Jack of all calls and master of few: vocal mimicry in the Tawny Lark (*Galerida deva*)

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ABSTRACT

Despite its prevalence across bird taxa, avian vocal mimicry remains a poorly studied field of animal behaviour. In order to advance our understanding of the function of avian vocal mimicry, the field requires that the range of vocal mimicry in birds is described. The Tawny Lark (or Sykes's Lark, *Galerida deva*) is endemic to central and western India. Recent work on other *Galerida* larks has found that the mimetic vocalisations match the biodiversity of their acoustic environment, thereby conferring a significant novel function in study of individual mimetic variation linked to biodiversity. Here, we provide a detailed account of the variety of mimetic sounds produced by the Tawny Lark. We also describe acoustic and peer-based analyses that gauge the accuracy of the mimicry. By providing a detailed description of mimicry, we provide a basis for future study of the function of mimicry in this species.

Keywords: vocal mimicry, repertoire, Tawny Lark, *Galerida deva*, larks, acoustic analysis, India, birds

1. INTRODUCTION

Avian vocal mimicry is a widespread phenomenon among birds with numerous intraspecific functions, ranging from mate attraction, discouraging intraspecific competitors, and teaching young to associate heterospecific alarm calls with danger during chick rearing (reviewed in Kelley *et al.*, 2008; Dalziell *et al.*, 2015). However, at present, anecdotal accounts comprise the majority of avian vocal mimicry studies. Thus, progress in the field requires detailed data on mimicry of individual species (Goodale and Kotagama, 2006; Dalziell *et al.*, 2015). In this paper, we provide a detailed description of vocal mimicry in the Tawny Lark (*Galerida deva*) and provide information on several aspects of the species it mimics.

The *Galerida* larks are well-known mimics, composed of six species of crested lark with similar morphological characteristics and display behaviours (de Juana *et al.*, 2004). *Galerida* song is most pronounced during the breeding season, with a peak during the pre-laying stage (Laiolo *et al.*, 2011). Song is often performed during flight, consisting of intermittent bouts of heterospecific (mimicry) or species-specific syllables (Laiolo *et al.*, 2011; Laiolo, 2012). *Galerida* larks are known to vocalise outside of breeding contexts, and will call during conspecific intrusion events and year-round while on territories (Laiolo, 2012). Calls pertaining to territorial defence are given mostly on the ground (Laiolo *et al.*, 2011). Although detailed description of vocal mimicry in some *Galerida* larks does exist (*Galerida cristata* and *Galerida theklae*; Laiolo *et al.*, 2011; Laiolo, 2012), little detailed description exists for any other species in the genus.

The Tawny Lark is a small, crested lark endemic and restricted to central and west-central India, often found in dry and scrubby areas (Ali *et al.*, 1987; Alström, 2004). Although considered to be a close relative of the *Galerida cristata* complex for decades, its taxonomic status remains uncertain with some systematists classifying it in its own genus (Alström *et al.*, 2013). Thus, while the Tawny Lark is currently considered a species of least concern (BirdLife International, 2012), it may be an evolutionarily significant lineage endemic to the Indian sub-continent (Alström *et al.*, 2013). When compared to the song structure of other *Galerida* larks (*G. cristata* and *G. malabarica*) in the Indian sub-continent, Tawny Lark song exhibits more variation in phrase rate with more emphasis on varied phrases rather than whistles (Ali, 1979; Alström, 2004). During the breeding season (March–September), males accompany their song with a flight display that involves slow wing flapping, soaring, and hovering typical of this genus (Ali *et al.*, 1987; Alström, 2004; de Juana *et al.*, 2004). Tawny Lark song is said to be almost identical to the song of the Singing Bush Lark (*Mirafra cantillans*) in sharing a complex flight display accompanied by vocal mimicry (Ali *et al.*, 1987; Alström, 2004).

Studies of other *Galerida* larks suggest that the vocal mimicry repertoires of species in the genus match the diversity represented by their acoustic environment. This thereby suggests a novel function in the study of individual trait variation linked to biodiversity (Laiolo, 2011). Here, we characterise the diversity of heterospecifics mimicked by Tawny Larks, using song data from 16 recordings. We describe the broad range of species mimicked by Tawny

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Lark individuals, using both acoustic and peer-based analyses.

2. METHODS

Tawny Lark flight songs were recorded opportunistically between September 2011 and November 2014 from the same locality in Amreli, Gujurat, India (21.62°N, 71.23°E). A total of 16 recordings were collected, and no recordings were obtained where there was no instance of mimicry. Recordings were made using a Sony ICD-UX512F recorder and self-made microphone setup at a 44.1 kHz sampling rate and 16 bit-depth. The audio files generated were in WAV and MP3 format (see Table S1 and S2). All recordings have been archived in the Macaulay Library of Natural Sounds (www.macaulaylibrary.org). Individuals were recorded by placing the recording device on the ground, and in some instances a parabolic dish was used to aid in localising the sound. Tawny Lark individuals were observed flying vertically from the ground during song. All songs were naturally produced and no playback was used to elicit any vocalisations. Recordings of complete songs were made, as characterised by the bird starting a song that lasted several minutes and then engaging in another activity such as foraging. The recordings were made in a matrix of dry scrub habitat and agricultural land.

Tawny Lark mimetic vocalisations were classified by sound by the recordist (VJ). The recordist was experienced with local species vocalisations and thus was able to match Tawny Lark mimetic sound to a model species. We assessed whether the species mimicked were passerine or non-passerine and resident or migratory. To minimise researcher bias of identification of mimetic vocalisations, we conducted a human assessment experiment based on methods modified from Igic and Magrath (2013). We selected a subset of five model species mimicked by the Tawny Lark (Black Drongo, *Dicrurus macrocercus*; Common Babbler, *Turdoides caudate*; Common Myna, *Acridotheres tristis*; Green Sandpiper, *Tringa ochropus*; and Red-wattled Lapwing, *Vanellus indicus*) based on the availability of good quality Tawny Lark mimetic and model species vocalisations. For each species, we generated four spectrograms of mimetic and model vocalisations using RavenPro 1.5 (Charif *et al.*, 2014). All recordings of Tawny Lark mimetic vocalisations were obtained from the field site. Recordings of model species were obtained from the field site or downloaded from the same region from Xeno Canto (Xeno Canto Foundation, 2012). A matching exercise using the generated spectrograms was presented to 10 researchers with experience analysing spectrograms. The researcher assigned multiple mimetic calls to model species vocalisations based on visual similarities of spectrograms. Spectrograms generated using the vocalisations of the Indian Peafowl (*Pavo cristatus*), a species that was not mimicked by the Tawny Lark, were used as a control.

An acoustic analysis was also performed using mimetic and model vocalisations of three species (Common Babbler, Black Drongo, Red-wattled Lapwing; Figures 1–3). Spectrograms and measurements of Tawny Lark mimetic vocalisations and model species vocalisations were generated using Raven Pro 1.4. The spectrogram settings used a time grid overlap of 96.9% and a resolution of 0.181 ms. The frequency grid resolution was 43.1 Hz with a DFT size of 1024 samples. A Blackman window function was used with a 10 dB clipping level. Spectrogram viewing settings were based on Magrath *et al.* (2007).

Because of the variability between the vocalisations of each species, different variables were assessed for each species in order to best capture the aspects of the vocalisation. For the Common Babbler vocalisations, we assessed element duration (s), element bandwidth (Hz), and the centre frequency of elements (Hz); for the Black Drongo, we assessed the number of elements, element duration (s) and element peak power (dB); and for the Red-wattled Lapwing, we assessed 90% duration of the vocalisation (s), the change in frequency between harmonics (Hz), and the peak power of harmonics (dB). We looked for differences in the measurements between model and mimetic vocalisations using a one-way ANOVA. Statistical analyses were completed using R (R Development Core Team, 2015).

Data on which model species were mimicked by each Tawny Lark individual is provided in Table S3. In addition, the accession numbers for the Macaulay Library recordings for each Tawny Lark individual is provided in Table S1.

3. RESULTS

A total of 34 model species were identified in the mimetic vocalisations of Tawny Larks from 16 recordings (Figures 1–4). Tawny Lark song consisted of bouts of mimicry interspersed occasionally with species-specific vocalisations; however, most of the vocalisations heard in all recordings were mimetic. The maximum number of species mimicked per song varied by individual (Figure 4). Two non-avian mimetic vocalisations were also identified (a shepherd's whistle and Indian Palm Squirrel, *Funambulus palmarum*) in one and four of the recordings, respectively. The passerine *versus* non-passerine and migratory *versus* non-migratory distribution of model species mimicked by the Tawny Lark are as follows: resident passerine ($n = 13$, 38%); migratory passerine ($n = 11$, 32%); resident non-passerine ($n = 7$, 21%); and migratory non-passerine ($n = 3$, 9%; Table S3).

The results from the human assessment experiment revealed a varied ability for researchers to accurately group the model and Tawny Lark mimetic vocalisations. The Common Babbler was correctly grouped $95 \pm 0.03\%$ (mean $\pm$ SE) of the time, the Black Drongo $75 \pm 0.07\%$ of

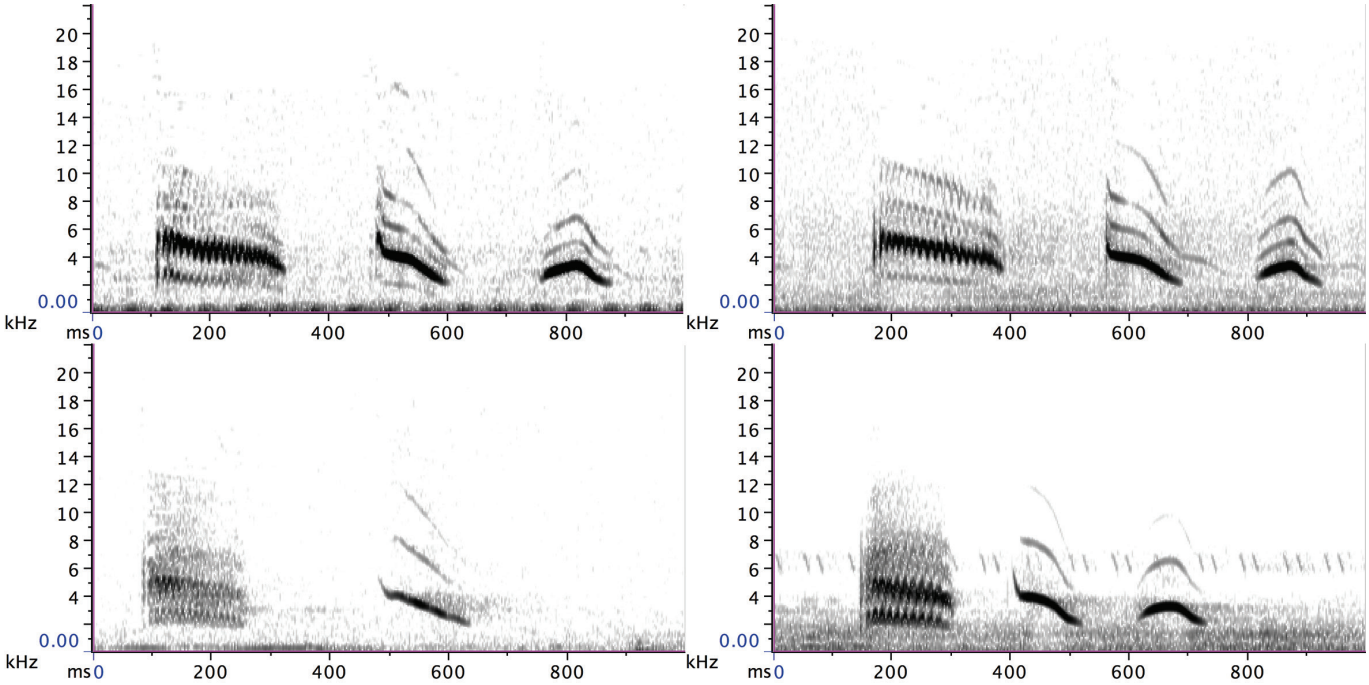

Figure 1 Spectrograms of Tawny Lark mimetic vocalisations of Black Drongo calls (top row) and Black Drongo vocalisations (bottom row) generated in RavenPro 1.5.

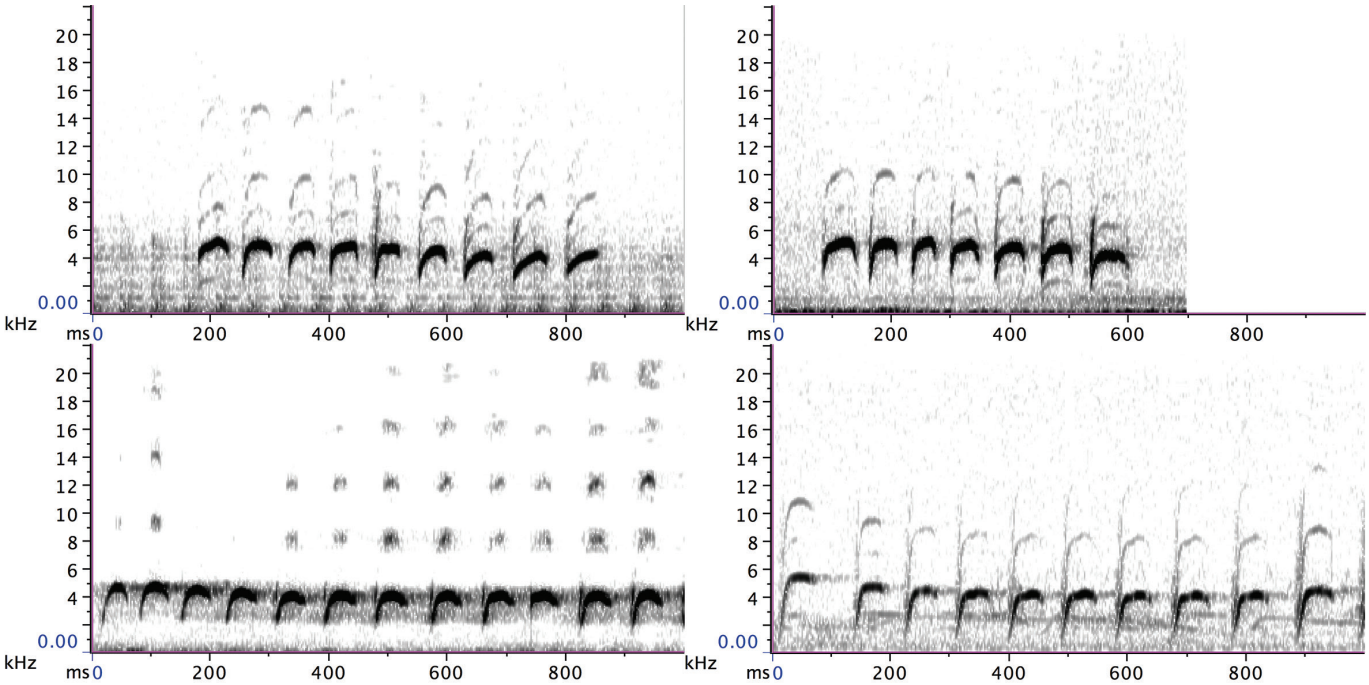

Figure 2 Spectrograms of Tawny Lark mimetic vocalisations of Common Babbler calls (top row) and Common Babbler vocalisations (bottom row) generated in RavenPro 1.5.

the time, the Red-wattled Lapwing 60 ± 0.08% of the time, the Common Myna (*Acridotheres tristis*) 23 ± 0.07% of the time, and the Green Sandpiper 15 ± 0.05% of the time (Figure 5). The control species, the Indian Peafowl, was correctly identified 100 ± 0.00% of the time (Figure 5).

The acoustic analysis of lark mimetic accuracy for the three model species tested varied (Table 1). For the Red-wattled Lapwing, mimetic and model songs differed significantly only in the frequency difference between harmonics 2 and 3, and the peak power at the peak time for the first harmonic. Mimetic and model vocalisations of the Black Drongo differed in duration of the first element, duration of the middle element, and peak power of the first element. For the Common Babbler, mimetic and model vocalisations did not differ significantly in any variable tested (Table 1).

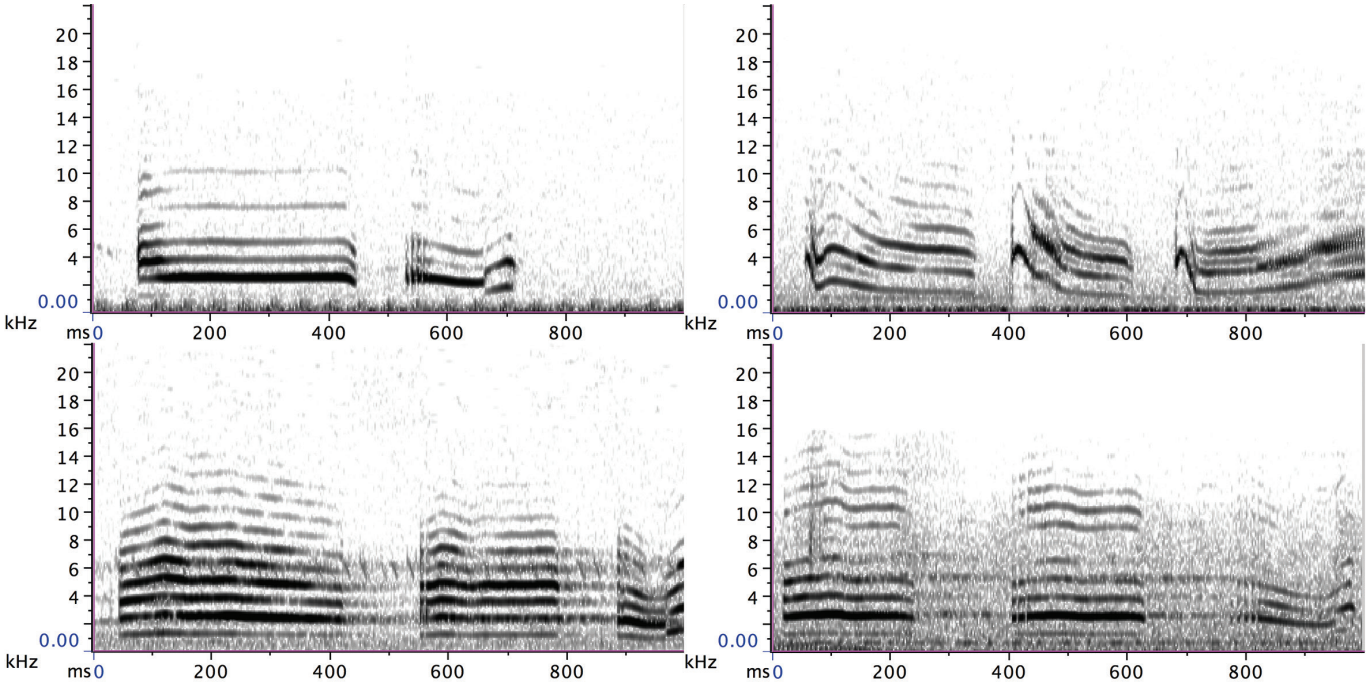

Figure 3 Spectrograms of Tawny Lark mimetic vocalisations of Red-wattled Lapwing calls (top row) and Red-wattled Lapwing vocalisations (bottom row) generated in RavenPro 1.5.

Table 1 Acoustic analysis to measure the accuracy of Tawny Lark mimicry. The table shows comparisons of call elements between model and mimetic vocalisations for three commonly mimicked species: Black Drongo, Red-wattled Lapwing, and Common Babbler

Acoustic Variable	*F* value	*P*
Black Drongo, *Dicrurus macrocercus* (*n*, mimic = 4, model = 4)		
Number of elements	0	1
Duration of the first element (s)	137.743	<0.01**
Duration of the middle element (s)	20.118	0.05*
Peak power of the first element (dB)	128.454	<0.01**
Peak power of the middle element (dB)	0.371	0.60
Red-wattled Lapwing, *Vanellus indicus* (*n*, mimic = 6, model = 9)		
Duration of the entire vocalisation (s)	1.001	0.34
Change in frequency between first and second harmonic (Hz)	2.168	0.18
Change in frequency between second and third harmonic (Hz)	8.236	0.02*
Peak power at the peak time for first harmonic (dB)	19.611	<0.01**
Peak power at the peak time for second harmonic (dB)	1.004	0.35
Peak power at the peak time for third harmonic (dB)	4.134	0.08
Common Babbler, *Turdoides caudata* (*n*, mimic = 4, model = 4)		
Duration of the first element (s)	1.908	0.40
Duration of the last element (s)	0.009	0.94
Bandwith (90%) of the first element (Hz)	2.643	0.35
Bandwith (90%) of the last element (Hz)	0.301	0.681
Centre frequency for the first syllable (Hz)	0.255	0.70
Centre frequency for the last syllable (Hz)	1.806	0.41

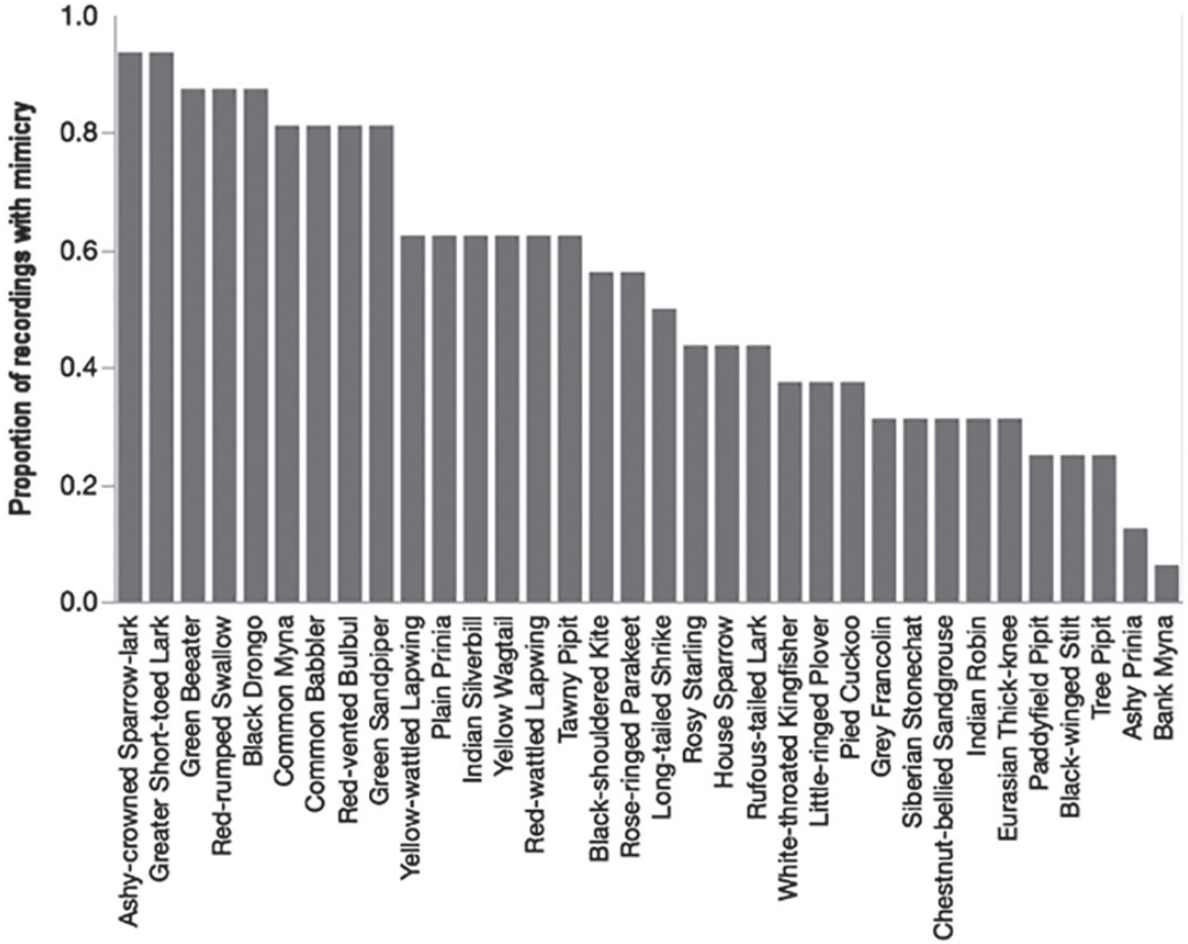

Figure 4 The proportion of Tawny Lark recordings ($n = 16$) with each mimicked species. Please refer to Table S3 for a detailed list of the model species mimicked during each recording.

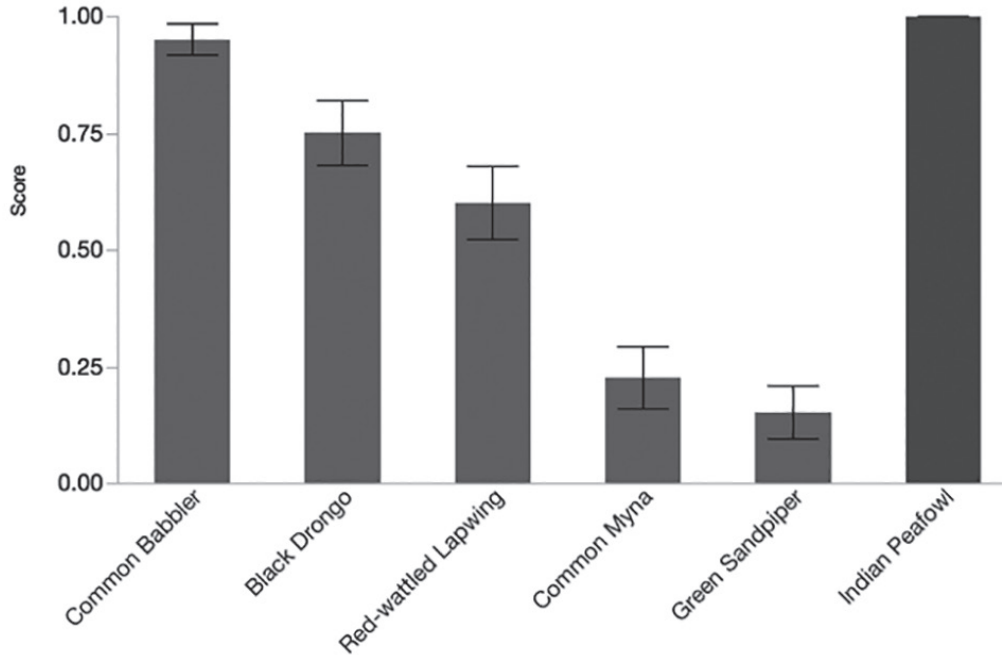

Figure 5 The mean accuracy of grouping of model species vocalisations and Tawny Lark mimetic vocalisations from a matching exercise conducted by human researchers ($n = 10$). Bars represent standard error.

4. DISCUSSION

We provide a detailed description and analysis of avian vocal mimicry in the Tawny Lark and associated species mimicked in 16 recordings of Tawny Lark song. Two independent acoustic analyses confirm that Tawny Larks mimic sympatric species with varied accuracy.

Tawny Larks mimic resident and migratory, as well as passerine and non-passerine, species. Thus, their mimetic repertoires include a wide taxonomic and ecological subset of avian taxa that occur in their acoustic environment. The most commonly mimicked species (the Ashy-crowned Sparrow-lark, present in 15 of 16 recordings) is a common species occupying the same habitats as Tawny Larks. The other commonly-mimicked species are also common open-country species, and hence likely regularly encountered by the Tawny Lark. Frequency of mimicked calls may be a function of sympatric species relative abundance. We were, unfortunately, unable to assess the relative abundance of other taxa within Tawny Lark habitat. Similarly, good quality recordings of only some mimicked taxa from the region were available, limiting our assessment of all model species.

A visual examination of the mimetic *versus* model vocalisations supports that some mimetic vocalisations match those of the model species relatively accurately (at least from a human perspective) while other mimetic vocalisations differed in structure. The acoustic analysis reveals that Tawny Lark mimetic calls are statistically indistinguishable from several acoustic variables of Common Babbler calls. Mimetic calls of Black Drongos and Red-wattled Lapwings also did not differ significantly in several acoustic variables. Notably, Common Babbler mimicry that was correctly classified by human observers with the highest accuracy was also statistically indistinguishable in acoustic variables from that of model species songs. The variables with diminished mimetic accuracy help to identify the limitations of the mimetic abilities in Tawny Larks and the extent of selection for their mimetic accuracy. Limitations on ability to mimic species may be driven by the Tawny Lark's evolutionary relationships with mimicked species, as 70% of the species mimicked are passerines (Zollinger and Suthers, 2004). We do not know whether the accuracy of mimicry is a sexually selected trait among *Galerida* larks; however, this genus is an ideal system to examine the sexual function of mimetic accuracy. Little sexual differences in plumage exist in this group, and hence inter-male differences in fitness can be more convincingly attributed to differences in mimetic accuracy and repertoire. Future research should emphasise the study of inter-individual variation in the accuracy of their mimicry, perhaps to shed more light on the function of mimicry in this taxon.

Moreover, while the species has been reported to be locally common, the grassland and scrub habitats of the Tawny Lark have seen extensive conversion to agricultural land-use practices in the past few decades (Singh *et al.*, 2009). Recent urbanisation has further altered the habitat and species composition of their native range considerably, and thus the future conservation of this species remains closely tied to the conservation of its grassland scrub habitats (Singh, 2009). The culmination of these circumstances calls for more comprehensive research to achieve a better understanding of this poorly-studied endemic Indian songbird. Further study of the Tawny Lark would provide an excellent opportunity to advance our understanding of the function of avian vocal mimicry, and the link of mimicry repertoire to the biodiversity of an area.

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6. ELECTRONIC SUPPLEMENTARY INFORMATION

The ESI, Tables S1, S2 and S3, is available through stl.publisher.ingentaconnect.com/content/stl/abr/supp-data/content-abr1700786_esi.

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