Gill et al. 2022). Four of these are rather small with very similar plumages: Williams's Lark *M. williamsi*, Singing Bush Lark *M. cantillans*, Friedmann's Lark *M. pulpa*, and White-tailed Lark *M. albicauda* (Sinclair and Ryan 2010; Ryan 2020a, b; Ryan and Sharpe 2020; Bradley 2021). Two other *Mirafra* species from southern Africa are extremely similar to these four species in appearance: Melodious Lark *M. cheniana* occurs in eastern South Africa, with a few records from southern Botswana and an isolated population in central Zimbabwe (there may also be a relict population in northern Botswana; (Davies 2011)), and Monotonous Lark *M. passerina*, which is more widely distributed in southern Africa, mainly north and west of *M. cheniana* (Ryan 2020c, d). In addition, Horsfield's Bush Lark *M. javanica* from Southeast Asia to Australia is similar to and sometimes considered conspecific with *M. cantillans*. All of these except *M. pulpa* and *M. albicauda* have been analysed phylogenetically and found to form a clade (Alström et al. 2013).

Larks have two centres of endemism within Africa: one in southern Africa, particularly in the Cape, Karoo, and Namib regions (Dean and Hockey 1989), and another in north-eastern Africa, particularly Ethiopia, Somalia, Kenya, and northern Tanzania (Fjeldså and de Klerk 2001). Some genera, such as *Spizocorys*, *Calendulauda*, and *Heteromirafra*, are largely or wholly confined to both regions but with different species represented in each (Archer and Godman 1961). This pattern of clustering of dry-country species into

species hotspots in southern and eastern Africa was studied by Moreau (1966), who suggested that the high number of dry-country endemics in both regions is due to their long and stable history of dry climates, perhaps longer and more stable in south-western Africa. A similar pattern of interrupted distribution is found also in other groups of animals, such as the harvester termites in the genus *Hodotermes* and their mammalian predators the Bat-eared Fox *Otocyon megalotis* and the Aardwolf *Proteles cristata*. The similarity in the taxonomic composition in these two hotspots of endemism is likely to be due to the fact that they have not always been separated, as they are now, by a humid zone from central Tanzania to Zimbabwe (Moreau 1966). An “arid corridor”, remnants of which are still apparent in western Tanzania, is likely to have linked the two repeatedly over time due to fluctuating climates, allowing exchange of animals between them.

In 1987, B.W.F. realised that what was generally assumed to be White-tailed Lark *M. albicauda* occurring in the Maasai Mara, Kenya and Serengeti, Tanzania (i.e., west of the Great Rift Valley) differed markedly (especially in song) from other populations of *M. albicauda* (Finch 2002, 2009). The identity of these birds, referred to below as “Mara Lark”, remained a mystery until it was originally suggested in a personal email sent by A.S.K. in 2020 that they appeared to match the highly disjunct *M. cheniana* rather than any known East African species.

We here analyse the taxonomic status of the “Mara Lark” based on analyses of songs and mitochondrial DNA. We conclude that the “Mara Lark” represents a presumably geographically isolated population of *M. cheniana*, and comment on its distribution and conservation status. We also for the first time include *M. albicauda* in a phylogenetic analysis (including the holotype) and describe its poorly documented song.

Material and methods

Field observations

B.W.F. studied “Mara Lark” in the field in the Maasai Mara in Kenya on multiple occasions between 1987 and 2019, and recognised that an identical form was present in Serengeti in Tanzania over the same period. R.S.H. and A.S.K. have studied the “Mara Lark” in the Maasai Mara in Kenya multiple times between 2010 and 2021. C.C. has sound recorded it in the Serengeti National Park, Tanzania in 2013 where it occurs sympatrically with *M. albicauda*. Rich Lindie videoed a singing bird in the Serengeti National Park, Tanzania in 2015 and Nik Borrow photographed a singing bird in the Serengeti National Park, Tanzania in 2018 (*Mirafra*

albicauda ML20546688). All localities with observations of “Mara Lark” are shown in Fig. 1.

B.W.F. has studied *M. albicauda* on multiple occasions in Kenya, Tanzania, and Uganda; C.C. has observed and sound recorded this species at multiple locations in Uganda, at Eluanata Dam in the Maasai Steppe east of the Great Rift Valley in Tanzania and especially in the Serengeti, west of the Great Rift Valley in Tanzania where it co-occurs with “Mara Lark”; J.G. has observed it in the Serengeti on several occasions, and P.A. has observed and sound recorded it in Nairobi National Park, Kenya in May 2018. D.d.S., D.E., J.G., P.F.D., and P.A. have ample experience with *M. cheniana* from South Africa.

Song

For sound analysis, we selected recordings of 8 *M. albicauda* individuals (4 individuals from Kenya, 3 from Tanzania, 1 from Uganda; 11 recordings in total), 4 “Mara Lark” individuals (all from Kenya, 4 recordings in total), 5 *M. cheniana* individuals (from throughout the range in South Africa, 5 recordings in total), and 4 *M. cantillans* individuals (3 individuals from Kenya and 1 from Somalia; 6 recordings in total). These include all of the species of larks that are potentially confusable with “Mara Lark”, and which occur in Kenya and Tanzania (Sinclair and Ryan 2010). The data were from our own recordings and additionally from xeno-canto (<http://www.xeno-canto.org>) and the Macaulay Library (<https://www.macaulaylibrary.org/>). The *M. albicauda* were identified based on our experience with songs of these birds from Kenya, Tanzania, and Uganda, as described in the literature (Britton 1980; Zimmerman and Turner 1996; Sinclair and Ryan 2010; Stevenson and Fanshawe 2002, 2020; Ryan 2020b); the birds identified as “Mara Lark” resembled *M. cheniana* from South Africa in song; and the *M. cantillans* were identified based on experience with songs of these birds from Kenya and Somalia. In several cases, the vocal identifications were confirmed by plumage characters (as described in the literature (Britton 1980; Zimmerman and Turner 1996; Sinclair and Ryan 2010; Stevenson and Fanshawe 2002, 2020; Ryan 2020a,b and c) and studied in museum collections). Our own recordings have also been uploaded to the Macaulay Library and to Xeno-canto. A list of the recordings studied is in Table S1. Additional recordings have been listened too, and multiple additional birds have been heard in the field.

The sampling frequency of all recordings was set to 48 kHz and sampling depth to 24 bits before analysis. Sonograms were created in Raven Pro 1.5 (Cornell Laboratory of Ornithology, Ithaca, USA), with the following settings: window size = 256 samples; window type = Hann; 3 dB filter bandwidth = 270 Hz; overlap = 50%; size = 2.67 ms; DFT size = 256 samples; spacing = 188 Hz. The contrast was kept

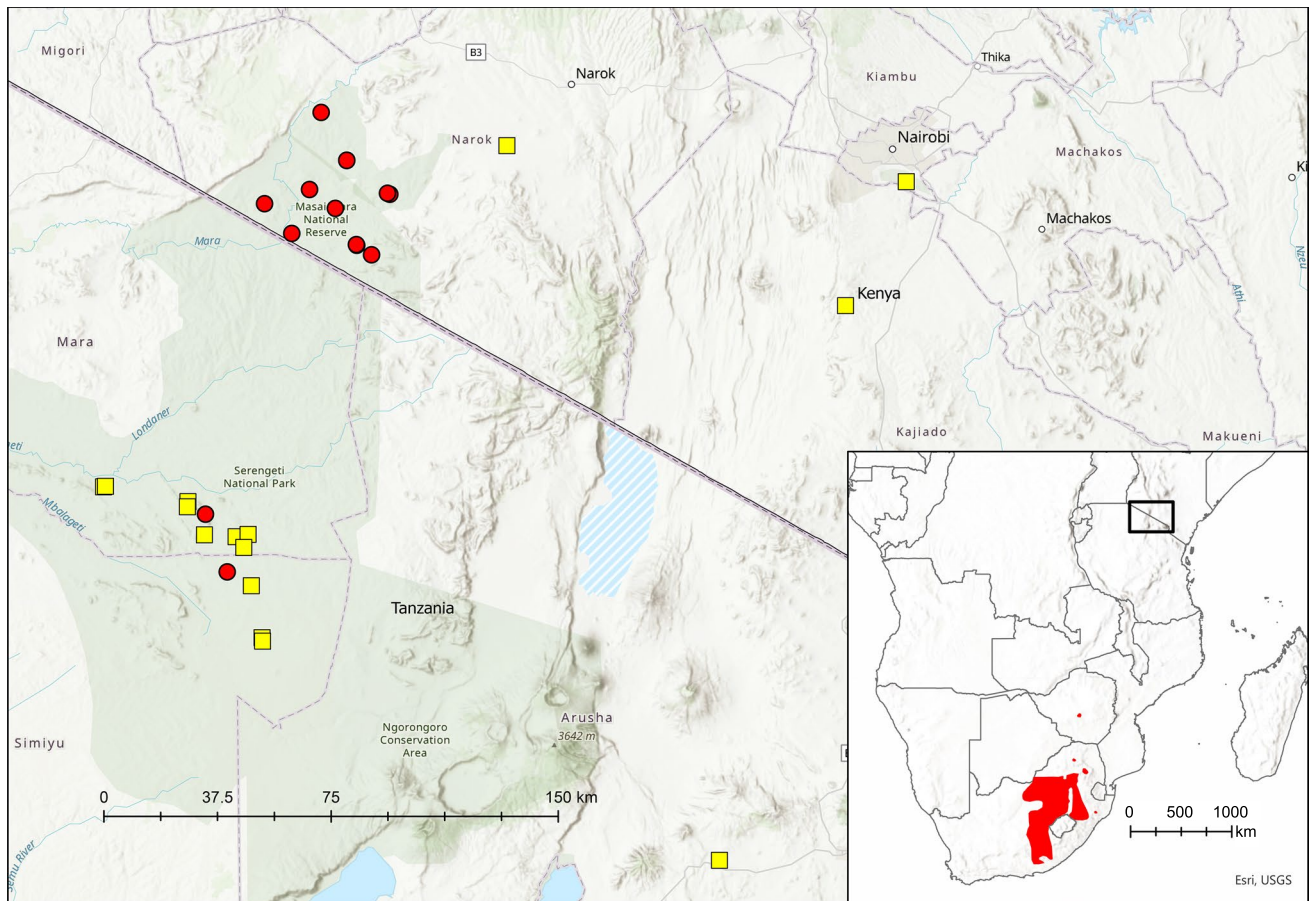


Fig. 1 Map showing recent point localities of “Mara Lark” (=Melodious Lark *Mirafra cheniana*; red circles) and White-tailed Lark *Mirafra albicauda* (yellow squares) from southern Kenya and north-

ern Tanzania. Note that both species are thinly scattered within their respective ranges. The inset map shows the previously known global range of *M. cheniana* (in red)

fixed at 93, and brightness was adjusted manually for each recording to give good visual separation between the song and the background noise. Strophes consist of notes, and different strophes are separated from each other by silent pauses. The following variables were measured for each strophe: duration (s), maximum frequency (Hz), and minimum frequency (Hz). The duration of intervals between strophes was also measured (s). In the simple parts of “Mara Lark” and *M. cheniana* songs (see below), the number of blocks of repeated notes (phrase) inside a strophe was counted. All analyses of songs were done by the same person (S.C.).

We used linear discriminant analysis (LDA) to assess similarity and clustering in song structure in multivariate space between “Mara Lark”, *M. cheniana*, *M. albicauda*, and *M. cantillans* based on the above measurements. In each analysis, we used correlation clustering to identify and remove strongly intercorrelated (at $r > 0.6$) variables. In the LDA analysis, all variables were scaled to zero mean and unit variance due to their greatly different scales of

measurement. Confusion matrices were used to assess the discriminatory power of the models.

To determine the identity and frequency of mimicked species in “Mara Lark” and *M. cheniana* songs (see below), we counted the number of times within a recording that a certain species was mimicked. For the song mimicry analysis, we selected recordings of 7 “Mara Lark” individuals, 6 from Kenya (the same 4 individuals from the sound analysis cited above, plus another 2; 8 recordings in total) and 1 from Tanzania. We also selected recordings of 24 *M. cheniana* individuals (the same 5 individuals from the sound analysis cited above, plus another 19; 32 recordings in total) (Table S1). This analysis was performed by three individuals for South African *M. cheniana* (D.E., J.G. and D.d.S.) and by one person for “Mara Lark” (B.W.F.).

Genetic analyses

A faecal sample of a “Mara Lark” was collected in Mara Naboisho Conservancy on 18 September 2020 immediately

Fig. 2 Photos of “Mara Lark”, Mara Triangle, Kenya, May 2021 (Pete Steward) (a), Mara Naboisho Conservancy, Kenya, March 2020 (R. Stratton Hatfield) (b), Mara Naboisho Conservancy, Kenya, September 2020 (this is the individual whose DNA was sequenced) (R. Stratton Hatfield) (c), Maasai Mara National Reserve, Kenya, September 2016 (R. Stratton Hatfield) (d), and Serengeti National Park, Tanzania, April 2018 (Nik Borrow) (e)



after it was deposited on a rock (Fig. 2c). This sample was dried and stored in an envelope at room temperature. DNA was isolated from the faecal sample using the QIAamp fast DNA Stool mini kit (QIAGEN, Valencia, CA, United States) according to the protocol: “Isolation of DNA from Stool for Human DNA Analysis” from the QIAamp fast DNA Stool mini handbook version February 2020. Two short overlapping fragments of the mitochondrial cytochrome *b* gene (Cytb) were amplified by means of Monoplex PCR and PCRs were run on a GeneAmp® PCR System 9700 (Online Resource 1 for primer sequences). The PCR product was visualized using the QIAxcel and purified using the QIAquick® PCR purification kit (QIAGEN) according to the protocol from this kit. For each of the PCR fragments, a sequencing PCR was performed on a pre-heated GeneAmp® PCR System 9700 using an input of purified PCR-product samples. PCR product was purified using the DyeEx® 2.0 Spin kit (QIAGEN) following the protocol for Dye-Terminator Removal. Purified sequencing PCR product was run on an AB3100 Genetic Analyzer. The two overlapping sequences were aligned and concatenated in BIOEDT 7.2.5. To exclude premature (numt induced) stop codons, open-reading frame

finder (<https://www.ncbi.nlm.nih.gov/orffinder/>) was used. All fragments aligned well against *M. cheniana* and *M. albicauda*, and there was no evidence of a chimeric sequence.

Four toepad samples of *M. albicauda*, including the holotype (ZMB 49.225) from Tanzania, were obtained (Table S2). These were extracted following the protocol described in Irestedt et al. (2006). Subsequently, Illumina library preparation followed the protocol published by Meyer and Kircher (2010), including pre-treatment with USER enzyme (New England BioLabs) to reduce post-mortem DNA damage patterns. In total, 11 samples with four sequencing libraries per sample (dual indexes) were then pooled in equimolar ratios and sent to SciLifeLab, Stockholm for paired-end sequencing using Illumina Next-Generation Sequencing (NGS) technology on one lane NovaSeq sequencing machines. Cytb sequences from two fresh samples of *M. cheniana* were obtained from unpublished whole-genome sequences (Alström et al. in prep.; Table S2). The raw reads were trimmed with Trimmomatic 0.36 (Bolger et al. 2014) by removing adapters identified as overrepresented sequences in FastQC 0.11.9 (Andrews 2010) and performing a 4-base wide sliding window trimming, cutting

when the average quality per base dropped below quality score 15. Bases at the start and end of the read were cut if they were below a threshold quality score of 3. Reads shorter than 50 nucleotides were discarded. The trimmed reads of *M. cheniana* DZUG U5759 were mapped to an *Eremophila alpestris* mitochondrial reference sequence in GenBank (NC 948,479) in Geneious 9.1.2 (www.geneious.com) with the Geneious mapper, medium–low sensitivity, iterated 10 times. The resulting consensus sequence was edited for quality and used as a template for a second round of mapping of *M. cheniana* DZUG U5759, using the same Geneious settings. The trimmed reads of *M. cheniana* DZUG U5760 and the four *M. albicauda* samples were mapped to the same template. The Cytb sequences were then extracted from the final respective consensus sequences supported by a sequencing depth of at least 10X. Cytb sequences of all other potential close relatives (except *M. pulpa*, for which no sequence data are available; corresponding to clade B1b in Fig. 1 in Alström et al. 2013), including one additional *M. cheniana*, as well as a few outgroup species (corresponding to clades B1a and B1d in Fig. 1 in Alström et al. 2013) were downloaded from GenBank (Table S2).

Sequences were aligned in SeaView 5.0 (Gouy et al. 2010). The best-fit model for phylogenetic analysis was determined by the Bayesian Information Criterion in jModeltest2 (Darriba et al. 2012). Phylogenetic analysis of the Cytb matrix was run under the best-fit model (HKY + G), a Yule speciation model, a strict molecular clock (with rate 1.0), and default priors in BEAST 1.10.4 (Suchard et al. 2018). 20 million generations were run, with trees sampled every 10,000 trees. Convergence to the stationary distribution of the single chains was inspected in Tracer v. 1.7.1 (Rambaut et al. 2014) using a minimum threshold for the effective sample size (> 200). The joint likelihood and other parameter values reported large effective sample sizes (> 1,000), and the trace plot had the shape of a “dense, straight, furry caterpillar”. Good mixing of the MCMC and reproducibility were established by multiple runs from independent starting points. The first 20% of the sampled trees were discarded as burn-in, well after stationarity had been reached, and the posterior probabilities were calculated from the remaining samples. Trees were summarized using TreeAnnotator v. 1.7 (in the BEAST package), choosing “Maximum clade credibility tree” and “Mean heights” and displayed in FigTree 1.4.4 (Rambaut 2016). Both jModeltest and BEAST were run on the CIPRES portal (Miller et al. 2010).

To evaluate how the “Mara Lark” differed from *M. cheniana* and *M. albicauda* in the 387-bp Cytb sequence that was available for the “Mara Lark”, as well as how other closely related lark taxa differ in the same region, an alignment was created for this stretch for the “Mara Lark”, three *M. cheniana*, four *M. albicauda*, a single *M. cantillans marginata* (from Tanzania), a single *M. javanica williamsoni*

(from Australia), three Horned Lark *Eremophila alpestris alpestris* (from Newfoundland, Canada), and four Horned Lark *Eremophila alpestris brandti* (from Gobi, Mongolia) (Table S2).

Morphology

Morphological comparisons between the “Mara Lark” and *M. cheniana* from South Africa and *M. albicauda* from East Africa were based on c.15 photos of the former and field observations (latter of course never side-by-side); nearly all the photos are available at Macaulay Library (<https://www.macaulaylibrary.org>), and a selection is shown in Fig. 2. It was not considered meaningful to try to quantify the differences, which mainly concerned minor differences in colour, and which were also affected by photos being taken under different light conditions, of birds at different stage of wear, etc. Measurements of specimens of *M. cheniana* and *M. albicauda* were taken in the Natural History Museum, Tring, UK by P.F.D., but no “Mara Larks” were available for comparison.

Results

Song characteristics of *Mirafra albicauda*, “Mara Lark”, *Mirafra cheniana*, and *Mirafra cantillans marginata*.

The song of *M. albicauda* (Fig. 3a–b) is usually composed of well-defined strophes that are separated by silent pauses of rather regular length; when given in flight (see below), the strophes average shorter (0.67–5.05 s, mean 2.75 ± 0.90 s, $n = 37$ strophes from 3 individuals) and the pauses shorter (0.78–3.42 s, mean 2.34 ± 0.79 s, $n = 32$ pauses from 3 individuals) than when given from a perch (strophes: 0.11–27.07 s, mean 4.40 ± 3.80 s, $n = 95$ strophes from 5 individuals; pauses: 0.30–18.61 s, mean 2.64 ± 3.36 s, $n = 89$ pauses from 5 individuals) (Table S3). The strophes consist of short, scratchy notes, which are sometimes interspersed with short, soft notes. Individual notes can be very different from each other in terms of frequency and shape, and usually, all notes in a strophe are unique as seen on a sonogram, although a few similar-sounding notes are often given in a sequence; occasionally, a single note may be repeated a few times before switching to another one. The notes are delivered at a rather slow, steady, chattering speed, usually with a slightly hesitant beginning; sometimes, the strophes are preceded by single notes that are well separated from the rest of the strophe. The notes are frequently given on somewhat rising and falling scales, producing an undulating rhythm, with an abrupt ending by a rather short, rather low-pitched note. In our sample, none of the strophes was repeated identically, and accordingly, each male has a very large repertoire of strophes. Unlike in “Mara Lark” and Melodious Lark,

Fig. 3 Songs of White-tailed Lark *Mirafra albicauda* in flight, Serengeti, Tanzania (Calan Cohen) (**a**, two strophes, April 2013; **b**, three strophes, May 2012); Singing Bush Lark *Mirafra cantillans* in flight Tug Wajale, Somalia, May 2010 (Michael Mills) (**c**; four strophes) and Nairobi, Kenya, May 2019 (Per Alström) (**d**; four strophes); “Mara Lark”, perched Mara Naboisho Conservancy, Kenya, March 2020 (Stratton Hatfield) (**e**); and Maasai Mara National Reserve, Kenya, March 2018 (Riley Chapman) (**f**); Melodious Lark *Mirafra cheniana* perched, Jagersfontein road, Free State, South Africa, October 2017 (Dawie de Swardt) (**g**); and Emthanjeni Local Municipality, Northern Cape, South Africa, October 2020 (Tony Archer) (**h**); “Mara Lark”, Maasai Mara National Reserve, Kenya, March 2018 (Glen Chapman) (**i**); and Maasai Mara National Reserve, Kenya, March 2018 (Riley Chapman) (**j**); Melodious Lark *M. cheniana* perched, Free State, South Africa, December 2017 (Per Alström) (**k**); and perched Blue Crane Route Local Municipality, Eastern Cape, South Africa, February 2020 (W. J. Rossouw) (**l**). Long silent pauses between the strophes have been shortened (indicated by three dots). Recordings **e–h** represent simple sequences of song and **i–l** more complex parts of song of “Mara Lark” and *M. cheniana*

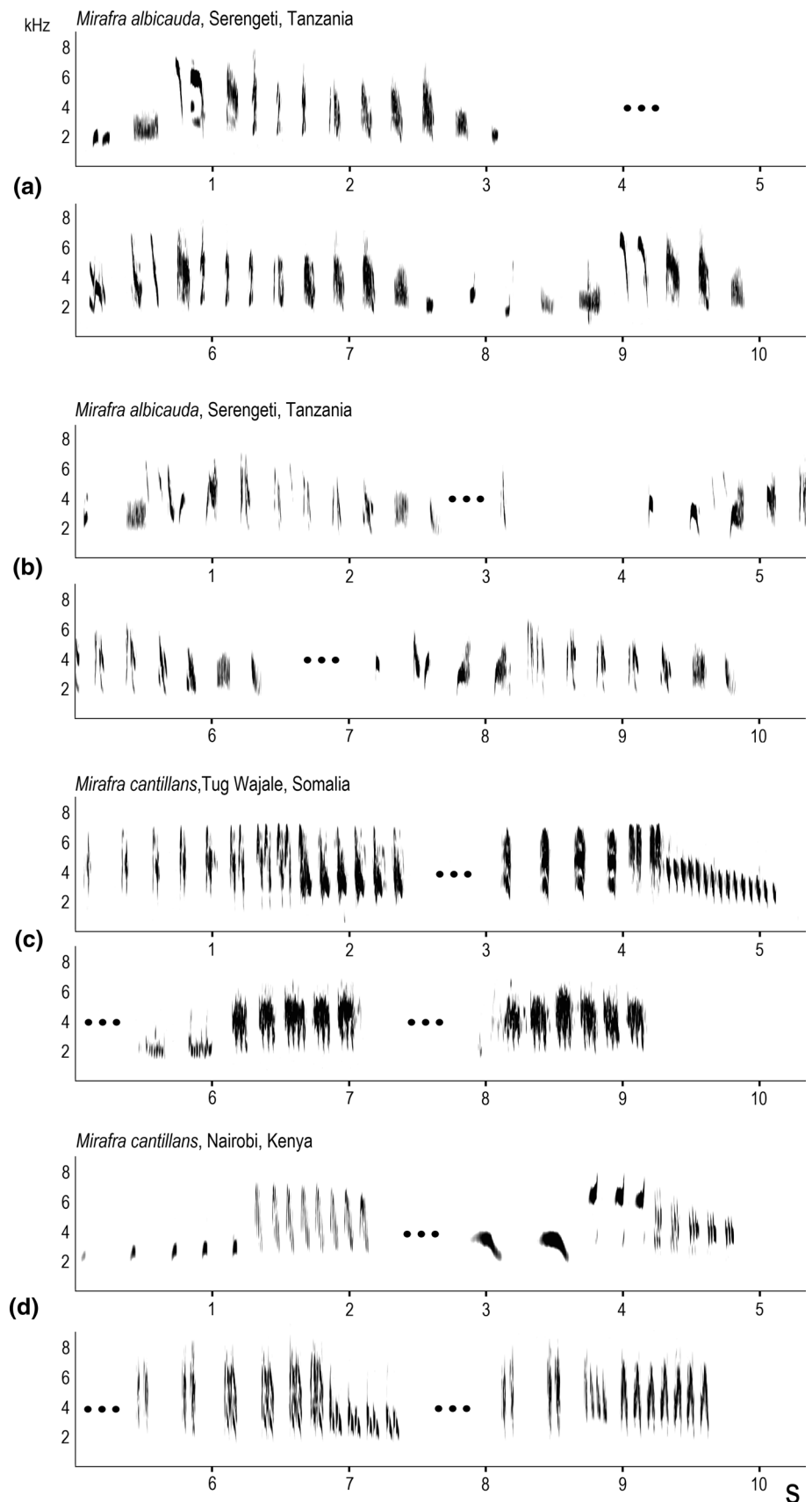


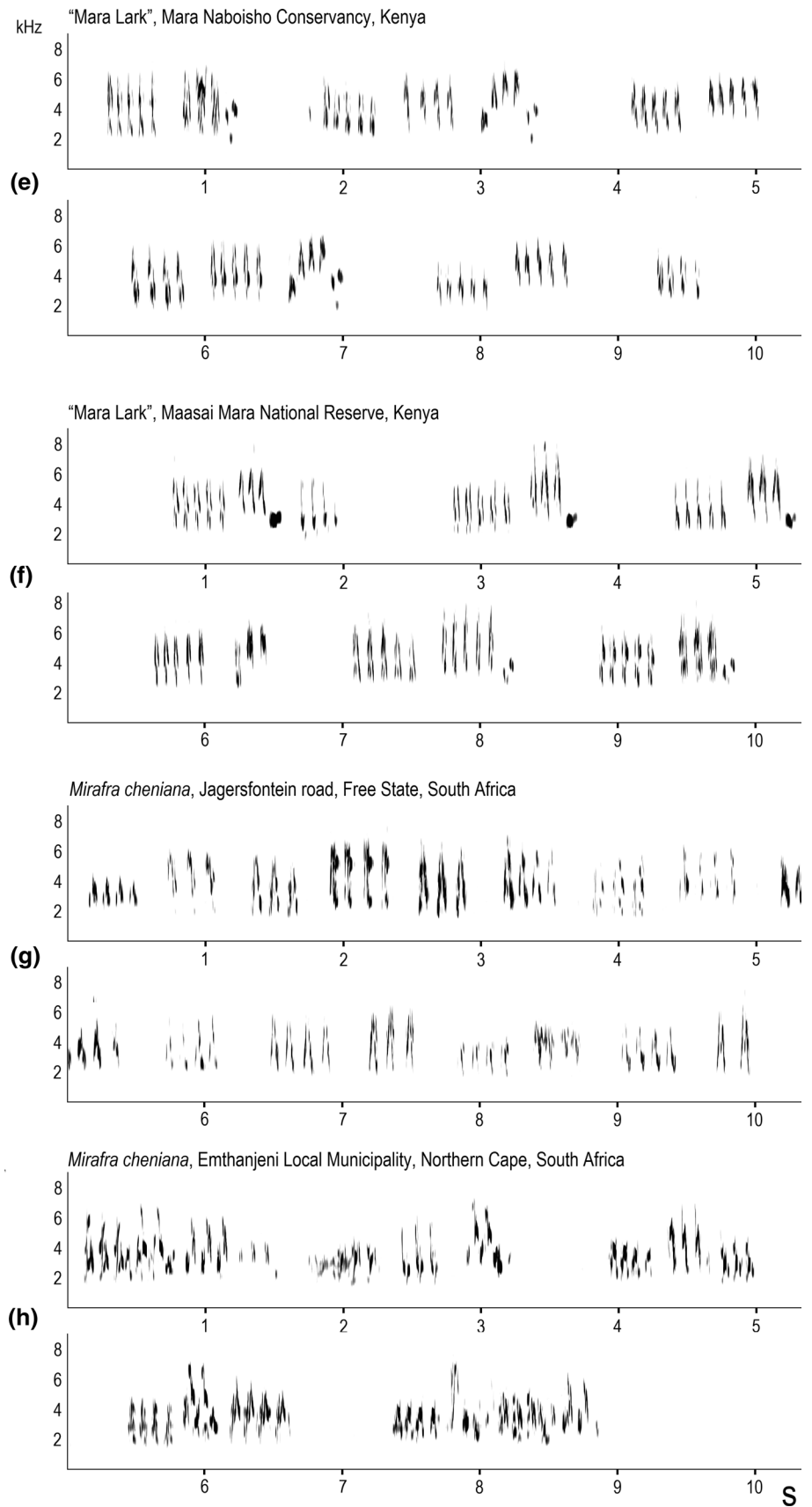
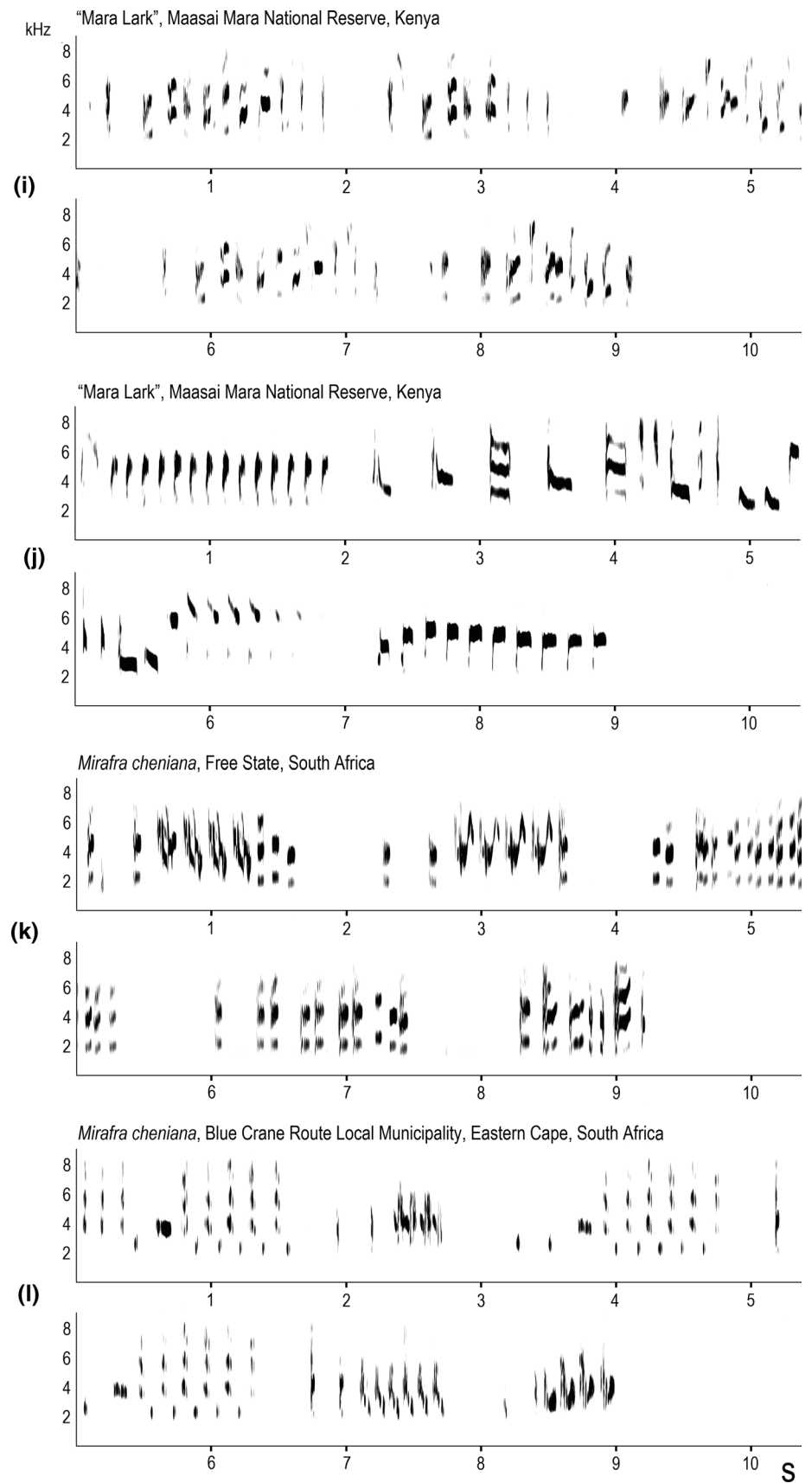
Fig. 3 (continued)

Fig. 3 (continued)

no apparent mimicry was included in the analysed songs of this species. Whilst the song is usually delivered in flight, it is more rarely given from the top of a low bush. In display flight, it traces a very large ellipse and may climb until lost to the naked eye. Hovering in one spot is only momentary after each repeated song phrase. The complete song-flight rarely lasts more than 15 min, but covers a large territory.

The song of “Mara Lark” is easily distinguishable from that of *M. albicauda* by being faster, more varied (often including mimicry) and more continuously flowing, with short, irregular pauses (most different compared to *M. albicauda* in flight). It is highly varied, and switches back and forth between monotonous spells of short rattling series of simple notes (Fig. 3e–f) and spells of much more complex notes, including mimicry (Fig. 3 i–j). The simple parts usually consist of rattling series (phrases) (1–6, mean 4.51 ± 0.70 , in $n = 217$ phrases from 4 individuals) of identical or marginally different short, dry, scratchy notes that are separated by short silent pauses (Table S3). Usually, two, sometimes three, phrases with different notes are given in rapid succession, separated by very brief intervals, and these “pairs” of phrases are separated by slightly longer silent pauses (0.52 – 7.13 s, mean 0.92 ± 1.01 s, $n = 102$ pauses from 4 individuals) (Table S3); the pitch usually differs slightly between the phrases in these “pairs” (first one being slightly higher pitched than the second or vice versa). The more varied parts are much more complex and melodious, and consist of a medley of highly varied notes of different pitch, duration, and quality, including their own improvised notes, masterful mimicry (see below), and notes that are considered to be modifications in tone and tempo of mimicked songs. The notes are usually arranged in series of various lengths that are separated by short pauses, but can also be rather continuously flowing; series of rapid repetitions of single notes are common. Similar-sounding, almost identical, series are often given a few times in succession. As in *M. albicauda*, the song can be given both in flight and from a perch such as the top of a bush, and there is no apparent difference in the frequency of the two song types depending on whether the song is given in flight or when perched. Unlike the display flight of *M. albicauda*, the bird remains over a small territory and hovers for long periods, tracing small circles and is rarely high enough not to be discerned by the naked eye. Such restricted range song-flights may exceed an hour in duration. The single recording of a bird by C.C. in 2013 from the Serengeti in Tanzania (ML274636) was not included in the vocal analyses because of inferior quality, but vocally confirms the presence of the “Mara Lark” as being in the Serengeti. Finally, “Mara Lark” singing males form loose associations in the same general area while *M. albicauda* in Kenya are always found singing in very low numbers with no local aggregations at any time of the year.

The song of *M. cheniana* from South Africa (Fig. 3k–l) is very similar to that of “Mara Lark” in its structure as both populations alternate between series of simple notes and more complex parts which include a high number of mimicked species. Because of the enormous variation both in a single recording and among recordings of different individuals, it is very hard to detect and quantify differences, if any, between *M. cheniana* and “Mara Lark”. However, the simple parts (Fig. 3g–h) usually comprise either rattling series of up to five identical notes (1–5, mean 3.07 ± 0.84 in $n = 415$ phrases from 5 individuals) with rather uniform pauses between the series (i.e., not “paired series”) or more complex series of notes (Table S3). In the more complex parts of the song, identical series of notes that are repeated a few times are not uncommon, unlike in our sample of “Mara Lark”, though this might be an effect of our smaller sample size of the “Mara Lark”. As in the above, the song may be given from a perch or in flight.

The songs of each of *M. albicauda*, “Mara” and Melodious Larks differ clearly from the song of *M. cantillans*, which occurs in the same geographical area as the two former species, although almost invariably separated by habitat. The song of *M. cantillans* from African populations (Fig. 3c–d) consists of short strophes (0.55 – 3.96 s, mean 2.16 ± 0.67 s, $n = 64$ unique strophes from 4 individuals) that are well separated by silent pauses (0.64 – 6.52 s, mean 2.48 ± 1.24 s, $n = 94$ pauses from 4 individuals) (Table S3). They usually begin somewhat falteringly with a series of a single note type and then change to a fast rattle consisting of one or two series of notes. The repertoire size seems to be much smaller than in the above-mentioned taxa. Unlike in “Mara Lark” and Melodious Lark, no apparent mimicry was included in the analysed songs of this species.

In the LDA, “Mara Lark” and *M. cheniana* are broadly overlapping along LD1 (which explains 91.9% of the variance), whereas they are fully separated along LD2 (explaining 6.4% of the variance) (Fig. 4). In contrast, *M. albicauda* and *M. cantillans* overlap on both axes, while they are widely separated from “Mara Lark” and *M. cheniana* along LD1. All songs were correctly classified, except one *M. albicauda*, which was classified as *M. cantillans* (Table S4).

Song mimicry in “Mara Lark” and *Mirafra cheniana*

As stated above, both “Mara Lark” and *M. cheniana* from South Africa include much mimicry in their songs. Table 1 lists the species that have been identified as mimicked in the songs of “Mara Lark” and *M. cheniana* from South Africa. The birds that are imitated have apparently been learned from the local avifauna, and accordingly, there are some geographical differences between “Mara Lark” and *M. cheniana* from South Africa. In the selected recordings, a total of 80 different species belonging to 22 different families

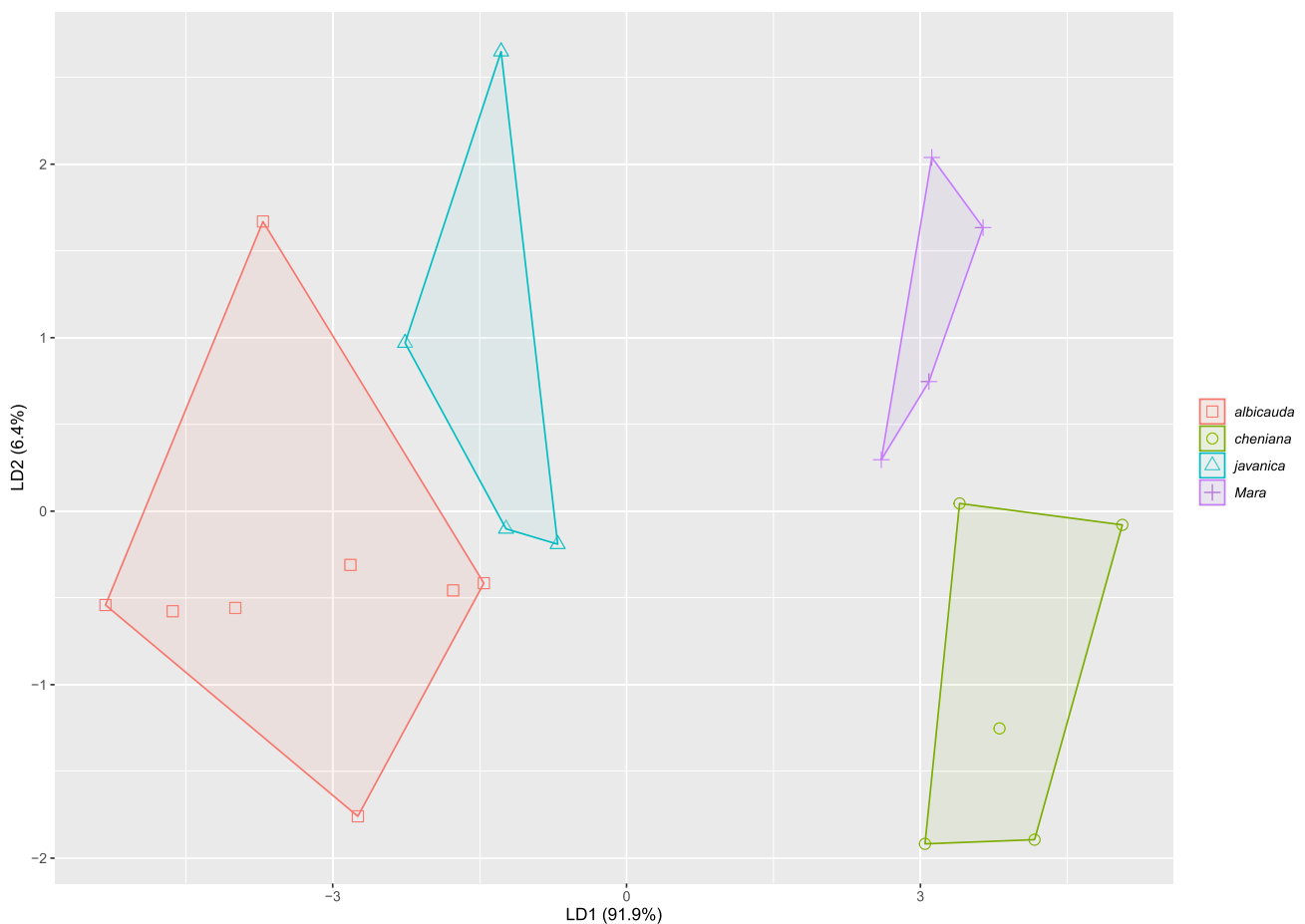


Fig. 4 Plot of LD1 versus LD2 of an LDA of songs of *Mirafra albicauda*, *M. cheniana*, *M. cantillans*, and “Mara Lark” based on duration, maximum frequency and minimum frequency of “strophes”, and duration of intervals between strophes

are imitated. The higher number of mimicked species by *M. cheniana* from South Africa is probably due to a larger number of available recordings for this population. The most frequently mimicked species by both populations belong to the families Cisticolidae, Alaudidae, and Hirundinidae; in particular, three species are mimicked consistently: Desert Cisticola *Cisticola aridulus*, Quailfinch *Ortygospiza atricollis*, and Grassland (African) Pipit *Anthus cinnamomeus*. Songs of Rufous-naped Lark *Mirafra africana* and Red-capped Lark *Calandrella cinerea* are incorporated by both “Mara Lark” and South African *M. cheniana*. In both “Mara Lark” and *M. cheniana*, mimicked songs are (i) often interspersed with their own songs and calls, (ii) characterized by frequent changes of the mimicked species, and (iii) interrupted by improvisation, unidentifiable song series, constituted by modified borrowed strophes.

Mitochondrial DNA

The Cytb tree (Fig. 5) identified the single “Mara Lark” as sister to the three *M. cheniana* from South Africa with

posterior probability 1.00. The four *M. albicauda* also formed a strongly supported clade. The latter was sister to the *M. javanica* + *M. cantillans* clade, but with poor statistical support (posterior probability 0.55).

The 387 bp sequence of the “Mara Lark” differed from the three South African *M. cheniana* at 5 positions (two individuals) or 7 positions (third individual). In comparison, three of the *M. albicauda* had identical sequences to each other in the same 387 bp sequence, whereas the fourth individual differed from the others by a single bp, and the single *M. javanica williamsoni* (Australia) and *M. cantillans marginata* (Tanzania) differed from each other at 6 positions in the same stretch of DNA. The three *E. alpestris alpestris* (Newfoundland, Canada) and four *E. alpestris brandti* (Gobi, Mongolia) had two fixed single-bp substitutions in the same 387-bp stretch of Cytb, with four additional, autapomorphic single-bp substitutions among these individuals (Online Resource 1).

Table 1 List of mimicked species by “Mara Lark” and South Africa Melodious Lark *Mirafra cheniana*

Common Name <i>species</i>	Family	"Mara Lark"	South Africa Melodious Lark
Spur-winged goose, <i>Plectropterus gambensis</i>	Anatidae	0	1
Helmeted guineafowl, <i>Numida meleagris</i>	Numididae	0	6
Grey-winged francolin, <i>Scleroptila afra</i>	Phasianidae	0	1
Red-winged francolin, <i>Scleroptila levaillantii</i>	Phasianidae	0	3
Harlequin quail, <i>Coturnix delegorguei</i>	Phasianidae	1	1
Common swift, <i>Apus apus</i>	Apodidae	0	1
Little swift, <i>Apus affinis</i>	Apodidae	3	2
White-rumped swift, <i>Apus caffer</i>	Apodidae	1	0
Diderick cuckoo, <i>Chrysococcyx caprius</i>	Cuculidae	0	9
Namaqua sandgrouse, <i>Pterocles namaqua</i>	Pteroclididae	0	2
Blacksmith lapwing, <i>Vanellus armatus</i>	Charadriidae	0	8
Crowned plover, <i>Vanellus coronatus</i>	Charadriidae	1	9
African wattled lapwing, <i>Vanellus senegallus</i>	Charadriidae	0	2
Three-banded plover, <i>Charadrius tricollaris</i>	Charadriidae	1	8
Little bee-eater, <i>Merops pusillus</i>	Meropidae	0	2
White-throated bee-eater, <i>Merops albicollis</i>	Meropidae	2	0
European bee-eater, <i>Merops apiaster</i>	Meropidae	1	14
Grey-backed fiscal, <i>Lanius excubitorides</i>	Laniidae	1	0
Southern fiscal, <i>Lanius collaris</i>	Laniidae	0	5
Spike-heeled lark, <i>Chersomanes albobasica</i>	Alaudidae	0	6
Short-clawed lark, <i>Certhilauda chuana</i>	Alaudidae	0	1
Chestnut-backed sparrow-lark, <i>Eremopterix leucotis</i>	Alaudidae	0	1
Rufous-naped lark, <i>Mirafra africana</i>	Alaudidae	6	5
Pink-billed lark, <i>Spizocorys conirostris</i>	Alaudidae	0	15
Large-billed lark, <i>Galerida magnirostris</i>	Alaudidae	0	6
Red-capped lark, <i>Calandrella cinerea</i>	Alaudidae	2	14
Somali short-toed lark, <i>Alaudala somalica</i>	Alaudidae	5	0
Dark-capped bulbul, <i>Pycnonotus tricolor</i>	Pycnonotidae	0	1
Banded martin, <i>Riparia cincta</i>	Hirundinidae	0	1
Barn swallow, <i>Hirundo rustica</i>	Hirundinidae	1	9
Greater striped swallow, <i>Cecropis cucullata</i>	Hirundinidae	0	15
Lesser striped swallow, <i>Cecropis abyssinica</i>	Hirundinidae	6	0
Rufous-chested swallow, <i>Cecropis semirufa</i>	Hirundinidae	9	6
Red-rumped swallow, <i>Cecropis daurica</i>	Hirundinidae	1	0
South African cliff swallow, <i>Petrochelidon spilodera</i>	Hirundinidae	0	4
Rattling cisticola, <i>Cisticola chiniana</i>	Cisticolidae	1	7
Levaillant's cisticola, <i>Cisticola tinnius</i>	Cisticolidae	0	3
Stout cisticola, <i>Cisticola robustus</i>	Cisticolidae	10	0
Croaking cisticola, <i>Cisticola natalensis</i>	Cisticolidae	2	0
Desert cisticola, <i>Cisticola aridulus</i>	Cisticolidae	2	17
Cloud cisticola, <i>Cisticola textrix</i>	Cisticolidae	0	25
Black-backed cisticola, <i>Cisticola eximius</i>	Cisticolidae	10	0
Pectoral patch cisticola, <i>Cisticola brunescens</i>	Cisticolidae	5	0
Pale-crowned cisticola, <i>Cisticola cinnamomeus</i>	Cisticolidae	0	1
Tawny-flanked prinia, <i>Prinia subflava</i>	Cisticolidae	1	0
Black-chested prinia, <i>Prinia flavicans</i>	Cisticolidae	0	11
Rufous-eared warbler, <i>Malcopus pectoralis</i>	Cisticolidae	0	5
Common myna, <i>Acridotheres tristis</i>	Sturnidae	0	4
Cape starling, <i>Lamprotornis nitens</i>	Sturnidae	0	1
Superb starling, <i>Lamprotornis superbus</i>	Sturnidae	2	0
Pied starling, <i>Lamprotornis bicolor</i>	Sturnidae	0	8
Red-billed oxpecker, <i>Buphagus erythrorhynchus</i>	Buphagidae	4	0
African stonechat, <i>Saxicola torquatus</i>	Muscicapidae	0	2
Sooty chat, <i>Myrmecocichla nigra</i>	Muscicapidae	4	0
Southern anteater-chat, <i>Myrmecocichla formicivora</i>	Muscicapidae	0	4
Marico sunbird, <i>Cinnyris mariquensis</i>	Nectariniidae	0	2
Cape sparrow, <i>Passer melanurus</i>	Passeridae	0	12
White-browed sparrow-weaver, <i>Plocepasser mahali</i>	Ploceidae	0	5
Scaly-feathered weaver, <i>Sporopipes squamifrons</i>	Ploceidae	0	2
Lesser masked weaver, <i>Ploceus intermedius</i>	Ploceidae	0	1
Southern masked weaver, <i>Ploceus velatus</i>	Ploceidae	0	8
Cardinal quelea, <i>Quelea cardinalis</i>	Ploceidae	1	0

Table 1 (continued)

Southern red bishop , <i>Euplectes orix</i>	Ploceidae	0	7
Red-collared widowbird , <i>Euplectes ardens</i>	Ploceidae	1	0
Long-tailed widowbird , <i>Euplectes progne</i>	Ploceidae	0	6
Common waxbill , <i>Estrilda astrild</i>	Estrildidae	0	8
Quailfinch , <i>Ortygospiza atricollis</i>	Estrildidae	7	35
Red-headed finch , <i>Amadina erythrocephala</i>	Estrildidae	0	8
Violet-eared waxbill , <i>Granatina granatina</i>	Estrildidae	0	4
Green-winged pytilia , <i>Pytilia melba</i>	Estrildidae	0	4
Cape wagtail , <i>Motacilla capensis</i>	Motacillidae	0	1
Cape longclaw , <i>Macronyx capensis</i>	Motacillidae	0	13
Yellow-throated longclaw , <i>Macronyx croceus</i>	Motacillidae	2	0
Rosy-breasted longclaw , <i>Macronyx ameliae</i>	Motacillidae	1	0
Grassland pipit , <i>Anthus cinnamomeus</i>	Motacillidae	8	43
Plain-backed pipit , <i>Anthus leucophrys</i>	Motacillidae	0	1
Tree pipit , <i>Anthus trivialis</i>	Motacillidae	1	0
Black-throated canary , <i>Crithagra atrogularis</i>	Fringillidae	0	6
Yellow canary , <i>Crithagra flaviventris</i>	Fringillidae	0	2
Cape canary , <i>Serinus canicollis</i>	Fringillidae	0	2

Numbers indicate the total number of times within our selected song recordings that a particular species was mimicked (“Mara Lark” $n=9$ recordings, South Africa Melodious Lark *M. Cheniana* $n=32$ recordings). Mimicked species present in Kenya but not in South Africa are highlighted in red, species found in South Africa but not in Kenya are highlighted in blue, and species shared by both regions are printed in black

Morphology

“Mara Lark” and *M. cheniana* are nearly identical in plumage, but “Mara Larks” appear to show more variation in plumage colour. Some worn “Mara Larks” show very white underparts and rufous lesser coverts, and these traits have not been recorded in *M. cheniana* in southern Africa. *Mirafra albicauda* is extremely similar, but is generally less warmly coloured overall, especially on the crown, nape, upperparts, and breast/flanks, and tends to show darker and more uniformly coloured centres to the tertials. The colour differences are most apparent in fresh plumage and can be negligible when worn. As we have not seen any specimens (alive or dead) of birds in the hand of “Mara Lark”, we cannot say whether there are differences in morphometrics. *Mirafra albicauda* is a larger bird than southern African *M. cheniana* with little or no overlap between the two in wing length (males only: mean 81.9 mm [range 77–86]; $n=15$ vs 74.5 mm [72–77]; $n=11$) or tarsus (23.5 mm [22.0–26.6]; $n=14$ vs 19.6 mm [17–21]; $n=11$).

Habitat

The habitat of “Mara Lark” and *M. cheniana* in South Africa is basically similar. It is characterized by extensive open, moderately grazed, often dominated by *Themeda triandra*, grasslands with minimal or no bush cover. In the west part of its South Africa distribution range, *M. cheniana* can also be found in drier grasslands. “Mara Larks” are found at 1500–1800 m above mean sea level over both vertisols

(black cotton clay) and planosols. “Mara Larks” appear to be resident, but during long wet periods, we have observed local irruptions into areas that recovered from recent overgrazing. *Mirafra albicauda* favours both lightly bushed, scrubby grasslands and more open grasslands, often over vertisols, and is very rarely seen in the open (even less frequently than “Mara Lark” and *M. cheniana*).

Discussion

Our results based on analyses of songs and mitochondrial DNA and studies of photographs taken in the field convincingly show that the lark population in south-western Kenya (“Mara Lark”) that has always been treated in the literature up to the end of 2020 as *M. albicauda* (Britton 1980; Zimmerman and Turner 1996; Stevenson and Fanshawe 2002; Ryan 2020a) is certainly not *M. albicauda*, but instead matches *M. cheniana*, which has previously been considered a Southern African endemic. That this population differs from *M. albicauda* has been known for some time based on perceived differences in song (Finch 2002, 2009). The phylogenetic analysis, which included a single sample of “Mara Lark” and samples of *M. cheniana* from South Africa and *M. albicauda* from Kenya and Uganda, as well as the holotype of *M. albicauda* Reichenow, 1891 from “Gonda, Tabora district, Tanganyika Territory” in Tanzania, confirms beyond doubt that the holotype of *M. albicauda* is not a “Mara Lark”. If that had been the case, *M. albicauda* would have become a junior synonym of *M. cheniana* A. Smith, 1843.

Phylogenetic tree showing relationships between various species of the genus *M.* The tree is rooted at the bottom left and branches upwards. Bootstrap values are indicated at the nodes. The species names and their source locations are listed to the right of the branches. The species **"Mara Lark"** is highlighted in bold. A scale bar at the bottom indicates a distance of 0.02.

Species and Source Locations (from top to bottom):

- M. albicauda* Kenya NHMUK 1901.2.22.246
- M. albicauda* Tanzania ZMB 49.225 holotype
- M. albicauda* Kenya ZMB 2000.9488
- M. albicauda* Uganda NHMUK 1916.12.1.840
- M. javanica williamsoni* Australia DQ008520
- M. cantillans marginata* Tanzania KF060473
- M. cheniana* South Africa KF060474
- M. cheniana* South Africa DZUG U5660
- M. cheniana* South Africa DZUG U5759
- "Mara Lark"** Kenya
- M. williamsi* Kenya KF060487
- M. passerina* South Africa AY165163
- M. africana harterti* Kenya KF060469
- M. fasciolata fasciolata* South Africa KF060477
- M. assamica* India KF060471

Scale bar: 0.02

Three other lark complexes, Rudd's Lark *Heteromirafra ruddi*–Archer's Lark *H. archeri*, Spike-heeled Lark *Chersomanes albofasciata*–Beesley's Lark *C. beesleyi* and Fawn-coloured Lark *Calendulauda africanoides*–Foxy Lark *C. alopex*, have similarly disjunct distributions between southern and eastern Africa as “Mara Lark”—*M. cheniana* (e.g., Gill et al. 2022), but are probably more anciently diverged,

approximately 6.5, 4, and 2 million years ago, respectively (Alström et al. 2013; Stervander et al. 2020). This may reflect different timings of movements along the “arid corridor” of eastern Africa as it has expanded and contracted over time.

The differences in song between the “Mara Lark” and southern African *M. cheniana* are partly based on the available subjects for mimicry. Peacock (2012) states that the three prime species mimicked in South Africa are Little Swift *Apus affinis*, Grassland (African) Pipit *Anthus cinnamomeus*, and Quailfinch *Ortygospiza atricollis*, which are frequently mimicked in our recordings from Kenya.

Conservation

Whilst the known distribution of the “Mara Lark” is geographically small, we believe that most of the population lies within formally gazetted protected areas and community-owned conservancies. More work is needed to ascertain the size of this population, but based on field observations, it is believed to be common in appropriate habitat.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-022-02013-z>.

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Data availability The datasets generated during and/or analysed during the current study are available online in GenBank, The Macaulay

Library and at www.xeno-canto.org or from the corresponding author on request.

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

Ethics approval No approval of research ethics committees was required to accomplish the goals of this study, because experimental work was conducted non-invasively.

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References

- Alström P (1998) Taxonomy of the *Mirafra assamica* complex. Forktail 13:97–107
- Alström P, Sundev G (2021) Mongolian Short-toed Lark *Calandrella dukhunensis* an overlooked East Asian species. J Ornithol 162(1):165–177. <https://doi.org/10.1007/s10336-020-01819-z>
- Alström P, Barnes NK, Olsson U, Barker FK, Bloomer P, Khan AA, Qureshi MA, Guillaumet A, Crochet P, Ryan PG (2013) Multilocus phylogeny of the avian family Alaudidae (larks) reveals complex morphological evolution, non-monophyletic genera and hidden species diversity. Mol Phylogenet Evol 69:1043–1056. <https://doi.org/10.1016/j.ympev.2013.06.005>
- Alström P, van Linschooten J, Donald PF, Sundev G, Mohammadi Z, Ghorbani F, Shafaeipour A, van den Berg A, Robb M, Aliabadian M, Wei C, Lei F, Oxelman B, Olsson U (2021) Multiple species delimitation approaches applied to the avian lark genus *Alaudala*. Mol Phylogenet Evol 154:106994. <https://doi.org/10.1016/j.ympev.2020.106994>
- Alström P, Gombobaatar S (2021) Mongolian Short-toed Lark (*Calandrella dukhunensis*), version 2.0. In Birds of the World (S. M. Billerman and B. K. Keeney, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.sstlar4.02>
- Andrews S (2010) FastQC: A quality control tool for high throughput sequence data. <http://www.bioinformatics.babraham.ac.uk/projects/fastqc/>
- Archer GF, Godman EM (1961) The Birds of British Somaliland and the Gulf of Aden. Volumes 1–4. Oliver and Boyd, Edinburgh and London, UK
- Beason RC (2020). Horned Lark (*Eremophila alpestris*), version 1.0. In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.horlar.01>
- Bolger AM, Lohse M, Usadel B (2014) Trimmomatic: A flexible trimmer for Illumina Sequence Data. Bioinformatics 30:2114–2120. <https://doi.org/10.1093/bioinformatics/btu170>

- Bradley J (2021). Friedman's Lark (*Mirafra pulpa*), version 2.0. In Birds of the World (Kirwan GM, Keeney BK) (Eds). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow-frilar1.02>
- Britton PL (1980) Birds of East Africa, their habitat, status and distribution. East African Natural History Society
- Clements JF, Schulenberg TS, Iliff MJ, Billerman SM, Fredericks TA, Gerbracht JA, Lepage D, Sullivan BL, Wood CL (2021) The eBird/Clements checklist of Birds of the World: v2021. Downloaded from <https://www.birds.cornell.edu/clementschecklist/download/>
- Darriba D, Taboada G, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nat Methods 9:772. <https://doi.org/10.1038/nmeth.2109>
- Davies GBP (2011) A disputed Botswana specimen of Melodious Lark, *Mirafra cheniana* (Aves: Alaudidae), revisited. Annals of the Ditsong National Museum of Natural History 1:171–179
- de Juana E, Suárez F, Ryan P, Alström P, Donald P (2004) Family Alaudidae (Larks). In: del Hoyo J, Elliott A, Christie DA (eds) Handbook of the Birds of the World, vol 9. Lynx Edicions, Barcelona, pp 496–601
- Dean WRJ, Hockey PAR (1989) An ecological perspective of lark (Alaudidae) distribution and diversity in the southwest-arid zone of Africa. Ostrich 60:27–34. <https://doi.org/10.1080/00306525.1989.9634502>
- Drovetski SV, Raković M, Semenov G, Fadeev IV, Red'kin YA, Mishmar D, (2014) Limited phylogeographic signal in sex-linked and autosomal loci despite geographically, ecologically, and phenotypically concordant structure of mtDNA variation in the holarctic avian genus *Eremophila*. PLoS ONE 9(1):e87570. <https://doi.org/10.1371/journal.pone.0087570.s001>
- Finch BW (2002) In Field Guide to the Birds of East Africa, Stevenson T and Fanshawe J, T & AD Poyser
- Finch BW (2009) Undescribed and unrecognised taxa in East Africa (8) – White-tailed Lark. African Bird Club Forum. <http://www.africanbirdclub.org/phorum/read.php?32,1279>
- Fjeldså J, De Klerk H (2001) Avian endemism in northeastern tropical Africa. Biologiske Skrifter 54:259–271
- Fjeldså J, Alström P, Olsson U, Cibois A, Johansson U (2020) Superfamily Sylvioidea, the Old World warblers and their allies. In: Fjeldså J, Ericson PGP, Christidis L (Eds) The Largest Avian Radiation: The Evolution of Perching Birds, or the Order Passeriformes. Barcelona: Lynx Edicions
- Ghorbani F, Aliabadian M, Olsson U, Donald PF, Khan AA, Alström P (2020a) Mitochondrial phylogeography of the genus *Eremophila* confirms underestimated species diversity in the Palearctic. J Ornithol 161:297–312. <https://doi.org/10.1007/s10336-019-01714-2>
- Ghorbani F, Aliabadian M, Zhang R, Irestedt M, Yan H, Sundev G, Lei F, Ma M, Olsson U, Alström P (2020b) Densely sampled phylogenetic analyses of the Lesser Short-toed Lark *Alaudala rufescens*-Sand Lark *A. raytal* species complex (Aves, Passeriformes) reveal cryptic diversity. Zoolog Scr 49:427–439. <https://doi.org/10.1111/zsc.12422>
- Gill F, Donsker D, Rasmussen P (Eds) (2022) IOC World Bird List (v. 12.1). <https://doi.org/10.14344/IOC.ML.12.1>
- Gouy M, Guindon S, Gascuel O (2010) SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Mol Biol Evol 27:221–224. <https://doi.org/10.1093/molbev/msp259>
- Guillaumet A, Crochet P-A, Godelle B (2005) Phenotypic variation in Galerida larks in Morocco: the role of history and natural selection. Mol Ecol 14:3809–3821. <https://doi.org/10.1111/j.1365-294X.2005.02696.x>
- Guillaumet A, Pons J-M, Godelle B, Crochet P-A (2006) History of the Crested Lark in the Mediterranean region as revealed by mtDNA sequences and morphology. Mol Phylogenet Evol 39:645–656. <https://doi.org/10.1016/j.ympev.2006.01.002>
- Guillaumet A, Crochet P-A, Pons JM (2008) Climate-driven diversification in two widespread Galerida larks. BMC Evol Biol 8:32. <https://doi.org/10.1186/1471-2148-8-32>
- Irestedt M, Ohlson JJ, Zuccon D, Källersjö M, Ericson PGP (2006) Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the Old World suboscines (Aves, Passeriformes). Zoolog Scr 35:567–580. <https://doi.org/10.1111/j.1463-6409.2006.00249.x>
- Meyer M, Kircher M (2010) Illumina sequencing library preparation for highly multiplexed target capture and sequencing. Cold Spring Harb Protoc. <https://doi.org/10.1101/pdb.prot5448>
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA pp. 1–8. <https://doi.org/10.1109/GCE.2010.5676129>
- Moreau RE (1966) The Bird Faunas of Africa and its Islands. Academic Press, London
- Peacock F (2012) The Definitive Guide to South Africa's Little Brown Jobs. Chamberlain's LBJs
- Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.7. Retrieved from <http://beast.bio.ed.ac.uk/Tracer>
- Rambaut A (2016) FigTree v1.4.4. Retrieved from <https://github.com/rambaut/figtree/releases>
- Ryan PG, Bloomer P (1999) The Long-billed Lark complex: a species mosaic in south-western Africa. Auk 116:194–208
- Ryan PG, Hood I, Bloomer P, Komen J, Crowe TM (1998) Barlow's Lark: a new species in the Karoo Lark *Certhilauda albescent* complex of southwest Africa. Ibis 140:605–619
- Ryan P, Sharpe CJ (2020). Williams's Lark (*Mirafra williamsi*), version 1.0. In Birds of the World del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E, (Eds). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.willar1.01>
- Ryan P (2020a) Singing Bushlark (*Mirafra cantillans*), version 1.0. In: Birds of the World del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (Ed). Cornell Lab of Ornithology, Ithaca, NY, USA <https://doi.org/10.2173/bow.sinbus1.01>
- Ryan P (2020b) White-tailed Lark (*Mirafra albicauda*), version 1.0. In: Birds of the World del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (Eds). Cornell Lab of Ornithology, Ithaca, NY, USA <https://doi.org/10.2173/bow.whtlar1.01>
- Ryan P (2020c) Latakoo Lark (*Mirafra cheniana*), version 1.0. In: Birds of the World del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (Eds). Cornell Lab of Ornithology, Ithaca, NY, USA <https://doi.org/10.2173/bow.latlar1.01>
- Ryan P (2020d) Monotonous Lark (*Mirafra passerina*), version 1.0. In: Birds of the World del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (Eds). Cornell Lab of Ornithology, Ithaca, NY, USA <https://doi.org/10.2173/bow.monlar2.01>
- Sinclair I, Ryan P (2010) Birds of Africa south of the Sahara. Struik Nature, Cape Town
- Spottiswoode CN, Olsson U, Mills MSL, Cohen C, Francis JE, Tøye N, Hoddinott D, Dagne A, Wood C, Donald PF, Collar NJ, Alström P (2013) Rediscovery of a long-lost lark reveals the conspecificity of endangered *Heteromirafra* populations in the Horn of Africa. J Ornithol. <https://doi.org/10.1007/s10336-013-0948-1>
- Stervander M, Alström P, Olsson U, Ottosson U, Hansson B, Bensch S (2016) Multiple instances of paraphyletic species and cryptic taxa revealed by mitochondrial and nuclear RAD data for *Calandrella* larks (Aves: Alaudidae). Mol Phylogenet Evol 102:233–245. <https://doi.org/10.1016/j.ympev.2016.05.032>
- Stervander M, Hansson B, Olsson U, Hulme MF, Ottosson U, Alström P (2020) Molecular species delimitation of larks (Aves: Alaudidae), and integrative taxonomy of the genus *Calandrella*, with

- the description of a range-restricted African relic taxon. *Diversity* 12:428. <https://doi.org/10.3390/d12110428>
- Stevenson T, Fanshawe J (2002) *Field Guide to the Birds of East Africa*. T & A. D. Poyser
- Stevenson T, Fanshawe J (2020) *Birds of East Africa, Kenya, Tanzania, Uganda, Rwanda, Burundi*. 2nd edition. Helm Field Guides
- Suchard MA, Lemey P, Baele G, Ayres DL, Drummond AJ, Rambaut A (2018) Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution* 4. <https://doi.org/10.1093/ve/vey016>
- Zimmerman DA, Turner DA, Pearson DJ (1996) *Birds of Kenya and Northern Tanzania*. Russell Friedmann Books

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