

## CHAPTER 4

# Vocalisations and aerial displays of the Short-clawed Lark *Certhilauda chuana*

### INTRODUCTION

The Short-clawed Lark is an endemic resident species of southern Africa. It has a disjunct distribution with a large western population largely restricted to south-eastern Botswana and adjacent provinces in South Africa, and a smaller, isolated population on the Polokwane Plateau in South Africa's Limpopo Province. It is an enigmatic species and at one stage it had the dubious distinction of being southern Africa's least known lark species (Maclean 1985b). This may partly be attributed to its highly localised distribution within its range, incorrect descriptions of vocalisations, behavioural, morphological and plumage characteristics in some publications, and the fact that the species has relatively few distinguishing characteristics to facilitate correct identification (Clancey 1985; Maclean 1985a; Sinclair 1987; Hustler, 1985; Robertson 1991; Dean & Keith 1992; Herremans 1997; Engelbrecht *et al.* 2007). Since Maclean's (1985b) statement, Herremans and Herremans (1992), Herremans *et al.* (1994) and more recently Engelbrecht (2005) studied aspects of the biology of the species and highlighted behavioural patterns that may aid correct identification.

The studies by Hustler (1985), Hunter (1991), Herremans & Herremans (1992) and Engelbrecht (2005) revealed that the species is sedentary, and once its vocalisations and/or characteristic aerial display flight is known, it is easy to locate and identify. Most of our present knowledge of the vocalisations of Short-clawed Larks is based on anecdotal

observations and phonetic descriptions of the species' various calls. Some of the descriptions are incorrect (Maclean 1985a;1985b) whereas others are based on unpublished data (Hockey *et al.* 2005) or an unpublished manuscript, i.e. Hustler (1980), which could not be traced. Thus, there is a clear need for a detailed description of the type and structure of Short-clawed Lark vocalisations. Such information combined with knowledge of the annual variation in singing and display of males would greatly facilitate correct identification of the species and it would be valuable for any conservation management plan involving the species. This study thus reports on the type and structure of vocalisations and the annual variation in singing and displays of Short-clawed Larks from the species' eastern population.

## MATERIALS AND METHODS

### ***Vocalisations***

For the purposes of this study, the vocalisations of the Short-clawed Lark were be categorized as follows:

- i. Territorial call (males only): The call can be described as a high-pitched, slow, drawn-out whistle comprised of 1 - 4 notes.
- ii. Agitated call (males only): A mixed warble of harsh raspy calls – *ree - teee - ree – tee - kreee – oooo*.
- iii. Contact call (both sexes): Can be interpreted as an alarm call to warn of incumbent danger – *pip-pee-u-pee-u, pee-u-wee-u* or a drawn-out *peee-u*.
- iv. Nestling distress call (nestlings and recently fledged young): This call is a single short, harsh note.

Recordings of vocalisations were obtained from various sites on the Polokwane Plateau in the Limpopo Province, South Africa (Table 4.1). Digital recordings were made with the aid of a Marantz PMD670 Professional digital recorder and a Sennheiser ME66 directional microphone. An estimate of quantitative variation in vocalisations was made by measuring the following variables for each call:

- i. The number of notes in a call,
- ii. Duration or delta time (DT) measured in milliseconds (ms),
- iii. Lowest frequency (LF) measured in kilohertz (kHz),
- iv. Highest frequency (HF) measured in kHz, and
- v. Delta frequency (DF), i.e. frequency range (kHz) of a call.

All call analyses were performed using the Raven 1.2 software package. For territorial calls, the duration (ms), lowest, highest and delta frequency (kHz) was measured for each individual note in a call as described by Lloyd *et al.* (1996). This could not be done for contact and agitated calls as these vocalisations showed too much variation in the structure of phrases.

### ***Frequency of singing and aerial display flights***

This aspect of the study was conducted in the 3200ha Polokwane Nature Reserve (23°58'S, 29°28'E). The frequency of singing (territorial, agitated and 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).

The aerial display flight, performed mainly during the breeding season is described by Herremans *et al.* (1994) as a vertical ascent followed by a stall at between 5 and 20m high and a near-vertical, nose-dive descent with closed wings and fanned tail. The wings are only opened again just before the bird alights. The descent is usually accompanied by a very high-pitched whistling call. In some cases, second or third display flights are performed in immediate succession. Display flights were thus recorded as single, double and triple displays.

The six territorial males were observed for 2-hourly intervals each over a 12-hour period from 06:00 – 18:00 for six days. Thus, data was collected at all six territories on any particular day. The order in which the territories were visited was alternated daily so that by the end of the 6-day observation period, data was obtained for all six 2-hourly intervals on separate days for each individual. Data was only collected on days with similar weather conditions, i.e. no over-cast conditions, strong wind, rain or excessively cold or warm conditions. Data was collected from a vehicle towards the edge of known territories. The data is presented in hourly-intervals.

All statistical analysis was performed with SPSS Version 14 (Norusi 1994) software package. Only individuals for which more than four calls were recorded were included in the statistical analysis. The Kruskal–Wallis was used to indicate whether significant differences occurred in various call variables recorded between individuals within the two populations.

## RESULTS

### ***Vocalisations***

Recordings of the different vocalisations were obtained from 25 adult individuals and two nestlings in a single nest. A total of 317 territorial notes, 171 agitated calls, 105 contact calls and 25 nestling calls were analysed.

### ***Territorial calls***

Territorial calls are produced by males only and are characterised by high-pitched clear notes of ascending, descending or a constant frequency (Fig. 4.1). Territorial vocalisations constitute two types of calls, namely a display and a perched call. The display call is a single note of relatively constant frequency produced during the descending phase of an aerial display. Only two display calls were recorded during the study. These display calls had a mean duration of 0.89s and a mean minimum, maximum and frequency range of 6.82kHz, 7.36kHz and 0.54kHz respectively.

Perched territorial calls are either produced from the ground (rarely) or more commonly, from a prominent perch on vegetation or a termite mound and comprise 1 - 4 notes. Only two 4-note territorial calls were recorded from a single individual. The total duration of these two calls was 2.81 and 2.93 seconds respectively. Due to the small sample size the 4-note calls were omitted from any further statistical analyses. Table 4.2 presents the number of single-, double- and triple-note calls and their relative contribution to the total number of territorial calls recorded.

Descriptive statistics for single note variables analysed for individuals within the eastern population are presented in Table 4.3. Significant differences (Kruskal-Wallis test = 13.45,  $d.f. = 4$ ,  $P < 0.05$ ) were obtained for the duration of the note for the eastern population, but

not for any of the other parameters analysed (Table 4.3). The results of the double- and triple-note territorial call variables analysed are presented in Tables 4.4 and 4.5. respectively. The structure of plural-note territorial calls showed considerable individual variation within and between individuals. Consequently, the Kruskal-Wallis test showed significant differences ( $P = <0.05$ ) between individuals for all the variables analysed (Tables 4.4 and 4.5).

### ***Agitated calls***

Agitated calls are also produced by males only. It is characterised by a rapid series of pulsed notes and clear whistles of varying duration, frequency and intensity. A sonogram of a typical agitated call is presented in Fig. 4.2. This call is generally associated with increased levels of excitement, e.g. aggressive encounters, or when a female is foraging nearby. The number of notes in a phrase ranged from 3 - 13 notes ( $\bar{x} = 5.69 \pm 1.46$ , range = 3 - 13). As with territorial calls, there was also considerable individual variation in the structure of agitated calls with regard to the number and placement of pulsed notes and clear whistles within a phrase. The Kruskal-Wallis test showed significant differences ( $P < 0.05$ ) between individuals for all the agitated call parameters analysed. Therefore, no attempt was made to analyse individual notes in agitated call phrases statistically.

### ***Contact calls***

These calls are produced by both sexes and consist of a single drawn-out note or a clear phrase with 2 - 4 notes that can be ascending, descending or remain relatively constant in frequency (Fig. 4.3). It was not always possible to identify the sex reliably and the contact call data was pooled for analysis. The summary statistics for contact calls are presented in Table 4.6. The Kruskal-Wallis test revealed significant differences ( $P < 0.05$ ) between individuals in contact calls for all the variables analysed.

### ***Nestling distress calls***

Distress vocalisations were produced by nestlings, usually only when handled. This type of call consisted of a short, shrill vocalisation of a relatively constant frequency. Calls were recorded from two individuals in a single nest. Short-clawed Lark nestlings are not known to have any other calls, e.g. soliciting calls. The results of the variables analysed are presented in Table 4.7.

### ***Frequency of singing and display***

The variation in the mean number of territorial, agitated and contact calls over a year is presented in Fig 4.4a-c. In order to account for some of the seasonal variation in calls, the sunrise and sunset times in the study area during the study period is presented in Table 4.8. Short-clawed Larks showed seasonal as well as daily variation in the frequency of the three kinds of vocalisations. Territorial calls were recorded throughout the year, albeit at low frequencies outside the breeding season, i.e. June and September (Fig. 4.4a). Territorial singing peaked 1 - 2 hours after sunrise in all seasons and gradually decreased during the day (Fig. 4.4a). A second, smaller peak in territorial singing was evident in the late afternoons in December and March (Fig 4.4a).

Contact calls were recorded throughout the day in all seasons (Fig 4.4b). The highest mean frequency of contact calls was recorded between 06:00 and 07:00 in September ( $\bar{x} = 35.17 \pm 16.88$ ; range: 15 – 63). The mean daily frequency of contact calls was highest in December ( $\bar{x} = 16.42 \pm 5.10$ ) and lowest in March ( $\bar{x} = 5.74 \pm 2.40$ ).

Similarly, the highest mean frequency of agitated calls was recorded between 06:00 and 07:00 in March ( $\bar{x} = 71.50 \pm 41.28$ ; range: 10 – 113), but it was recorded at a low frequency

throughout the year (Fig 4.4c). Although agitated calls showed a peak in the early morning in all seasons, this pattern was not as obvious as in territorial calls (Fig. 4.4c).

A total of 504 display flights were recorded during the survey. The frequency of single display flights were 95.6%, for double display flights it was 4.2% and only a single triple display flight (0.2%) was recorded during the study. Figure 4.5 presents the number of single display flights performed by males over the four seasons. Although display flights were recorded in all four seasons, it reached its highest frequency 1 - 2 hours after sunrise in the peak-breeding season (December). Display flights were recorded throughout the day in December, but generally only in the morning in the other seasons. The daily and seasonal frequency of double display flights followed the same pattern as for single display flights, i.e. it peaked early in the morning in December. The single triple display flight was performed in December between 09:00 and 10:00.

## DISCUSSION

### ***Vocalisations***

The vocalisations recorded in the present study correspond with the descriptions of the territorial, agitated and contact calls of the species described in Hockey *et al.* (2005). Short-clawed Lark vocalisations are fairly simple and stereotyped consisting of only three types of calls in the adult. The species' calls comprise either clear whistles, pulsed notes or a combination of these, similar to the territorial calls of species in the Long-billed Lark *Certhilauda* spp. complex as mentioned by Ryan and Bloomer (1999). Herremans & Herremans (1992) reported small dialectal differences in the calls of individuals across small geographical barriers such as ridges. However, the extent of individual variation in the calls



of males from the eastern population made it impossible to recognise any dialects. In the present study, individuals in the Polokwane Nature Reserve showed just as much variation in their calls within the reserve as between individuals recorded at various sites elsewhere on the Polokwane Plateau. The results of the present study therefore suggest that the extent of individual variation in calls will mask the identification of any dialects. Nevertheless, despite the marked individual variation in territorial calls it remains a reliable aid in identification and is often the first indication of the presence of the species.

Maclean's (1985a) description of Short-clawed Lark vocalisations appear to be that of the alarm and agitated calls of the species and no mention is made of the territorial call of the species, unless it is included under "... other clear whistles". Moreover, Maclean (1985a) also described a *kwert-kwert* and *krerr-krerr-krerr* alarm call of Short-clawed Larks. This description is clearly erroneous as this call has never been described in other literature and was never heard during field observations. This call's description is more likely to be that of the Rufous-naped *Mirafra africana* or Sabota Lark *Calendulauda sabota*. Hockey *et al.* (2005) described the territorial call of males as long, hoarse whistles or a rapid series of pleasant whistles. This description is open to interpretation but does not accurately describe the drawn-out plaintive whistle or series of 2 - 4 clear notes of males recorded in the present study.

A characteristic of the Short-clawed Lark that was observed throughout the current study and which has not previously been described as an identification feature for this species is the black inner "mouth" which is clearly visible when the birds call. This feature was particularly prominent in calling territorial males but was also observed in female birds as shown in Fig. 1.1.

In the present study territorial calls were recorded throughout the year albeit at very low frequencies in the non-breeding season (Fig 4.4a). According to Herremans & Herremans (1992) and Engelbrecht (2005), territorial calls start to increase in the pre-breeding season and peak between the latter part of September to December, i.e. the main breeding season. During the present study, the frequency of territorial singing showed a slight increase between June and September, but was still well below the frequencies recorded for the peak breeding season. This can be attributed to a later start to the breeding season during this study when compared with that of Engelbrecht (2005). In two consecutive seasons of observations, Engelbrecht (2005) first found eggs 101 and 106 after the northern solstice, compared with 129 days in the present study. Furthermore, in the present study the data was collected in the first week of September and the slight increase observed indicates that the survey may have been conducted in the very early stages of the pre-breeding season.

The frequency of territorial calls and aerial displays peaked 1 - 2 hours after sunrise (Fig 4.4a and 4.5). Following this “advertising” period, aerial displays and territorial singing gradually decreased as the males started foraging for the next 60 - 90 minutes. A second increase in aerial displays and territorial calls was evident after this foraging period Fig 4.4a). The second morning peak in territorial singing 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. In the breeding season, there was a third increase in territorial calling towards the late afternoon.

Short-clawed Larks generally forage during the first hour after sunrise and the most commonly heard call during that time was the contact call (Fig. 4.4b). Unlike with 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. Upon arrival at a given territory for data recording, both sexes usually

uttered the contact call for varying periods to warn of impending danger. Thus, this may partly explain the relatively high frequency of this type of call in all four seasons. The peak-breeding season (December) showed the highest mean daily frequency of contact calls. This may be explained by active breeding in three of the territories at the time the data was recorded. Adults are extremely alert and wary when breeding and will give contact calls at regular intervals particularly when both adults are foraging and feeding nestlings.

The daily frequency of agitated calls showed a clear peak in March, i.e. the late-breeding season. Engelbrecht (2005) noted that the late-breeding season coincides with increased levels of excitement as fledglings disperse from their natal territories and adult birds divorce at the end of the breeding season. The high mean daily frequency of agitated calls can therefore be attributed to dispersal of juveniles and divorce of breeding pairs. The peak-breeding season also showed a relatively high frequency of agitated calls. This is to be expected during the breeding season as males attempt to settle territorial disputes or accompany females while foraging.

### ***Display Flight***

Species in the Long-billed Lark complex, which includes the Short-clawed Lark, are perhaps best known for their characteristic and spectacular display flights. The display flight is commonly described as a vertical ascent and descent during which the male calls a drawn-out whistle (Herremans *et al.* 1994). This is a somewhat erroneous description as a typical display flight rather resembles a parabolic curve and the male may or may not give a call during the display flight. A typical display flight starts with a male flying approximately 1m above the ground for a distance of between 10 - 60m, followed by a steep ascent with wings closed to a height of between 6 - 10m, followed by a steep descent with wings closed and tail fanned out. The display flight is often associated with a drawn-out display call which is

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 of the ascent and the end of the descent is usually approximately 30 - 35 metres but can be greater, particularly during windy conditions.

Herremans *et al.* (1994) reported that there is an association between the height of the display flight and the average height of trees in a given territory. Males in territories with tall trees have higher display flight apexes with display flight apexes which may exceed 20m as reported by Herremans *et al.* (1994). No attempt was made to relate tree height to the display flight apex in the present study, but casual observations suggest that the display flight apex height in the study area is relatively constant within the 6 - 10m range. However, the average tree height is relatively similar in Short-clawed territories in the Polokwane Nature Reserve where the study was conducted. This makes it difficult to assess whether there is an association between the display flight apex height and tree height for males from the eastern population.

The results indicate that single display flights dominate in the eastern population and triple display flights are extremely rare. Interestingly, casual observations of display flights of males from the western population suggest that double-and triple-display flights are considerably more common in that population. Herremans *et al.* (1994) also report double-, triple- and even quadruple-display flights by males from this population. Engelbrecht (2005) mentioned that only certain males in the Polokwane Nature Reserve regularly perform multiple display flights and suggested that 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 the lack of tree cover in an individual's territory with double-and triple-display flights requiring in excess of 100m of open terrain to perform. Thus, the number of display flights that a male

can perform may be related to the size and vegetational and geographical structure of its territory. This, in turn, may be directly related to an individual's fitness – fit males are better able to occupy and defend large territories in which to perform multiple display flights and hence improve their chances of attracting a female.

In conclusion, this study presents the first detailed analyses and description of Short-clawed Lark vocalisations and displays. Unlike with the western population, the parameters analysed failed to reveal any dialects associated with the vocalisations of Short-clawed Larks from the eastern population. This is largely due to considerable variation in the number and placement of pulsed and whistle notes in their different calls. Although Short-clawed Larks call and display throughout the year and during most parts of the day, most vocalisations and displays peak in the first 1 - 3 hours after sunrise in the peak-breeding season. This would thus be the best time to perform monitoring surveys for this species. The results obtained are therefore of considerable value to organizations involved in the monitoring, management and conservation of this localised species of conservation concern.

**Table 4.1.** Sampling localities for analysis of vocalisations of territorial male Short-clawed Larks *Certhilauda chuana* from the eastern population of the species.

<b>Locality name</b>	<b>Coordinates</b>
Polokwane Nature Reserve	S 23 58 467, E 29 31 060
Polokwane Nature Reserve	S 23 58 074, E 29 31 017
Polokwane Nature Reserve	S 23 58 062, E 29 31 006
Polokwane Nature Reserve	S 23 58 445, E 29 30 539
Polokwane Nature Reserve	S 23 58 444, E 29 51 102
Perskebult	S 23 47 197, E 29 20 979
Mothibaskraal	S 23 55 470, E 29 38 163
South of Moshate Village	S 23 51 226, E 29 49 052
Eduan Park (Polokwane)	S 23 52 605, E 29 28 362
South-east of Eerstegoud	S 23 58 138, E 29 23 345
Polokwane Nature Reserve	S 23 59 577, E 29 29 139
Polokwane Nature Reserve	S 23 58 319, E 29 28 108
Polokwane Nature Reserve	S 23 58 074, E 29 51 432

**Table 4.2.** The number of single-, double- and triple-note territorial calls recorded for Short-clawed Lark males from the eastern population of the species. The relative percentage contribution of each note to the total number of notes is presented in parenthesis.

<b>Number of notes</b>	<b>N of calls</b>	<b>N of notes</b>
Single	49	49 (30.1%)
Double	82	164 (50.3%)
Triple	32	96 (19.6%)
Total	163	309 (100%)

**Table 4.3.** Single-note territorial call ( $n = 49$ ) variables analysed for Short-clawed Lark males from the eastern population of the species. DT = delta time (ms), LF1 = Lowest Frequency (kHz), HF1 = Highest Frequency (kHz), DF1 = Delta frequency (kHz).

<b>Variable</b>	<b>Mean</b>	<b>SD</b>	<b>Median</b>	<b>Range</b>	<b><i>P</i></b>
<i>DT</i>	0.78	0.16	0.78	0.14 - 1.13	0.01*
<i>LF</i>	4.77	1.19	4.83	1.95 - 7.08	0.33
<i>HF</i>	5.94	1.11	6.14	3.86 - 7.80	0.11
<i>DF</i>	1.17	0.76	0.95	0.34 - 3.54	0.57

\* Significant difference between individuals ( $P < 0.05$ )

**Table 4.4.** Double-note territorial call variables analysed for Short-clawed Lark males from the eastern population of the species. DT1, DT2 and DT<sub>Tot</sub> = delta time of the first and second note and total phrase respectively (ms), LF1, LF2 and LF<sub>Tot</sub> = Lowest Frequency of the first and second note and total phrase respectively (kHz), HF1, HF2 and HF<sub>Tot</sub> = Highest Frequency of the first and second note and total phrase respectively (kHz), DF1, DF2 and DF<sub>Tot</sub> = Delta frequency of the first and second note and total phrase respectively (kHz).

<b>Eastern population (<i>n</i> = 82)</b>					
<b>Variable</b>	<b>Mean</b>	<b>SD</b>	<b>Median</b>	<b>Range</b>	<b><i>P</i></b>
<i>DT1</i>	0.45	0.28	0.50	0.06-0.91	0
<i>DT2</i>	0.92	0.37	0.76	0.15 – 1.64	0
<i>DT<sub>Tot</sub></i>	0.89	0.42	0.95	0.12 – 2.34	0
<i>LF1</i>	5.23	1.16	5.61	3050.80 – 7817.80	0
<i>LF2</i>	4.07	0.84	3.93	3050.80 – 6440.70	0
<i>LF<sub>Tot</sub></i>	4.55	1.07	4.10	3084.70 – 6881.40	0
<i>HF1</i>	6.48	0.88	6.27	4678.00 – 8466.10	0
<i>HF2</i>	6.18	1.08	6.37	4508.50 – 7694.90	0
<i>HF<sub>Tot</sub></i>	6.79	0.88	6.98	4203.40 – 8466.10	0.04
<i>DF1</i>	1.25	0.54	1.13	419.50 – 2915.30	0
<i>DF2</i>	2.11	1.21	2.07	305.10 – 4339.00	0
<i>DF<sub>Tot</sub></i>	2.24	1.13	2.07	474.60 – 4843.20	0



**Table 4.5** Triple-note territorial call variables analysed for Short-clawed Lark males ( $n = 32$ ) from the eastern population of the species. DT1, DT2, DT3 and DT-Tot = delta time of the first, second and third note and total phrase respectively (ms), LF1, LF2, LF3. LF<sub>Tot</sub> = Lowest Frequency of the first, second and third note and total phrase respectively (kHz), HF1, HF2, HF3. HF<sub>Tot</sub> = Highest Frequency of the first and second and third note and total phrase respectively (kHz), DF1, DF2, DF3. DF<sub>Tot</sub> = Delta frequency of the first and second and third note and total phrase respectively (kHz). Significant differences ( $P = <0.05$ ) were noted between individuals for all the variables analysed.

<b>Eastern population (<math>n = 32</math>)</b>				
<b>Variable</b>	<b>Mean</b>	<b>SD</b>	<b>Median</b>	<b>Range</b>
<i>DT1</i>	0.16	0.14	0.13	0.07 - 0.68
<i>DT2</i>	0.63	0.10	0.66	0.22 - 0.71
<i>DT3</i>	0.58	0.91	0.56	0.48 - 0.84
<i>DT<sub>Tot</sub></i>	1.72	0.21	1.71	1.26 - 2.42
<i>LF1</i>	5.44	0.78	5.83	3.46 - 6.13
<i>LF2</i>	4.43	1.40	3.59	3.35 - 6.95
<i>LF3</i>	5.19	0.71	5.52	3.27 - 5.75
<i>LF<sub>Tot</sub></i>	3.65	0.33	3.52	3.28 - 4.37
<i>HF1</i>	6.41	0.80	6.81	4.50 - 7.05
<i>HF2</i>	6.09	0.97	5.59	4.71 - 7.96
<i>HF3</i>	6.26	0.54	6.47	4.67 - 6.74
<i>HF<sub>Tot</sub></i>	7.04	0.35	6.94	6.47 - 7.93
<i>DF1</i>	0.97	0.34	0.95	0.37 - 2.10
<i>DF2</i>	1.65	0.57	1.86	0.44 - 2.30
<i>DF3</i>	1.07	0.43	0.98	0.33 - 2.40
<i>DF<sub>Tot</sub></i>	3.38	0.37	3.36	2.57 - 4.27

**Table 4.6.** Contact call ( $n = 105$ ) variables analysed for Short-clawed Larks from the eastern population of the species. DT = delta time (ms), LF1 = Lowest Frequency (kHz), HF1 = Highest Frequency (kHz), DF1 = Delta frequency (kHz), NN = Number of Notes.

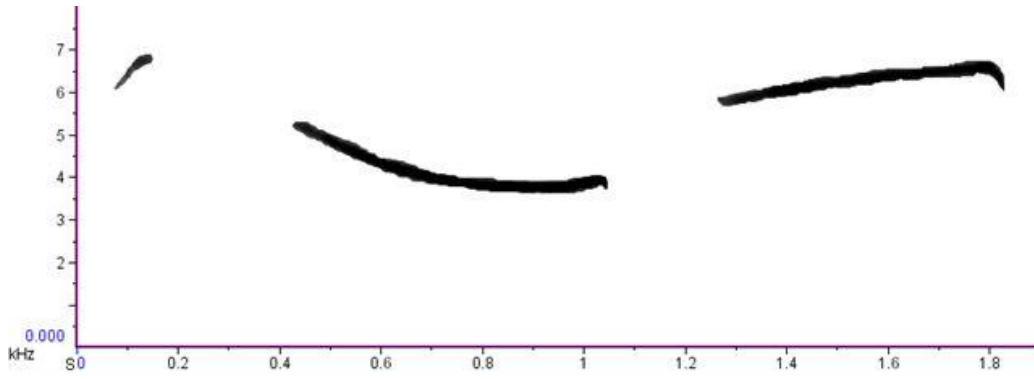
	Mean	SD	Range
<i>DT</i>	1.00	0.32	0.14 - 1.75
<i>LF</i>	2.08	0.17	1.83 - 3.28
<i>HF</i>	3.58	0.13	3.22 - 4.20
<i>DF</i>	1.50	0.19	0.81 - 2.07
<i>NN</i>	2.30	0.79	1 - 4

**Table 4.7.** Nestling distress ( $n = 25$ ) call variables of the Short-clawed Lark. DT = Delta Time (ms), LF1 = Lowest Frequency (kHz), HF1 = Highest Frequency (kHz), DF1 = Delta Frequency (kHz).

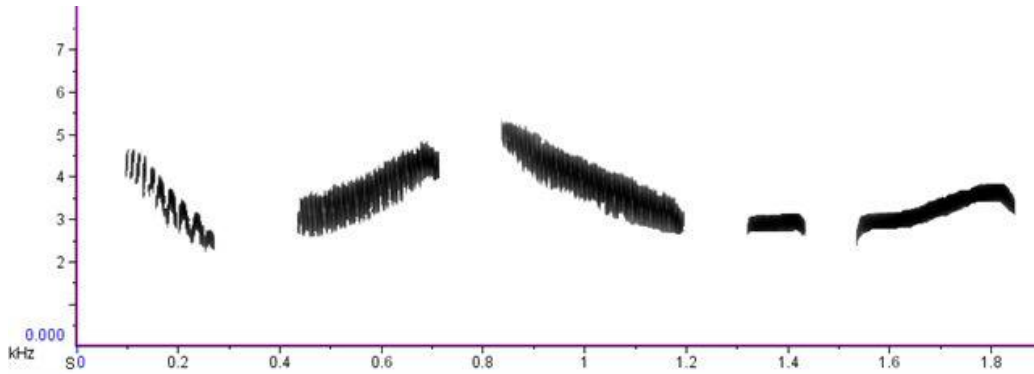
	Mean	SD	Range
<i>DT</i>	0.16	0.04	0.12 - 0.27
<i>LF</i>	3.13	0.24	2.20 - 3.41
<i>HF</i>	4.09	0.30	3.08 - 4.47
<i>DF</i>	0.95	0.18	0.54 - 1.25

**Table 4.8.** Sunrise and sunset times in the study area when call and display data was collected.

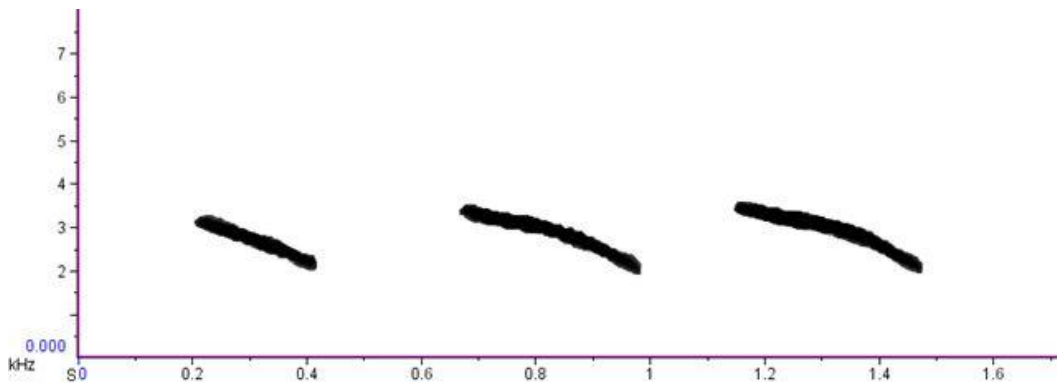
	March	June	September	December
<b>Sunrise</b>	05:58	06:37	06:14	05:06
<b>Sunset</b>	18:31	17:23	17:51	18:35



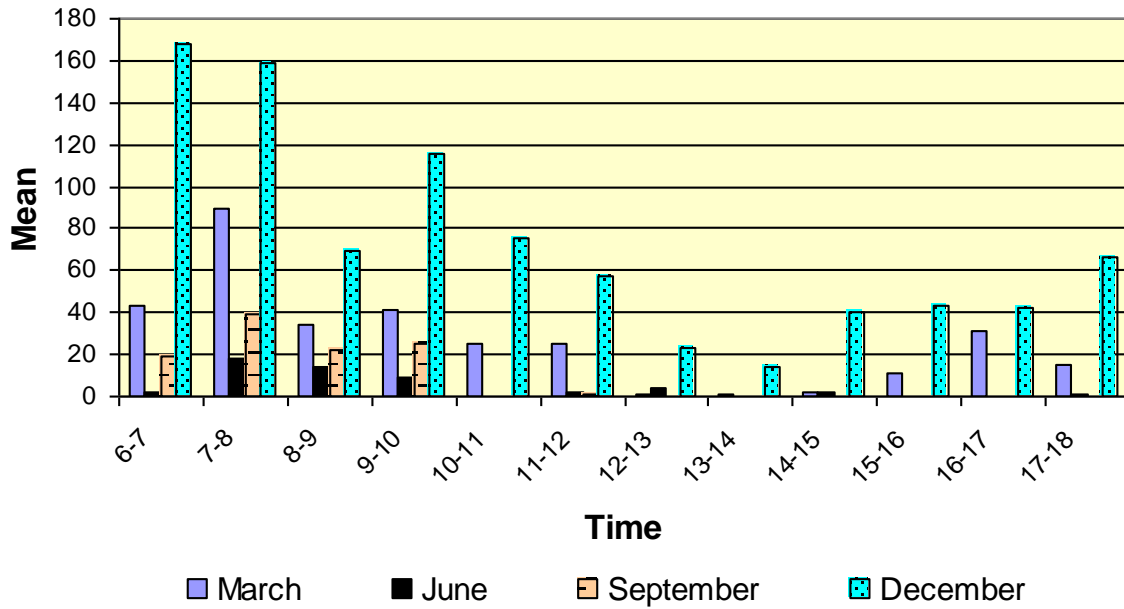
**Fig. 4.1.** Sonogram of a triple-note Short-clawed Lark territorial call.



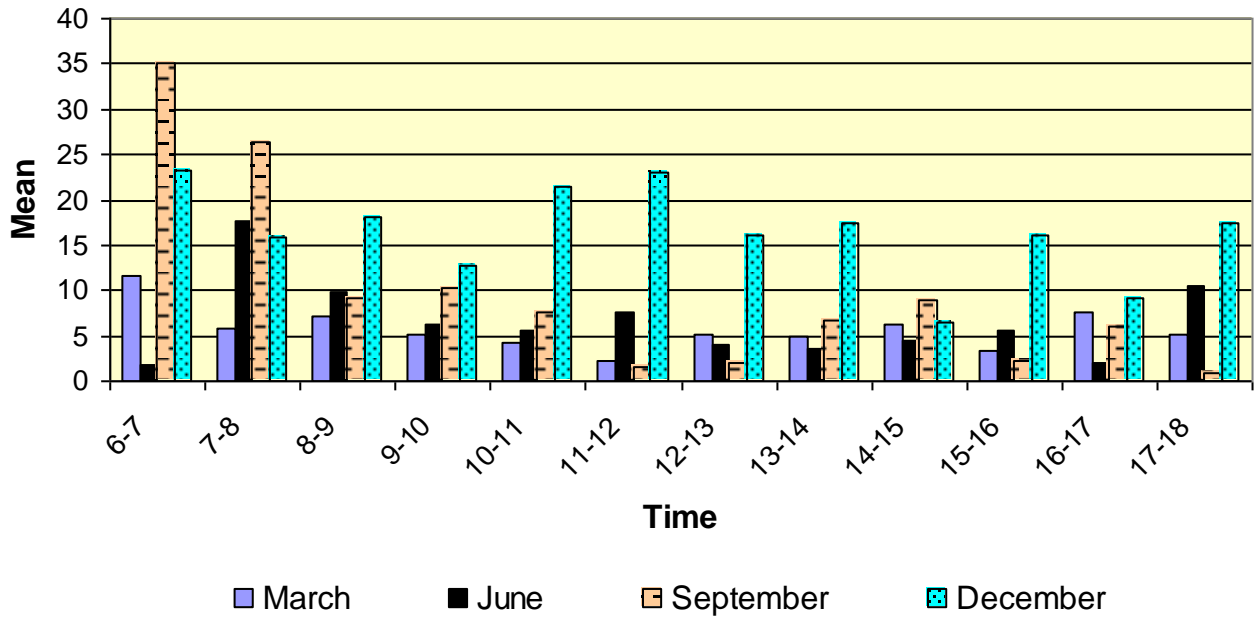
**Fig. 4.2.** Sonogram of a typical agitated call by a male Short-clawed Lark.



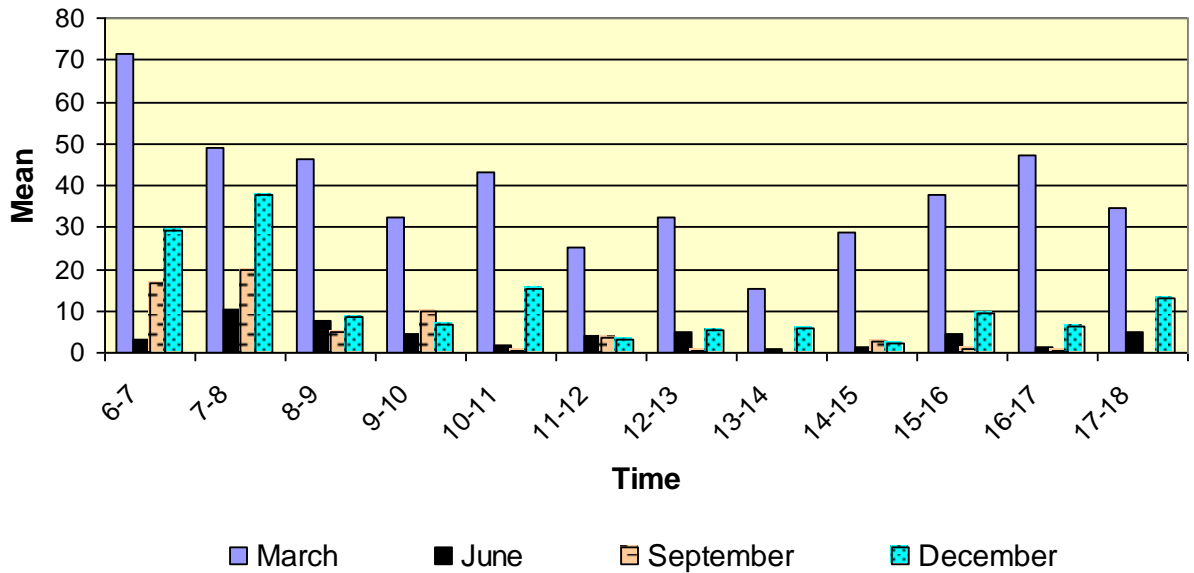
**Fig. 4.3.** Sonogram of a 3-note Short-clawed Lark contact call.



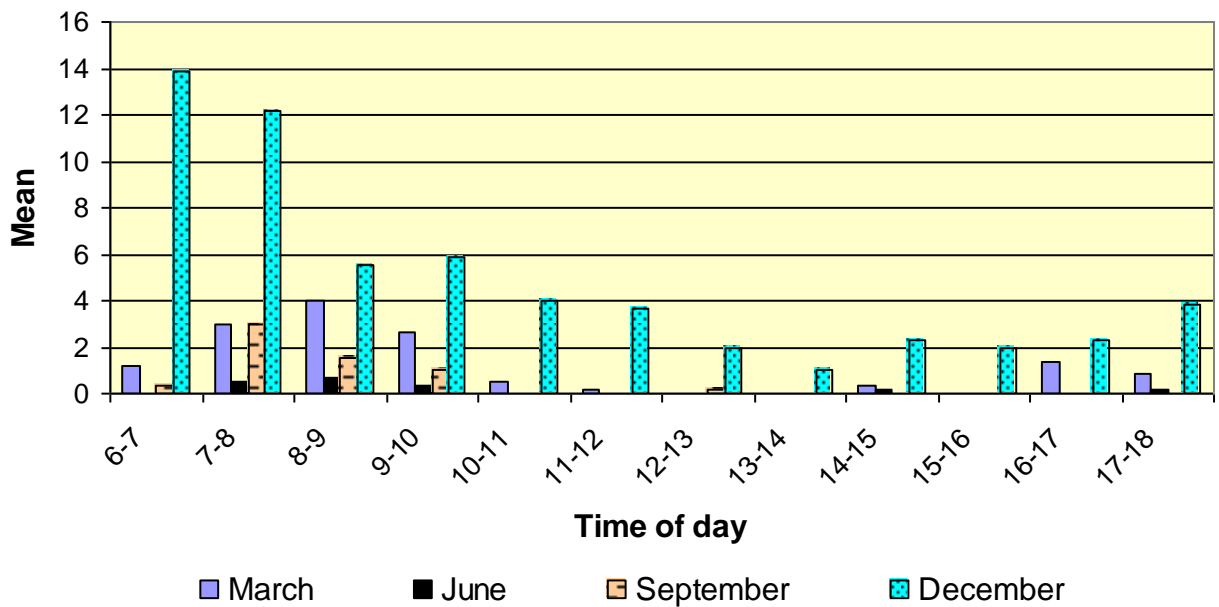
**Fig. 4.4a.** The mean frequency of territorial calls by male Short-clawed Larks over a year.



**Fig. 4.4b.** The mean frequency of Short-clawed Lark contact calls over a year.



**Fig. 4.4c.** The mean frequency of agitated Short-clawed Lark calls over a year.



**Fig. 4.5.** Mean number of single display flights by male Short-clawed Larks over four seasons