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Vocalizations and seasonal variation in singing and aerial displays of the Short-clawed Lark *Certhilauda chuana*

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Abstract

The southern African endemic Short-clawed Lark *Certhilauda chuana* is listed as 'Least Concern' globally. As a result of its highly localized distribution in South Africa, it is regarded as a species of conservation concern. It is afforded legal protection in all three provinces in which it is found. Its calls are distinctive and a valuable aid to correctly identify the species for monitoring purposes. However, descriptions of the various calls are ambiguous in some publications, and the existence of local dialects complicates the correct identification of the species. Here we report on the vocal repertoire and annual variation in vocalizations and displays of Short-clawed Larks from the species eastern population. The vocal repertoire comprises of three categories and seven types of vocalizations: song (including a territorial and display flight song by males only), contact-type calls (including agitated, alarm and nestling feeding calls) and nestling calls (distress and begging). Each male has a limited territorial song repertoire of only 3–6 'signature' phrases. The limited number of phrases facilitates recognition of neighbours and strangers for a resident, territorial species such as Short-clawed Lark. Vocalizations and aerial display frequency peaked 1–3 hours after sunrise in the peak (December) and late (March) breeding seasons. Knowledge about the vocal repertoire and seasonal variation in the frequency of the different vocalizations and aerial display flights will be valuable from an atlasing point of view and for designing a monitoring protocol for the species.

Keywords: Short-clawed Lark, *Certhilauda*, Alaudidae, vocalizations, calls, aerial display, 'dear neighbour', dialects
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Short-clawed Lark is a resident southern African endemic with a disjunct distribution. A large population in eastern Botswana and the adjacent North West and Northern Cape Provinces in South Africa represent the species' western population. A smaller population restricted to the Polokwane Plateau in South Africa's Limpopo Province represents an isolated eastern population. Despite its local and global conservation status of 'Least Concern' (Engelbrecht and Grosel 2015; Birdlife International 2021), Short-clawed Lark is generally regarded as a species of conservation concern in South Africa. Both the eastern and western populations in South Africa are afforded protection under provincial legislation as a Schedule 2 'Specially Protected Wild Animal' (Limpopo Environmental Management Act, Act No. 7 of 2003), a Schedule 2 'Specially Protected Species' (North West Biodiversity Management Act, Act No. 4 of 2016), and a Schedule 2 'Protected Species' (Northern Cape Nature Conservation Act, Act No. 9 of 2009).

It is an enigmatic species, and at one stage, it had the dubious distinction of being southern Africa's least known lark species (Maclean 1985a). This accolade may have been attributed to its highly localized distribution within its range, incorrect descriptions of vocalizations, behavioural, morphological and plumage characteristics in some publications, and the fact that the species has relatively few distinguishing features to aid correct identification (Clancey 1985; Maclean 1985a; Sinclair 1987; Robertson 1991; Dean and Keith 1992; Herremans 1997). Since Maclean's (1985a) statement, Herremans and Herremans (1992), Herremans et al. (1994), Duvivier (2005), Engelbrecht (2005), Engelbrecht et al. (2007), Brewster et al. (2010) and Engelbrecht et al. (2021a) investigated various aspects of the species ecology, highlighting features that may aid correct identification.

Herremans and Herremans (1992) and Engelbrecht (2005) found males are territorial and defend territories throughout the year. In the Polokwane Game Reserve, one male occupied the same territory for more than 15 years, from 2005 to 2021 (Engelbrecht 2021). Although males remain in the same territory year after year, a breeding pair usually divorces at the end of the breeding season (March to June), with females dispersing in search of a new mate for the forthcoming breeding season (Engelbrecht 2005).

Once Short-clawed Lark's vocalizations and its characteristic aerial display flight are known, it is easy to locate and identify. However, most of our present knowledge of the vocalizations of Short-clawed Larks is based on anecdotal observations and phonetic descriptions of its various calls, some descriptions being incorrect (see Maclean 1985a; 1985b). Although several authors cite a paper by Hustler (1980), this paper cannot currently be found anymore and was therefore not included in this paper. To complicate matters further, Herremans and Herremans

(1992), Duvivier (2003; 2005) and, more recently, Engelbrecht et al. (2021) showed distinct dialects within the species western and eastern meta-populations. These dialects exist in the absence of any significant geographical barriers, and the boundaries of different dialects are still poorly known. Thus, there is a clear need for a detailed description of the type and structure of Short-clawed Lark vocalizations. Such information combined with knowledge of the annual variation in singing and displays of males would greatly facilitate the correct identification of the species. It would also be valuable for any conservation management plan or monitoring programme involving the species. Here we report on the type and structure of vocalizations and annual variation in vocalizations and displays of Short-clawed Larks from the species' eastern population.

METHODS

Vocalizations

Recordings of vocalizations were obtained from various sites on the Polokwane Plateau in the Limpopo Province, South Africa, from 2005 to the present (see Appendix 1). Digital recordings were made with a Marantz PMD670 or PMD661 MKIII Professional digital recorder and a Sennheiser ME66 or ME67 directional microphone.

We used the definitions of Catchpole and Slater (2008) to describe the units of vocalizations. An element is the simplest unit and is defined as a continuous line on a sonogram. A syllable is more complex and comprises two or more elements lasting a few hundred milliseconds. Several syllables grouped together form a phrase, while songs constitute phrases repeated in a variable or repetitive sequence.

The Raven 1.6 software package was used for call analyses and to create sonograms (Center for Conservation Bioacoustics 2019). The number of elements, duration (ms), lowest, highest and delta frequencies (kHz) were measured for each phrase in territorial song and contact calls. Detailed analyses of agitated calls were not possible as these vocalizations showed too much variation in the structure of syllables and phrases.

Seasonal variation in vocalizations and aerial display flights

This aspect of the study was conducted in the Polokwane Game Reserve (-23.94, 29.47, 1 300 m above sea level). The number of songs (territorial and agitated), contact calls and aerial display flights of six territorial males were recorded at 3-monthly intervals between June 2005 and March 2006. The four intervals correspond with the non-breeding season (June), early-breeding season (September), peak-breeding season (December) and late-breeding season (March). Display flights were recorded as single-, double- or triple-displays in a single flight. All display flights end with the single-note display song.

The six territorial males were observed for six days in each season. Each territory was visited on a rotational basis for 2-hourly intervals from 06:00–18:00 on each day. Thus, data were collected at all six territories on any particular day. The order in which the territories were visited was alternated daily. Therefore, at the end of the 6 -day observation period, data were obtained for all six, 2-hourly intervals on separate days for each individual. Data were only collected on days with similar weather conditions, i.e., no over-cast conditions, strong wind, rain or excessively cold or warm conditions, using a vehicle as a hide. The data are presented in hourly intervals.

Statistical analyses were performed with SPSS Version 26.0 software package.

RESULTS

Vocalizations

The vocal repertoire of Short-clawed Lark can be assigned to three categories representing seven types of vocalizations:

1. Song

1.1 Territorial song (males only): A single element or series of clear, high-pitched, drawn-out whistles delivered from a perch (e.g., Engelbrecht D, XC675342. Accessible at www.xeno-canto.org/675342; Engelbrecht D, XC675353. Accessible at www.xeno-canto.org/675353).

1.2 Display song (males only): A single element delivered towards the end of a display flight (e.g., last note in Engelbrecht D, XC675378. Accessible at www.xeno-canto.org/675378; last note in Engelbrecht D, XC675371. Accessible at www.xeno-canto.org/675371).

2. Contact-type calls

2.1 Contact calls, including alarm calls (both sexes): A single or series of clear whistles, lower-pitched than territorial calls. These calls range from contact calls between a pair described as a drawn-out *peeeu* (e.g., Engelbrecht D, XC675385. Accessible at www.xeno-canto.org/675385) to a more urgent alarm call to warn of impending danger - *pip-peeu-peeu, peeu-weeu* (e.g., Engelbrecht D, XC675388. Accessible at www.xeno-canto.org/675388).

2.2 Agitated call (both sexes, mainly males): A mixed warble of harsh raspy elements and syllables: *ree-teee-ree–tee-kreee-oooo* (e.g., Engelbrecht D, XC675383. Accessible at www.xeno-canto.org/675383; Engelbrecht D, XC675384. Accessible at www.xeno-canto.org/675384).

2.3 Chattering call (male only): a rapid chattering call (https://youtu.be/LoXQSh2eO1c).

3. Nestling calls

3.1 Nestling distress call (nestlings and recently fledged young): A single, short, harsh and grating call.

3.2 Nestling begging call (nestlings and fledged young): A short, high-pitched *peep* call (https://youtu.be/8EFxveQM7rQ).

We recorded 502 territorial song phrases (n = 20 individuals), 13 display songs (n = 11 individuals), 34 contact phrases (n = 6 individuals), 126 agitated call phrases (n = 13 individuals), 2 chattering calls from the same individual, 25 nestling distress calls (n = 2 individuals) and nestling begging calls at a single nest. No vocal mimicry was recorded in this study.

Territorial song

Territorial songs were delivered by males only and were characterized by high-pitched, clear elements of either an ascending, descending or a constant frequency (Fig. 1). Phrases were given in relatively quick succession with a mean pause duration of 4.70 ± 2.36 s (range: 1.36–31.23, n = 480) between successive phrases.

Territorial songs were delivered from the ground or, more commonly, from a prominent perch such as a bush, fence post or termite mound. This type of song covered a broad frequency range (2 033.80–8 666.60 Hz) since the individual elements in a phrase were delivered over a range of frequencies. A brief, sometimes barely audible introductory note may or may not be included in a phrase (Fig. 1). Short-clawed Lark territorial song on the Polokwane Plateau comprised 1–7 elements, averaging 2.42 ± 1.17 (n = 502). However, if the western and eastern dialects on the Polokwane Plateau are separated, the territorial song of males from the west of the plateau average significantly more elements than birds from eastern regions of the plateau (western: 2.64 ± 1.47 elements per phrase, range: 1 –7, n = 169; eastern: 2.30 ± 0.97 elements per phrase, range: 1–6, n = 333; Mann-Whitney U-test = 3 1240.0, P = 0.026). Furthermore, the territorial song of birds representing the western dialect is more 'musical' compared to birds singing the eastern dialect. The number of elements in a phrase and their relative contribution to the total number of perched territorial phrases recorded is presented in Table 1. Single element territorial songs of Short-clawed Lark males averaged 0.89 ± 0.15 s (range: 0.53–1.30, n = 115), while 2-element phrases averaged 1.29 ± 0.27 s (range: 0.85–2.02, n = 166), 3-element phrases 1.79 ± 0.36 s (range: 1.21–1.79, n = 156), 4-element phrases 1.82 ± 0.40 s (range: 1.08–2.32, n = 48), 5-element phrases 1.67 s (n = 1), 6-element phrases 2.04 ± 0.06 s (range: 1.99–2.21, n = 11) and 7-element phrases averaged 2.48 ± 0.03 s (range: 2.45–2.51, n = 5).

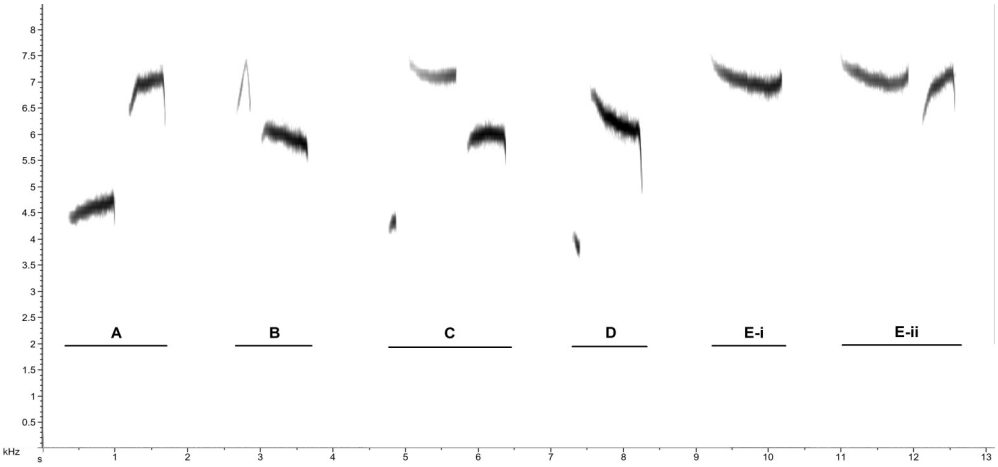

Figure 1. A collection of the five territorial song phrases of a single Short-clawed Lark male. Note the introductory notes of phrases B to D. Phrase E-ii was interpreted as the alternative expression of this individual's more common phrase E-i.

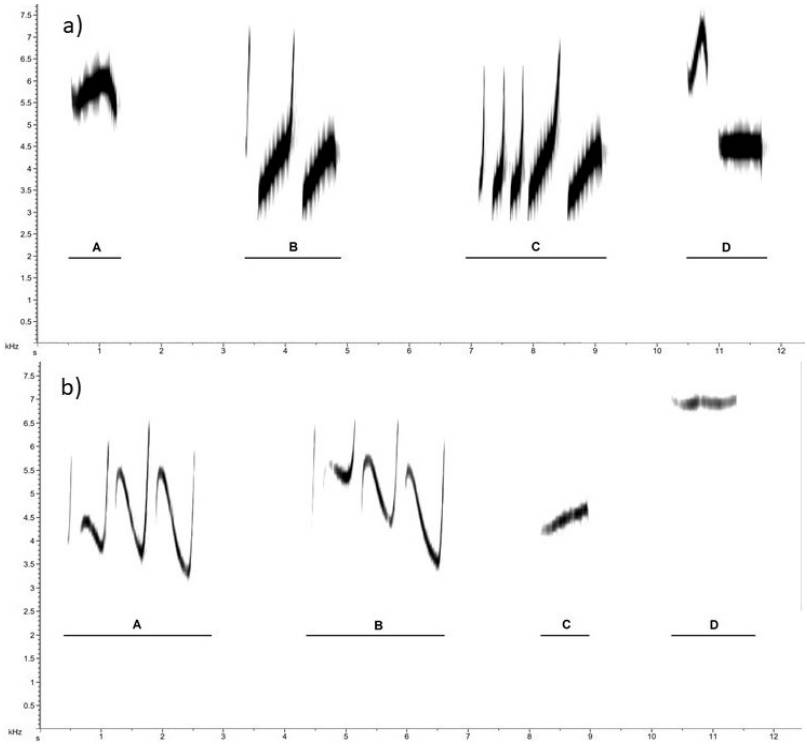

Figure 2. Four territorial song phrases of two males: a) is a sonogram of a male representing the eastern dialect and b) a male representing the western dialect on the Polokwane Plateau. The more musical nature of the western dialect is visible in these sonograms.

Despite the great variety of territorial song phrases recorded in this study, each male possessed a limited number of 3–6 unique or 'signature' phrases (n = 17 males where a minimum of 2 minutes of continuous recording during a territorial call bout was obtained; e.g., Engelbrecht D, XC675519. Accessible at www.xeno-canto.org/675519; Engelbrecht D, XC675342. Accessible at www.xeno-canto.org/675342; Fig. 2). Some elements/phrases of an individual showed minor deviations from the 'standard' signature elements/phrases (Fig. 1E-i and E-ii). Each individual's unique phrases are repeated in a seemingly random pattern, sometimes with slight variation in the frequency of some elements and the presence or absence of a short introductory note. Sequences of 20 consecutive phrases of five males are presented in Table 2.

Display song

The flight display song was a single element of relatively constant frequency lasting 1.04 ± 0.07 s (range: 0.96–1.13 s, n = 13). It was delivered during the last part of an ascent and the descending phase of an aerial display flight. The mean frequency of display calls was 6 163.71 ± 1 832.49 Hz (n = 13). However, there appear to be two types of display flight calls: a high-frequency display call averaging 7 334.64 ± 152.23 Hz (n = 9) and a lower frequency display call averaging around 3 529.13 ± 49.14 Hz (n = 4).

Contact calls

Both sexes called contact calls, and it usually consisted of a single drawn-out note or a clear phrase with 2–4 elements ($\bar{x}$ = 2.56 ± 0.82 s, n = 34) (Fig. 3). Contact calls were delivered along a gradient ranging from contact calls between a foraging pair or the unhurried calls when a potential threat was first noticed (e.g., Engelbrecht D, XC675385. Accessible at www.xeno-canto.org/675385) to more urgent alarm calls when the level of threat escalated (e.g., Engelbrecht D, XC675388. Accessible at www.xeno-canto.org/675388). There were, however, some minor variations in this type of call. For example, on rare occasions, a trill was introduced in the contact call (DE, pers. obs.). An individual recorded at Ditenteng on the western edge of the Polokwane Plateau had an unusual contact call showing significant frequency modulation (see Fig. 3). Contact calls were delivered in a frequency range of 1 727.7 to 3 978.3 Hz, making this category of vocalizations the lowest in the frequency range of Short-clawed Lark. It was not always possible to identify the sex reliably, and the contact call data were therefore pooled for analysis.

Table 1. The number of elements in phrases of the territorial song of Short-clawed Lark males from the Polokwane Plateau. The relative contribution of each type of phrase to the total number of phrases recorded is presented in parenthesis.

Number of elements	*n* of calls	*Relative contribution (%)*	*n individuals*
1	115	22.9	18 (85.7%)
2	166	33.1	19 (90.5%
3	156	31.1	16 (76.2%)
4	48	9.5	5 (23.8%)
5	1	0.2	1 (4.8%)
6	11	2.2	2 (9.5%)
7	5	1.0	1 (4.8%)
Total	502	100%	

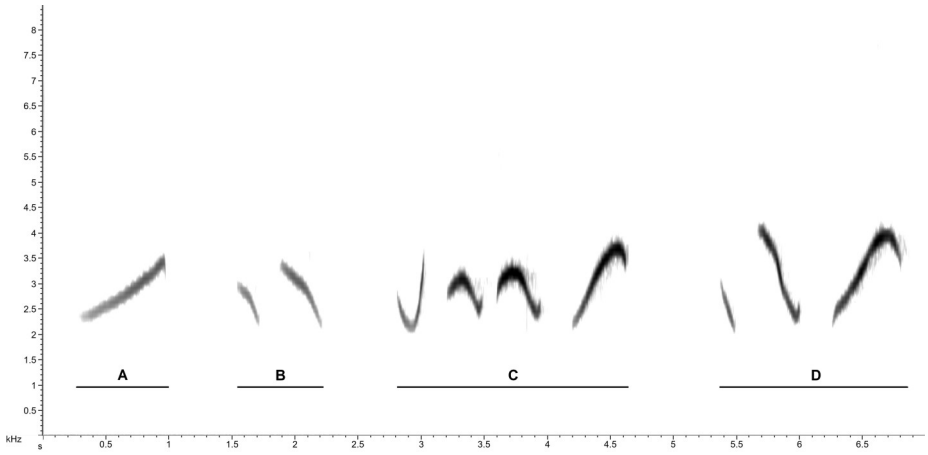

Figure 3. Contact calls of Short-clawed Lark on the Polokwane Plateau. A and B are typical contact calls, but C and D were unusual contact calls of a bird at Ditenteng on the western plateau.

Table 2. Sequences of phrases in territorial song bouts of five Short-clawed Lark males on the Polokwane Plateau. All five territorial song sequences included a minimum of 2 minutes of continuous recording. Each letter represents a unique phrase for an individual. Note that a letter of one individual is different from the same letter of another individual, e.g. A in #4 is not the same as phrase A in any other individuals.

Locality	Sequences of 20 consecutive territorial call phrases																			
Polokwane	A	B	C	A	D	A	B	E	B	C	D	A	B	C	A	B	A	C	E	B
Papkuil	A	B	C	B	D	B	D	D	B	C	B	D	B	D	B	C	D	B	A	B
Moletzie	A	B	D	B	C	E	C	A	B	D	B	E	C	A	B	D	B	C	E	C
Dikgale	A	E	E	E	E	B	C	D	B	C	B	E	C	D	E	C	B	E	C	C
Kgwareng	A	B	C	B	A	D	C	B	E	A	D	E	A	D	C	A	D	C	D	E

Agitated calls

This type of vocalization was delivered in different contexts. It may be a contact call, but it is sufficiently distinct from other calls to warrant its recognition as a separate call. It was frequently associated with aggressive intraspecific encounters between males or when a male performed sentinel duties near an active nest. Both sexes also called a slightly muted and attenuated agitated call to stimulate nestlings to gape for food (see https://youtu.be/L8t2sL8P2ss). As a result of the small sample size for the nestling feeding version of the agitated call, no further analyses of this type of call were performed.

Agitated calls were characterized by a rapid series of pulsed elements, e.g., trills, syllables, and clear whistles of varying duration, frequency and intensity (Fig. 4). These calls were produced over a broad frequency range of 1 908.8 and 7 501.2 Hz (n = 20 agitated calls bouts of different males) with brief pauses between successive phrases ($\bar{x}$ = 8.40 ± 10.66 s, range: 1.37—71.07, n = 112). The duration of individual agitated call phrases (excluding the nestling feeding agitated call) ranged from 0.69 to 3.21 s ($\bar{x}$ = 1.53 ± 0.42 s, n = 126). The mean number of syllables in an agitated call phrase was 5.44 ± 1.58 notes (range: 2-–10, n = 126). Like the territorial song, there was also considerable individual variation in the structure of agitated call phrases concerning the number and placement of pulsed elements, syllables, clear whistles, and the duration of the different elements and syllables within a phrase. There was also evidence that each individual possessed a suite of unique elements and syllables arranged in a different order in phrases, resulting in a tremendously varied repertoire for this call. As a result of the complex configuration of elements and syllables in agitated call phrases and the extensive variation within and between individuals, no attempt was made to analyze individual notes in agitated call phrases statistically.

Chattering call

This call was heard on two occasions when nesting behaviour was recorded on video (https://youtu.be/LoXQSh2eO1c). In both instances, a male performed the chattering call and delivered it just before the termination of a brooding bout. Its purpose is not known, but it may represent an alternative expression of the agitated call.

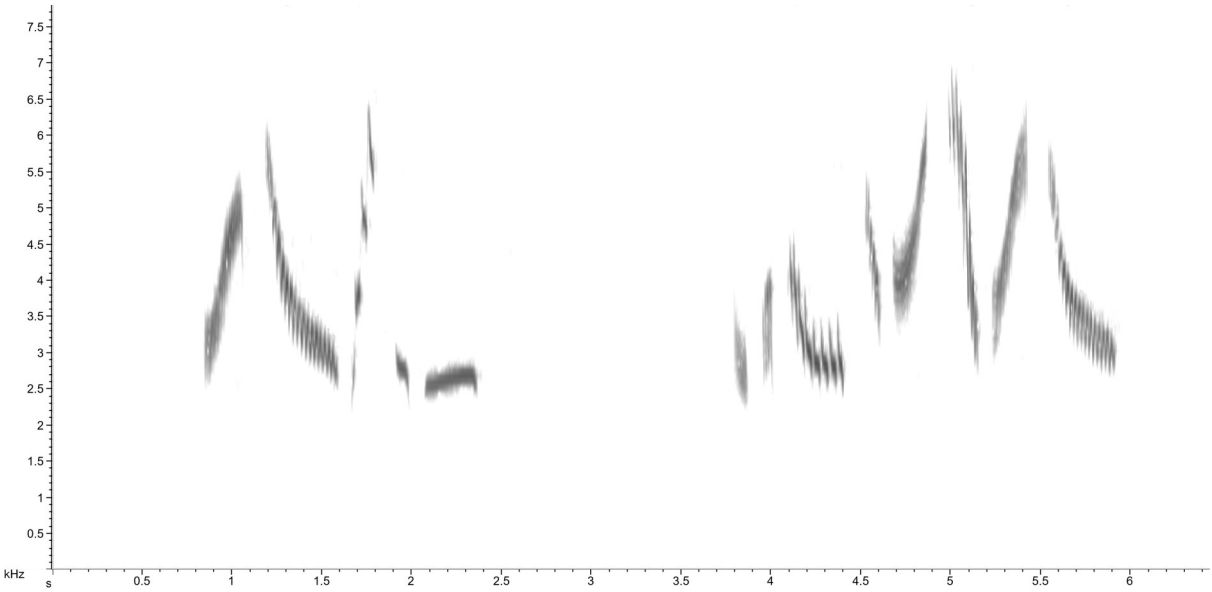

Figure 4. Two agitated call phrases of a Short-clawed Lark showing the frequency modulation, trills and whistles typical of this call.

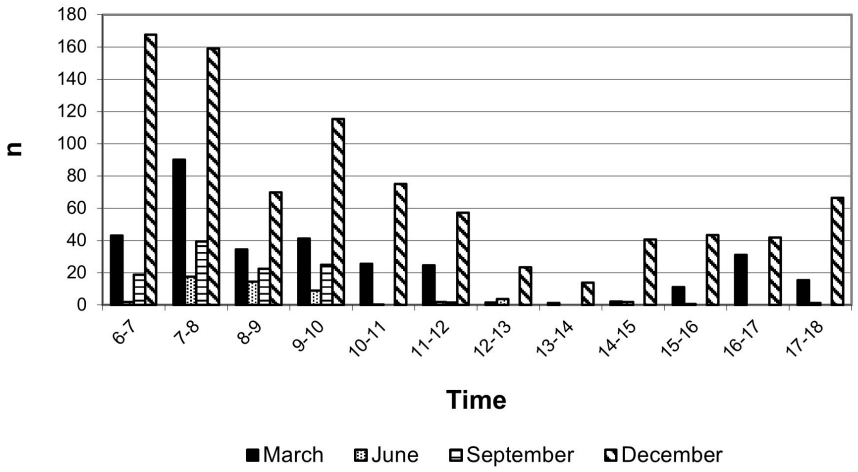

Figure 5. Annual variation in the mean frequency of territorial song of Short-clawed Lark males.

Nestling calls

Two types of nestling calls were recorded. The begging call is a soft *peep* and was heard after a parent called the nestling feeding call (see agitated calls above) and during feeding (e.g., see https://youtu.be/8EFxveQM7rQ). Distress vocalizations were produced by nestlings, usually only when handled. This type of call consisted of a short, piercing vocalization of a relatively constant frequency. Vocalizations were recorded from two individuals in a single nest. The results of the variables analyzed are presented in Table 3.

Seasonal variation in the frequency of vocalizations and display flights

Vocalizations

The annual variation in the mean number of territorial songs, contact calls and agitated calls of Short-clawed Lark males is presented in Figs. 5–7. As the sunrise and sunset times may affect activity levels in different seasons, the sunrise and sunset times during data collection were as follows: March (05:58 and 18:31), June (06:37 and 17:23), September (06:14 and 17:51) and December (05:06 and 18:35).

Territorial singing was recorded throughout the year, but the average number of territorial song phrases per day peaked in December ($\bar{x}$ = 873.50 ± 190.13; range: 637–1094) and was lowest in the non-breeding season, i.e. June ($\bar{x}$ = 52.83 ± 38.44; range: 5–96) (Fig. 5). In all seasons, territorial singing peaked within 2 hours after sunrise and gradually decreased during the day (Fig. 5). Another smaller peak in territorial singing was evident in the late afternoons in December and March (Fig 5).

Contact calls were recorded throughout the day in all seasons but were most frequent within the first 2 hours after sunrise (Fig. 6). The mean daily number of contact calls was highest in December ($\bar{x}$ = 193.17 ± 80.50; range: 105–312) and lowest in March ($\bar{x}$ = 68.83 ± 34.63; range: 19–100).

Agitated calls were recorded throughout the year but peaked in March ($\bar{x}$ = 463.5 ± 160.89; range: 301–762) and were lowest in June ($\bar{x}$ = 50.5 ± 15.54; range: 32–77) (Fig. 7). The highest mean number of agitated call phrases delivered per hour were recorded in March ($\bar{x}$ = 71.50 ± 41.28; range: 10–113; between 06:00 and 07:00). Although agitated calls peaked in the early morning in all seasons, this pattern was not as apparent as it was with territorial singing (Fig. 7).

Displays

A total of 504 display flights were observed during the study period. The relative frequency of single display flights was 95.6%; for double display flights, it was 4.2%; and only a single triple display flight (0.2%) was recorded during the study. Seasonal variation in the frequency and timing of

Table 3. Nestling distress call variables of Short-clawed Lark (n = 25 calls). DT = delta time (ms), LF1 = lowest frequency (kHz), HF1 = highest frequency (kHz), DF1 = delta frequency (kHz).

	Mean	SD	Range
DT	0.16	0.04	0.12–0.27
LF	3.13	0.24	2.20–3.41
HF	4.09	0.30	3.08–4.47
DF	0.95	0.18	0.54–1.25

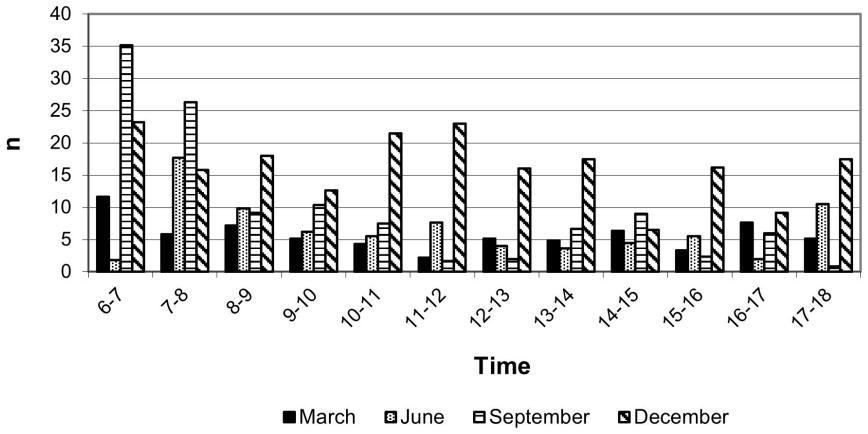

Figure 6. Annual variation in the mean frequency of contact calls (including alarm calls) of Short-clawed Larks.

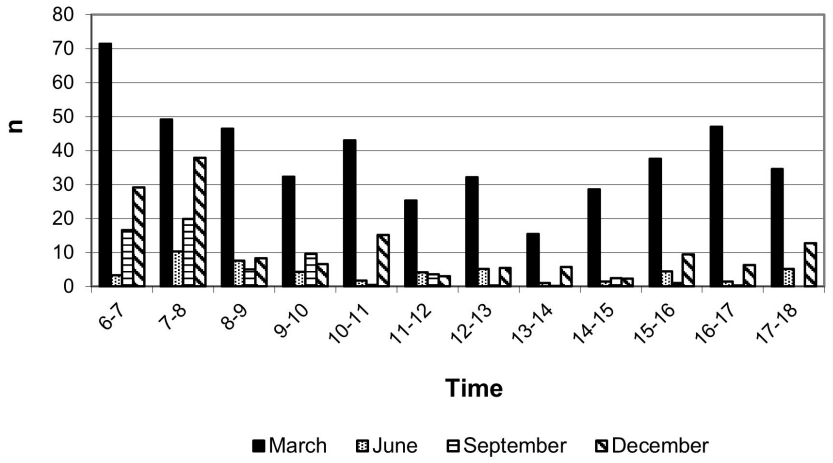

Figure 7. Annual variation in the mean frequency of agitated call bouts of Short-clawed Larks.

single display flights performed by males over the four seasons is presented in Fig. 8. Display flights were performed throughout the year but peaked in December ($\bar{x}$ = 58.5 ± 9.97 display flights per day; range: 41–68), and was lowest in June ($\bar{x}$ = 1.83 ± 1.83; range: 0–4). The frequency of displays was greatest 1–3 hours after sunrise in all seasons (Fig. 8). In December, display flights were recorded throughout the day, but mainly in the morning in the other seasons. The daily and seasonal frequency of double display flights followed the same pattern as single display flights (Fig. 9). Except for one individual, all males were observed performing double-display flights. The single triple display flight was recorded in December between 09:00 and 10:00 by the same male that also executed the most double-display flights (*n* = 7) during the study.

DISCUSSION

Vocalisations

In many respects, the species' vocalizations are similar to the vocalizations of other *Certhilauda* larks (*cf.* Hockey *et al.* 2005). No vocal mimicry was recorded in this study, confirming the general notion that species in the Long-billed Lark (*Certhilauda* spp.) complex do not exhibit heterospecific vocal mimicry. Short-clawed Lark vocalizations are somewhat stereotyped, consisting of only two categories of vocalizations in adults, song and contact-type calls, each with subtypes. There are two subtypes of song: territorial and display flight songs. Contact-type calls are varied and include contact calls ranging from unvarying, gentle contact calls between a pair such as during foraging, to a more urgent alarm type of contact call when there is a potential threat.

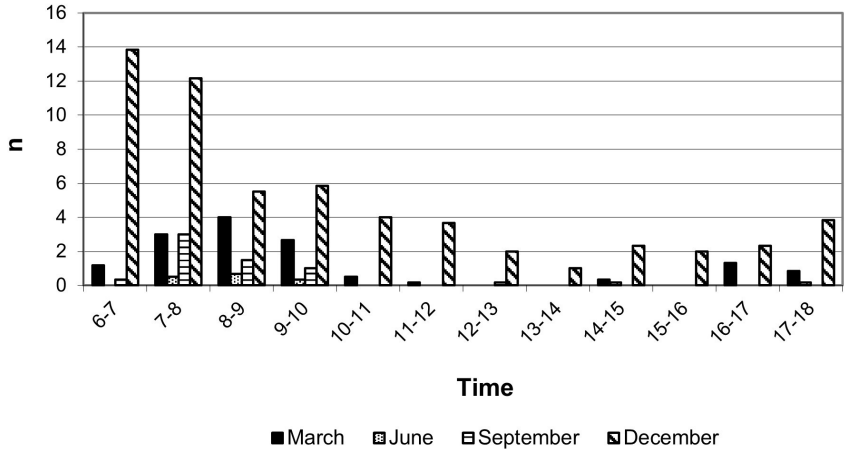

Figure 8. Mean number of single display flights of Short-clawed Lark males over four seasons.

Another contact-type call is an agitated call. This call appears to be an all-purpose call. It was associated with aggressive intraspecific interactions between males, sentinel duties near an active nest, or to stimulate nestlings to gape for food. Lastly, an uncommon chattering call was recorded twice during video recording of nesting behaviour.

Maclean's (1985b) description of Short-clawed Lark vocalizations appears to be its alarm call (*pip peeu peeu, peeu weeu*) and agitated call (*wip peee prrr pip peet pree*). No mention is made of the territorial song of the species unless it is included under '… other clear whistles'. Moreover, Maclean (1985b) also described a *kwert kwert* and *krerr krerr krerr* alarm call of Short-clawed Larks. This call has never been described in other literature, nor was it ever heard during field studies.

Engelbrecht et al. (2021) reported dialectal differences in territorial song in the eastern population of the species. The territorial song of males on the western Polokwane Plateau are more 'musical' and complex than the stereotypical, simpler territorial songs of males from the plateau's eastern regions. Herremans and Herremans (1992) and Duvivier (2005) studied Short-clawed Lark in Botswana and noted dialectal differences across insignificant geographical barriers such as ridges and bush-encroached hills. According to Herremans (2005), the territorial songs of males in northeastern Botswana are more complex and melodious and are characterized by a 'rapid series of pleasant whistles' (e.g., Herremans M, XC667444. Accessible at www.xeno-canto.org/667444). This description seemingly fits the western dialect of the species eastern population in the Limpopo Province (see Engelbrecht et al. 2021). Furthermore, according to Herremans (in litt.) and Duvivier (2005), the territorial song of the southwestern and south-central populations in Botswana is more monotonous with fewer syllables (e.g., Herremans M, XC667441. Accessible at www.xeno-canto.org/667441). This description matches the territorial song of birds on the eastern Polokwane Plateau.

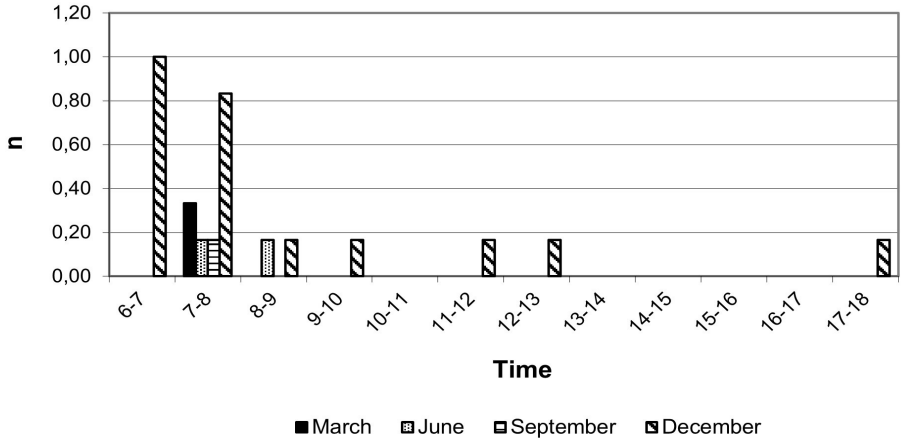

Figure 9. Mean number of double display flights of Short-clawed Lark males over four seasons.

Interestingly, the territorial songs of Short-clawed Lark on the eastern Polokwane Plateau are more similar to the songs of males at Botsalano (nearly 400 km to the west in the North West Province, South Africa) than they are to males a mere 8 km away on the western Polokwane Plateau (Engelbrecht et al. 2021). In addition to dialectal differences in territorial song, Herremans (in litt.) also noted dialectal differences in the alarm notes of the northeastern (with trills, e.g. Herremans M, XC667448. Accessible at www.xeno-canto.org/667448) and southwestern (without trills, e.g., Herremans M, XC667447. Accessible at www.xeno-canto.org/667447) populations in Botswana. Trilled contact (including alarm) calls were uncommon in this study. Still, it would be interesting to obtain more recordings and map their distribution to determine if they coincide with the plateau's two territorial song dialects.

The seemingly similar dialectal differences in territorial songs evident over weak geographic barriers on a local scale (i.e. northeastern vs southwestern Botswana, and western Polokwane Plateau vs eastern Polokwane Plateau) appear to be maintained over large geographical distances with more substantial geographic constraints (i.e. northeastern Botswana and western Polokwane Plateau vs southwestern Botswana and eastern Polokwane Plateau). That the territorial songs and alarm calls of males from northeastern Botswana and the western Polokwane Plateau are similar (or the same) but differ from populations south of Ranaka-Ntlhantlhe in southwestern Botswana and the eastern Polokwane Plateau, may open a taxonomic can of worms. Such a scenario may suggest the existence of two cryptic species. The recent discovery of an isolated population at Bojanala, south-east of Pilanesberg in the North West Province (Engelbrecht and Grosel 2019), added another level of complexity to the dialectal conundrum. Alarm calls from this population are trilled and resemble alarm calls of the northeastern dialect in Botswana (e.g., Perrins N, XC493148. Accessible at www.xeno-canto.org/493148).

The propensity for establishing and maintaining dialects in a sedentary species such as Short-clawed Lark is not surprising. Although males are territorial and defend their territories throughout the year, Marr et al. (2016) showed the habitat in occupied territories can become unsuitable within 2–3 years if grazing, browsing or fire are withheld. Conversely, unsuitable habitat can become suitable within a relatively short period if open savannah is created through wood harvesting for fuel, frequent fires to reduce grass cover, clearing of bush for crop farming or poor land management practices such as overgrazing. Thus, populations can expand their ranges if suitable conditions are created, either naturally through drought, grazing/ browsing by herbivores or as a result of human activities such as subsistence agriculture. If conditions become unsuitable, ranges may contract, leaving sub-populations isolated and setting the scene for the establishment of dialects. Should the populations be isolated for a sufficient period, this may cause genetic drift and ultimately speciation. Therefore, it is conceivable that the dialects in Short-clawed Lark may result from one or more historic or prehistoric bottlenecks caused by range expansions and contractions. The results of this study highlight an urgent need for comprehensive analyses of Short-clawed Lark vocalizations and genetic relationships of individuals representing the different dialects. Should the dialects have a taxonomic basis and represent cryptic species, some of these populations would require urgent conservation action. They are almost wholly confined to rural subsistence farming areas and may also have small ranges.

The present study recorded territorial songs throughout the year, albeit at very low frequencies in the non-breeding season. According to Herremans and Herremans (1992) and Engelbrecht (2005), territorial singing increases in the pre-breeding season and peaks in the primary breeding season. Although the frequency of territorial singing increased slightly between June and September in this study, it was still well below the frequencies recorded in the peak breeding season. The apparent anomaly between this study and Herremans and Herremans (1992) and Engelbrecht (2005) may be attributed to interannual variation in the onset of breeding in the eastern population. For example, in the 2016/17 breeding season, laying in the first nest of the season commenced 54 days (DE, unpublished data) after the northern solstice; in the 2002/2003 and 2003/2004 breeding seasons, it was 101 and 106 days respectively (Engelbrecht 2005), and in the 2005/2006 season, it was 129 days (the latest date for the onset of breeding in this population to date; DE, unpublished data). In this study, territorial song frequencies were recorded during the first week of September of the 2005/2006 breeding season, and the slight increase observed suggests recordings may have been made in the early stages of the pre-breeding season in that year.

The present study confirms Engelbrecht's (2005) findings that Short-clawed Larks occupy permanent territories that they advertise by singing and defending against rivals throughout the year, albeit at a much-reduced frequency during the non-breeding season. These findings are not entirely unexpected in a highly territorial species such as the Short-clawed Lark. In many species, including the Short-clawed Lark, non-breeding or unmated birds may become 'floaters' in a population when resource availability constrains the number of suitable breeding territories an area can support (Engelbrecht 2005; Penteriani et al. 2011). Such floaters or territory-prospecting males present a threat to resident territorial males and elicit appropriate territorial defence behaviour. Many territorial species exhibit tolerance towards conspecific neighbours, termed the 'dear enemy' effect, but respond strongly to the intrusion of conspecific strangers, e.g., floaters or males from distant territories (Temeles 1994). Neighbouring males will tolerate one another if they recognize specific visual or auditory cues, e.g., certain song phrases, in their neighbour's vocal repertoire.

This study revealed Short-clawed Lark males possess a limited number of 'signature' territorial song and agitated call phrases.

For example, the number of unique territorial phrases of 17 males for which a minimum of two minutes of continuous recording was obtained ranged from three to six, with a mean of 4.4 unique phrases. Even when delivered in an infinite combination of sequences, a small number of signature phrases would be instantly recognizable to neighbours. A male giving an unrecognized territorial song or agitated call phrase will be regarded as a threat to the territory holder and elicit a strong response. However, this truce between neighbours may be flexible and depend upon the stage of the breeding cycle and the spatial position of the calling bird, as was demonstrated in the Skylark *Alauda arvensis* (Briefer et al. 2008, 2009, 2011).

Many social, environmental and intrinsic factors determine when and for how long an individual or species will participate in the dawn chorus (Hutchinson 2002; Bruni et al. 2014). The dawn chorus may serve several purposes: attracting a mate, mate guarding, territory defence against rival males, or advertising territory occupancy. Following this 'reassertion' period, aerial displays and territorial singing gradually decreased as the males started foraging for the next 60–90 minutes. A second peak in aerial displays and vocalizations followed this foraging period (Figs. 5–8), but this was not as prominent as the first and gradually decreased as ambient temperatures increased. During the hottest part of the day, the birds generally foraged or sought shelter from the heat. There was a third increase in territorial singing and aerial displays towards the late afternoon in the breeding season.

Short-clawed Larks generally foraged during the first hour after sunrise, and contact calls dominated vocalizations at this time (Fig. 6). Unlike the other calls, contact calls were recorded at a relatively constant frequency throughout the day in all seasons. This may be an artefact of the sampling strategy as the contact call is associated with an alarm note (Engelbrecht 2005). Upon arrival at a given territory for data recording, both sexes usually delivered the contact call for varying periods to warn of impending danger. The peak-breeding season (December) showed the highest mean daily frequency of contact calls. This seasonal peak in contact calls may partially be attributed to active breeding in three territories when the data were recorded. Adults are vigilant and wary when breeding and give alarm calls at regular intervals when faced with a potential threat.

The daily number of agitated call phrases showed a distinct peak in March, i.e., the late-breeding season. Engelbrecht (2005) noted that the late-breeding season coincides with increased excitement levels. The increased frequency in agitated calls in late summer may be due to i) immature birds gaining independence and starting to leave their natal territories, ii) adult pairs that are still actively breeding, or iii) non-breeding females starting to disperse (Briefer et al. 2008; Engelbrecht 2014). The pair-bond in Short-clawed Lark usually dissolves at the end of the breeding season. Females then disperse from that season's nesting territory, searching for a new mate for the forthcoming breeding season (Engelbrecht 2005; Engelbrecht 2014). The frequency of agitated calls also showed an increase in the peak-breeding season as males called during aggressive territorial disputes or while guarding their mates during foraging and nest construction, courtship or while performing sentinel duties while a female was incubating.

Display flights

Species in the Long-billed Lark complex, which includes the Short-clawed Lark, are perhaps best known for their characteristic and spectacular display flights. Herremans *et al*. (1994) described the aerial display flight as a vertical ascent followed by a stall between 5 and 20 m high and a near-vertical, nose-dive descent with closed wings and a fanned tail while the male calls a drawn-out whistle. In our opinion, a typical display flight is better described as a male flying approximately 1 m above the ground for 10–60 m, then ascending steeply with wings closed to a height of 6–10 m, followed by a steep descent with the wings still closed and the tail fanned out. The display flight is almost invariably associated with a drawn-out call (i.e. the flight song) lasting about 1 s and produced during the last quarter of the ascent and during the descent. Following the descent, the male may land on the ground, alight onto a prominent perch or proceed to perform another display flight. The distance between the start and end of the parabolic phase of the display flight is usually 30–35 m, occasionally more, particularly during windy conditions.

Herremans *et al.* (1994) noted an association between the height of the display flight and the average height of trees in a given territory; males in regions with tall trees having higher display flight apexes - sometimes exceeding 20 m. We did not attempt to relate tree height to the display flight apex in the present study, but casual observations show the display flight apex height of Short-clawed Lark on the Polokwane Plateau consistently falls within the 6–10 m range. Our observations agree with the description of Robertson (1991) for birds observed north of Zeerust: '… suddenly rose vertically to a height of no more than ten metres …'.

This study showed single display flights dominate on the Polokwane Plateau while triple display flights are scarce. Interestingly, incidental observations of display flights of males at Botsalano Game Reserve in South Africa's North West Province suggest that double-and triple-display flights are considerably more common in the western population of the species (DE, pers. obs.). Robertson's (1991) description '… before levelling out and flying low over the grass, repeating the ascent/descent pattern' of males north of Zeerust (and representing the western meta-population) suggests repeat-display flights are common in that region. Herremans *et al.* (1994) also reported double-, triple- and even quadruple-display flights by males in south-eastern Botswana.

Engelbrecht (2005) reported that only certain males in the Polokwane Game Reserve regularly performed multiple

display flights and suggested this may be related to the individual fitness of males. However, the possibility also exists that the number of display flights may be linked to tree cover in an individual's territory. Double-and triple-display flights usually require more than 100 m of open terrain to execute. A dense tree cover may impose constraints on the ability of a male to perform multiple display flights. Thus, the number of display flights a male can perform may be constrained by the vegetation and geographical structure of his territory. In turn, this may be directly related to an individual's fitness; fit males are better able to occupy and defend large territories to perform multiple display flights and improve their chances of attracting a female.

Management implications

The results support the evidence provided by Engelbrecht et al. (2021) that there exist local dialects in the eastern population of the species. Knowledge of the extent of variation in calls will facilitate the monitoring of the species. It is vital to improving the geographic coverage of recordings of Short-clawed Lark vocalizations to delineate the geographic boundaries of these dialects for both the Polokwane Plateau population and the larger western population in Botswana and the North West Province. Given the distribution patterns of these dialects in both the western and eastern meta-populations, DNA analysis of representatives of the different dialects will improve our understanding of gene flow, or its absence, in populations of this species and whether these dialects may have a genetic basis. The results also showed promise to use territorial songs and agitated calls for individual identification of males. Although Short-clawed Larks vocalize and display throughout the year and during most parts of the day, most vocalizations and displays peak 1–3 hours after sunrise in the peak-breeding season (December). From a management perspective, this would be the best time to perform monitoring surveys for this species without using playback. Alternatively, we found that alternating short bouts of playback (particularly of its song) with more extended periods of listening in suitable Short-clawed Lark habitat will also elicit a response from a resident male. Still, the response may be variable and may require repeated visits to confirm presence or absence. Therefore, the results obtained are valuable for monitoring programmes and conservation of this localized species of conservation concern in South Africa.

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Dedication

This paper is dedicated to the memory of my dear co-worker Joe Grosel, who sadly passed away while this paper was under review. Joe was the initial inspiration for me to start a life-long passion for studying Short-clawed Lark. Together, we spent years and travelled thousands of kilometres in search of Short-clawed Larks to unravel the life history secrets of this enigmatic lark.

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Appendix 1. Sampling localities for Short-clawed Lark vocalisations on the Polokwane Plateau