AN INVESTIGATION INTO PHENOTYPIC VARIATION AND THE ECOLOGY OF THE SABOTA LARK *CALENDULAUDA SABOTA*

by

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DECLARATION

I declare that “**AN INVESTIGATION INTO PHENOTYPIC VARIATION AND THE ECOLOGY OF THE SABOTA LARK *CALENDULAUDA SABOTA***” is my own work and that all the sources that I have used or quoted have been indicated and acknowledged by means of complete references and that this work has not been submitted before for any other degree at any other institution.

Surname, Initials (title)

Date

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PREFACE

This dissertation was written and formatted according to the guidelines given in the University of Limpopo's *Postgraduate Manual 2014* provided by the office of Research Development and Administration. The dissertation is comprised of five chapters. Chapter 1 gives a general overview of larks to provide some background information to readers unfamiliar with this family as well as the purpose of the study. This is followed by a desktop study of the ecology of the Sabota Lark based on an analysis of data from various databases (Chapter 2). Chapter 3 presents the results of a field-based study of the breeding biology and ecology of the Sabota Lark in the Limpopo Province. The results of an investigation into the geographic variation and sexual size dimorphism of the Sabota Lark from across its range using museum study skins is presented in chapter 4. The dissertation concludes with a summary of the major findings of the study, some recommendations and avenues for future research projects on the species (Chapter 5).

Chapters 2, 3 and 4 were written and formatted as research papers which can be submitted for publication with minimum editing. This inevitably resulted in some repetition of information in these chapters but I attempted to keep it to a minimum. Tables and figures are arranged at the end of each chapter, and a single list of references appears at the end of the dissertation, formatted according to the manuscript requirements of the Journal of African Zoology.

The results for this study have been presented at several local and national conferences and the details are provided below (* presenting author):

- **Mashao M.L.* and Engelbrecht G.D.** Breeding biology and ecology of the Sabota Lark (*Calendulada sabota*) in the Limpopo Province, South Africa. Paper read at the Faculty Research Day. Bolivia Lode, Polokwane, August 2012.
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ABSTRACT

The Sabota Lark *Calendulauda sabota* is the most common and widely distributed lark in southern Africa. There is evidence that the species is expanding its range in some areas, particularly in KwaZulu-Natal and the Northern and Western Cape Provinces, but its range seems to be decreasing in other areas, most notably the North West and Free State Provinces. Despite its extensive geographic range, very little is known about the general ecology of the species. To complicate matters even further, the species arguably exhibits the most extensive morphological variation with regard to bill size and shape and overall body size of any lark species. This leads to difficulties in identifying the species with obvious implications for successful management programmes involving this species. It is therefore evident that a detailed study of the taxonomy, ecology and geographic variation of the species is overdue.

As a result of its wide geographic range, the species inhabits a range of habitats from mesic savannahs in the east of the subcontinent to desert margins in the west. As such, two groups are generally recognized, namely a slender-billed group occupying the mesic and semi-arid woodlands and savannahs of southern Africa, and a thick-billed group inhabiting the semi-arid and arid Karoo, savannahs and desert margins in the west of the species range. These two groupings formed the basis of a desktop study comparing the breeding biology of the two groups and an investigation into phenotypic variation in the different subspecies of the Sabota Lark.

A desktop study of the breeding biology and ecology of the Sabota Lark was carried out using data requested from various databases at the Animal Demography Unit, University of Cape Town, and the National Museum, Bloemfontein. Data were obtained from the Nest Record Card Scheme (NERCS), SAFRING and SABAP1 databases. The following data were included in the analysis: breeding seasonality, habitat and nest site characteristics, clutch size, egg dimensions and descriptions, duration of the incubation and nestling periods, morphometric data, and the pattern and timing of moult. To analyse diet, stomach contents of adult birds were obtained from the collection in the National Museum, Bloemfontein.

The results of the desktop study showed that the preferred breeding site of the species was open areas with extensive areas of bareground. Although most nests were domed, the quality of domes varied from thick to almost see-through, and two nests were not domed, illustrating that there is considerable individual variation in nest construction. The study also revealed geographic variation with regard to the onset of breeding between the thick- and slender-billed groups. However, breeding in both groups coincided with the wet season in the east and west of the subcontinent and the geographic variation can therefore be attributed to geographic variation in the onset of the wet season. The results also showed geographic variation in clutch size with clutch sizes being larger in the west compared to the east. This may be attributed to greater variability in rainfall which restricts breeding to periods of good rainfall, resulting in opportunistic breeding with larger than normal clutch sizes. Analysis of SAFRING data showed that the thick-billed group is significantly larger than the slender-billed group with regard to mass and wing length. Inspection of primary moult data in the SAFRING database confirms the ‘generic’ post-breeding moult pattern typical of the majority of larks. Stomach content analysis showed that the species feeds on a mixture of vegetable matter (mainly seeds) and invertebrates. All stomachs analysed had some grit to aid with digestion.

A field-based study of the breeding ecology of the Sabota Lark was conducted at two localities in the Limpopo Province, namely the Polokwane Nature Reserve and De Loskop farm, during the 2011/2012 and 2012/2013 breeding seasons. This study confirmed the results of the desktop study that the species breeds during the wet season with a peak in December. The preferred breeding site had a large amount of grass cover with smaller amounts of forbs and debris providing cover and nest concealment. Nests were placed either next to a grass tuft, forb or stone. Nest building and incubation duties were performed by females only, while males helped in brooding and provisioning the nestlings. This brooding behaviour has not been recorded for any *Calendulauda* larks before. Mean clutch size and egg dimensions compared well with the results of the desktop study. The mean incubation period of the Sabota Lark was found to be 12.3 ± 0.5 days, with a mean nestling period of 12 days.

Although only the female performed incubation duties, some males did contribute to brooding nestlings, mainly by providing shade. This behaviour is unusual amongst larks. The relative contribution of males to feeding nestlings was greater than that of the females, but this may be due to females performing most of the brooding duties.

The overall breeding success of 32.9% estimated using Mayfield’s method was considerably greater compared to other ground nesting birds at the study sites. Known causes of breeding failure included predation, flooding and trampling.

Storer’s Dimorphism Index (SDI) results revealed that males were on average larger than females but this was not consistent across the different subspecies and was not statistically significant. The results of this study showed that geographic variation in the Sabota Lark is complex and merits a more detailed study with larger sample sizes. One of the major findings is that of the eight subspecies of the Sabota Lark studied, four groups can be formed, namely i) a thick-billed group, ii) a slender-billed group, with iii) *C. s. ansorgei* and iv) *C. s. waibeli* sharing characters of both groups sufficiently different to be treated as separate groups. The most important parameter contributing towards the similarity within these groups and the dissimilarity between the groups were tail and wing lengths.

The study showed that the various citizen science databases may be a source of valuable data to get a better understanding of the biology and ecology of poorly known species. It is also the first detailed study of the breeding biology and ecology of the Sabota Lark and has made a significant contribution to our knowledge of larks in general. This study is sure to form the basis of future studies on this species and other larks. The results of the analysis of geographic variation revealed unexpected patterns of variation and groupings with the Sabota Lark complex which may form the basis of future studies elucidating the real diversity in the family Alaudidae.

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CHAPTER 1

Despite their predominantly dun-coloured plumage and preference for open, structurally simple habitats in some of the most austere environments on Earth, larks have been celebrated in literature for millennia (Beer 1995). Their drab appearance belies an exceptionally rich vocal repertoire that has attracted adulation and inspired poets (see Beer 1995) and their ability to perform sustained display flights is truly awe inspiring. But what is a lark? Below follows a brief overview of the Alaudidae.

1.1. An overview of the larks (Alaudidae) of the world

1.1.1. Morphological aspects

The larks (Alaudidae) represent a group of approximately 96 species of medium-sized, primarily terrestrial passerines, characterised by their superficial similarity and conservative plumage colouration. They constitute a well-defined family whose members all share three unique morphological features of the syrinx and tarsus, namely: (1) the syrinx lacks a bony ossified pessulus, (2) they possess five pairs of syringeal muscles while other passerines have six to eight, and (3) the posterior surface of the tarsus is latiplantar and scuttelate (covered with small scales) as opposed to the rounded tarsi and lack of scales on the posterior surface of the tarsus of other passerines (Rand 1959; Ames 1971).

Larks differ greatly in body size, colouration and bill size and shape (de Juana *et al.* 2004). They range in size from approximately 12 g in some of the *Spizocorys* larks to 75 g in the Greater Hoopoe Lark *Alaemon alaudipes* but by far the majority of lark species weigh in at around 30 g (de Juana *et al.* 2004). As larks are primarily terrestrial, they move about with agility and generally prefer to run rather than fly when disturbed. There appears to be a correlation between leg length and diet since insectivorous species tend to have longer legs and are therefore better runners, while granivorous larks have shorter tarsi which are more suitable for walking and searching for small seeds on the ground (de Juana *et al.* 2004).

Larks have ten primaries, although the length of the tenth primary varies considerably. In some genera, e.g. *Calandrella* it is vestigial and in others, e.g. *Alaemon*, it is very well-developed (de Juana *et al.* 2004). These different wing formulae can be useful to distinguish between closely related species, e.g. Melodius Lark *Mirafra cheniana* and Monotonous Lark *Mirafra passerina* (Davies 2011). If corrected for body size, male larks have larger wings than females (de Juana *et al.* 2004). This may be an adaptive response to sustained display and song flights – the energetic cost of these flights may be mitigated by a reduction in wing-loading. There are also differences in the wing-loading of migratory vs resident larks: the former has long, narrow wings and a high wing-loading for fast flight, whereas resident species tend to have shorter, broader wings and a lower wing-loading. A final aspect of interest regarding the wings of larks, is their strikingly large inner secondaries. These essentially form a “cloak” over the underlying primaries and outer secondaries, protecting them from UV radiation and abrasion (de Juana *et al.* 2004).

The generally dull, earthy-coloured plumage of larks provides camouflage for a primarily terrestrial group inhabiting open, exposed environments with little cover. Most larks share a similar plumage pattern ranging from light tan to reddish-brown dorsally and paler whitish to buff below with varying amounts of streaking below. However, there is considerable variation in dorsal plumage colouration, even intra-specifically, to match the colour of the substrate where they live (MacDonald 1953; Willoughby 1969; Maclean 1970a; Ryan & Bloomer 1997). For example, Red Larks *Certhilauda burra* inhabiting the red sand dunes have a predominantly red colouration whereas species inhabiting the eastern plains are predominantly brown with broad streaking. Maclean (1970a) grouped larks into two groups based upon dorsal plumage colouration, namely those with generalised and those with specialised plumage patterns and colouration. The former is mostly seen in almost all migrant and nomadic larks, e.g. *Spizocorys*, *Calandrella* etc. It comprises a mixture of dark streaking on the feathers and it offers some degree of crypsis in virtually any environment (Barnes 2009). Species exhibiting the specialised plumage pattern, e.g. Dune Lark *Calendulauda erythrochlamys,* tend to be uniformly coloured dorsally and the colouration matches the substrate closely (Ryan & Bloomer 1999; Barnes 2009).

As a family, larks display some of the greatest variation in bill structure within a family. This is an excellent example of adaptive radiation and is only matched by a few families, e.g. Galapagos Finches (Thraupidae), the Hawaiian Honeycreepers (Drepanididae) and Madagascar Vangas (Vangidae), to name but a few (Melo & Ryan 2012). The diversity of bill structures within the Alaudidae reflects a wide variety of diets and associated foraging techniques. This evolutionary feature has allowed many larks to survive in hostile environments which are completely devoid of other birds (Donald 2004). Insectivorous species tend to have long, slender bills and collect much of their food by digging in the ground, such as the Greater Hoopoe Lark. The generalist species have short, strong bills and are generally omnivorous. Species whose diet is mainly granivorous, e.g. Stark's Lark *Spizocorys starki* have short, deep bills (Maclean 1970a).

In addition to interspecific variation in bill structure related to diet and foraging techniques, some species also exhibit intraspecific geographical variation in bill size and shape (Clancey 1966). The Sabota Lark *Calendulauda sabota* arguably provides the best example of this phenomenon. This species is divided into a slender- and large-billed group. The former inhabits the mesic to semi-arid grassland and savannas of the eastern and central parts of southern Africa, whereas the latter inhabits the arid and semi-arid Karoo, savannas and desert margins in the western parts of the subcontinent (Dean 2005).

Most species of larks exhibit sexual size dimorphism (SSD) with males being larger than females. This phenomenon occurs frequently in species that are monomorphic in plumage colouration (Cramp 1988). Interestingly, juvenile Dupont's Lark *Chersophilus duponti* also exhibit SSD (Vögeli *et al*. 2007). Although SSD is more evident in resident, insectivorous species, it is by no means restricted to this group and even the most granivorous species are mildly dimorphic with regard to size, particularly in bill and wing length (de Juana *et al*. 2004; Engelbrecht 2005; Dikgale 2012; Engelbrecht & Mathonsi 2012). Engelbrecht (2005) showed that Short-clawed Lark *Certhilauda chuana* males are on average 8–11% larger than females for certain measurements. The Raso Lark *Alauda razae* shows extreme SSD in bill size between males and females, with the bill of males being on average 23.1% longer than those of females (Donald *et al*. 2003). It is generally believed that the SSD in bill length shown by so many resident species allows the sexes to forage at different levels and possibly occupy different niches, thus reducing intraspecific competition between the sexes (Donald *et al.* 2003). Granivorous species are usually nomadic or prone to local movements, and since seeds are usually an abundant food source, there is very little competition for resources between the sexes (McKechnie 2007). These species show little or no variation with regard to bill length, but they may exhibit SSD with regard to wing and tail length.

Despite the mild SSD shown by most species, the sexes are generally monomorphic with regard to plumage colouration. A few species are mildly sexually dichromatic, such as those in the genera *Ramphocoris*, *Eremophilia, Melanocorypha* and *Pinarocorys* (Keith *et al.* 1992), but most members of the genus *Eremopterix* (sparrow-larks) exhibit strong sexual dichromatism. Male sparrow-larks are strikingly coloured whereas females possess the more typical cryptic plumage of larks.

1.1.2. Distribution

Although larks are found on all continents except Antarctica, the family's distribution and diversity is highly skewed (Figure 1.1). The family is best represented in Africa (78 species), followed by Eurasia (37 species) whereas Australasia and the New World each support a single species (de Juana *et al.* 2004). In terms of endemism, Africa also surpasses the other continents: of the 78 species occurring in African, 60 (77%) are endemic to sub-Saharan Africa. In contrast, only 17 of the 37 (46%) Eurasian species are endemic to that continent. Furthermore, all 21 currently recognized alaudid genera are represented in Africa, as opposed to 13 genera in Eurasia and one each in Australasia, i.e. *Mirafra javanica*, and the New World, i.e. *Eremophila alpestris*.

Within Africa, their distribution and diversity is also highly skewed (de Juana *et al.* 2004). Although lark diversity peaks in the arid and semi-arid regions of the continent, two centres of endemism stand out. These are the south-western arid zones which include South Africa, Namibia and Botswana, and the north-eastern arid zone which includes Kenya, Ethiopia and Somalia (Barnes 2007). Together these two centres of endemism support 62% of Africa's endemic larks. In the south-western arid zone, 26 of the 31 species in that area are endemic or near-endemic. Similar high levels of endemism are present in the north-eastern arid zone where 23 of the 34 species are endemic to that region (Barnes 2007).

Throughout their distribution range, the majority of larks inhabit open, structurally simple areas with sparse vegetation cover in semi-arid to arid regions (de Juana *et al.* 2004). Within this broad description of their preferred habitat, they occupy a wide range of niches, e.g. grassland, deserts, savannas, steppes, scrub, coastal marshes, pastures and heaths from sea-level to sometimes over 5000 m in Alpine vegetation. The majority of species occupy areas with annual precipitation of between 400 mm and 800 mm per annum (Dean & Williams 2004).

1.1.3. Phylogenetics

Although larks can be clearly defined based on tarsal scuttelation and shape as well as syringeal musculature, their relationships to other passerines have been contentious for many years. Using traditional morphological characters, they were initially placed at the "beginning" of the passerine tree near the sub-oscine passerines (Peters 1960). With the advent of genetic-based classification systems in the 1990s (Sibley & Ahlquist 1990), this traditional belief was shattered and they were placed in the superfamily Passeroidea. More recently, DNA sequence data has shown them to belong to the superfamily Sylvioidea (Ericson & Johansson 2003; Alström *et al.* 2006; Fregin *et al.* 2012). Within the Sylvioidea they form an unlikely but distinct sister clade with the monotypic and ecologically radically different genus *Panurus* (Panuridae) (Ericson & Johansson 2003; Alström *et al*. 2006; Fregin *et al*. 2012; Alström *et al*. 2013).

Traditional classification systems designated lark genera based on morphological criteria. However, certain morphological features such as bill structure and plumage vary considerably with diet and habitat and as such they are unreliable characters for phylogenetic assessment (Cramp 1988; Alström *et al.* 2013). Recent studies using molecular methods to resolve taxonomic relationships within the family has revealed exceptionally high levels of disagreement between morphologically-based taxonomy and phylogenetic relationships as inferred from DNA sequences (Ryan *et al.* 1998; Ryan & Bloomer 1999; Guillaumet *et al.* 2005; Barnes 2007; Alström *et al.* 2013).

Alström's (2013) phylogeny of the Alaudidae using DNA sequences from two mitochondrial and three nuclear loci revealed that larks can be grouped into three major clades:

- Alaudids. This clade includes the genera *Alauda, Galerida, Lullula, Spizocorys, Calandrella, Eremophila, Melanocorypha, Eremalauda and Alaudula*.
- Ammomanids which include the genera *Alaemon, Ammomanopsis, Chersomanes, Certhilauda, Ramphocoris, Ammomanes* and *Eremopterix*, and *Pinarocorys*.
- Mirafrids. This clade is comprised of the genera *Calendulauda, Heteromirafra, Corypha, Mirafra* and *Megalophoneus*.

Despite advances in lark taxonomy brought about by using molecular methods, there are still many unresolved relationships and species diversity is likely to be underestimated (Alström *et al.* 2013). In particular, the mirafrid clade has been especially problematic and it has been referred to as the "dumping ground" of species with uncertain taxonomic affinities (Barnes 2007). For example, the Madagascan Lark *Mirafra hova* was traditionally placed within the genus *Mirafra*, yet Alström *et al.* (2013) found that the species should be included in the genus *Eremopterix* within the ammomanid clade. The phylogeny proposed by Alström *et al.* (2013) revealed two major clusters within the mirafrid group. The one cluster included the typical *Mirafra* larks and the genera *Heteromirafra* and *Corypha*. The other cluster included a well-defined group of *Mirafra*-like larks which lacks the rufous wing-panel of typical *Mirafra* larks (Ryan & Bloomer 1999; Alström *et al.* 2013). The genus *Calendulauda* was resurrected to include the members within this cluster.

1.1.4. Demographics

Larks exhibit the full spectrum of movement patterns shown by birds. These movements range from sedentary to small scale local movements, nomadism, partial and regular migration. These movement patterns are not fixed and several species have resident, nomadic and partially migratory populations in different parts of their range, e.g. Chestnut-backed Sparrow-lark *Eremopterix leucotis* and Pink-billed Lark *Spizocorys conirostris* (Dean *et al.* 1992; Dikgale 2012; Engelbrecht & Mathonsi 2012). Although migratory larks are well represented amongst Eurasian species, e.g. Bimaculated *Melanocorypha bimaculata* and White-winged *Melanocorypha leucoptera* Larks, the Dusky Lark *Pinarocorys nigricans* is the only truly migratory southern African lark. It leaves its breeding quarters in northern Angola and Zambia in late October and November and migrates through Zimbabwe and Mozambique to north-eastern South Africa, southern Botswana and parts of western Mozambique (Keith *et al*. 1992). It returns to its breeding quarters between about April to June following a more direct route via Botswana and western Namibia. Examples of nomadic and sedentary species include Stark's Lark *Spizocorys starki* and Karoo Lark *Calendulauda albescens* respectively.

1.1.5. Diet

Despite the differences in bill structure highlighted above, the diet of all adult larks comprises a mixture of seeds and invertebrates (de Juana *et al.* 2004). However, the relative importance of each differs amongst species, and even within the same species between different seasons, e.g. Spike-heeled Lark *Chersomanes albofasciata* and Raso Lark (Burton 1971; Donald *et al*. 2003; de Juana *et al*. 2004). In terms of their diet, larks can broadly be divided into four groups: resident insectivores, nomadic insectivores, resident granivores and nomadic granivores (Dean & Hockey 1989; Maclean 1993). In most larks, the diets of nestlings are almost exclusively insectivorous, but some of the mainly granivorous species, e.g. Pink-billed Lark and Chestnut-backed Sparrow-lark, supplement the nestlings' diet with small seeds from various plants and grasses (Dikgale 2012; Engelbrecht & Mathonsi 2012). Once more, there are sometimes intraspecific differences in the diet of the sexes. For example, males of the Raso Lark have longer bills and mainly dig for bulbs, whereas females have a more insectivorous diet (Donald *et al*. 2003).

Larks also display varying degrees of dependency on water. The mainly granivorous species often assemble at surface water bodies whereas the more insectivorous species never drink water. They fulfil their water requirements by reabsorbing a considerable amount of water in the intestine or they obtain sufficient water from their prey (Tieleman 2002). Some species have a tendency to drink surface water regularly (e.g. Botha's Lark *Spizocorys fringillaris*, Pink-billed Lark and Red-capped Lark *Calandrella cinerea*). Others such as Stark's Lark drink water regularly during the dry season but less often after rain because of the abundance of insects and green vegetation in their habitats. Once again, there are also intraspecific differences in dependency on water. For example, Sabota Lark populations in the mesic east of the species range have never before been recorded drinking water but birds in the arid west have been recorded drinking water (Engelbrecht 2012).

Desert larks have developed physiological and behavioural adjustment that enables them to survive desert environments with high ambient temperature, lack of surface water and low primary production (Tieleman *et al*. 2004). Due to a lack of surface water in the areas they inhabit, they reabsorb a considerable amount of water in the intestine, while other species get all their water requirements from their diet of mainly insects and freshly parts of insects. Several species also have various behavioural adaptations to reduce evaporative water loss. For example, Spike-heeled Larks often spend the hottest parts of the day in underground burrows (Keith *et al.* 1992). Other species perch on elevated objects to take advantage of convection currents and reduce radiation from the soil surface, whereas others perch on low-growing vegetation. Williams (1996), Williams & Tieleman (2001) and Tieleman *et al*. (2003) showed that the reductions in the rate of energy expenditure and evaporative water loss of desert larks are adjustments to their environment and thus natural selection favours individuals with low rates of energy expenditure and water loss.

1.1.6. Voice

Lark vocalizations have inspired generations of poets and authors and are therefore arguably the most endearing feature of this family. The fabled song and display flights of the Eurasian Skylark *Alauda arvensis*, for example, have resulted in its introduction to distant continents and islands (Donald 2004). Due to their generally cryptic plumage colouration, male larks invest more in song and other vocalizations in order to attract their mates during the breeding season (de Juana *et al*. 2004). The vocalizations of larks are rich and varied and include song, and various other calls, e.g. territorial, distress, alarm, feeding, flight, contact and begging calls. A fascinating feature of lark vocalizations is their ability to mimic the calls of other species. Mimicry is often incorporated into the song of many lark species. Interestingly, although mimicry is common in members of the alaudid and mirafrid clades, it is uncommon in the ammomanid clade and has thus far only been recorded in the Chestnut-backed Sparrow-lark (Dikgale 2012). Interestingly, some species have replaced their song and calls with wing-clapping display flights, e.g. Flappet *Mirafra rufocinnamomea*, Cape Clapper *Mirafra apiata* and Eastern Clapper Larks *Mirafra fasciolata* (Ryan & Marshall 2005) and hardly have other vocalizations.

1.1.7. Moult

Moult is the periodic shedding and replacement of feathers. Although replacement of worn feathers is the main reason, birds also moult for other reasons. In some species, males undergo a pre-breeding moult into a more showy plumage. Many birds also have juvenile and immature plumages which serve various purposes, e.g. camouflage or avoiding intra-specific adult aggression (Amadon 1966). Feather moult is energetically costly and therefore most birds schedule it so that it does not coincide with other energetically demanding activities such as breeding or migration. Replacement of worn feathers may affect flight efficiency temporarily, but will provide improved flight performance at the completion of moult. It can also result in reduced insulative properties of feathers, thus resulting in increased metabolic costs (Gill 1995). Moulting birds meet their nutrient demands by increasing their daily nutrient intake, making reductions in other nutrient demanding functions such as breeding and migration, and catabolising body tissues (Ankney 1979).

Timing and duration of moult differ greatly between species. Adult larks moult either before the breeding season e.g. Short-toed Lark *Calandrella brachydactyla* or, as with the majority of larks, at the end of the breeding season. Juveniles undergo a complete post-juvenile moult when they are 4–6 weeks old. Adult larks, residents and short-distance migrants, have only one complete moult per year which normally occurs after the breeding season (de Juana *et al*. 2004). Other species of larks, e.g. Grey-backed Sparrow-lark *Eremopterix verticalis* and Gray's Lark *Ammomanopsis grayi*, have two complete moults per annum (de Juana *et al*. 2004). It has been suggested that excessive abrasion by windblown sand and vegetation as well as UV radiation exacts a heavy toll on feathers which necessitates a bi-annual moult. The usual moult is quite rapid and takes place soon after breeding, while the second moult is prolonged and takes place throughout the dry season when food is scarce (de Juana *et al*. 2004). There are several examples of species that undergo a partial moult during the breeding season and moult only the innermost secondaries such as in the Short-clawed Lark (Herremans & Herremans 1992) and the Chestnut-backed Sparrow-lark (Dikgale 2012). It is worth noting that the timing and duration of moult can differ geographically for species with large distribution ranges (Serra 1998; Underhill 2003).

1.1.8. Breeding biology

The breeding biology of larks can broadly be summarised as follows: larks are monogamous and defend territories of varying sizes; they breed as isolated pairs or in loose colonies; they nest on the ground; females are responsible for nest construction and usually perform incubation alone; clutch sizes are highly variable; nestlings grow rapidly and are fed by both parents; breeding success is poor; and there is a relatively long post-fledging dependence period (de Juana *et al.* 2004). However, there are exceptions and deviations from this general pattern for literally every point above. Having said this, we lack basic breeding data for the majority of larks and these generalisations are likely to dissolve as breeding data becomes available for more and more species. The poor state of our knowledge about the breeding of larks may be attributed to the harsh habitats so many species inhabit, and the difficulty in studying relatively small, terrestrial, ground-nesting species. The breeding biology of the Eurasian Skylark is undoubtedly the best known of all larks (*cf* Donald 2004). A few other Eurasian larks have also been studied in detail e.g. Crested Lark *Galerida cristata,* Thekla Lark *Galerida theklae,* Greater Short-toed Lark *Calandrella brachypetala,* Lesser Short-toed Lark *Calandrella rufescens* (Hartley 1946; Suarez *et al*. 2002; Suarez *et al*. 2005; Lesiński 2009) but comparatively little is known of the breeding ecology of the majority of African larks.

Breeding in larks is either seasonal or opportunistic in response to erratic or above average rainfall. In some cases breeding can also be triggered by favourable conditions such as temperature (de Juana *et al.* 2004) and food availability. There is a positive correlation between rainfall, primary production and food availability (Maclean 1970b; Lloyd 1999). Since most larks feed their young invertebrates, breeding is scheduled to coincide with the flush of insect life following good rains. Those species feeding their young seeds usually breed after the peak of the wet season so that breeding coincides with seed set by grasses (Engelbrecht & Mathonsi 2012; Dikgale 2012).

The onset of breeding is marked by an increase in males singing and displaying (de Juana *et al*. 2004). Males establish and defend territories against conspecifics. Many granivorous species (*Eremopterix* and *Spizocorys*) breed opportunistically when food is abundant after rains in arid areas. These species may aggregate in large numbers in these patches and breed in loose colonies with the nests sometimes spaced only a few metres apart. The predominantly insectivorous species' breeding season also coincides with the wet season, but they tend to defend permanent territories and their nests are usually evenly spaced and well apart, e.g. *Certhilauda* and *Calendulauda*.

Breeding in desert-dwelling larks follows after good rain (>20 mm for insectivorous species and >40 mm for granivorous species) when primary production is high and there is much food (seeds and invertebrates) available for nestlings (Maclean 1970c; Dean 2004; de Juana *et al.* 2004). Other factors associated with rainfall which may also act as stimuli for breeding are availability of material for nest construction and sheltered nest sites at the bases of grass tufts (Maclean 1970b; Dean *et al*. 1992; Dean 2004; de Juana *et al*. 2004). Species such as Sclater's Lark breed opportunistically after sufficient rain because it prefers the seeds of Eight-day grass *Enneapogon desvauxii* which grows, germinates and set seeds in just eight days after the onset of rain (Lloyd 1997). Factors that determine the onset of breeding in desert-dwelling larks differ from those related to larks of temperate climates. For example, in temperate climates, breeding is also influenced by favourable temperatures (Lloyd 1999; Donald 2004).

Although most larks are monogamous, the nomadic Monotonous Lark's breeding strategy includes polygyny upon arrival on the breeding grounds, but changes to monogamy as the season progresses (Engelbrecht & Grosel 2011). There is also evidence that extra-pair paternity occurs in the family and may be more common than thought (Donald 2004; Sanchez *et al.* 2004; Hutchinson & Griffith 2008). Few species are sufficiently well-studied, but most studies have shown that pairs remain together for the duration of the breeding season followed by divorce in the non-breeding season (Donald 2004; Engelbrecht 2005; Engelbrecht & Mathonsi 2012; Dikgale 2012).

With the exception of the obligate biparental breeders (*Spizocorys* and *Eremopterix*), nest construction is usually performed by females only but males have been recorded assisting with nest construction in Rufous-tailed Lark *Ammomanes phoenicura*, Desert Lark *Ammomanes deserti*, Sykes's Lark *Galerida deva* and Malabar Lark *Galerida malabarica* (de Juana *et al*. 2004). Nevertheless, males constantly guard their mates during the nest construction and laying period. Incubation is usually performed by females only but in the genera *Spizocorys* and *Eremopterix* both parents incubate and brood the eggs and nestlings. There are unconfirmed reports of biparental incubation in the Australasian Bushlark *Mirafra javanica*, Malabar Lark, Syke's Lark and the Oriental Skylark *Alauda gulgula* (de Juana *et al*. 2004).

Despite the differences in habitat types occupied by larks, most species construct their nests adjacent to or under a grass tuft, rock or within low vegetation. They built an open-cup or domed nest in small hollows and the nest type is rather consistent in genera. The material used in nest construction differs greatly and depends on the surface substrate and the material available, e.g. grass, plant fibres, rootlets, forbs, bark, small sticks, dead leaves, sedges, feathers, clods, dung, and cobweb (Maclean 1970a; de Juana *et al*. 2004; Tarboton 2011; Engelbrecht & Mathonsi 2012; Dikgale 2012).

The number of eggs laid in a season and the size of the clutch vary considerably, from one (Sclater's Lark) to eight (Calandra and Black Larks *Melanocorypha yeltoniensis*) (de Juana *et al.* 2004). Clutch sizes of larks in temperate regions usually vary between 2–4 eggs and those in arid regions average 2–3 eggs. There is a general tendency for clutch sizes to decrease with an increase in aridity (Serlé *et al*. 1977; Cannings & Threlfall 1981; Morel & Morel 1984; Lepage & Lloyd 2004; Tieleman *et al.* 2004). Some species also show regional variation in clutch size. For example, the Chestnut-backed Sparrow-lark normally lays two eggs in its southern breeding range but in Senegambia in the north of its range it lays only a single egg (Morel & Morel 1984; Engelbrecht & Dikgale 2014). In addition to regional clutch size variation, several lark species also show seasonal variation in clutch size (Donald 2004; Engelbrecht 2005; Suárez *et al.* 2005; Engelbrecht & Mathonsi 20012). For example Short-clawed Lark and Eurasian Skylark clutch sizes tend to be larger in the middle of the season compared with the beginning and end of the season. In the case of the nomadic Grey-backed Sparrow-lark *Eremopterix verticalis*, clutch size is usually two eggs, but may increase to 4–5 eggs within a week of good follow-up rains on the breeding grounds (Lloyd 1999).

Eggs are laid at daily intervals and normally early in the morning (de Juana *et al*. 2004). Incubation commences in most species upon clutch completion, but once again there are exceptions. The Pink-billed Lark commences with incubation upon laying of the first egg, but some species, e.g. Chestnut-backed Sparrow-lark sometimes have a variable onset in incubation (Engelbrecht & Dikgale 2014). Generally the incubation period ranges from 11–13 days, although 8–10 day periods are known for sparrow-larks (Lloyd 1998; Engelbrecht & Dikgale 2014) and 15–16 days for Black and Short-clawed Larks. As with many ground-nesting species, the eggs are cryptically patterned with small, irregular spots varying in colour.

Both sexes assist with food provisioning and nest sanitation, although only females brood the young in the majority of species (de Juana *et al*. 2004). Although both sexes contribute to feeding of nestlings and fledglings, several studies have shown that this is not necessarily symmetrical (Engelbrecht 2005; Engelbrecht & Mathonsi 2012: Engelbrecht & Dikgale 2014). Invertebrates form the bulk of the diet of nestlings and even the most granivorous larks feed their nestlings a mixture of seeds and invertebrates. Development of nestlings is rapid and in most species nestlings fledge after 8–11 days in the nest, but as early as six days in the Eurasian Skylark and as late as 14 days in other species (de Juana *et al.* 2004; Donald 2004). Rapid development of the legs enables nestlings to leave the nest well before they are able to fly (Donald 2004; Engelbrecht 2005; Engelbrecht 2008; Engelbrecht & Lonzer 2008; Engelbrecht & Mathonsi 2012; Engelbrecht & Dikgale 2014). Early fledging has the advantage of reducing the period of vulnerability to predation of the entire clutch. Nestlings can spend up to two weeks hiding in vegetation after fledging.

In common with many ground-nesting species, larks suffer high nest losses. Breeding success in many species is between 10–30% and in some transformed habitats as many as 80–90% of nests are lost (Maclean 1970b; Suárez & Manrique 1992; Donald 2004; Praus & Weidinger 2010; Engelbrecht & Mathonsi 2012; Engelbrecht & Dikgale 2014). Nest predation is often regarded as a primary cause of breeding failure in most passerine species and it seems to hold for larks too (Donald *et al.* 2002; Klug 2005; Johnson *et al*. 2012). Other causes of nest failure include flooding, trampling, starvation, exposure and natural causes. However, larks are capable of producing several replacement clutches in a season, sometimes within a week of a previous nest loss (de Juana *et al*. 2004; Donald 2004; Engelbrecht 2005). Although data is limited, most resident larks seem capable of double, repeat-brooding attempts but Engelbrecht (2005) recorded triple repeat-brooding attempts for the Short-clawed Lark.

1.2. The genus *Calendulauda*

The genus *Calendulauda* consists of eight species, namely: Sabota Lark, Red Lark *Calendulauda burra*, Karoo Lark, Dune Lark, Barlow's Lark *Calendulauda barlowi*, Pink-breasted Lark *Calendulauda poecilosterna,* Foxy Lark *Calendulauda alopex* and Fawn-coloured Lark *Calendulauda africanoides* (Alström *et al*. 2013). All currently recognized *Calendulauda* species were previously placed within the genus *Mirafra*, but genetic evidence showed it is a relatively well-defined cluster within the mirafrid clade and the genus *Calendulauda* was resurrected to accommodate this group (Ryan *et al*. 1998; Alström *et al*. 2013). With the exception of the Fawn-coloured Lark, all members of the genus *Calendulauda* can be distinguished from *Mirafra* larks by the absence of a rufous wing-panel in the former.

1.3. The Sabota Lark *Calendulauda sabota*

As mentioned above, the Sabota Lark was originally described as *Mirafra sabota* Smith, 1836 until genetic evidence revealed that it should be placed in the genus *Calendulauda*

(Ryan & Bloomer 1999; Barnes 2007). Other synonyms for the species include: *Megalophonus sabota* Layard, 1867, *Megalophonus naevius* Ayres, 1871, *Alauda naevia* Sharpe, 1871, *Mirafra naevia* Shelley, 1882, *Alauda sabota* Sharpe, 1871 and *Mirafra plebeia* Shelley, 1896 (Pätzold 1994).

The Sabota Lark is characterised by its heavily streaked, bold head markings, a blackish eye stripe, prominent pale supercilium and thin, black moustachial streaks (Plate 1.1). It is a very common and widely distributed species, inhabiting semi-arid and arid savannahs, deserts, the Karoo and rocky outcrops on the margins of the Namib Desert (Dean 1997; Dean 2005). It is considered a resident and sedentary species of southern Africa and neighbouring countries including Angola (Clancey 1966). However, populations in the drier parts of its range are locally nomadic. An isolated population occurs in the Cabinda province of Angola (Keith *et al*. 1992).

Given its wide distribution, wide habitat tolerance and resident behaviour, it is not surprising that the species exhibits the greatest degree of geographical variation in plumage colouration, body size and bill shape of any lark. No fewer than eight subspecies are recognised by Dean (2005), mainly with regard to plumage coloration of the dorsal surface and bill size. These subspecies are generally grouped into two groups, namely the slender-billed group with a mostly eastern distribution, and the thick-billed group restricted to the arid and semi-arid south-western and western parts of southern Africa (Clancey 1966; Hall & Moreau 1970). The thick-billed group is characterised by heavy bills, darkest and dorsally most heavily streaked populations in the south and the lightest in the extreme north of this group's distribution range (Clancey 1966), and consists of three subspecies: *C. s. naevia* (Strickland, 1852)*, C. s. bradfieldi* (Roberts, 1928) and *C. s. herero* (Roberts, 1936). The slender-billed group comprised of five subspecies: *C. s. sabota* (Smith, 1836)*, C. s. waibeli* (Grote, 1922)*, C. s. ansorgei* (Sclater, 1926)*, C. s. sabotoides* (Roberts, 1932) and *C. s. suffusca* (Clancey, 1958).

Apart from obvious differences in bill size and plumage coloration between the two groups, they also differ with regard to behaviour and physiology. For example, the slender-billed group has never been observed drinking surface water and obtain all their water requirements from their diet and metabolic water. However, members of the thick-billed group have been observed drinking water (Engelbrecht 2012). The phenotypic variation has never been quantified for the eight subspecies of the Sabota Lark and there is a debate as to whether the observed variation in this species simply represents clinal variation along a rainfall gradient, the validity of some subspecies and whether some subspecies, or at least the two groups, represent distinct species (Clancey 1966; de Juana *et al.* 2004; Dean 2005). *Caledulauda sabota bradfieldi* in particular, has also been the centre of a long-standing taxonomic debate and there have been calls for its recognition as a valid species (Roberts 1928; Engelbrecht 2012).

Despite the species widespread distribution in a range of habitats, high reporting rate in suitable environments and the interest shown by taxonomists overs the years, its breeding biology and ecology remains poorly known. From the little information reported about the Sabota Lark, Maclean (1970b) gave the description of the shape of the nest and nest-site characteristics of the species. Keith *et al*. (1992) gives the mean clutch size as 2.3 with a range from 2–4 eggs. The eggs are typically cryptically coloured with a whitish base colour, speckled and spotted with shades of brown and slate with large spots concentrated at the obtuse end (Keith *et al.* 1992).

The Sabota Lark's diet includes a mixture of seeds and invertebrates, with seeds dominating the diet of the thick-billed group and it appears that invertebrates comprise the main component of the diet of the slender-billed group (De Juana *et al.* 2004; Dean 2005; Kopij 2005). Although the diet of the nestlings is not known, it is likely to be mainly invertebrates. There is no data available on any other aspects of the breeding biology of the Sabota Lark.

1.3.1. Current study

Managing our rich biodiversity requires, amongst others, a thorough understanding of all its components. Unfortunately, this is lacking for the majority of species which complicates effective conservation planning. In light of the foregoing it was decided to perform a desktop and field study of the biology and ecology of the Sabota Lark *Calendulauda sabota*. The aim of the desktop study was to collate all the current information in various databases such as the Nest Record Card Scheme (NERCS), the

South African Bird Ringing Unit (SAFRING), the first Southern African Bird Atlas Project (SABAP1) and diet records held by the National Museum, Bloemfontein. Collating all this information will reveal to what extent we can improve our knowledge of the biology of poorly known species by using historic data held in various databases. These databases may shed light on various aspects of a species' biology such as breeding seasonality, habitat and nest-site characteristics, nest dimensions, clutch size, egg dimensions, duration of the incubation and nestling periods, roles of sexes, diet, moult and morphometrics from across the species' range. This information will then be used as a baseline for a thorough field study of various aspects of the biology and ecology of the species as well as a morphometric study of geographic variation in the species using museum study skins. The information gleaned from both the desktop and the field studies will then give an indication of how well the two approaches compare.

The aim of this study was:

- To improve our knowledge of geographic morphological variation and the ecology of the Sabota Lark through desktop and field based research.

The objectives of this study were:

- To collate and summarise all existing information of the species biology and ecology using data from NERCS, SABAP1, SAFRING and the National Museum, Bloemfontein.
- To quantify and describe geographic morphological variation and sexual size dimorphism of the eight subspecies using museum study skins.
- Determine the roles and relative contribution of the sexes in different stages of the breeding cycle, i.e. nest construction, incubation, nestling and post-fledging stages.
- Describe the nest dimensions, structure and site characteristics.
- Describe various egg parameters, including the fresh egg mass (g), egg dimensions (mm), egg elongation index, egg volume and the egg weight coefficient (Kw).

- Determine the duration of incubation and brooding on- and off-bouts of females.
- Determine the rate of food delivery to nestlings and the relative contribution of the sexes to food provisioning.
- Describe the growth and development of nestlings and fit their growth data to a logistical growth curve model.
- Calculate the breeding success of the species independently for the different stages of the nesting cycle, i.e. the laying and incubation, hatching and nestling period.
- Compare the breeding characteristics of the Sabota Lark with other species in the family.
- Determine the diet and relative composition of the diet of nestlings.
- To determine the diet of the adults by analysing the stomach contents of preserved specimens held by the National Museum, Bloemfontein.
- To describe the timing and pattern of primary moult using SAFRING data and museum study skins from across the species' range.

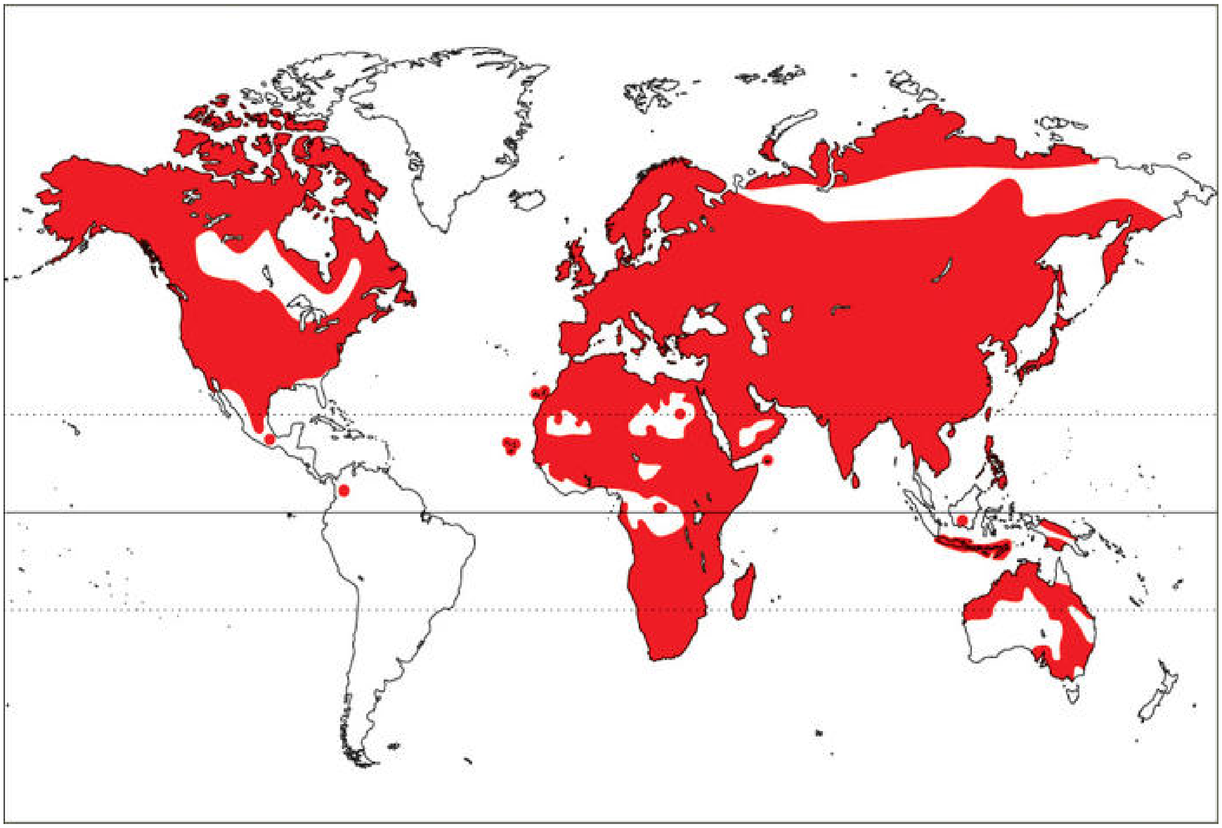

Figure 1.1. The global distribution of the family Alaudidae (de Juana *et al.* 2004).

Plate 1.1. The Sabota Lark *Calendulauda sabota.* (Photo credit: G.D. Engelbrecht).

CHAPTER 2

A desktop study of the biology of the Sabota Lark *Calendulauda sabota*

2.1. Introduction

The Alaudidae forms an important component of the African avifauna. All 21 genera in the family are represented on the continent and approximately 80% of the 96 species occur in Africa, with 60 species endemic to the continent (de Juana *et al.* 2004). The level of endemism and diversity exhibited by the Alaudidae is amongst the highest of any bird family in Africa (de Juana *et al.* 2004).

The Sabota Lark *Calendulauda sabota* is a southern African near-endemic with the largest distribution range of any southern African lark (*cf.* Dean 1997). It occupies a range of habitats ranging from arid and semi-arid savannahs, the Karoo and desert margins of the Namib Desert (Dean 1997). Beyond biogeographical southern Africa, it inhabits the coastal plains of southern Angola and there is also an isolated population in the province of Cabinda in the extreme northwest of Angola (de Juana *et al.* 2004). Throughout its range it is a common resident within its preferred habitat.

Given such a wide distribution range in a variety of habitat types, it is not surprising that the Sabota Lark exhibits considerable phenotypic variation across its range, particularly with regard to overall body size, bill size and shape, and plumage colouration. Furthermore, there are also some behavioural differences between arid western and mesic eastern races. For example, Sabota Larks in the more mesic eastern parts of southern Africa have never been observed drinking surface water (but see Skead 1974), but Engelbrecht (2012) reported individuals representing *C. s. bradfieldi* drinking surface water in the Karoo. Given the considerable phenotypic variation across its range, Dean (2005) recognized eight subspecies in southern Africa. However, differences between some of these subspecies are negligible and based on small sample sizes and it is possible that detailed morphological and genetic studies will show that some of these subspecies may not be valid (Barnes 2007). The nine subspecies are usually divided into two groups, namely a thick- and a slender-billed group. The thick-billed races are sometimes treated as separate species from the slender-billed group but there is only limited genetic evidence to support such a split (de Juana *et al.* 2004). The slender-billed group inhabits the more mesic eastern parts of southern Africa whereas the thick-billed group occupies the arid, western parts of the subcontinent (Clancey 1966). Apart from obvious differences in the size and shape of the bill, the species also conforms to Gloger’s (1833) rule with the eastern races being smaller, and more heavily streaked and darker than western races (Clancey 1966; de Juana *et al*. 2004; Dean 2005). Although the two groups are largely allopatric, the observed variation is said to be broadly clinal with a broad contact zone in the north-eastern Northern Cape Province and the western Free State Province as well as in northern Damaraland in Namibia (Dean 2005).

Despite the prominence of larks amongst the African avifauna, the majority of species are poorly known. This may be attributed to their generally drab appearance, the difficulty in studying small, ground-nesting passerines and their preference for structurally simple habitats in sometimes austere environments. Most studies to date have focussed on resolving taxonomic or phylogenetic issues or describing geographic variation between subspecies (Clancey 1966; Ryan & Bloomer 1999; Barnes 2007; Alström *et al*. 2006; Alström *et al*. 2013). In comparison, there is only limited information available on aspects of the biology of the majority of species. The few detailed biological and/or ecological studies that have been conducted on larks have revealed interesting intra- and interspecific differences in various life history strategies (*cf.* Engelbrecht 2005; Engelbrecht & Mathonsi 2012; Engelbrecht & Dikgale 2014). However, there is a considerable amount of data available in various databases held by different institutions, which may shed some light on aspects of the biology and ecology of several species without the necessity of field studies. For example, Tjørve (2007) showed that Nest Record Card Scheme (NERCS) data can provide valuable insights into a species breeding biology. Other databases which may also prove to contain valuable information include museum records and data collected by various citizen science projects such as the Southern African Bird Atlas Projects (SABAP), bird ringing (the South African Bird Ringing Unit - SAFRING) and the Birds in Reserves Project (BIRP) to name but a few.

In order to undertake large-scale scientific research, enough data needs to be collected. An efficient way to obtain such data is through “citizen science”, a research procedure that involves the public in gathering data (Bhattacharjee 2005; Cooper *et al*. 2007). Citizen science projects have advanced scientific knowledge and helped participants learn about various taxa (Bonney *et al*. 2009). Above all, citizen science projects have proved valuable in finding rare species and even species new to science, as well as assisted with documenting the decline in numbers of native species (Dickinson 2010). To date, citizen science has been used successfully, and several products have been published (Hochachka *et al*. 1999; Hames *et al*. 2002; Cooper *et al*. 2005, 2007; Bonter & Harvey 2008; Bonter *et al*. 2009).

The aim of this study was to perform a desktop study of the biology of the Sabota Lark by collating data in various databases held by museums and other academic institutions. This data have been collected by professional and citizen scientists over many years and represent a largely untapped resource of potentially valuable information about various aspects of a species’ biology. This study has improved our limited knowledge of the biology of the Sabota Lark, and served as a base for a field study on the breeding ecology of the species. It will also reveal to what extent these databases may shed light on the biology of poorly known species. Furthermore, by collating and summarising the data in the various databases, it will contribute to a more comprehensive understanding of the geographic variation, reproductive traits and life history strategies of African larks.

2.2. Methods

2.2.1. Data collection

Data from the following databases held by the Animal Demography Unit (ADU) at the University of Cape Town, South Africa, were used in this study: NERCS, SAFRING and

SABAP1. For analysis of diet, stomach contents were obtained from the National Museum, Bloemfontein.

2.2.2. Breeding

Most records provided insufficient data for calculation of some breeding parameters, e.g. breeding success. The following information was captured from the NERCS records (where provided): breeding seasonality (back dated when possible), habitat and nest site characteristics, clutch size, egg dimensions and descriptions, duration of the incubation and nestling periods and the roles of the parents in breeding. The approximate laying date, expressed as the month in which laying commenced, was estimated assuming 12 days incubation and 11 days nestling period which seems to be the norm for similar sized southern African larks (*cf.* Hockey *et al.* 2005). Data from the SAFRING database was used to determine if the species exhibits sexual size dimorphism, the extent of geographical size variation and the pattern and timing of primary moult in the species. Prior to analysis, SAFRING data were prepared to exclude obvious errors in the data, e.g. excessively high or low values for certain parameters and biometric parameters which were in the wrong columns. The following biometric parameters were included: mass, wing length, culmen length, tail length and tarsus length: The SABAP1 database was primarily used to obtain information on the timing of breeding across the species range. In all instances, locality data was used to assign a record to a specific subspecies (as recognized by Dean 2005) and groups, i.e. slender- or thick-billed. This was done in order to determine if there is geographical variation for any of the parameters analysed in this study. The results were analysed using SPSS version 22 and Microsoft Excel. All results are reported as mean ± SD.

2.2.3. Diet

Stomachs of Sabota Larks representing both the slender- and thick-billed groups were obtained from the National Museum, Bloemfontein. After dissection, the stomach contents were placed in tubes and preserved in 70% alcohol. Each tube was labelled with the museum accession number, subspecies name, locality and date of collection. To analyse the stomach contents, the contents of each stomach were placed in a petridish with 70% alcohol and sorted in the laboratory using a stereo-microscope (Leica EZ4). The contents were classified as grit, plant or animal matter. Plant material included seeds or the remains of, for example leaves or flowers. The only animal matter recorded was of invertebrates and, where possible, this was classified to order level using keys in Scholtz & Holm (1986). Invertebrates were in varying stages of breakdown and they were identified mainly based on features of the head capsule and mandibles since these parts usually remain undigested or persist longer than the softer body parts. Seeds showed varying degrees of resistance to digestion and it was often impossible to distinguish partially digested seeds from other soft parts of a plant.

2.3. Results

2.3.1. NERCS

The NERCS database had a total of 76 nest record cards dating from 1886 to 1992 and represented records from throughout the species’ range. There were interesting fluxes in records over the years (Figure 2.1). Details on cards varied from extremely sparse to very detailed. As the majority of cards represent a single visit, it was not possible to calculate certain parameters such as breeding success.

Breeding seasonality

Analysis of NERCS records showed that breeding has been reported in all months except August. It should be noted that the records are from across the species’ range and it is therefore not surprising that breeding has been reported in most months. Using the backdating technique on cards where sufficient information is provided, laying started in late September, with a peak in February (19.1%, n = 16) followed by a gradual decline in breeding records towards winter. Surprisingly, there were a few records during the winter months, e.g. May (1.2%, n = 1) and July (2.4%, n = 2) (Figure 2.2).

A closer inspection of breeding seasonality revealed geographic variation in the onset of breeding between the thick- and slender-billed groups. The slender-billed group started breeding towards the end of September, peaking in December, followed by a decline in breeding with single records each in March and April. The thick-billed group started breeding in January until July with a peak in February and with single records each in May and June. There was a single “aseasonal” breeding record for the thick-billed group in October (Figure 2.3).

Habitat and nest-site characteristics

Fifty four (71.1%) of the NERCS cards provided information about the species preferred habitat and nest-site characteristics. Most records described the macro-habitat as open *Acacia* savanna with sparse vegetation cover. Most nests (51.3%, n = 39) were built at the base of a grass tuft. The grass species that are mentioned include *Brachiaria* spp., *Stipagrostis uniplumis*, *Stipagrostis hochstetteriana* and *Monachina genestifolium.* Thirteen nests (17.1%) were situated adjacent to a forb, e.g. a “composite”, a “small succulent plant”, *Rhigozum* shrub, small *Aloe* species such as *A. davyana* and *A. transvaalensis*, and saplings of *Acacia* spp. or *Colophospermum mopane.* One nest was placed underneath a rock and another beneath a dry cowpat.

Nest description

Most records described the typical domed nests of the genus, but there appears to be considerable variation with regard to how well the dome is developed. Descriptions of the dome varied from “flimsy” and “partial” to “thick” and “well developed covering the entrance”. Interestingly, two records explicitly mentioned the absence of a dome.

Two records included descriptions of an apron, i.e. an extension of the nest entrance. In both instances the material used for the apron was dead grass. NERCS nest entrance records (n = 12) revealed a preference for nests entrances facing in a southerly direction with 41.7% of the nests facing south, 16.7% south-west and 8.3% south-east. Two nests faced north (16.7%) and another two faced east (16.7%).

Description of the eggs, their dimensions and clutch size

All records described the eggs as having a white base and speckled with brown and grey spots, with the spots more concentrated at the obtuse end. A summary of the egg dimensions and clutch sizes for the thick- and slender-billed groups reported on NERCS cards are presented in Table 2.1. Once again the results showed evidence of geographical variation in egg dimensions and clutch size. Not surprisingly, eggs of the thick-billed group tended to be larger than those of the slender-billed group albeit not statistically significant (Mann-Whitney U test, $P > 0.05$). Clutch sizes ranged from 1 to 5 (mean = 2.6 ± 0.7, n = 67) but the mean clutch size of the thick-billed group was significantly larger than that of the slender-billed group (T-test, $P < 0.001$) (Table 2.1).

Duration of the incubation and nestling periods and breeding success

Very few nests included multiple observations over a sufficiently long period to determine the duration of the incubation and nestling periods or breeding success. However, one record indicated that incubation is at least 10 days long, and most records of the nestling period showed that nestlings are fully feathered and capable of moving around when 10 days old. There was also a record that reported fledged young flying approximately 10 m just after fledging.

2.3.2. SABAP1

Breeding seasonality

SABAP1 breeding records (n = 87) represent the species entire range. SABAP1 breeding records span all months of the year except July, with the highest reporting rate during the wet season in southern Africa, i.e. from October to April (92.0%, n = 80). Once more the results showed geographical variation in the onset of breeding between the thick- and slender-billed groups. The breeding season of the former lasted from August to May, but breeding peaked in March/April. For the slender-billed group, SABAP1 breeding records spanned August to June, but with a definite peak between November and January. Most records from the extremes of the breeding seasons were single records and may represent opportunistic breeding attempts (Figure 2.4).

2.3.3. SAFRING

Geographical variation and sexual size dimorphism (SSD)

The SAFRING database contained mensural data for n = 488 individuals. As not all parameters were recorded for every individual, and since males and females appear monomorphic in the hand, most records stated “sex unknown”. Thus, sample sizes of known sex were too small for any meaningful statistical analysis of sexual dimorphism. Following preparation of the SAFRING data for analysis, the results of males and females were pooled for both groups. The results revealed significant size differences between the thick- and slender- billed groups of the Sabota Lark for mass and length of the wing chord and culmen length (Mann-Whitney U-test, $P < 0.05$), but not for tail and tarsus length (Figure 2.5).

Moult

The analysis of primary moult data from the SAFRING database revealed a post-breeding moult strategy which started in February/March, with primary moult completed in about May/June for the slender-billed group. The limited data for the thick-billed group confirms a post-breeding moult with primary moult 50–70% completed by June/July, suggesting a later onset of primary moult.

2.3.4. Diet

Analysis of stomach contents (n = 35) of the Sabota Lark’s showed that their diet includes a mixture of vegetable matter (mainly seeds) and invertebrates, with a small amount of grit present in all stomachs (Plate 2.5). One stomach contained small pieces of glass which was recorded as grit (Plate 2.5). The majority of stomachs (91.4%) contained grass seeds (vegetables). Invertebrate remains included mostly beetles (Coleoptera, 57.1% of stomachs) and termites (Isoptera, 54.3% of stomachs). Other invertebrates recorded were ants (Hymenoptera, 11.4%) and grasshoppers (Orthoptera, 8.6%) (Plate 2.1–2.6). The percentage of stomachs that contained a given order of invertebrates is presented in figure 2.6. There were single records of a soft-bodied worm, a small snail, maggots (Diptera) and a faecal sac in stomachs.

2.4. Discussion

NERCS records showed interesting temporal variation in the number of records submitted over the years. The periods when there were a marked decrease in the number of cards submitted appears to coincide with periods of global and national instability (Figure 2.1). For example, there were no records in the 1930's which coincided with the Great Depression of the early 1930's. There were also no records for the period 1940–1945 which coincided with World War II when there were other priorities to natural history studies. The majority of NERCS records (63.2%, n = 48) date from the mid-1960s to mid-1970s when there was a resurgence in interest in natural history studies. Since then, there has been a marked drop in records and this period once again coincides with political instability in South Africa and its neighbouring countries. The last record for the Sabota Lark in the NERCS database was in 1992 and it is possible that political restructuring and a shift in priorities may be responsible for the absence of records since then. There has also been a global shift in which funding agencies view natural history research. The present emphasis is on high-tech, high turn-over studies and very few funding agencies provide financial support for long-term natural history studies. With technological innovation, there has also been an explosion of various citizen science projects. This may have resulted in the pool of potential citizen scientists dividing their efforts between several projects. However, this does not explain why no new records have been submitted to NERCS since 1992 whereas other projects flourish. In light of the above, the NERCS manager/s may have to rethink their "marketing" strategy.

Breeding seasonality

The timing of breeding is a very important factor determining the reproductive performance of birds. Birds respond to conditions such as temperature, rainfall, food abundance or the availability of nesting materials for suitable breeding and to maximize their breeding success (Immelman 1971; Lloyd 1999; Dawson *et al.* 2001; Barrientos *et al.* 2007). The results of the analysis of NERCS and SABAP1 breeding records confirm that breeding in both groups coincided with the wet season (Dean 1997). This is also the general pattern for most southern African passerines and in particular the mirafrid larks (*cf.* Hockey *et al.* 2005). However, the peak of the breeding season differed between the thick- and slender-billed groups. The slender-billed group's peak breeding was between November and January which coincides with the peak of the wet season in the eastern parts of the sub-continent that this group inhabits (Hockey *et al*. 2005). The thick-billed group's breeding season peaked a few months later with most records in February to April. Once again, this coincides with the peak of the wet season in the north-western parts of the subcontinent. Although both groups appear to have an extended breeding season, the reality is that there are very few breeding records outside the two breeding peaks. The breeding records in mid-winter and October for the large-billed group may relate to opportunistic breeding in response to erratic rainfall in the arid areas this group generally inhabits. However, it is also possible that observer effort is lower during the colder, winter months, resulting in fewer records during this period. Observer effort in relation to season may be difficult to quantify though.

Habitat and nest site characteristics

The preferred habitat of the Sabota Lark as revealed by analysis of NERCS records is similar to that described in the literature (Dean 2005). They prefer to nest in open areas with sparse grass cover as this enables incubating bird sufficient view to see potential predators from a distance away, yet provide sufficient cover to conceal the nest. The majority of nests were placed adjacent to vegetation which further assists with concealment, but also helps to create a favourable micro-climate in the vicinity of the nest (de Juana *et al*. 2004).

Nest entrance orientation may have an influence on the embryonic development, breeding success and nestling growth (Cook *et al*. 2003; Lloyd & Martin 2004). Despite the small sample size, nest entrance directions were randomly spaced although there was a tendency for nest entrances to face in a southerly direction. The nests of many ground-nesting species in southern Africa are biased towards facing in a southerly direction as this provides at least some shade during the heat of the day, e.g. Pink-billed Lark *Spizocorys conirostris* and Chestnut-backed Sparrow-lark *Eremopterix leucotis* (Engelbrecht & Mathonsi 2012; Engelbrecht & Dikgale 2014). Thus, the nest entrance direction may also contribute to creating a suitable micro-climate within the nest. However, unlike the Pink-billed Lark and Chestnut-backed Sparrow-lark which construct open nests, Sabota Larks build domed nests which provide some shade to the nest contents. This questions the thermoregulatory hypothesis of facing nest entrances in a southerly direction. Future studies on the nest micro-habitat characteristics of the Sabota Lark should establish whether or not nest entrance directions are randomly distributed or not.

Nest description

Like other *Calendulauda* species, the nest of the Sabota Lark is a domed cup, lined with finer grasses and rootlets. The presence of a dome is considered to be a diagnostic feature of larks in the mirafrid clade, which includes the genus *Calendulauda* (Barnes 2007)*.* It is worth noting that two records indicated that the nest was undomed. This suggests that the presence of a dome is not necessarily a diagnostic feature of mirafrid larks. There was also considerable variation with regard to how well the dome was constructed. Descriptions of the dome ranged from “flimsy” and “partial” to “thick” and “well developed covering the entrance”. It has been suggested that variation in dome shape vary with experience of individuals with inexperienced or first time breeders tending to construct nests without a dome and more experienced breeders enclose their nests (Boyer 1988). Thus, an element of learning may be involved in nest construction (Boyer 1988). Variation in the quality of lark nests has been reported in several studies (Engelbrecht 2005; Engelbrecht & Mathonsi 2012; Engelbrecht & Dikgale 2014).

Two NERCS records mentioned the presence of an apron i.e. an extension of the nest entrance, sometimes referred to as a “rampart”. In cup-shaped nests, the extension may encircle the entire nest or only partially, whereas in domed nests it extends from the entrance. Different materials are usually used to build an apron and they differ from species to species. Species such as Chestnut-backed Sparrow-lark and Pink-billed Lark include sticks, small stones, animal dung and earth clods for their aprons (Tarboton 2011; Engelbrecht & Mathonsi 2012; Engelbrecht & Dikgale 2014). There is much speculation about the functional significance of an apron and hypotheses suggest improving camouflage, thermoregulation and experience (Orr 1970; Afrik *et al*. 1991; de Juana *et al.* 2004; Engelbrecht 2005; Engelbrecht & Dikgale 2014).

Egg descriptions, egg dimensions and clutch size

The description of eggs on NERCS cards is similar to that given by Dean (2005). According to Maclean (1970), dark spotted eggs of *Mirafra* spp. and *Spizocorys conirostris* are usually associated with disruptive backgrounds such as tall grass or tumbled rocks. Although eggs tended to be larger for the thick-billed group (not statistically significant though), this may simply be due to the larger overall size of this group.

The mean clutch size of 2.5 in this study corresponds well with the mean clutch size of 2.3 reported for the species across its range (Keith *et al.* 1992). There was an unusual record of a clutch of five eggs in the NERCS database which is larger than the clutch size of any southern African lark. This is clearly unusual and may be a case of egg-dumping by another female/s (Gill 1995) or a case of mistaken identity by the observer.

According to the NERCS records, the Sabota Lark exhibits geographic variation in clutch size: the thick-billed group had significantly ($P < 0.005$) larger clutch sizes compared with the slender-billed group. This is unusual as other studies of larks found a general tendency for clutch sizes to decrease with an increase in aridity (Tieleman *et al*. 2004).

Duration of the incubation, nestling periods and breeding success

Incubation periods in larks vary from 11–17 days and it is usually undertaken by females only (de Juana *et al*. 2004). However, a few species share incubation and brooding duties such as *Eremopterix* and *Spizocorys* larks. Very few cards are sufficiently detailed to provide information such as duration of the incubation or nestling period, but there is a record which indicated that incubation is at least 10 days long. Furthermore, the records show that nestlings are fully feathered and capable of moving around at age 10 days. Most lark nestlings are able to walk or hop around from age 8–10 days and fledge at around 9–12 days old (de Juana *et al.* 2004; Donald 2004; Engelbrecht 2005; Maphisa *et al*. 2009). The NERCS cards therefore seem to provide a reasonable estimate for the duration of the nestling period of the Sabota Lark.

Geographical variation and sexual size dimorphism

There were significant size differences between thick- and slender-billed Sabota Larks for some parameters. Unfortunately, the true extent of geographic size variation in the Sabota Lark is masked as males and females of each group were pooled due to small sample sizes if they were separated. A source of additional variation that cannot be accounted for is observer differences in measurements and the results must therefore be interpreted with caution.

Moult

Little is known of the timing and pattern of moult in larks. Timing and duration of moult are very important because they can have an impact on the birds breeding success and future survival (Gill 1995). Reduction in flight performance during moult, may affect bird’s ability to escape from predators (Gill 1995). Since moult is an energy demanding aspect of a bird’s annual cycle (Lindström *et al*. 1993; Klaassen 1995; Murphy 1996; Langston & Rohwer 1996), most larks follow the general pattern of a complete post-breeding moult to avoid the competing demands of breeding and moulting at the same time (de Juana *et al.* 2004). Another reason why moult and breeding do not overlap is the inherent, genetically programmed circadian rhythms of birds which dictates when these activities take place within the annual cycle (Van Niekerk 2009). In some species, particularly within the tropics, an overlap in moult and breeding sometimes occur as well as in areas with irregular rainfall where there is opportunistic breeding (Payne 1969; Foster 1975; Britton 1978; Moreno 2004). The usual post-breeding moult is rapid and takes advantage of food abundance following rains, and the second moult is prolonged and occurs throughout the dry season (de Juana *et al*. 2004). However, some species such as Gray’s Lark *Ammomanopsis grayi*, Stark’s Lark *Spizocorys starki* and Grey-backed Sparrow-lark *Eremopterix verticalis* of the Namib Desert in Namibia have two (complete) annual moults (Willoughby 1971; de Juana *et al*. 2004).

Analysis of data in the SAFRING database shows that the Sabota Lark undergoes the usual lark pattern of scheduling moult to commence at the end of the breeding season. Since the two groups exhibit geographical variation in the onset and termination of their breeding seasons, it is not surprising that there is geographic variation in the onset of moult. The slender-billed group started February/March and completed moult in about May/June in the eastern part of southern Africa, whereas the thick-billed group was only 50–70% completed in about June/July. The results of this study contradict Hall's (1956) finding that moult of the slender-billed group in north-eastern Botswana was nearly completed in November. Since it is not clear which feathers were moulting, it complicates providing an explanation for this seemingly out of season strategy. It is possible that it may be a partial pre-breeding moult or perhaps only the inner secondaries that were replaced as is common for larks (Herremans & Herremans 1992; de Juana *et al.* 2004).

Diet

Generally, larks have a mixed and varied diet of seeds and invertebrates, depending on the species bill morphology or foraging behaviour (de Juana *et al.* 2004; Donald 2004). Larks exhibit different foraging behaviour, e.g. species such as Rufous-naped Lark *Mirafra africana*, Karoo Lark *Calendulauda albescens* and Dusky Lark *Pinarocorys nigricans* sometimes scratch through herbivore dung searching for undigested seeds or larvae of coprophagous beetles, the Large-billed Lark *Galerida magnirostris* digs for its food, while the Greater Hoopoe-lark *Alaemon alaudipes* extracts beetle larvae from the sand (de Juana *et al*. 2004). Southern African larks can conveniently be divided into resident insectivores, nomadic insectivores, resident granivores and nomadic granivores with respect to their main diet and nature of seasonal movements (Dean & Hockey 1989; Kopij 2005). However, there are many exceptions to this and some species may have seasonal shifts in dietary preferences. In species such as Spike-heeled Lark *Chersomanes albofasciata*, males have longer bills than females. This sexual size dimorphism in bill morphology may be related to feeding habits since it is more evident in insectivorous species than granivorous species (Burton 1971; de Juana *et al*. 2004). This type of adaptation is believed to reduce competition for food between sexes in arid environments where resources are limited (Cramp 1988).

The analysis of stomach contents revealed that the diet of both groups included a mixture of vegetable matter, e.g. leaves and seeds, and invertebrates. According to

Willoughby (1971) and Kopij (2005) the species is primarily granivorous and occasionally feeds on insects. Willoughby's (1971) records are based on specimens representing the thick-billed group, but Kopij's (2005) samples included specimens representing both groups. The results of this study confirm the findings of these authors, irrespective of the different habitat types in which the specimens were collected.

There is a correlation between diet and the need to drink water in most species of larks. More granivorous species tend to drink water regularly, while insectivorous species fulfil their water requirements through their diet and metabolic processes (Williams 1996; Williams & Tieleman 2001; Tieleman *et al.* 2004). The thick- and slender-billed groups differ with regard to behaviour, bill morphology and possibly physiology (Engelbrecht 2012). Although Skead (1974) mentions that the Sabota Lark "occasionally" drinks water, there are no other records in the literature. According to Engelbrecht (2012), slender-billed Sabota Lark do not drink water, nor were any birds observed drinking during the course of this study. However, Engelbrecht (2012) observed individuals representing the thick-billed group drinking water, suggesting that their diet may comprise a larger portion of seeds. Future studies on the diet of this species should attempt to look at seasonal and regional variation.

2.5. Conclusion

The results of this desktop study showed that various databases exist with a wealth of information which may contribute to our knowledge and understanding of the life history of poorly known species. The present study provided valuable information on the breeding biology and ecology of the species. The study revealed geographical variation in body size, the onset of the breeding season, clutch size and moult. The results of this study also confirm the previous findings that the Sabota Lark's diet includes a mixture of vegetable matter and invertebrates, but it is not clear if the species exhibits geographical variation in its diet. Future studies on the diet of the species should determine if there is seasonal and regional variation in the diet of this species.

Table 2.1. Egg dimensions (thick-billed: n = 12 eggs; slender-billed: n = 9 eggs) and clutch sizes (thick-billed: n = 26; slender-billed: n = 41) of the thick- and slender-billed groups of Sabota Lark *Calendulauda sabota* as obtained from NERCS records. Significant differences were set at $P < 0.05$.

	Thick-billed	**Slender-billed**	
	Mean ± SD., range	Mean ± SD., range	*P*
Length (mm)	21.2 ± 0.7, 19.9–21.8	20.6 ± 0.8, 19.6–21.8	0.3
Width (mm)	15.4 ± 0.3, 14.9–15.7	15.2 ± 0.5, 14.3–15.6	0.3
Clutch size	2.9 ± 0.8, 1–5	2.3 ± 0.5, 1–3	< 0.001

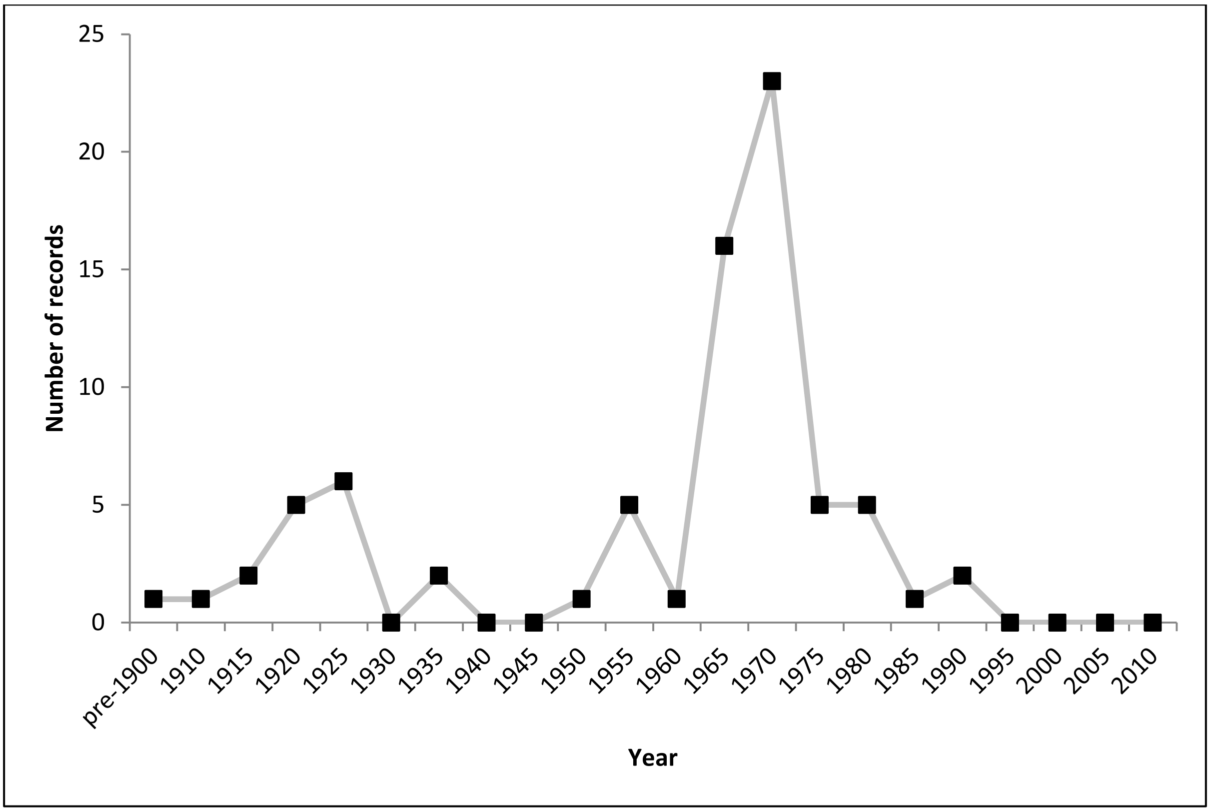

Figure 2.1. Temporal distribution of NERCS cards of the Sabota Lark *Calendulauda sabota* from 1886–2010 to the present (n = 76).

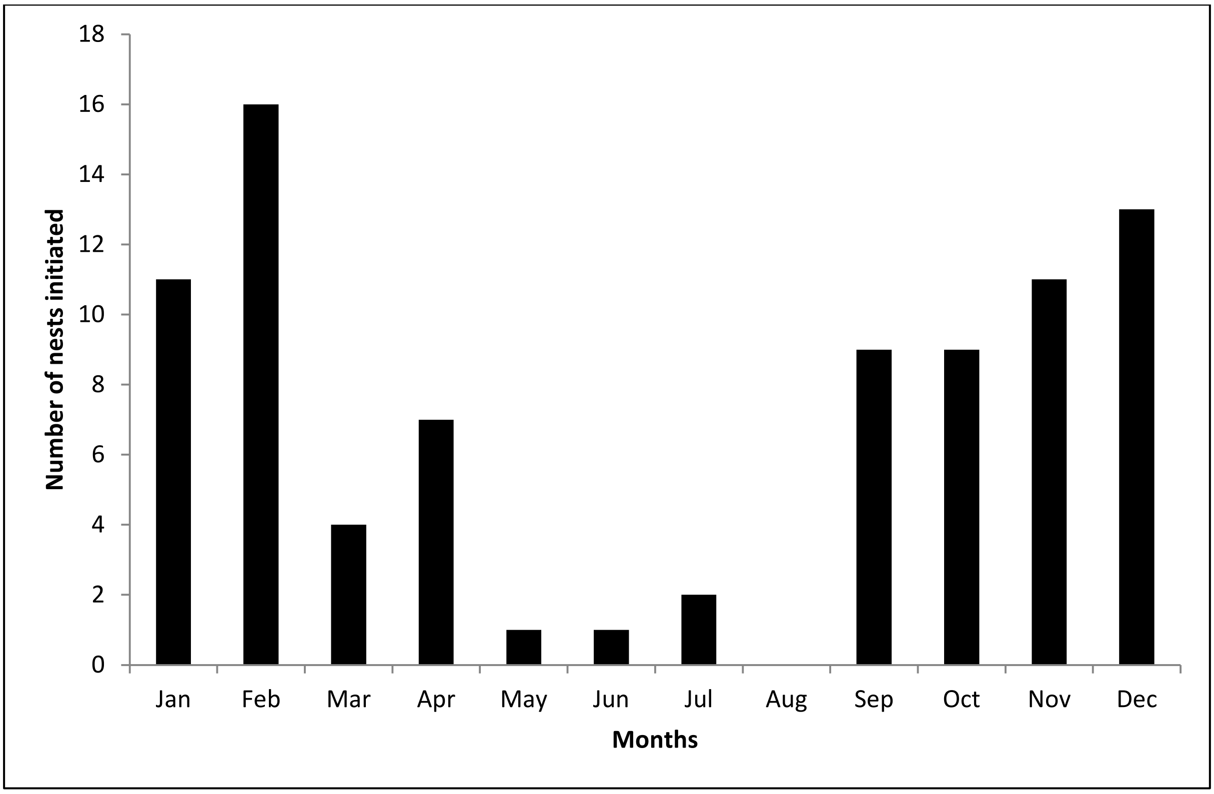

Figure 2.2. Frequency of Sabota Lark *Calendulauda sabota* nests reported with eggs or nestlings from 1886–1992 (n = 76) as obtained from the NERCS database.

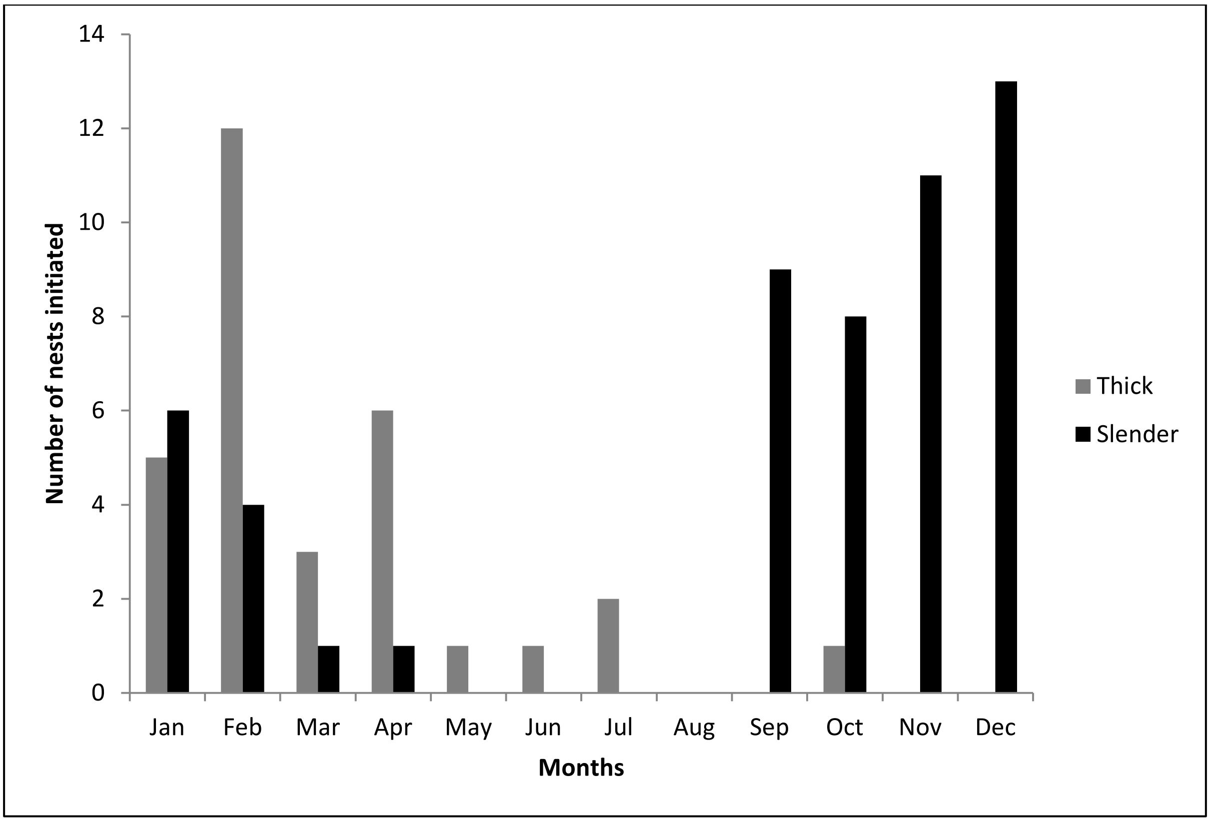

Figure 2.3. Seasonal and geographical variation in the onset of breeding of the slender- and thick-billed groups of the Sabota Lark *Calendulauda sabota* from across the species range. Data obtained from the NERCS database.

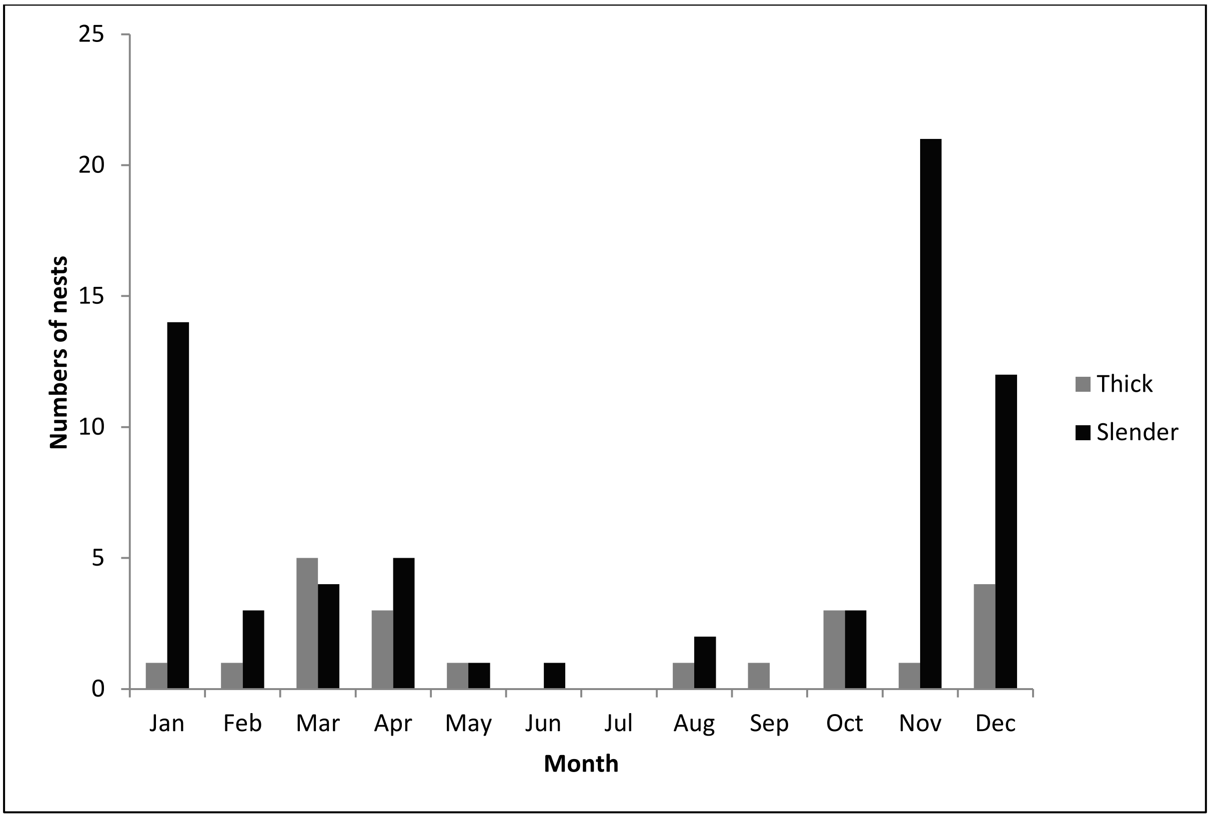

Figure 2.4. Records of the breeding activities of the thick- and slender-billed groups of the Sabota Lark *Calendulauda sabota* across its range. Data obtained from the SABAP1 database.

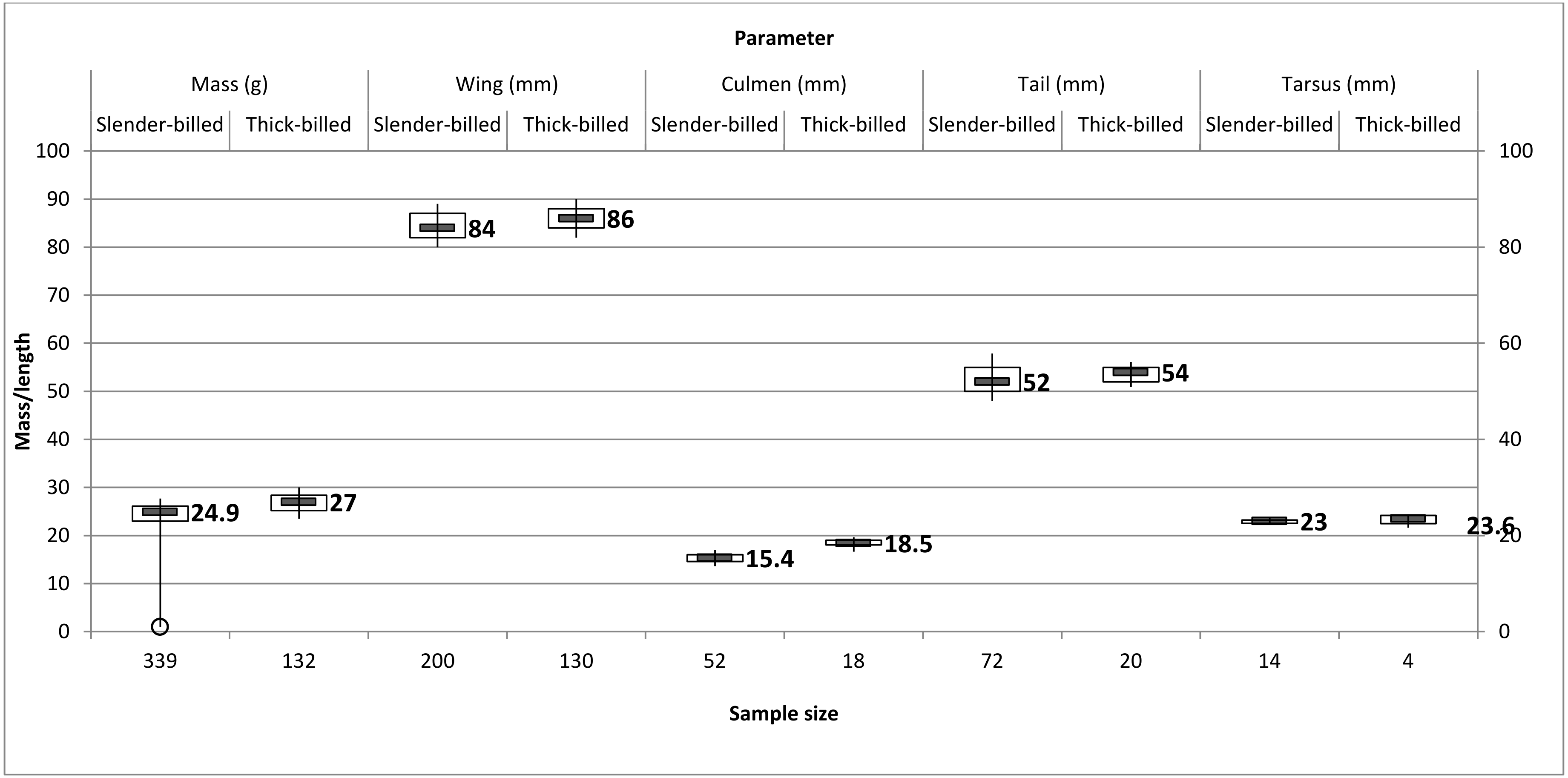

Figure 2.5. Mass and biometrics of adult slender- and thick-billed Sabota Larks *Calendulauda sabota* in the SAFRING database. The box represents the interquartile range "x" represent the maximum and minimum values and the solid bar the median.

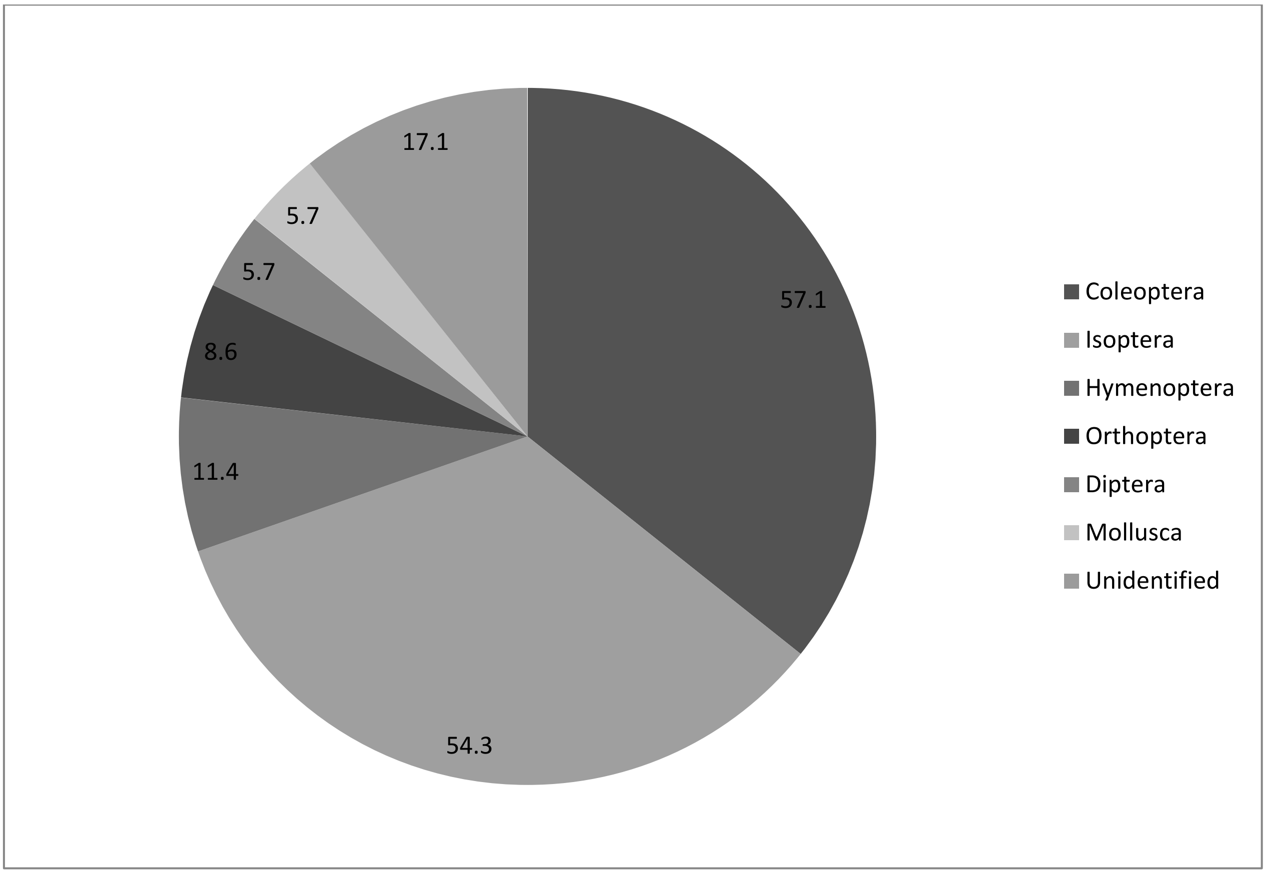

Figure 2.6. Composition percentage of invertebrates found in the Sabota Lark C*alendulauda sabota* stomachs.

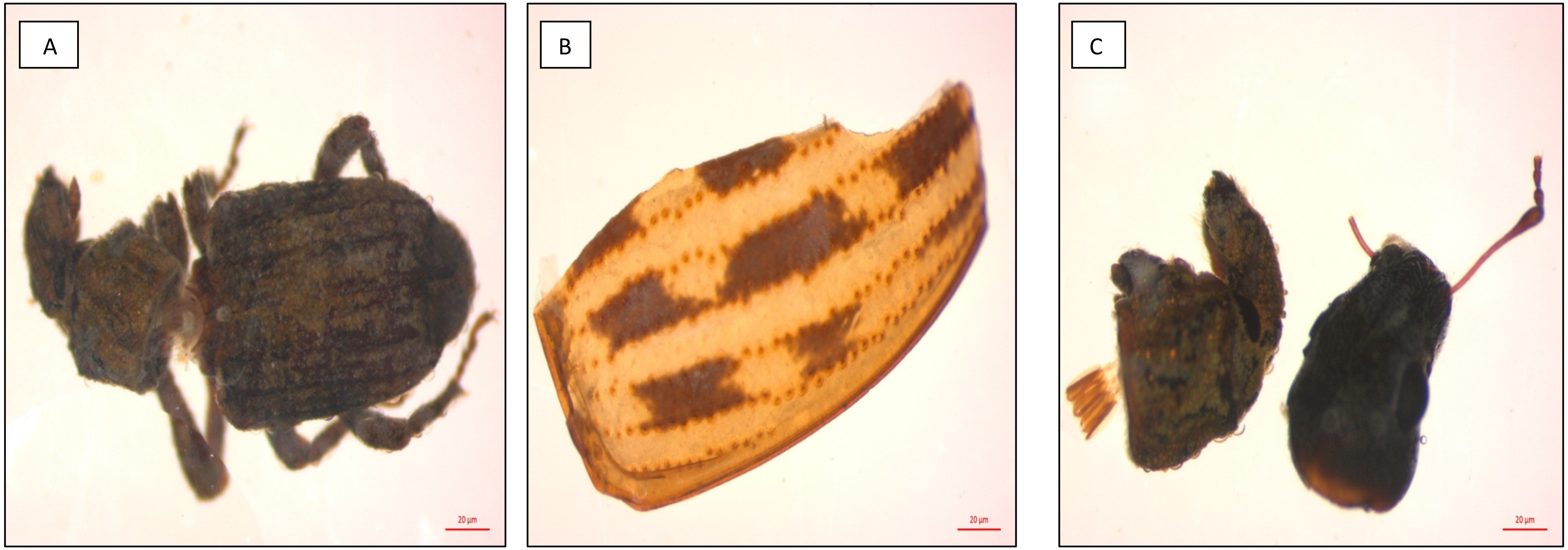

Plate 2.1. Different body parts of beetles (Order Coleoptera) found in the stomach of the Sabota Lark *Calendulauda sabota*, (A) full body part, (B) wing and (C) head regions.

Plate 2.2. Different body parts of ants (Order Hymenoptera) found in Sabota Lark *Calendulauda sabota* stomachs, (A) full body part, (B) legs and thorax, and (C) full body part.

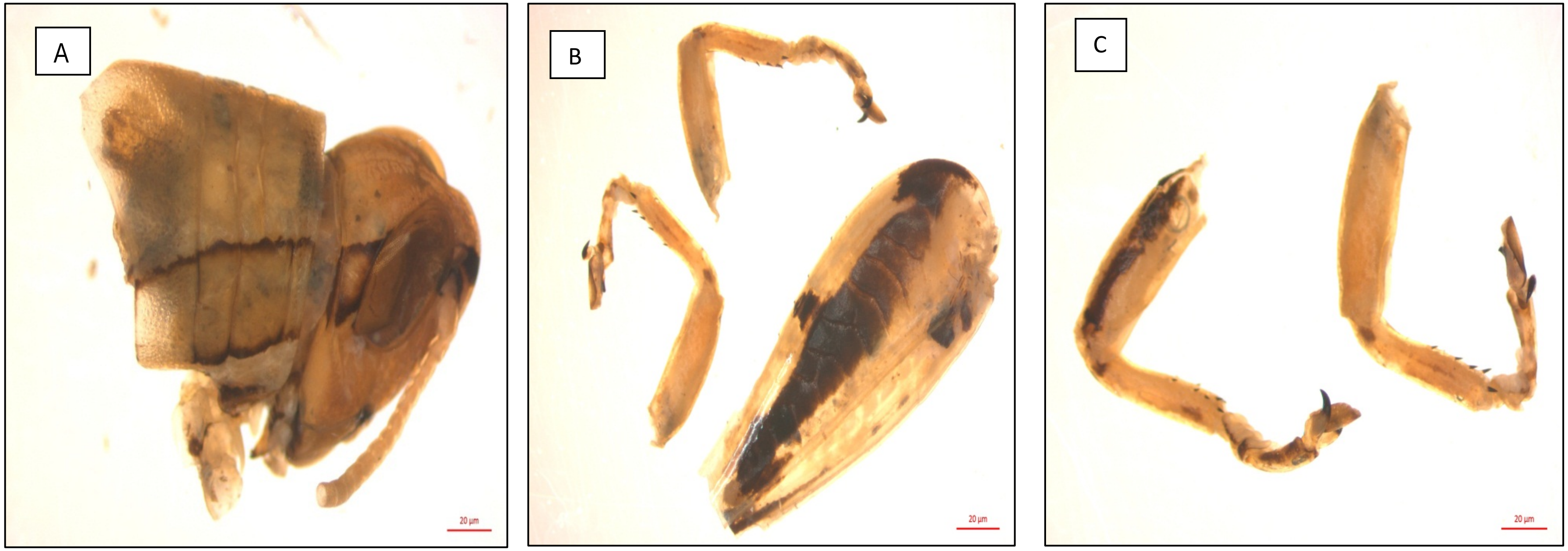

Plate 2.3. Different body parts of grasshoppers (Order Orthoptera) found in Sabota Lark *Calendulauda sabota* stomachs, (A) head, (B) and (C) legs.

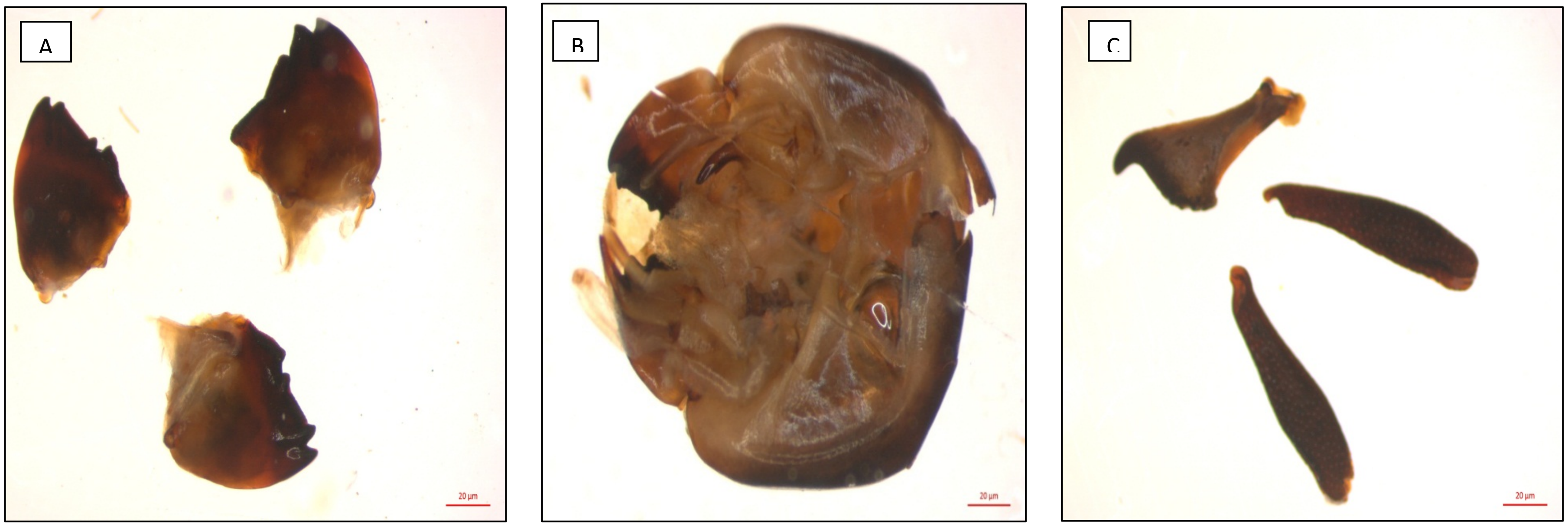

Plate 2.4. Different body parts of termites (Order Isoptera) found in Sabota Lark *Calendulauda sabota* stomachs, (A) and (B) mouth parts, and (C) legs.

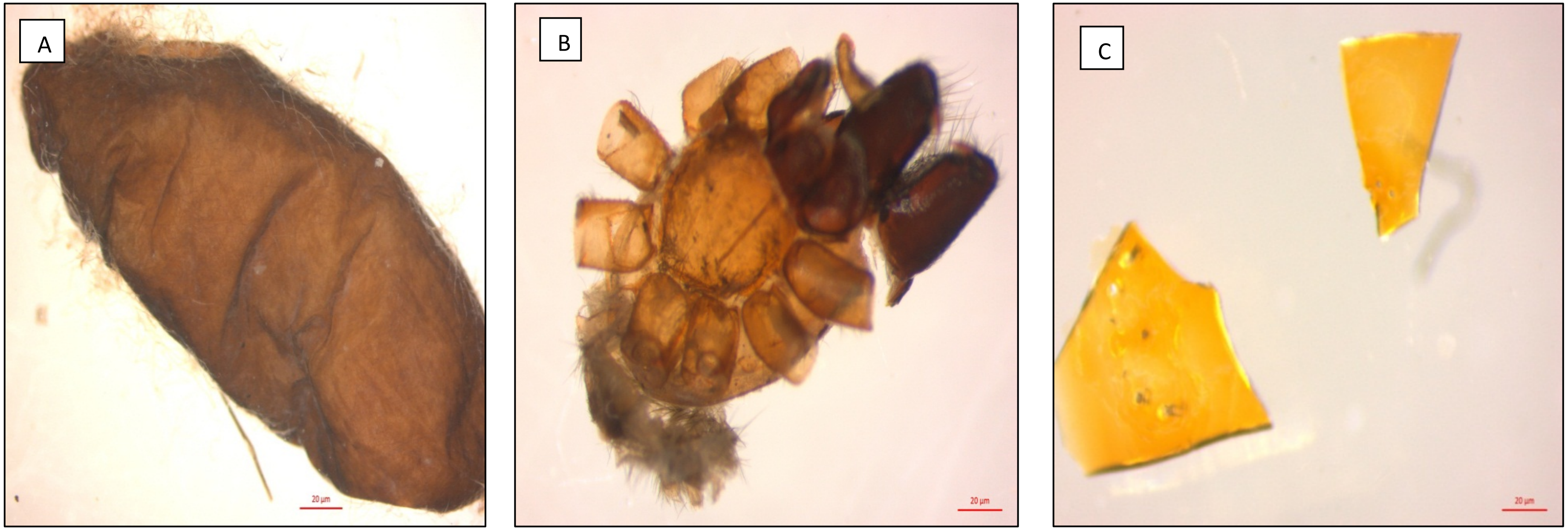

Plate 2.5. Different items found in Sabota Lark *Calendulauda sabota* stomachs, (A): the faecal sac, (B) Arachnid (spider) and (C) pieces of glass probably used as grit.

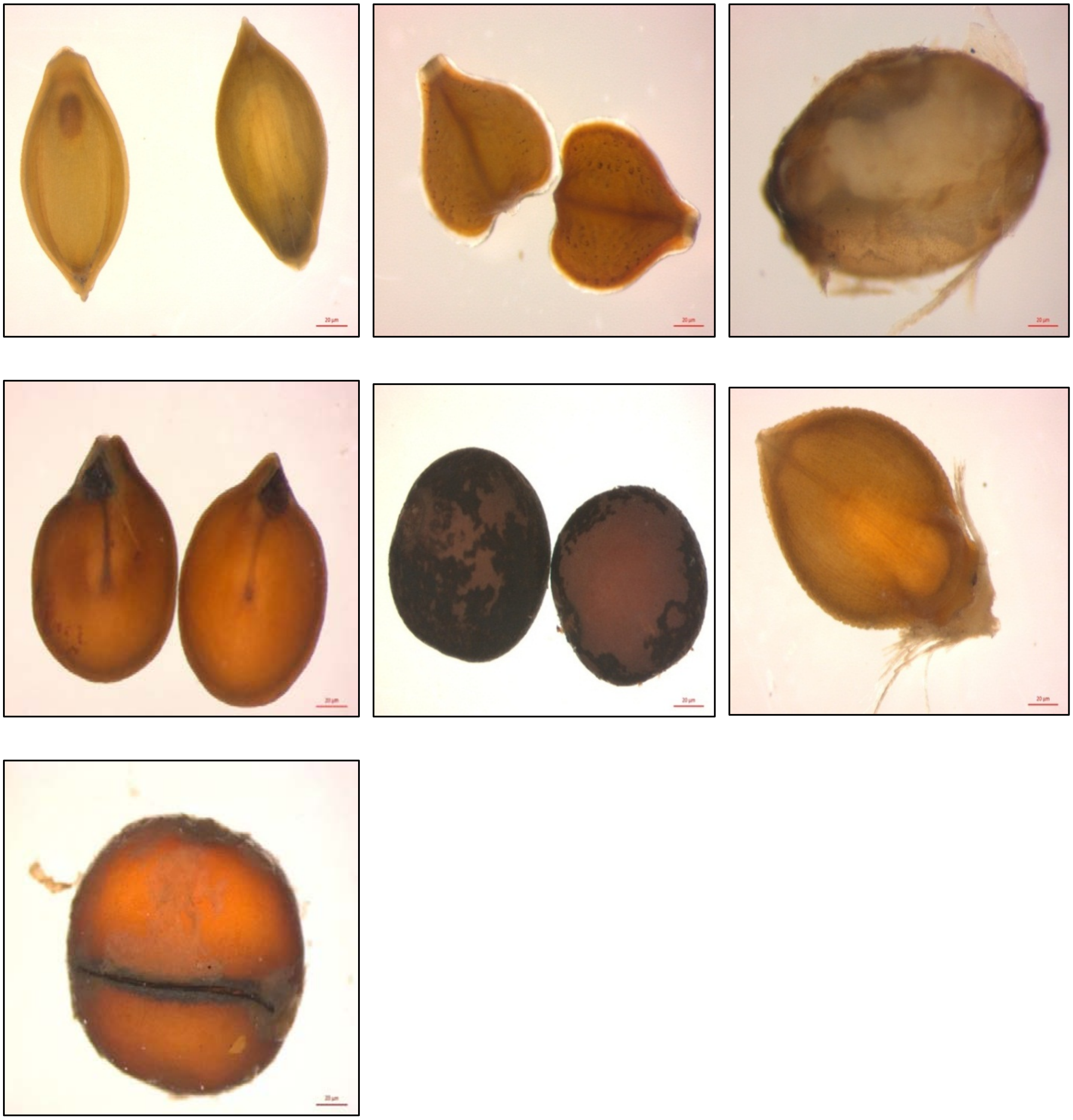

Plate 2.6. Different types of seeds found in the Sabota Lark *Calendulauda sabota* stomachs.

CHAPTER 3

Nesting ecology of the Sabota Lark *Calendulauda sabota* in the Limpopo Province, South Africa

3.1. Introduction

The larks represent a speciose family of approximately 96 species of medium-sized passerines inhabiting structurally simple, sparsely vegetated habitats in deserts, semi-deserts, grasslands, savannahs, rocky plains and steppes (Cramp 1988; de Juana *et al.* 2004). The family is remarkably diverse in aspects such as diet, water requirements, types of vocalizations (including the ability to perform inter-specific mimicry), display flights, and the types of movements they exhibit (de Juana *et al.* 2004; Engelbrecht & Mathonsi 2012). As such they provide an ideal opportunity to elucidate questions related to the evolution of various life history characteristics. Unfortunately our generally poor knowledge of these characters hinders attempts to explain the evolution of these characters.

The breeding ecology and nesting success of most lark species are generally poorly known. For the majority of species, particularly those in Africa, breeding information is limited to anecdotal observations or brief descriptions of one or two aspects of its ecology. However, well documented studies on the breeding ecology of species can contribute to the development or testing of various life history theories. Furthermore, such studies are the core foundation to understanding variation in reproductive strategies because they provide important natural history data which may make a meaningful contribution to successful biodiversity, habitat management programmes, and improve our knowledge and understanding of birds (Roff 1992; Stearns 1992; Dowling 2003).

In an attempt to address this gap in our knowledge of African larks, I present data on the breeding ecology of the Sabota Lark *Calendulauda sabota* collected in South

Africa's Limpopo Province. According to the first Southern African Bird Atlas Project (SABAP1), the Sabota Lark is the most widespread lark in southern Africa (*cf.* Harrison *et al.* 1997). Given its widespread geographic range, it is not surprising that the species exhibits the greatest geographic variation in size, bill shape and size, plumage variation, behaviour, physiology, diet and some breeding parameters of any other lark (see Chapter 1; Clancey 1966; Engelbrecht 2012). Its phenotypic geographic variation has resulted in a detailed taxonomic study by Clancey (1966), resulting in the recognition of nine subspecies, although only eight are found in southern Africa. These eight subspecies are divided into two groups occupying different parts of the subcontinent. There is evidence of geographical variation in certain ecological parameters (see Chapter 2). Ecological information about the species is generally sparse: Willoughby (1971) and Dean (2005) provided details of the species' diet, Maclean (1970a) described the nest structure and dimensions and entrance directions of nests in the Kalahari Desert and Keith *et al.* (1992) gave information on the breeding success based on a sample of seven nests. Apart from these studies, little else is known about the species breeding ecology. For example, we lack information about basic breeding parameters such as the duration of the incubation and nestling periods, growth and development of young, roles of the sexes in the breeding cycle (Dean 2005). The aim of the present study was to describe in detail for the first time the breeding ecology of one of the most common and widespread southern African larks. The results of this study can then serve as a basis for future studies investigating geographic variation in breeding parameters and other life history strategies of the Sabota Lark as revealed in Chapter 2.

3.2. Materials and methods

3.2.1. Study site

The study was conducted on the Polokwane Plateau, mainly in the Polokwane Nature Reserve (PNR) (23°58'S, 29°28'E; 1 350 masl) and at Al3 De Loskop (DLK) farm (23°30'S; 29°19'E; 1090 masl) Limpopo Province, South Africa. The Polokwane Plateau falls within the savannah biome. The vegetation in PNR is described as Polokwane

Plateau Bushveld and is characterised by open *Themeda* grassland with scattered *Acacia* trees and bush clumps (Mucina & Rutherford 2006). DLK is situated in the Makhado Sweet Bushveld vegetation unit and is characterised by a mixture of short, open, *Acacia*-dominated scrub with a poorly developed grass layer, fallow lands, crop fields and a perennial earth dam. Both sites experience a moderate climate with a mean summer day-time high of 28°C and a mean night-time low of 5°C. The area is situated in a summer rainfall region with a mean annual precipitation (MAP) of 478 mm (Mucina & Rutherford 2006).

3.2.2. Nest searching and monitoring

Breeding data of the Sabota Lark were collected during the 2011/2012 and 2012/2013 breeding seasons. The onset of the breeding season was determined by weekly visits to the study areas throughout the year and using parental behaviour cues such as carrying nesting material, food or faecal sacs. Once the first evidence of breeding activity was recorded, nest searches were carried out 2–3 times a week. When a nest was found, data were usually recorded every 2–3 days while the nest was active, but sometimes daily to determine critical parameters such as duration of the incubation and nestling periods.

3.2.3. Clutch size and egg data

At each nest, clutch size was recorded as the number of eggs or young, i.e. the brood size present at the time. Egg dimensions (maximum length and width, to the nearest 0.1 mm) were recorded using Vernier callipers and mass (weighed to the nearest 0.1 g) was determined using a portable digital scale. Fresh egg mass (FEM) was taken as the mass of an egg measured within four days of laying. Egg volume (V) was calculated according to the formula $V = LW^2$, where L = maximum length and W = maximum width (Hoyt 1976). The fresh egg mass was used to calculate an egg weight coefficient (K_w), as described by Hoyt (1979): $K_w = mass/L \times W^2$. The weight coefficient was used to estimate the mass of eggs (EEM) found to be older than three days and the resulting EEM was used to assess female investment in each clutch, by expressing total clutch mass as a percentage of the mean mass of an adult female. An index of egg elongation was calculated as L/W (Preston 1969).

3.2.4. Nestling growth and development

To assist with individual identification, nestlings were marked initially on the thigh with a non-toxic marker pen and later with a SAFRING metal ring and two colour rings when they were 7–8 days old. Nestling growth and development parameters were recorded within the first 90 min after sunrise every 1–3 days for the duration of the nestling period. Parameters recorded include: plumage development, mass measured using a portable digital scale (to the nearest 0.1 g), length of the tarsus, head length and wing chord (all to the nearest 0.01 mm) as described by de Beer *et al*. (2001). Nestlings were only measured once the parents voluntarily left the nest, to reduce disturbance at the nest.

The growth rate of each nestling was determined by fitting the growth curve to a logistic equation (Ricklefs 1967, 1968): $x\ (t) = A / 1 + \exp\ (- K\ (t - t_i))$ where x (t) is the mass or length at age *t*, A = the asymptote of the growth curve, K = relative growth rate as a proportion of the asymptote/day, and t_i = age at inflection point of the growth curve or maximum growth rate. The logistic model is rather inflexible as it is symmetrical around the inflection point, which is fixed at 0.5 of the upper asymptote (Tjørve & Tjørve 2010). The value of x at the inflection point is found at t = t_i and the model thus reduces to: $A / (1 + \exp\ (0)) = A/2$. Despite this limitation, the logistical model is one the most useful and often applied models (Tjørve & Tjørve 2010). The $t_{10–90}$, i.e. the time required to complete growth from 10% to 90% of the asymptote, was also calculated. For a logistic growth curve, this is calculated as: $t_{10-90} = 4.394/K$.

3.2.5. Roles of the sexes

Sabota Larks are sexually monomorphic and therefore one or both parents were caught and fitted with a unique combination of coloured plastic rings to aid in individual identification. Adults were sexed by means of the presence of a brood patch in females and its absence in males.

To determine the roles and relative contribution of the sexes during the nesting cycle, parental activity was recorded with digital video-recorders (Sony HDR-XR160). The video-recorders were placed approximately 1–3 m from the nest where possible but sometimes closer or further depending on the specific site characteristics, e.g. vegetation or rocks. All cameras were concealed to minimize their visibility. Recording started within the first hour after sunrise and continued for ~6–11 hrs. To determine the relative contribution of parents in different stages of the nesting cycle, the incubation and nestling stages were divided into an early-, middle- and late incubation or nestling stage. This corresponds to 0–3 days (early), 4–7 days (middle) and 8–11 days (late) for the incubation period, and 0–2 days (early), 3–5 days (middle) and 6–8 days (late) for the nestling period. Recording of provisioning rates were discontinued after day 8 as it was found that nestlings sometimes leave the nest for short periods from day 9 onwards and they may or may not be fed outside the view of the camera, leading to underestimates of the actual provisioning rate.

To describe the incubation and brooding patterns, the following parameters were considered: mean on-bout duration (mean incubation or brooding bout duration in minutes), mean recess duration (mean time spent away between two incubation or brooding on-bouts in minutes) and nest attentiveness (the percentage of total hours spent within or standing on the cup lip during a recording session). A bird standing on the cup lip was considered to be attending the nest as birds often stood on the cup lip when they were shading the nestlings. During the nestling period, the number of feeding trips/nestling/hour was also included. A feeding visit was only recorded if the adult was actually observed providing a food item to the nestling/s irrespective of the number of food items. Moreover, the video footage was used to identify the food items delivered.

3.2.6. Nest dimensions and nest site characteristics

Nest dimensions were recorded during the incubation and early nestling periods as nest dimensions can change considerably during the nesting cycle as a result of wear and tear. Nests dimensions recorded as described by Hansell (2000) included nest width, cup diameter, cup depth, entrance width and the presence/absence and size of an apron, i.e. an extension of a nest entrance, constructed of various materials such as grasses, sticks and dung. The following nest micro-habitat features were recorded by visually estimating the percentage cover within a 1 m^2 quadrant around the nest: grass, forbs, bare ground, stones and debris. Nest entrance orientation was determined with the aid of a handheld GPS.

3.2.7. Breeding success

Mayfield's (1975) breeding success estimator was used to calculate the breeding success by estimating daily survival rates using the number of exposure days, eliminating the need to monitor nests from initiation. The daily survival rates during incubation (DS_I) and nestling period (DS_N), as well as the hatching rate (HR) were determined to estimate the overall breeding success of the species in the particular area.

3.2.8. Data analysis

Most data are reported as descriptive statistics and include the mean, standard deviation, range and sample size. Means are presented ± S.D., with the exception of daily nest survival rates which are presented as ± S.E. and are calculated as the binomial standard error for a sample (Zar 1999). The analysis was performed using Microsoft Office Excel (2010), SPSS Version 22 (2013) or R Version 3.0.3 (2013). The Chi-square test was used to test if there was any correlation between breeding success and the presence or absence of an apron. One-way Analysis of Variance (ANOVA) was performed to test if grass, forbs or stones covaries with the breeding success of the species. The Spearman correlation test was used to test the relationship between bare ground or debris and the breeding success. To test if nest entrance directions were biased towards a particular direction, Rayleigh's test of uniformity was used with the ORIANA version 4 software package (Kovach Computing Services, Pentraeth, United Kingdom) to obtain circular graphs and mean vectors (r) for nest entrance orientation. Mean vector length is a unitless measure (0–1) of the dispersion of the data, with a value of 0 being widely dispersed (uniform) and 1 being tightly concentrated. Differences or effects were considered significant when $P < 0.05$.

3.3. Results

A total of 57 nests were found during this study: 31 in PNR and 26 at DLK. These included 30 nests during the 2011/12 and 27 in the 2012/13 breeding seasons.

3.3.1. Breeding seasonality

Breeding activity was recorded from October to February which coincides with the wet season in the study areas (Figure 3.1). The start of the breeding season was marked by an increase in singing by males. In both years, this commenced in early September and it continued throughout the breeding season. Males were particularly vocal during nesting and this was a good cue that there was an active nest nearby. Despite intensive search efforts, no active nests were recorded outside this period.

3.3.2. Nest construction, dimensions and micro-habitat characteristics

Details of nest dimensions, nest structure, nest micro-habitat characteristics and entrance directions were not recorded at all nests and therefore sample sizes differ for certain parameters. Females were solely responsible for all aspects of nest construction and incubation, but males accompanied females during trips to collect nesting material. Nest construction started with the female digging a cup, followed by construction of the dome (if present), then adding material for the cup as well as lining for the cup. However, nest construction and maintenance and adding material for lining was an ongoing activity throughout the incubation period and sometimes during the early stages of the nestling period too. Nests were constructed entirely of course grass blades with finer grasses and rootlets used as lining.

Of the 47 nests where nest data were collected, the majority (83.0%, n = 39) were placed next to a grass tuft (Plate 3.1), with the remainder placed next to a forb (8.5%, n = 4; Plate 3.2), sapling or small shrub (8.5%, n = 4; Plate 3.3). Although an apron was present at most nests (59.6%, n = 28), there was considerable variation with regard to its size and composition. Material used for the apron included grasses, twigs, stones and dung. (Plate 3.3 and 3.4; Plate 3.5 shows an example of a nest without an apron).

Although most nests were domed (93.6%, n = 44, Plate 3.1–3.5), there was also considerable variation as to how well developed the domes were. Domes ranged from completely absent (4.3%, n = 2) or a partial dome (2.1%, n = 1), to flimsy and nearly see-through, to extremely thick and well-developed.

The results of nest dimensions and nest micro-habitat characteristics in this study are presented in Table 3.1. It shows that the Sabota Lark’s preferred nest site is in fairly open areas with a relatively high amount of grass cover and smaller amounts of cover provided by forbs, debris and stones. There was no correlation between the breeding outcome (success vs failure) and the any of the nest micro-habitat parameters that were recorded (Spearman’s Rho, $P < 0.05$). The sample size of percentage cover of stones was too small for meaningful analysis and was omitted from further calculations. Nest entrance directions were not randomly orientated (Rayleigh’s Uniformity Test, Z = 18.1, $P < 0.001$; Figure 3.2). The mean vector length was 28.7° ± 56.5, n = 47), but entrance directions were not particularly tightly clustered around the mean ($r = 0.6$). The majority of nests faced in a northern or north-easterly direction (72.9%) with 12.5% facing in a north-westerly direction and 14.6% facing south.

3.3.3. Clutch size, dimensions, egg mass and egg description

The mean clutch size of the species at the study site was 2.7 ± 0.5, n = 57 ranging from 2–3 eggs per clutch. However, there was a significant difference in the clutch size between years: 2011/2012: $\bar{x}$ = 2.5 ± 0.5, median = 3, n = 30; 2012/2013: $\bar{x}$ = 2.8 ± 0.4, median = 3, n = 25; T-test, $P < 0.05$). The results of egg dimensions, fresh egg mass (FEM), estimated egg mass (EEM) and egg volume (EV) recorded in this study are presented in Table 3.2. The mean EEM of $\bar{x}$ = 2.4 g ± 0.2 in this study represents 10.1% of the mean mass of adult females at the study area ($\bar{x}$ = 23.8 ± 1.6 g, range: 22.00–26.7, n = 15). The mean EEM of two-egg clutches was $\bar{x}$ = 5.1 ± 0.4 g (range: 4.5–5.6, n = 6) representing 21.3% and three-egg clutches ($\bar{x}$ = 7.2 ± 0.7 g, range: 6.0–8.0, n = 11) represented 30.3% of the mean mass of adult females.

The base colour of eggs were creamy-white in colour and speckled with shades of brown and slate-grey spots. The brown spots were more concentrated at the obtuse end of the egg (Plate 3.6). However, there was considerable variation with regard to the degree of spotting, even within a clutch.

3.3.4. Incubation period

Eggs were laid within two hours after sunrise at daily intervals. Only females were recorded incubating. Incubation started upon clutch completion, resulting in a synchronous hatching pattern with all eggs hatching on the same day, albeit sometimes hours apart. The incubation period, i.e. the interval between the laying of the last egg of a clutch and the hatching of that egg was 12.3 ± 0.5 days (range: 12–13, n = 6). During that period, males acted as a sentry by perching on a nearby tree or shrub, continuously calling and warning the incubating female when a potentially threatening situation arose e.g. when an observer approaches the nest.

A total of 12351 min of footage was recorded during the incubation period. Nest attendance in the three stages ranged between 67.8% and 78.4% (Figure 3.3) and was greatest in incubation stage 2. The results of the analysis of incubation shift lengths and recess durations in the three stages of the incubation period are presented in Figure 3.4. Although the duration of incubation on-bouts increased as the incubation period progressed, there were no significant differences in the duration of incubation on-bouts between the different stages or in the duration of recess bouts (T-test, $P > 0.05$).

Egg shells were usually removed soon after hatching and dropped a considerable distance away from the nest. There was only one incident where a female was observed eating the egg shells soon after the nestlings hatched (Plate 3.5).

3.3.5. Nestling period

The mean duration of the nestling period was 11.7 ± 0.9 days (range: 11–13 days, n = 20). Although females did most of the brooding of nestlings, some males assisted with brooding, mainly by shading nestlings while standing on the cup lip. This is a form of temperature control and it was interpreted as brooding. At one nest, a male actually entered the nest and brooded the young for a few minutes.

The growth and development of the Sabota Lark nestlings has not been described before and Table 3.3 provides a summary of the main developmental events during the nestling period. Faecal sacs were swallowed during the first few days of the nestling stage and later disposed of away from the nest.

The diet of nestlings was composed entirely of invertebrates. Prey items that were identified include grasshoppers (Orthoptera), termites (Isoptera), ants (Hymenoptera), phasmatodeans (Phasmatodea), mantids (Mantodea), spiders (Arachnida), moths and butterflies (Lepidoptera) as well as various soft-bodied invertebrates, e.g. worms, which could not reliably be identified to order level.

Typical of ground-nesting birds, growth was rapid with $K > 0.30$ for most parameters (Table 3.4). Once again, with the exception of head length, the $t_{10\text{-}90}$ was reached at or around fledging for the most parameters. Both sexes contributed to feeding the nestlings, although the contribution between the sexes varied considerably.

The roles and relative contributions of the parents were recorded for 7829 min during the nestling period. Figure 3.5 provides a summary of nest attendance and the duration of brooding on-bouts and recesses during the different stages of the nestling period respectively. As expected, nest attendance decreased as the nestling period progressed, but brooding was nevertheless recorded in all three stages (Figure 3.6a and Figure 3.6b).

The results revealed that male Sabota Larks generally made more food deliveries compared with females in all three stages of the nestling period (Figure 3.7). There was a steady increase in the number of food deliveries as the nestlings got older, peaking at approximately seven food deliveries per hour (Figure 3.8).

3.3.6. Breeding success

The daily survival rates for the different stages in the breeding cycle as well as the overall breeding success are presented independently for the 2011/2012, 2012/2013 and the two breeding seasons combined in Table 3.5. Of the 124 eggs laid in 57 nests, 87 hatched and 63 nestlings fledged successfully, giving a crude breeding success estimate of 51.0%. The overall Mayfield breeding success was calculated using the mean incubation period of 12.3 days and the mean nestling period of 11.7 days, resulting in a breeding success rate of 36.4% for the duration of this study (Table 3.5). Although breeding success was considerably greater in the 2011/12 breeding season compared with the 2012/13 season, it was very similar at the two study sites. There were also very little differences in the DSR during different stages of the nesting cycle (Table 3.5). There was a difference in the overall breeding success of nests facing in the preferred entrance directions, i.e. north or north-east (24.5%) compared to nests facing in other directions (40.8%). However, this may be due to the small sample size (n = 9 nests) of nests that don’t face in the preferred entrance directions. Two instances of repeat-brooding were recorded and given the relatively high nest failure rate, replacement broods were a common phenomenon. Known causes of breeding failure included predation by snakes (Plate 3.7), birds (Plate 3.8), natural causes and trampling.

3.4. Discussion

The results of this study conform in large with the general pattern of breeding in many lark species, but some aspects appear to be unique or are reported here for the first time.

3.4.1. Breeding seasonality

The breeding season of the Sabota Lark in this study compared well with laying dates given by Dean (2005). Its breeding season was relatively brief and coincided with the early- and peak wet-season in the study area, i.e. laying was initiated between October and January. Although the breeding phenology in this study is similar to that of the slender-billed group across its range (*cf.* Chapter 2), the breeding season was more condensed. Laying in this study spanned only four months whereas nesting of the slender-billed group has been recorded in eight months (September to April) (*cf.*

Chapter 2). The more extended breeding season across its range is not surprising as there are geographic and temporal differences in the onset of the wet season across the species range.

The relative brevity of the breeding season in this study is somewhat surprising. Although the onset of the breeding season corresponds with the main flux of initiation of breeding of birds in the study area, the Sabota Lark’s breeding season ends relatively early compared with other species in the area (D. Engelbrecht, unpublished data). For example, breeding of the Short-clawed Lark *Certhilauda chuana* in the study area has been recorded from late-September to April (Engelbrecht 2005). Such an extended breeding season allows for multiple brooding attempts for a ground-nesting species facing high nest losses. According to Engelbrecht (2005), triple repeat-brooding attempts within a single season were a relatively common occurrence in the Short-clawed Lark and partially offset the high nest losses experienced by this species. Despite intensive search efforts, no instances of triple repeat-brooding were recorded in this study. However, there were two instances of double-brooding and, given the relatively poor breeding success in the study area, replacement-broods were common. Thus, the relatively short breeding season and high incidence of nest losses limit the likelihood of triple repeat-brooding attempts by Sabota Lark in the study area. The proximate reasons as to why their breeding season terminates early compared with most other birds in the study area, remains a matter of conjecture as there is still sufficient food available to rear nestlings.

3.4.2. Nest construction, dimensions and micro-habitat characteristics

In the majority of larks, females are solely responsible for collecting nest material and nest construction although males may accompany females as part of a mate-guarding strategy (de Juana *et al*. 2004). This pattern was confirmed in this study. The nest construction period, i.e. the period from the start of nest construction until the first egg was laid, was relatively short (1–3 days). However, this is mostly due to the definition of the term “nest construction”; namely the period from the start of nest construction until the first egg is laid. The shell of the nest and lining of the nest cup was not nearly completed at the time laying started, but the female continued adding material to the nest throughout the incubation period and even during the early stages of the nestling period. The same trend of continuing with nest construction after laying has commenced appears to be common amongst lark species (Engelbrecht 2005; Engelbrecht & Mathonsi 2012; Engelbrecht & Dikgale 2014).

The results of nest micro-habitat characteristics showed that Sabota Larks prefer to place their nests in areas with a fair amount of vegetative cover, but also with a small amount of open areas such as bare ground or rocks. The combination of a large amount of vegetative cover and the domed nest structure served well to conceal the nest contents. Within the study area, the Sabota Lark was usually the only lark species breeding in the habitat occupied by them. Most of the other lark species preferred nesting in more open habitats.

The construction of domed nests was traditionally considered to be one of the defining features of mirafrid larks. However, several studies have shown this to be an inconsistent feature, particularly amongst members of the genus *Calendulauda* (Maclean 1970; Boyer 1988; Engelbrecht & Lonzer 2008). The results of this study further supports the notion that it is not a reliable character as a dome was absent at two nests and one nest was only partially domed, e.g. built-up on one side only. Moreover, there was considerable variation with regard to the quality of the dome at those nests where it was present. These results confirm the findings presented in Chapter 2 that the construction of domed nests in the Sabota Lark is not a consistent feature. This variation in nest size, shape and quality of birds is poorly known but it has been reported for a few species (Haggerty 1986, 1995; Mertins 1987; Boyer 1988; Powell & Rangen 2000; Engelbrecht 2005; Engelbrecht & Mathonsi 2012). For example, Haggerty (1995) reported variation in the presence or absence and development of a dome in Bachman's Sparrow *Aimophilla aestivailis* nests within a single breeding season.

There are essentially four hypotheses to explain variation in the shape and dimensions of nests within a season, namely 1) thermoregulatory: nests in more exposed sites may need more insulative material, 2) concealment: more exposed nests may need more material to conceal it from predators, 3) energetic: a female may have less disposable energy to collect material later in the season for nest construction, and 4) individual variation: young or inexperienced females may still learn nest construction techniques (Boyer 1988; Powell & Rangen 2000; Engelbrecht 2005). It is possible that any or a combination of these hypotheses may explain the variation in nests observed in this study.

The nest entrance orientation evidently serves a thermoregulatory function in many lark species (Maclean 1970; Boyer 1988; de Juana *et al.* 2004; Engelbrecht & Mathonsi 2012; Engelbrecht & Dikgale 2014). For example, thermoregulatory benefits can be achieved through radiation and nests facing into or away from the prevailing winds. In this study, most nest entrances were orientated towards the north-east and it is possible that it may also serve a thermoregulatory function. Since the nests are usually domed, the eggs are shaded to a large extent for most of the day when the female is on an incubation recess. It is possible that nests with a northern orientation will be warmer than nest facing more towards the south, resulting in slower cooling of the eggs during recesses with obvious benefits to the developing embryos. Interestingly, Maclean's (1970) study found Sabota Larks in the Kalahari Desert orientate their nests towards the south and analyses of NERCS data also showed a tendency towards south facing nests (Chapter 2). However, this is based on a sample size of only three nests. The results of this study also showed that nest entrance directions may contribute to breeding success but the sample size in this study was too small to make definitive conclusions on this matter. Clearly, this aspect of the ecology of Sabota Larks warrants further investigation. It is interesting that the nest entrance orientation of three open, cup-nesting lark species (Pink-billed Lark *Spizocorys conirostris*, Chestnut-backed Sparrow-lark *Eremopterix leucotis* and Red-capped Lark *Calandrella cinerea*) in the study area are all towards the south so as to maximize shade during the hottest parts of the day (Engelbrecht & Mathonsi 2012; Engelbrecht & Dikgale 2014; D. Engelbrecht unpublished data).

3.4.3. Clutch size and egg dimensions

The mean clutch size of 2.7 (range 2–3) in this study corresponds well with the mean of 2.3 reported by Keith *et al*. (1992) for the species from across its range, and 2.5

calculated from the NERCS data (*cf.* Chapter 2). There was no evidence of seasonal variation in clutch size for this species, possibly due to the shortness of the breeding season. The mean clutch size is similar to that of other resident larks in the area, e.g. Short-clawed Lark ($\bar{x}$ = 2.3; Engelbrecht 2005) and Rufous-naped Lark ($\bar{x}$ = 2.8; D. Engelbrecht unpublished data). Small clutch sizes are typical of ground-nesting species in the tropics suffering high nest failure rates (Martin 2002).

3.4.4. The incubation period

The mean duration of the incubation period of 12.3 ± 0.5 days recorded in this study matches the range of 11–13 days reported for most other larks (de Juana *et al*. 2004). In common with most other larks, only the female performed incubation duties and incubation commenced upon clutch completion (de Juana *et al*. 2004).

The female's behaviour during incubation revealed interesting patterns of variation in nest attendance in the different stages of the incubation period. Although nest attendance remained relatively constant at around 75% throughout the incubation period, there was a steady increase in the duration of the incubation on-bouts as the incubation period progressed. There are two plausible explanations for this: 1) in the early stages, the female makes regular trips to collect nest material and complete construction, and 2) greater sensitivity of developing embryos to extreme temperature fluctuations in the days prior to hatching.

3.4.5. The nestling period

The length of the nestling period compares well with the 12–14 days reported for most other larks (de Juana *et al.* 2004). However, the nestlings are able to move around well when they are 8–10 days old. In common with all other larks, male Sabota Larks assist their mates with food provisioning to the nestlings. With the exception of obligate biparentally breeding species such as the *Eremopterix* and *Spizocorys* larks, male larks do not assist the female with brooding the young. However, in this study males were frequently observed shading the nestlings by standing for extended periods on the cup lip at the nest entrance. As this is a form of thermoregulation, it was regarded as brooding in this study. Even more surprising was observing one male actually entering the nest and brooding the nestlings. This is as far as can be established, the first recorded instance where a male lark in the mirafrid clade entered a nest to assist with brooding the young.

Although the relative contribution of males to brooding was relatively small, males compensated for this by making more nest visits to deliver food compared with females. Furthermore, they also delivered food at a faster rate compared with females. In many species, males tend to deliver more food as they are freed from the constraints of brooding and they do not develop a functional brood patch. Hence heat transfer from males to their young is likely to be suboptimal (but see Auer *et al.* 2007). Thus, it appears as if there is some role division in the parental care strategies of the Sabota Lark.

3.4.6. Nestling growth and development

Lark nestlings grow extremely rapidly and growth takes place at or near the physiologically maximum rate possible (de Juana *et al.* 2004). This is particularly true for the growth of the wing and tarsus where the growth rate (K) typically exceeds 0.3 (Engelbrecht & Mathonsi 2012; Engelbrecht & Dikgale 2014). As the nestling period is short, the two parameters (tarsus and wing) associated with locomotion grow very rapidly to enable the fledglings to move around after fledging. For example, the $t_{10\text{-}90}$ is reached at about the time of fledging (Table 3.4). The rapid growth of the tarsus is also required to support the mass of fledglings as they are not able to fly at the time of fledging but they are able to walk and jump small distances. This rapid growth and fledging at a very young age are adaptations to cope with high nest losses. Early fledging and scattering of the young is an anti-predation strategy to reduce the likelihood of a predator depredating the entire brood.

3.4.7. Breeding success

As ground-nesting birds, larks generally suffer high nest losses (de Juana *et al.* 2004; Donald 2005). The breeding success of most larks is unknown, but for those species that it is known, it ranges from 4% for Stark's lark *Spizocorys starki* (Lloyd 2005) to as high as 61% for the Red-capped Lark. Predation is typically invoked as the main factor responsible for nest failure, but there are many other factors too, including trampling, exposure, flooding, nest abandonment and natural causes such as infertile eggs or nestlings that are runts (de Juana *et al*. 2004). All of the foregoing were responsible for nest losses in this study too. Nest predation has an important influence on avian productivity (Ricklefs 1969; Rotenberry & Wiens 1989; Martin 1993) and parental behaviour (Pietz & Granfors 2005), and it can result in nest abandonment (Anderson 2010).

This study has confirmed that predation is one of the main factors responsible for nest losses. Predators of ground-nesting birds include a range of species but small mammalian carnivores, snakes, lizards, birds and squirrels are the main predators (de Juana *et al*. 2004). In most instances, the identity of nest predators is a matter of conjecture as biologists are usually only left with indirect clues to identify potential predators and several studies have shown that this is an unreliable method of determining the nest predator (Moors 1983a; Williams & Wood 2002, Staller *et al*. 2005; Engelbrecht 2011; Pietz *et al*. 2012). However, in this study the identified predators included the Boomslang *Dispholidus typus* and Common Fiscal *Lanius collaris*.

Interestingly, the nest-microhabitat features recorded in this study had no effect on the nest outcome. Thus, whether or not there was an apron present or not or a large amount of cover for concealment of the nest, predation occurred regardless. The overall breeding success of 32.9% calculated in this study is slightly lower than the 44% reported for the Short-clawed Lark (Engelbrecht 2005) in PNR, but considerably higher than the 12.8% for the Pink-billed Lark (Engelbrecht & Mathonsi 2012) and 16.6% for the Chestnut-backed Sparrow-lark (Engelbrecht & Dikgale 2014) at DLK. Even when the breeding success of the localities are separated, the breeding success of Sabota Larks at DLK was still greater compared with that of the Pink-billed Lark and Chestnut-backed Sparrow-lark in the same area, although in different macro-habitats.

Although there were some differences between years and localities, the overall daily survival rate was very similar in the different stages of the nesting cycle. This is somewhat unusual as there usually are differences in the daily survival rate during different stages. For example, some predators may be stage specific, e.g. Rhombic Egg-eater *Dasypeltis scabra* feeding specifically on eggs. It is often assumed that greater activity at the nest and begging calls of nestlings during the latter stages of the nestling period may lead to greater nest losses during this stage. To counter this, parents may reduce their feeding trips by increasing prey loading to avoid the risk of predation (MacColl & Hatchwell 2003). The data obtained in this study suggests that nest failure is more or less equally likely during the different stages of the nesting cycle.

3.5. Conclusion

The present study has provided valuable information about the breeding biology and ecology of the Sabota Lark in particular, but also of larks in general. It has confirmed a lot of what is already known about the family, but also revealed some interesting new information. For example, the study has shown that despite the relatively short breeding season, the species is capable of double repeat-brooding attempts. Furthermore, the observations that males assist with brooding young seems to be unique amongst the mirafrid larks at present. Future studies on parental care using video-surveillance may show this behaviour to be more common than generally thought. Thus, this study has demonstrated that common and widespread species are often overlooked in ecological studies but that they can make major contributions to our knowledge of birds.

Table 3.1. Nest dimensions (mm) and micro-habitat characteristics (% cover, ± S.D., range) of the Sabota Lark *Calendulauda sabota* on the Polokwane Plateau (n = 47 nests).

Nest characteristics	**Parameter**	**Mean ± S.D.**	**Range**
Nest dimensions	Nest width	112.6 ± 7.1	100–128
	Cup diameter	68.8 ± 11.1	54–87
	Cup depth	28.6 ± 5.7	14–38
	Entrance width	61.8 ± 2.3	55–65
Micro-habitat	Grass	52.6 ± 14.2	25–80
	Forbs	14.1 ± 9.2	5–40
	Bare ground	23.3 ± 11.5	5–50
	Debris	14.1 ± 12.1	5–45
	Stones	8.9 ± 4.7	5–15
	Other	7.5 ± 2.5	5–10

Table 3.2. Clutch size, egg dimensions (L = length, W = width, mm), egg elongation index, egg volume (mm^3), FEM = fresh egg mass (g) and EEM = estimated egg mass (g) and clutch mass (CM = clutch mass) of the Sabota Lark *Calendulauda sabota* on the Polokwane Plateau.

Parameters	**Mean ± S.D.**	**Range**	**N**
Clutch size	2.7 ± 0.5	2–3	55
Egg length	20.8 ± 1.0	18.3–23.0	46
Egg width	15.0 ± 0.5	14.0–15.9	46
Elongation index	1.4 ± 0.1	1.3–1.5	46
Egg volume	4708.8 ± 410.1	3776.8–5386.8	46
FEM	2.5 ± 0.2	2.1–2.9	22
EEM	2.4 ± 0.2	2.0–2.8	22
CM (2 eggs)	5.1 ± 0.4	4.5–5.6	6
CM (3 eggs)	7.9 ± 2.5	6.0–15.0	11

Table 3.3. Main developmental events of Sabota Lark *Calendulauda sabota* nestlings as recorded in the Limpopo Province, during the 2010/2011 and 2011/2012 breeding seasons.

Day	**Description**
0	Eyes closed. Skin is a dark, purplish-black colour with tufts of straw-coloured down on capital, humeral, spinal and crural tracts. Rarely some individuals have tufts of down on the caudal end of the ventral feather tracts. All the feather tracts including the ventral feather tract in some individuals. Primary, secondary and caudal neosoptiles visible. Culmen and nostrils are blackish-horn coloured but the tip of the bill is a paler grey colour. Gape flange is a pale whitish-yellow colour and the inside of the mouth is bright yellowish-orange with two laterally situated tongue spots at the back of the tongue and one at the distal tip of the tongue. In some individuals, the distal tongue spot is absent. The upper and lower mandibles also have a black spot on each tip.
1	No feather tracts have erupted yet but are visible under the skin.
2	Eyes open slits, to fully open in some individual. First primaries begin to erupt, the becoming darker approaching blackish colour.
3	Eyes fully open. Primaries and most secondaries in pin. First feathers on ventral and spinal track erupt.
4	Most feathers in pin on all tracts.
5	First ventral in brush, the rest of pin feathers continue to grow.
6	All feather tracts have at least some feathers in brush except primaries, primary coverts and tail which are still in pin. First feathers

Day	Description
	on capital tracts only start to erupt.
7	All feathers on all tracts erupted. Some primaries and most secondaries in brush. Most secondary coverts but no primary coverts in brush yet.
8	Most primaries and secondaries between 15 and 25% in brush. First primary coverts and most secondary coverts in brush.
9	All feathers continue to grow. Primaries ± 30–40% in brush.
10	Feathers continue to grow. Primaries approximately 50% in brush.

Table 3.4. Means of the parameters of the logistic growth curve for the increase in mass (g) and growth of the head (mm), tarsus (mm) and wing (mm) length of the nestlings of the Sabota Lark *Calendulauda sabota* (n = 20).

Parameter	**A**	**K**	***t***	$t_{10\text{-}90}$
Mass	21.2	0.5	4.8	8.6
Head length	32.0	0.2	2.2	19.1
Tarsus length	28.5	0.3	4.3	13.2
Wing length	86.3	0.4	8.2	12.7

Table 3.5. The overall breeding success (%), daily survival rate during the incubation (DSI) and nestling (DSN) periods, and the hatching rate (HR) during the nesting period of the Sabota Lark *Calendulauda sabota* in the Limpopo Province.

	2011/2012	**2012/2013**	**PNR**	**DLK**	**Overall**
DS_I	0.95 ± 0.1	0.98 ± 0.1	0.96 ± 0.1	0.98 ± 0.1	0.97 ± 0.1
HR	0.91 ± 0.2	0.94 ± 0.2	0.80 ± 0.1	0.91 ± 0.2	0.93 ± 0.1
DS_N	0.97 ± 0.1	0.91 ± 0.1	0.96 ± 0.2	0.93 ± 0.1	0.95 ± 0.1
Overall (%)	**36.4**	**26.1**	**29.1**	**30.7**	**32.9**

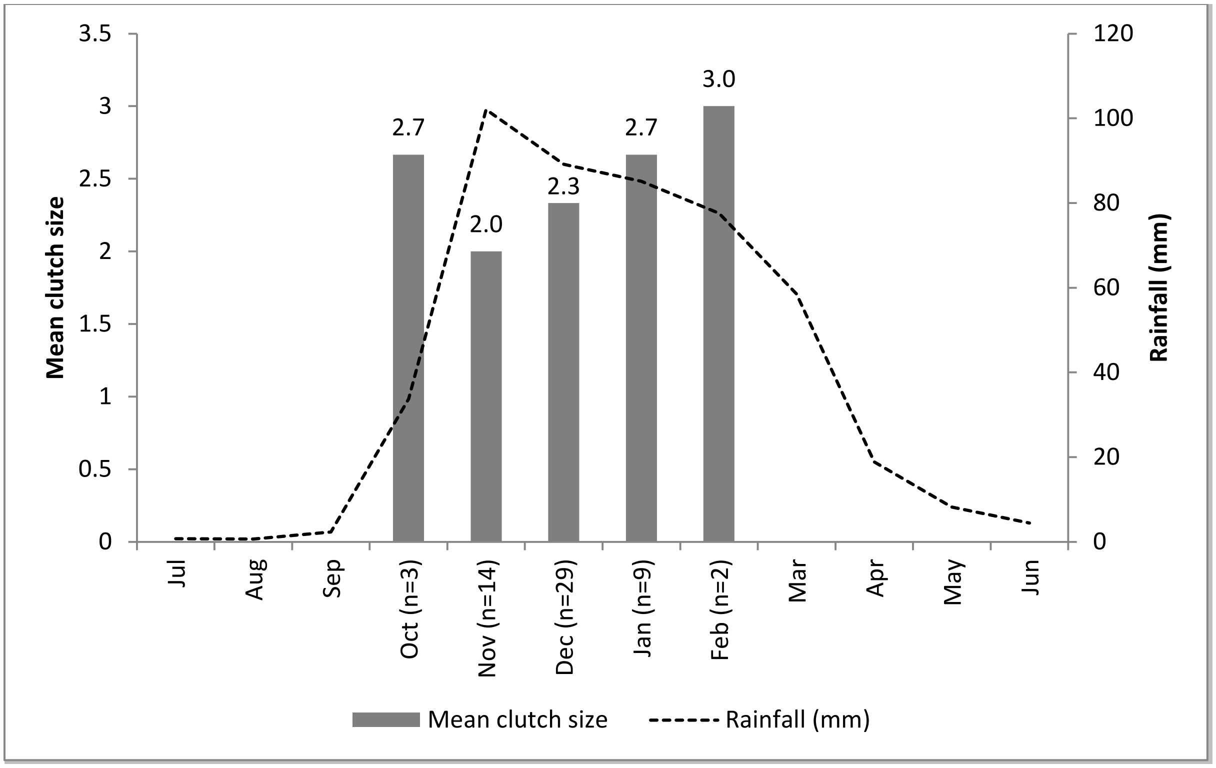

Figure 3.1. Mean monthly rainfall and clutch size of Sabota Larks *Calendulauda sabota* on the Polokwane Plateau in the 2011/12 and 2012/13 breeding seasons.

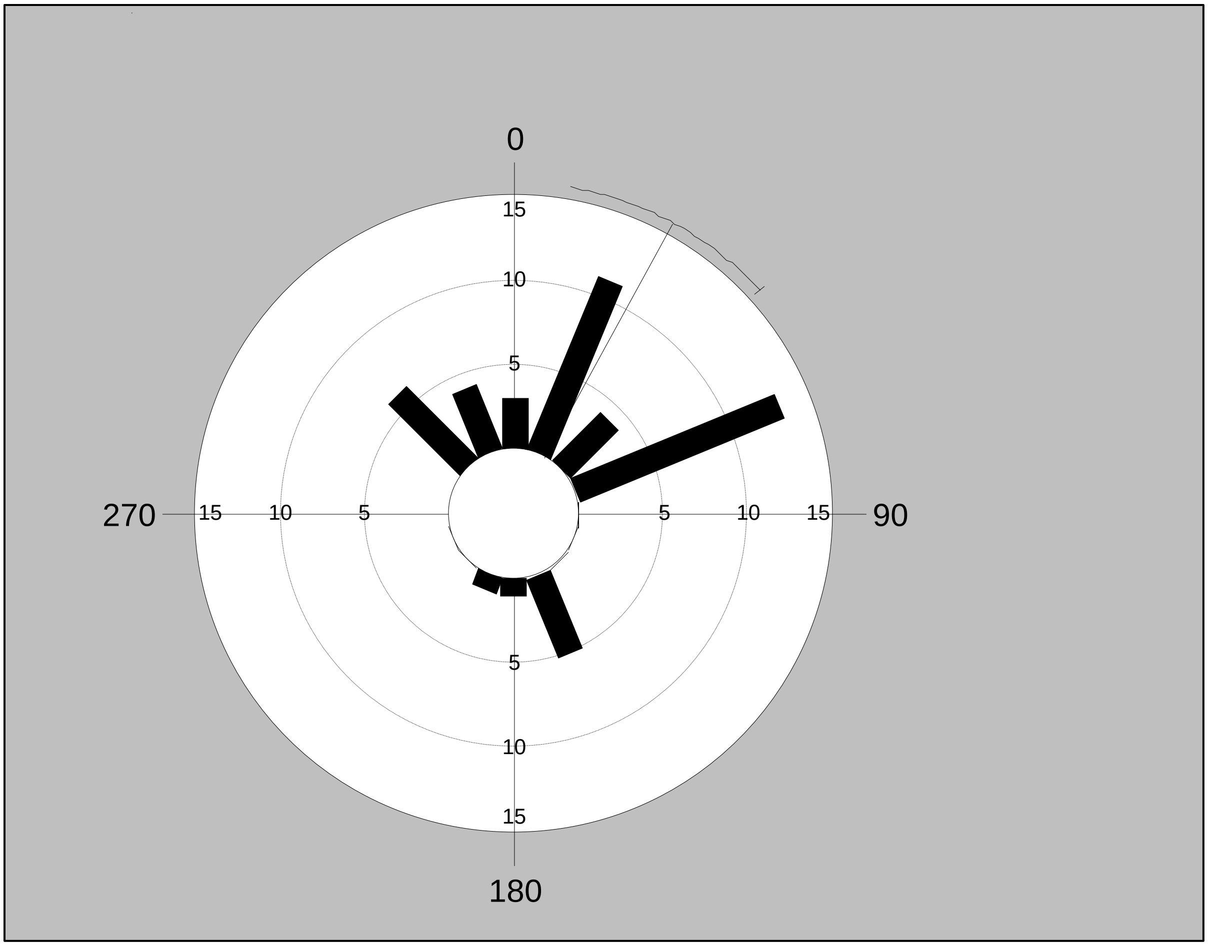

Figure 3.2. Orientations of Sabota Lark *Calendulauda sabota* nest entrances on the Polokwane Plateau. Bars along radial axes indicate numbers of nests along 16 cardinal directions. Numbers on the outside represent compass bearing. The mean vector length is depicted by the thin, solid line.

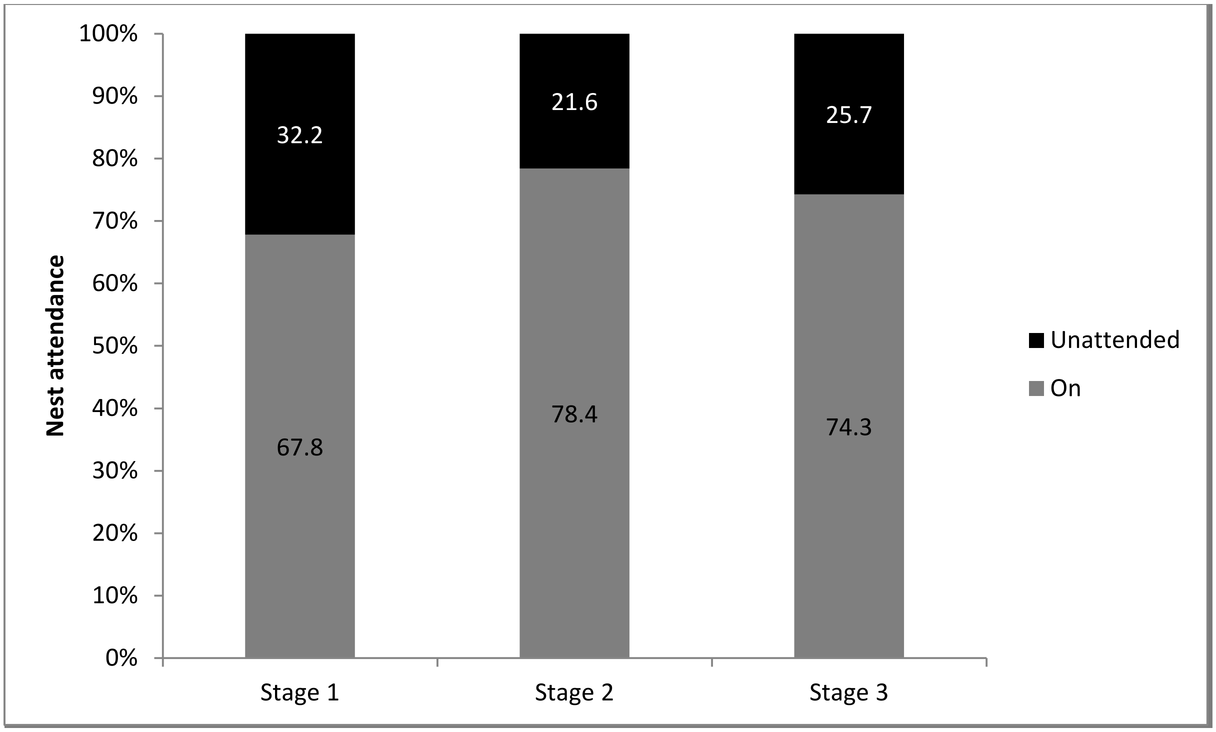

Figure 3.3. Nest attendance by female Sabota Larks *Calendulauda sabota* during different stages of the incubation period.

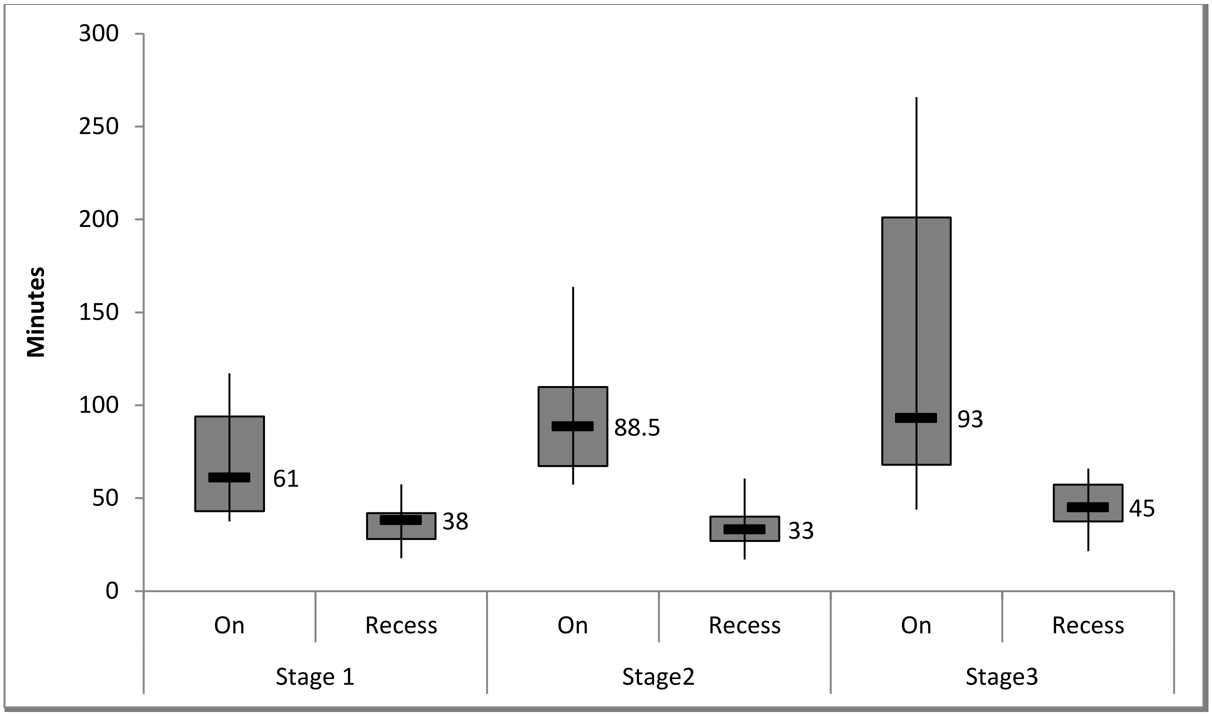

Figure 3.4. Duration of incubation on-bouts and recess bouts during different stages of the incubation period of the Sabota Lark *Calendulauda sabota.* The filled rectangles represent the median and the boxes represent the interquartile range.

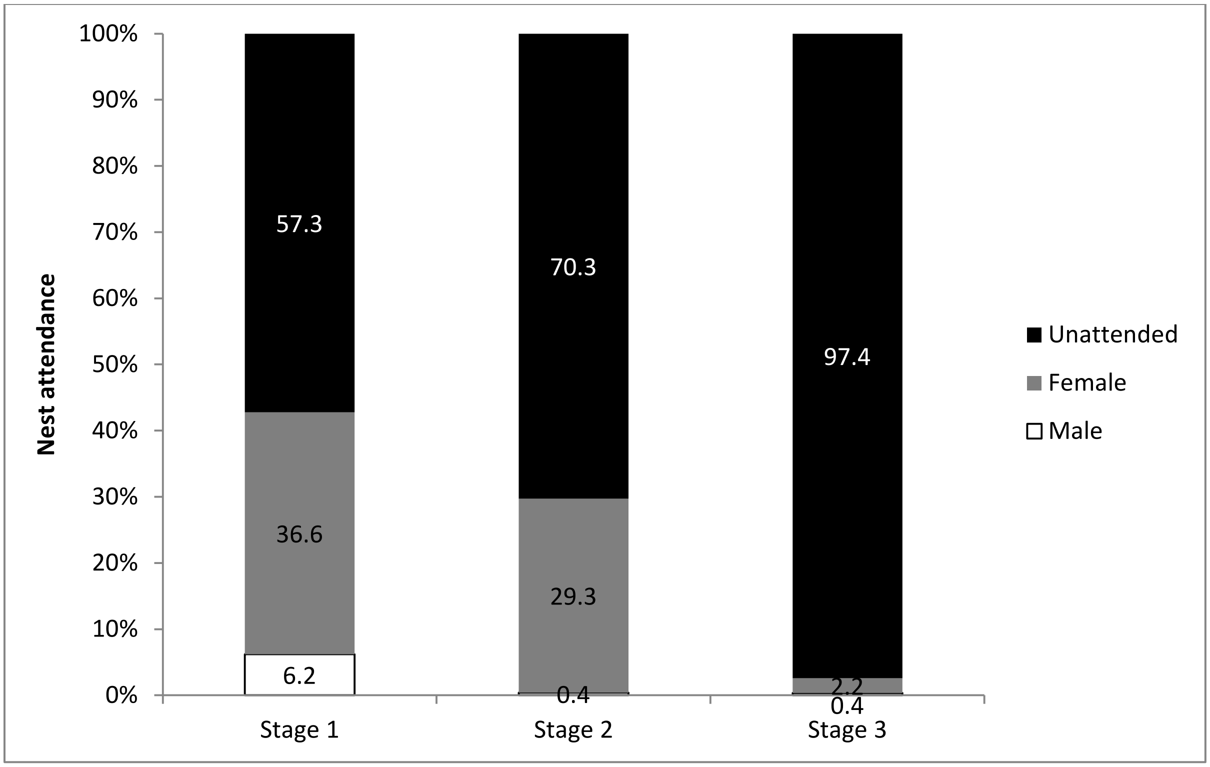

Figure 3.5. Nest attendance by male and female during the early-, middle- and late stages of the nestling period in the Sabota Lark *Calendulauda sabota.*

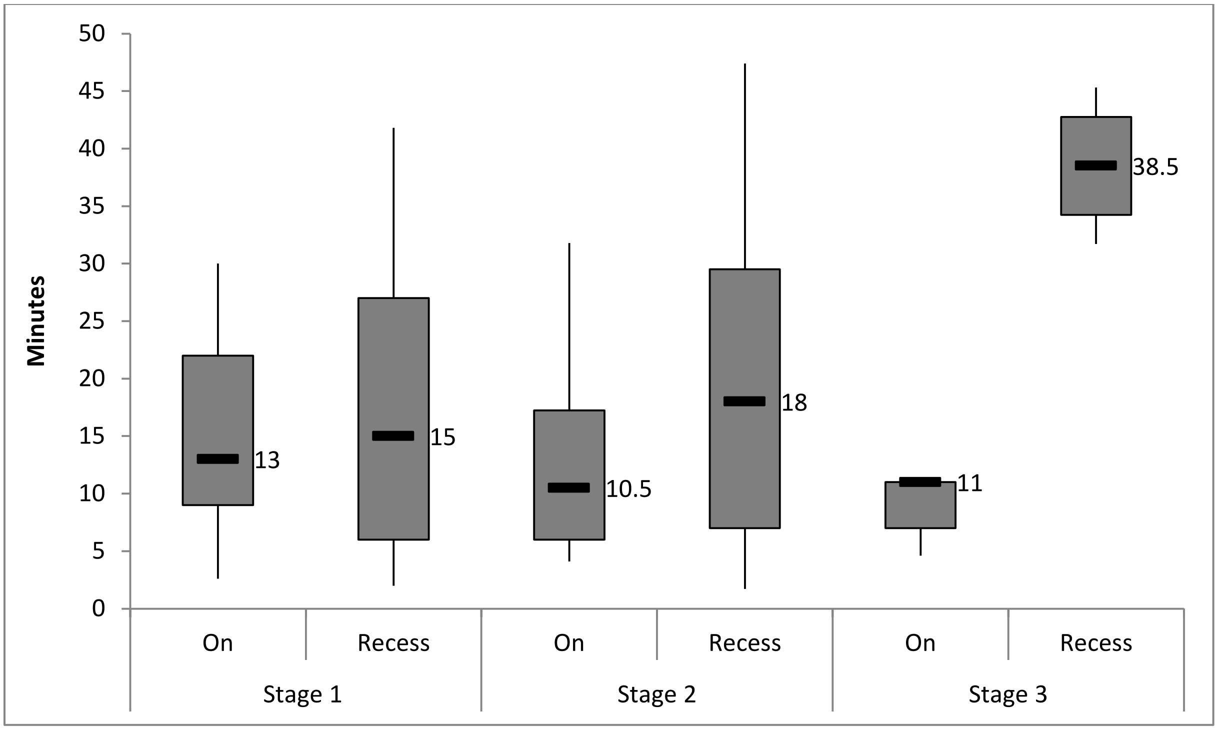

Figure 3.6a. Duration of brooding on-bouts and recess bouts of the female Sabota Lark *Calendulauda sabota* during different stages of the nestling period. The filled rectangle represents the median and the boxes represent the interquartile range.

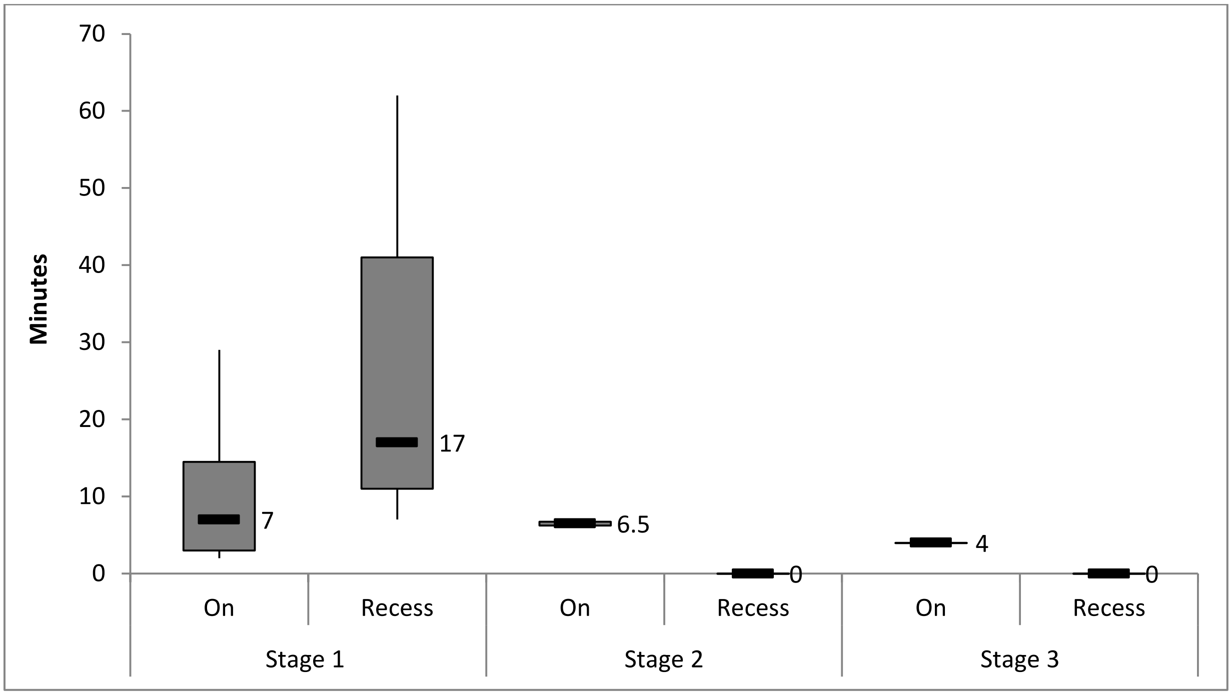

Figure 3.6b. Duration of brooding on-bouts and recess bouts of the male Sabota Lark *Calendulauda sabota* during different stages of the nestling period. The filled rectangles represent the median and the boxes represent the interquartile range.

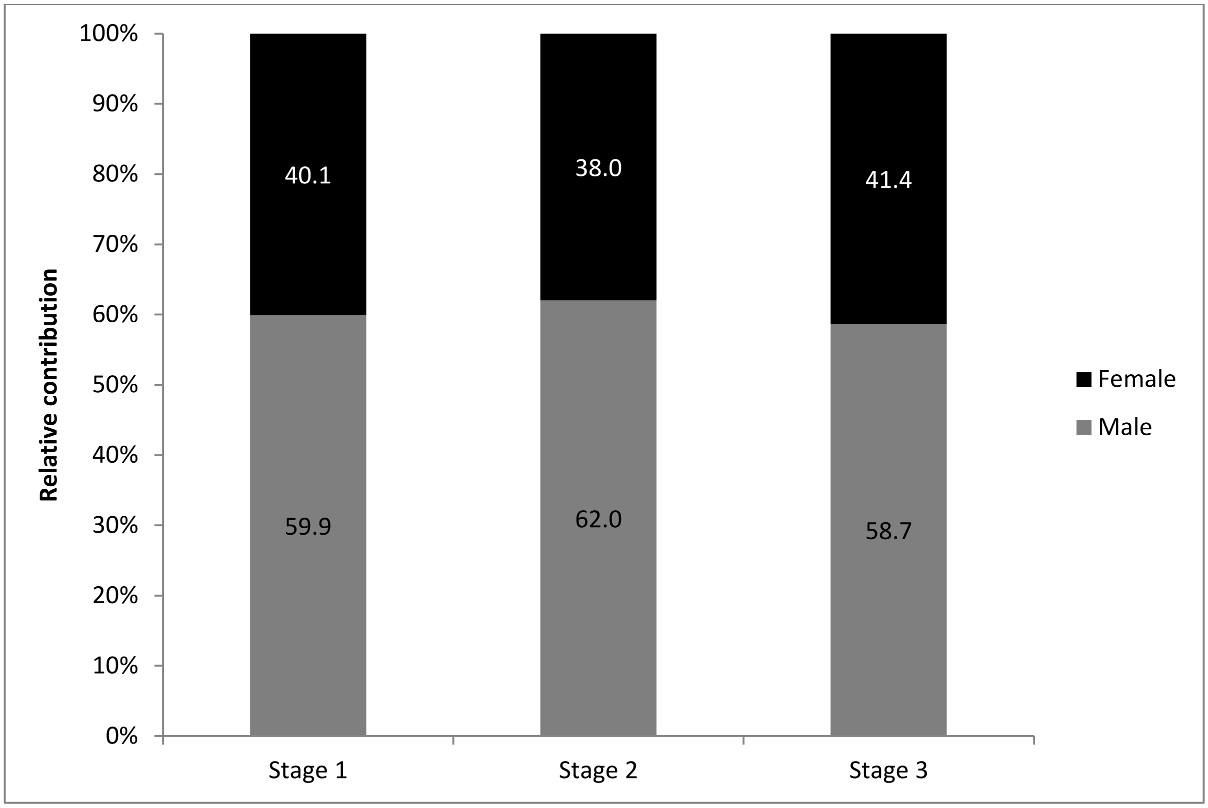

Figure 3.7. The relative contribution of food delivered by male and female Sabota Larks *Calendulauda sabota* during different stages of nestling period.

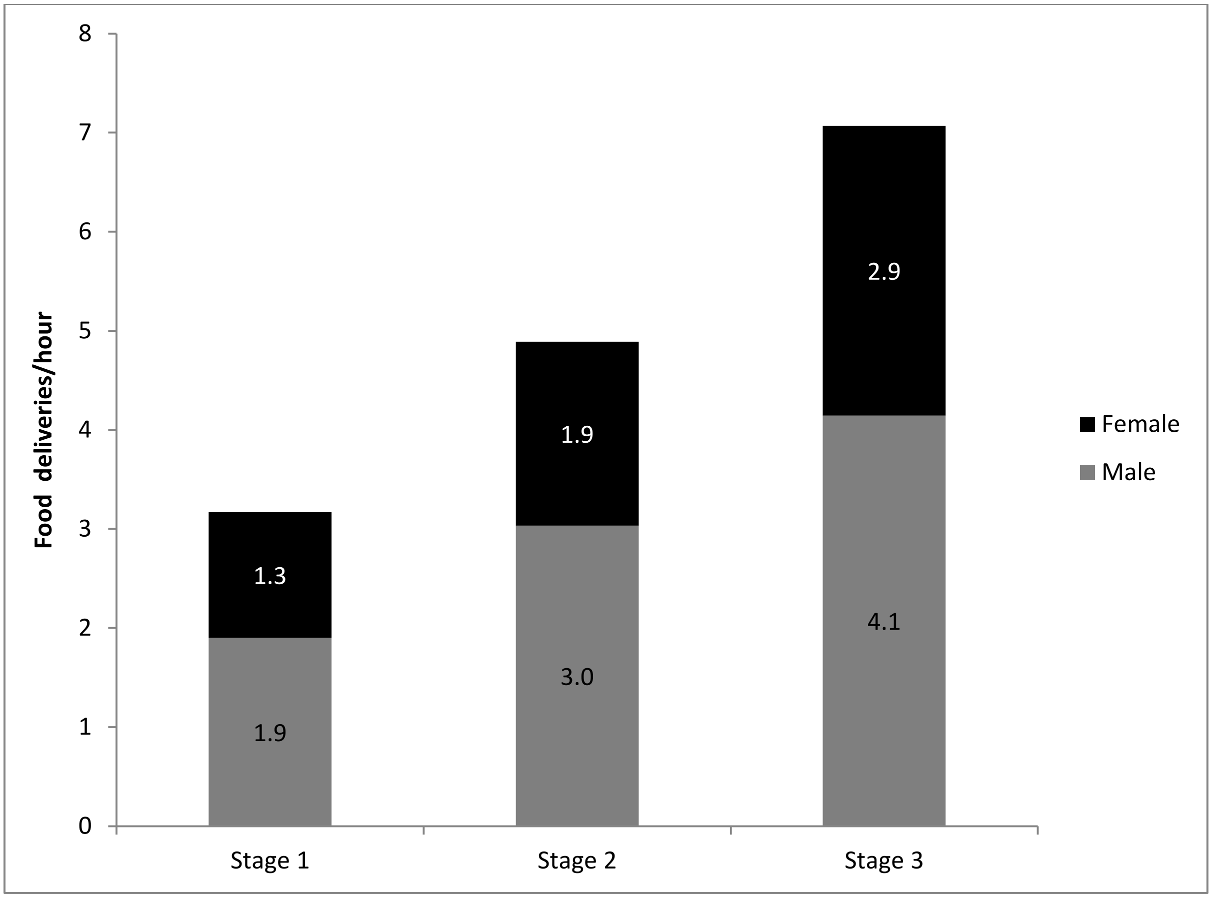

Figure 3.8. Mean number of food deliveries per hour by male and female Sabota Larks *Calendulauda sabota.*

Plate 3.1. A Sabota Lark *Calendulauda sabota* nest placed next to a tuft of a grass (Polokwane Nature reserve, Limpopo province, 2011).

Plate 3.2. A Sabota Lark *Calendulauda sabota* nest placed next to a forb.

Plate 3.3. A Sabota Lark *Calendulauda sabota* nest placed next to a sapling and with an apron.

Plate 3.4. A Sabota Lark *Calendulauda sabota* nest with no apron, placed next to a tuft of grass.

Plate 3.5. Female Sabota Lark *Calendulausa sabota* feeding on an egg shell just after hatching.

Plate 3.6. Eggs and a newly hatched nestling of the Sabota Lark *Caledulauda sabota.*

Plate 3.7. Female Boomslang *Dispholidus typus* depredating nestlings of the Sabota Lark *Calendulauda sabota* in the Polokwane Nature Reserve.

Plate 3.8. A Common Fiscal *Lanius collaris* predating on a 4 day old Sabota Lark *Calendulauda sabota* nestling in the Polokwane Nature Reserve.

CHAPTER 4

Geographical variation and sexual size dimorphism in the Sabota Lark *Calendulauda sabota*

4.1. Introduction

The Sabota Lark *Calendulauda sabota* is a southern African near-endemic species, extending only marginally into Angola (Clancey 1966). The species has a widespread distribution in the arid- and semi-arid savannahs, edges of the Namib Desert, Karoo and grasslands of southern Africa (Clancey 1966; Hall & Moreau 1970). During the first Southern African Bird Atlas Project, it was the lark species that was recorded in the most quarter degree grid squares compared to all other southern African lark species (see Dean 1997).

Given its broad distribution range and largely sedentary behaviour (non-migratory) in a variety of biomes, it is not surprising that the species displays extensive geographical variation, especially with regard to size and plumage features. Clancey (1966) was the first to investigate geographical variation in the species, resulting in the description and recognition of eight subspecies. A ninth subspecies, *Calendulauda sabota plebeja,* is apparently isolated from all the other subspecies and occurs in a small area on the coast of north-western Angola in the province of Cabinda. Dean (2005) concurred with Clancey (1966) and this taxonomic arrangement is followed in this chapter. The eight subspecies can be divided into two groups namely: a thick-billed group with its distribution largely centred in the more arid western parts of southern Africa, and a slender-billed group occupying the more mesic savannahs in the east of the subcontinent. The taxonomic separation between these two groups is based mainly on morphological characteristics, e.g. overall body size and size and shape of the bill, and to a lesser extent on plumage features, e.g. the amount of dorsal streaking (Clancey 1966). Members of the slender-billed group are notably smaller and have more extensive streaking giving them an overall darker appearance, compared with the distinctly larger and less streaked (paler) western races. It is not known if the two groups are allopatric, but there is a potential narrow contact zone in South Africa in the north-eastern Northern Cape, the western Free State, western parts of the Eastern Cape, as well as in northern Damaraland in Namibia (Clancey 1966; Dean 2005). However, the phenotypic variation has never been quantified for these subspecies and it is not known if the geographical variation is clinal or not (Clancey 1966; de Juana *et al.* 2004; Dean 2005).

Despite the interest shown by taxonomists over the years and the species' widespread distribution in southern African, the Sabota Lark remains one of the least known of southern African larks. Prior to this study, there has been no formal, detailed study of any aspect of this species' biological and ecological requirements. All our present knowledge of the species is based on anecdotal observations (Dean 1971; Dean 1987; Nuttal 1993; Skinner 1995; Tarboton 2011). There is some evidence that in addition to the phenotypic differences, there may be ecophysiological (e.g. different water requirements and dependence on surface water) and behavioural differences (e.g. differences in vocalizations and social behaviour) between the slender- and thick-billed groups which may or may not have a taxonomic basis (Engelbrecht 2012).

Geographical variation in most species results from phenotypic plasticity, which is defined as the tendency of an adult organism with the same genotype to vary under different environments and conditions (Tieleman *et al*. 2003). In most of the geographical range of bird species, phenotypic variation is gradual, but change is more abrupt in the contact zone (Babin 2005). Most larks exhibit geographical variation in relation to upper plumage colouration linked to soil colour and vegetation density e.g. Karoo Lark *Calendulauda albescens,* Eastern Clapper Lark *Mirafra fasciolata,* Red-capped Lark *Calandrella cinerea* and Spike-heeled Lark *Chersomanes albofasciata* (Willoughby 1969; Ryan & Bloomer 1997). In addition to phenotypic variation in plumage colouration, geographical variation may also be reflected in a range of parameters, e.g. bill size, voice or behaviour (Clancey 1966; Payne 1973; Payne 1984; Ryan & Marshall 2005; Engelbrecht 2005; Grosel 2007; Engelbrecht 2012). However, most studies focussing on intra-specific geographical variation usually only consider variation in various morphological parameters to resolve taxonomic issues (Johnson & Marten 1992; Johnson 2002). In recent years, traditional taxonomic studies have been usurped by studies of genetic analysis of populations. However, most studies still rely on morphometric data to support the findings of the genetic analyses.

Sexual dimorphism is generally defined as the morphological variation between the sexes of adults of the same species (Fairbairn 1997). In larks, sexual dimorphism is expressed as differences in vocalizations, sexual size dimorphism and sexual dichromatism. There are several examples of larks species where sex specific calls exist, e.g. Skylark (Donald 2005) and Short-clawed Lark (Engelbrecht 2005). Males usually have specific songs and territorial calls which does not form part of the vocal repertoire of females (de Juana *et al.* 2004). Sexual size dimorphism (SSD) in larks is especially common amongst resident insectivorous species and is almost absent in the more nomadic granivorous species. In larks, SSD is usually manifested as differences in the bill and wing length. In the case of the former, it has been suggested that differences in bill length between the sexes is the result of intra-specific niche differentiation where the sexes employ different foraging strategies and have slightly different diets, thus avoiding excessive competition for food resources in marginal habitats, e.g. the Spike-heeled and Raso Lark *Alauda razae* (Hockey *et al*. 2005; Barnes 2007). SSD is also particularly common in species where the sexes are monochromatic, i.e. no plumage differences, and is linked to sexual selection by females for larger males that have to defend territories (Cramp 1988). Thus, SSD seems to have evolved in response to selection pressures that differ between males and females (Badyaev & Martins 2000) or due to sex differences in selection on body size (Cox & Calsbeek 2009). The last form of dimorphism is sexual dichromatism. Although some larks shows minor differences in plumage colouration between the sexes, e.g. species of the genus *Pinarocorys*, *Ramphocorys* and *Eremophilia* (Keith *et al.* 1992; de Juana *et al.* 2004), it is best developed in the sparrow-larks (*Eremopterix* spp.). It has been suggested that the brighter plumage of the male enables easy recognition of the sexes in these semi-nomadic species when individuals arrives in a breeding area (Barnes 2007). Females, in contrast, are more cryptically coloured allowing for effective camouflage when incubating. Despite the bright plumage of the male, the colouration is disruptive and it is also very well camouflaged when breeding.

Sabota Larks are resident throughout their range, although populations in the arid western parts of its range may be prone to local movements (Dean 1997). Being sexually monochromatic but resident, one would therefore expect the species to exhibit sexual size dimorphism, especially in the west of its range where resources may be relatively scarce to the more mesic eastern parts of its range. However, according to the literature (Dean 2005), the sexes are alike in size and plumage colouration. The aim of this study was to quantify the extent of geographical morphological variation and sexual size dimorphism of the species across southern Africa using data obtained from museum skins.

4.2. Methods

4.2.1. Data collection

Biometric data of Sabota Larks were obtained from museum study skins requested from the following South African natural history museums: National Museum Bloemfontein, Iziko Museum of Cape Town, Ditsong National Museum of Natural History, Durban Natural Science Museum, East London Museum and the McGregor Museum in Kimberley.

The following measurements were recorded as described by Eck *et al*. (2011): culmen length (from the base of the bill at the union with the skull to the tip of the culmen), culmen-nare length (from the distal end of the nares to the tip of the culmen), bill depth (vertically perpendicular to the nares), bill width (horizontally perpendicular to the nares), length of the tarso-metatarsus (hereafter referred to as the tarsus length, from the notch of the first undivided anterior scute to the notch at the proximal end of the tarsus), wing length (maximum length of the flattened wing chord), and tail length (maximum length of the rectrices). Wing length was measured using a stopped wing ruler, a plain ruler to measure the tail length and digital Vernier calipers were used for all other measurements. Not all measurements were taken from all birds as some of the study skins were damaged, therefore, the sample sizes varied. As these measurements form part of a larger database of morphological data of African larks, and to ensure measurement consistency, all measurements were recorded by Prof. D. Engelbrecht only.

For sexual size dimorphism, Storer's Dimorphism Index (SDI; Storer 1966) was applied as follows:

$$SDI = (100^{*}\ (\text{parameter of female} - \text{parameter of male}))\ /\ (0.5^{*}(\text{parameter of female} - \text{parameter of male}))$$

The mean parameters were used for both males and females. A positive SDI value would represent reversed sexual dimorphism i.e. females being larger than males.

4.2.2. Statistical analysis

Descriptive statistical analyses for sexual size dimorphism, including the mean, standard deviation and range, were determined for all the measured parameters. One-way analysis of variance (ANOVA) was performed to test for any significant differences in any of the parameters measured between the different subspecies. Significance was assessed at a level of $P < 0.05$. Where significant differences were found, a Tukey post-hoc test was used to determine which taxa differed for which parameter/s. These statistical analyses were performed using SPSS version 22 software (SPSS, Inc. Chicago).

In order to determine geographical variation between the thick- and slender-billed groups, multivariate statistical analysis was performed using PRIMER-E package version 6 (Clark & Warwick 2001). Geographical data were imported into PRIMER-E and the raw data were square root transformed to reduce the confounding effect at large valued parameters. A distance matrix was compiled using Euclidean and the transformed data. A cluster analysis was performed on the distance matrix, whereby the relative similarity of the subspecies could be visualised in the form of a dendrogram.

A Non-metric Multidimensional Scaling (NMDS) plot of the distance matrix was used to visualize the variation between the sample groups. The distances between pairs of samples on the NMDS plot reflect the relative multivariate distance between the samples. This plot highlights any possible groupings between the subspecies of the Sabota Lark.

Permutational Multivariate Analysis Of Variance (PERMANOVA) of the distance matrix was used to test whether the differences between the group of subspecies were statistically significant. A significant result for the PERMANOVA indicates that there is a significant difference in the position of the centroids, dispersion about the centroid or both. A Distance-based test for homogeneity of multivariate dispersions (PERMDISP) of the distance matrix was used to determine whether the dispersion of each group around their group centroid varied significantly between groups (Anderson *et al*. 2008).

A SIMPER analysis was performed to determine the physical parameters driving putative groupings of the Sabota Lark. The SIMPER analysis used Euclidean distance at square root transformed data of each parameter to the similarity within the group and those contributing to the dissimilarity between groups. Parameters that contribute the most are those with the highest similarity or dissimilarity percentage (Clark & Warwick 2001).

4.3. Results

A total of 410 study skins representing adults of all eight southern African subspecies of the Sabota Lark were measured for the various parameters and the data were analysed. Sample sizes vary for individual parameters as a result of the condition of some of the study skins, e.g. some specimens had damaged bills or missing legs.

4.3.1. Sexual size dimorphism

A summary of the results of sexual size dimorphism including the mean, standard deviation, ranges, sample sizes and the SDI values of all the measured parameters for all the subspecies of both sexes of the Sabota Lark are shown in Table 4.1. Although most subspecies of the Sabota Lark do not exhibit statistically significant sexual size dimorphism for the various parameters, there were statistically significant differences ($P < 0.05$) between the sexes of *C. s. herero* (bill depth, bill width and tarsus length), *C. s.*

ansorgei (tail length), *C. s. sabota* (bill depth) and *C. s. suffusca* (bill width). However, the results should be interpreted with caution as the sample sizes were small for some subspecies, particularly *C. s. naevi* and *C. s. ansorgei*.

Negative SDI values were calculated for most parameters and showed that males were on average larger than females. Unfortunately, sample sizes were too small for some subspecies to make any meaningful interpretation from the results. Within both the thick- and slender-billed groups, sexual dimorphism were mostly expressed in bill depth, bill width and wing length (Table 4.1).

4.3.2. Geographical variation

The dendrogram results produced by Euclidean cluster analysis of mensural parameters confirmed that the eight subspecies of the Sabota Lark can be divided roughly into thick- and slender-billed groups (Figure 4.1).

Although, there was no clear separation between the two groups from the dendrogram, the NMDS plot based on thick- and slender-billed forms revealed separation between the thick- and slender-billed groups with some overlap between the groups (Figure 4.2). To highlight which subspecies of the Sabota Lark overlapped, the NMDS was performed based on the subspecies (Figure 4.3) and revealed that *C. s. ansorgei* belonging to the slender-billed group, was grouping with the thick-billed group and *C. s. waibeli* of the slender-billed group appeared to be an intermediate group. These results indicate that the eight subspecies of the Sabota Lark could be grouped as thick-billed, slender-billed, *C. s. waibeli* (the intermediate) and *C. s. ansorgei.*

To confirm whether males and females possessed different mensural characteristics, a one-way PERMANOVA was performed. The results supported the SDI results (sexual size dimorphism above), showing that males were significantly larger than females (PERMANOVA, $P < 0.05$; PERMDISP, $P > 0.05$).

Due to the statistically significant difference between the sexes and the smaller sample sizes for females, further analysis was performed for males only. The results revealed a statistically significant difference in the position of centroids between *C. s. ansorgei* and

C. s. naevi, *C. s. sabota* and *C. s. sabotoides*, *C. s. waibeli* and *C. s. naevi* and *C. s. herero* and *C. s. naevi* ($P < 0.05$). The PERMDISP analysis performed revealed non-significant differences between the dispersion of the centroids of the subspecies ($P > 0.05$).

Since the eight subspecies of the Sabota Lark could be classified into four groups, pair-wise PERMANOVA was performed to confirm whether there were statistically significant differences between revised groups. The PERMDISP analysis indicated that there was no significant difference in dispersion between the groups. The PERMANOVA analysis returned a significant result ($P < 0.05$), confirming in conjunction with the PERMANOVA results, that the position of the centroids of the revised groups was statistically significant ($P < 0.05$).

The results from the SIMPER analysis showed that tail length and wing length were the most important parameters contributing to the similarities within the groups thick-billed, slender-billed and *C. s. ansorgei*. In the group *C. s. waibeli* tail length and culmen-nare length contributed the most (Table 4.2). The comparison between the thick-billed and *C. s. ansorgei* groups, and between slender-billed and *C. s. ansorgei* groups (Table 4.3) showed that tail length and wing length contributed most to the dissimilarity between the groups. Tail length and culmen-nare length were the most important parameters contributing towards the dissimilarity between the thick- and slender-billed groups. Lastly, tail length and culmen length contributed the most towards the dissimilarity between *C. s. waibeli* and *C. s. ansorgei*. Thus, tail length and wing length appeared to be parameters contributing most to both the similarities within the groups and dissimilarities between the groups.

Calculated average squared distance showed that variability within the groups was similar or of the same magnitude between the groupings of the Sabota Lark. The calculated distance showed how the groups are related to each other (Figure 4.4). The thick-billed group seem to be closer related to the *C. s. ansorgei* group, while slender-billed group was closer related to *C. s. waibeli* group.

4.4. Discussion

4.4.1. Sexual size dimorphism

Adaptation to different ecological niches can result in differences between the sexes with regard to body size or morphological characteristics. These may manifest itself in differences in, for example, bill length, as one of the sexes preferentially forages at a different depth to the other sex (Donald *et al*. 2003). Overall size differences between the sexes can also results in niche differentiation as the larger sex can theoretically consume larger food items. The flight efficiency hypothesis explained by Andersson & Norberg (1981) was based on sexual selection whereby females preferred mating with small bodied males selected during the flight performance.

Although the Sabota Lark exhibits sexual size dimorphism, it was not consistent for a given parameter nor was it statistically significant for the majority of the subspecies. The SDI values obtained in this study were also relatively small and suggest only minor levels of sexual size dimorphism is present in the Sabota Lark. The SDI values showed that most subspecies of the Sabota Lark had higher values for parameters related to the flight apparatus (tail length) and bill dimensions e.g. bill width and bill depth (Table 4.2). A longer tail length in males may result from selection to enhance flight efficiency during display flights. Although not really known as a species that exhibits extensive display flights, males do perform these display flights from time to time. A typical display flight takes place at a great height and can last in excess of 15 min (Engelbrecht, pers. obs.). Thus, it is clear that a longer tail length may provide benefits during the energetically costly display flights. (Andersson 1994; Savalli 1995; Pryke & Andersson 2005).

Bill width and bill depth measurements appeared to be the most consistently dimorphic characters for majority of the subspecies. Males generally had larger bills (width and depth) compared with females, but the difference was not statistically significant for all the subspecies and there was a good degree of overlap in the measurements. Sexual differences in feeding apparatus are usually viewed as ecologically driven dimorphism as sexes exploit different ecological niches (Selander 1966). However, there are also examples where sexual dimorphism in bill length of Swamp Sparrows *Melospiza georgiana* is driven by mate choice (Olsen *et al.* 2013). In the study of Olsen *et al*.

(2013), bill size was found to increase with age. Thus, by selecting males with larger bills, females are choosing mates that can defend their territory in the coming years and pass their good genes on to their offspring.

4.4.2. Geographical variation

To determine phenotypic geographical variation in the Sabota Lark, the results confirmed separation between the thick-billed and slender-billed groups. However, the subspecies *C. s. ansorgei* which was historically assigned to the slender-billed group, grouped with the thick-billed group. From a distribution point of view, the results of this study which groups *C. s. ansorgei* with the thick-billed group makes more sense. The distribution map provided by Dean (2005) suggests that *C. s. ansorgei* may be isolated from the other slender-billed subspecies by a strip occupied by *C. s. herero* and *C. s. naevi*. Furthermore, *C. s. ansorgei, C. s. herero* and *C. s. naevi* all occupy similar, very arid environments in the north-western parts of the subcontinent. The subspecies *C. s. waibeli* showed characteristics that were intermediate between the slender-billed and thick-billed groups and may represent a transition type from the mesic and semi-arid woodlands and savannahs in the east, to the semi-arid and mostly arid woodlands and desert margins in the north-west of the subcontinent.

In this study, the significant difference found for PERMANOVA and the non-significant for PERMDISP suggest that the difference between the four groups and the eight subspecies may be due to location effect. Variation between the groups and subspecies was indicated by flight parameters. However, separation of subspecies into four groups shows that geographical variation might have an effect on the morphological characteristics of the Sabota Lark.

The results of this study support Hall & Moreau's (1970) suggestion that the Sabota Lark can be separated into a slender-billed (*C. s. sabota*, *C. s. sabotoides*, *C. s. suffusca*), thick-billed (*C. s. bradfieldi*, *C. s. herero*, *C. s. naevi*) and an intermediate group (*C. s. waibeli*), but with *C. s. ansorgei* as a separate group with affinities to the thick-billed group. The grouping of *C. s. ansorgei* with the thick-billed group certainly makes more sense from a biogeographical point of view. The result of this study now confirms that the thick-billed group is restricted to arid Karoo, desert margins and coastal plains of the western parts of southern Africa, and the slender-billed group is mainly restricted to semi-arid savannah and woodland habitats in the more mesic eastern parts of the subcontinent. The morphological differences between the two groups lend support to calls for the recognition of the two groups as distinct species but a preliminary genetic study of the differences between the two groups gave only limited support to this view (Ryan, pers. comm.). Of particular interest is the recognition of *C. s. waibeli* as a distinct but intermediate group within the Sabota Lark complex. A more detailed genetic study of this complex and representing all the known subspecies is necessary to unequivocally address the taxonomic status of the Sabota Lark groups.

4.5. Conclusion

In conclusion, morphometric data in this study revealed that a population level SSD in the Sabota Lark is not statistically significant, although, males are on average larger than females for the majority of parameters. The SDI revealed that *C. s. herero* is the most sexually dimorphic of all the subspecies. The high SDI values for wing length in majority of the species may reflect behavioural adaptations for sustained display flight. Multivariate analysis revealed four groups of the Sabota Lark with *C. s. waibeli* as an intermediate group between the thick- and slender-billed groups. It is recommended that these results be confirmed by genetic analysis of the different subspecies.

Table 4.1. Analysis of sexual size dimorphism in the different subspecies of the Sabota Lark *Calendulauda sabota*. Shaded cells indicate statistically significant differences (*P* < 0.05, one-way ANOVA). All measurements in mm.

	Mean ± SD			
	♂ (n)	**♀ (n)**	***P***	**SDI**
		C. s. bradfiledi		
Culmen	16.9 ± 1.0 (49)	16.6 ± 0.8 (11)	0.5	-2.3
Cumen-nare	12.1 ± 0.7 (48)	11.9 ± 0.7 (11)	0.9	-2.4
Bill depth	6.2 ± 0.3 (50)	6.1 ± 0.2 (11)	0.2	-2.8
Bill width	5.7 ± 0.4 (50)	5.6 ± 0.4 (11)	0.5	-4.0
Tarsus	24.7 ± 0.8 (50)	24.7 ± 1.1 (11)	0.5	-0.0
Tail	55.4 ± 2.5 (46)	53.0 ± 2.4 (11)	0.9	-4.3
Wing	87.5 ± 3.0 (50)	85.7 ± 2.8 (11)	0.9	-2.1
		C. s. herero		
Culmen	17.7 ±0.9 (50)	17.0 ± 1.0 (23)	0.6	-4.2
Cumen-nare	12.3 ± 0.6 (49)	11.6 ± 0.8 (22)	0.2	-5.9
Bill depth	6.1 ± 0.2 (51)	5.8 ± 0.3 (23)	<0.05*	-5.0
Bill width	5.6 ± 0.4 (51)	5.2 ± 0.2 (23)	<0.001**	-8.2
Tarsus	24.4 ± 0.9 (51)	23.9 ± 0.6 (25)	<0.05*	-2.2
Tail	54.8 ± 2.9 (52)	50.7 ± 2.6 (25)	0.90	-7.7
Wing	87.3 ± 2.3 (52)	83.0 ± 2.2 (25)	0.71	-5.0
		C. s. naevi		
Culmen	17.4 ±0.5 (3)	17.3 ± 0.9 (4)	0.3	-0.6
Cumen-nare	12.2 ± 0.5 (3)	12.0 ± 0.8 (4)	0.6	-1.2
Bill depth	6.1 ± 0.2 (3)	5.5 ± 0.4 (4)	0.4	-10.3
Bill width	5.2 ± 0.2 (3)	5.3 ± 0.2 (4)	0.7	-1.5
Tarsus	23.6 ± 0.6 (3)	24.7 ± 1.5(4)	0.1	4.6
Tail	53.3 ± 2.5 (3)	52.0 ± 1.8 (4)	0.7	-2.5
Wing	84.3 ± 1.5 (3)	83.8 ± 4.4 (4)	0.2	-0.7
		C. s. ansorgei		
Culmen	17.3 ±0.8 (19)	16.8 ± 0.4 (2)	0.3	-3.5
Cumen-nare	11.5 ± 0.7 (18)	11.1 ± 0.2 (2)	0.1	-4.1
Bill depth	5.9 ± 0.3 (19)	5.4 ± 0.6 (2)	0.3	-8.5
Bill width	5.5 ± 0.4 (19)	4.8 ± 0.6 (2)	1.0	-13.6
Tarsus	24.4 ± 1.0 (19)	23.6 ± 0.5 (3)	0.5	-3.3
Tail	53.2 ± 3.4 (19)	49.7 ± 0.6 (3)	<0.05*	-6.9
Wing	85.5 ± 2.9 (19)	83.3 ± 0.6 (3)	0.1	-2.6
		C. s. sabota		

	Mean ± SD			
	♂ (n)	**♀ (n)**	***P***	**SDI**
Culmen	15.2 ±0.8 (53)	14.6 ± 0.8 (20)	0.8	-3.8
Cumen-nare	10.1 ± 0.6(50)	9.6 ± 0.5 (20)	0.4	-4.9
Bill depth	5.3 ± 0.3 (53)	5.1 ± 0.2 (20)	<0.001**	-4.6
Bill width	4.9 ± 0.3 (53)	4.7 ± 0.4 (20)	0.3	-4.8
Tarsus	23.7 ± 1.0 (53)	23.5 ± 0.8 (21)	0.2	-0.8
Tail	51.9 ± 3.2 (52)	49.6 ± 3.0 (21)	0.9	-4.7
Wing	84.5 ± 2.5 (53)	81.3 ± 2.2 (21)	0.5	-3.9
		C. s. sabotoides		
Culmen	15.6 ±0.6 (31)	15.1 ± 0.3 (13)	0.1	-3.7
Cumen-nare	10.0 ± 0.4 (29)	9.7 ± 0.5 (13)	0.4	-2.2
Bill depth	5.2 ± 0.3 (31)	5.1 ± 0.2 (13)	0.4	-1.0
Bill width	4.7 ± 0.4 (32)	4.4 ± 0.4 (13)	1.0	-6.2
Tarsus	23.2 ± 0.7 (35)	23.4 ± 0.7 (14)	1.0	1.2
Tail	52.3 ± 3.0 (35)	47.9 ± 2.3 (14)	0.4	-8.9
Wing	84.0 ± 2.4 (35)	80.9 ± 3.2 (14)	0.4	-4.5
		C. s. waibeli		
Culmen	15.6 ± 1.0 (8)	16.3 ± 0.9 (3)	0.8	4.5
Cumen-nare	11.1 ± 1.2 (8)	10.8 ± 0.3 (3)	0.1	-3.1
Bill depth	5.7 ± 0.4 (8)	5.2 ± 0.1 (3)	0.2	-7.7
Bill width	5.0 ± 0.5 (8)	5.0 ± 0.0 (3)	0.3	0.2
Tarsus	23.8 ± 0.8 (8)	22.7 ± 0.7 (3)	0.8	-4.8
Tail	53.5 ± 4.3 (8)	52.3 ± 3.1 (3)	0.5	-2.2
Wing	84.6 ± 4.4 (8)	82.7 ± 2.9 (3)	0.6	-2.3
		C. s. suffusca		
Culmen	15.3 ±0.8 (38)	14.9 ± 0.8 (13)	0.3	-2.6
Cumen-nare	9.8 ± 0.6 (38)	9.1 ± 0.5 (12)	0.5	-7.4
Bill depth	4.7 ± 0.4 (39)	5.0 ± 0.3 (13)	0.5	7.6
Bill width	4.7 ± 0.4 (39)	4.5 ± 0.5 (13)	<0.05*	-3.1
Tarsus	23.0 ± 1.9 (41)	22.8 ± 0.8 (13)	0.4	-1.1
Tail	49.8 ± 1.8 (41)	46.2 ± 2.4 (13)	0.5	-7.5
Wing	82.4 ± 2.2 (41)	78.7 ± 3.1 (13)	0.1	-4.7

Table 4.2. Summary of SIMPER results showing the contribution percentages of the mensural parameters for the similarities within the slender-billed, thick-billed, *C. s. waibeli* and *C. s. ansorgei* groups of the Sabota Lark *Calendulauda sabota*. All measurements in mm.

Parameters	**Slender-billed**	**Thick-billed**	***C. s. ansorgei***	***C. s. waibeli***

Tail length	37.0	43.2	36.6	54.6
Wing length	23.1	24.2	16.9	6.4
Culmen length	8.1	12.3	16.4	7.2
Culmen-nare length	9.0	9.2	11.4	11.1
Bill depth	3.6	4.4	3.8	3.4
Bill width	7.3	7.4	7.1	10.7
Tarsus	5.8	5.2	7.3	6.6

Table 4.3. Summary of SIMPER results showing the contribution percentages of the mensural parameters for the dissimilarities between the groups of the Sabota Lark *Calendulauda sabota*. All measurements in mm.

Parameters	***C. s. ansorgei* and slender-billed**	***C. s. ansorgei* and thick-billed**	***C. s. ansorgei* and *C. s. waibeli***	**Thick- and slender-**

				billed
Tail length	28.8	35.3	34.9	26.1
Wing length	18.4	19.4	15.2	16.5
Culmen length	17.4	13.7	19.4	15.0
Culmen-nare length	16.5	13.7	12.7	22.8
Bill width	8.6	7.0	7.2	8.3
Bill depth	5.8	0.0	0.0	7.2
Tarsus length	0.0	6.4	5.7	0.0

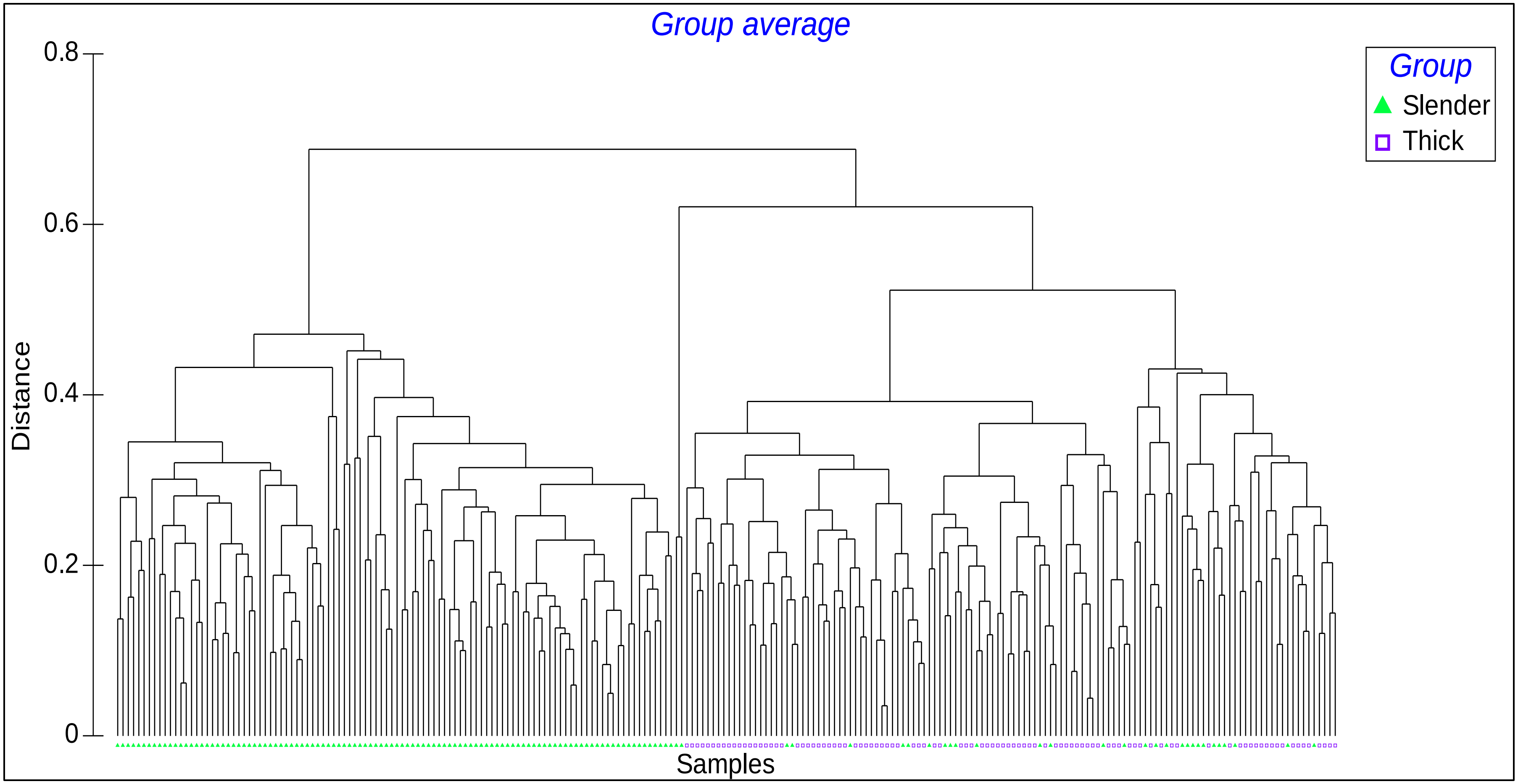

Figure 4.1. Dendrogram from Euclidean distance cluster analysis showing groupings of the Sabota Lark *Calendulauda sabota* according to geographical location.

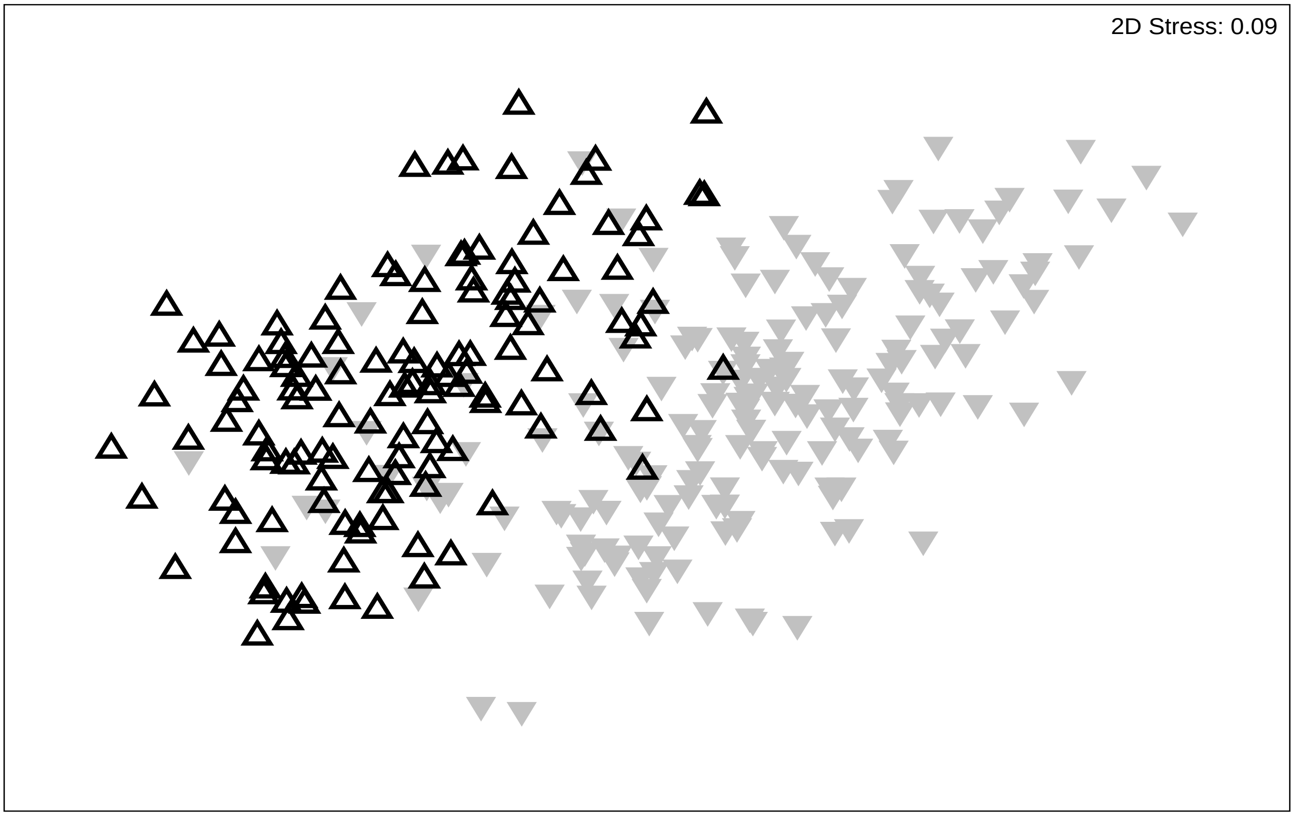

Figure 4.2. Multidimensional scaling ordination of both male and female data for geographical variation of the Sabota Lark *Calendulauda sabota* across its range. Groups established from the cluster analysis are indicated by different shapes and colours (n = 184 slender-billed (▼) and 133 thick-billed samples (Δ)).

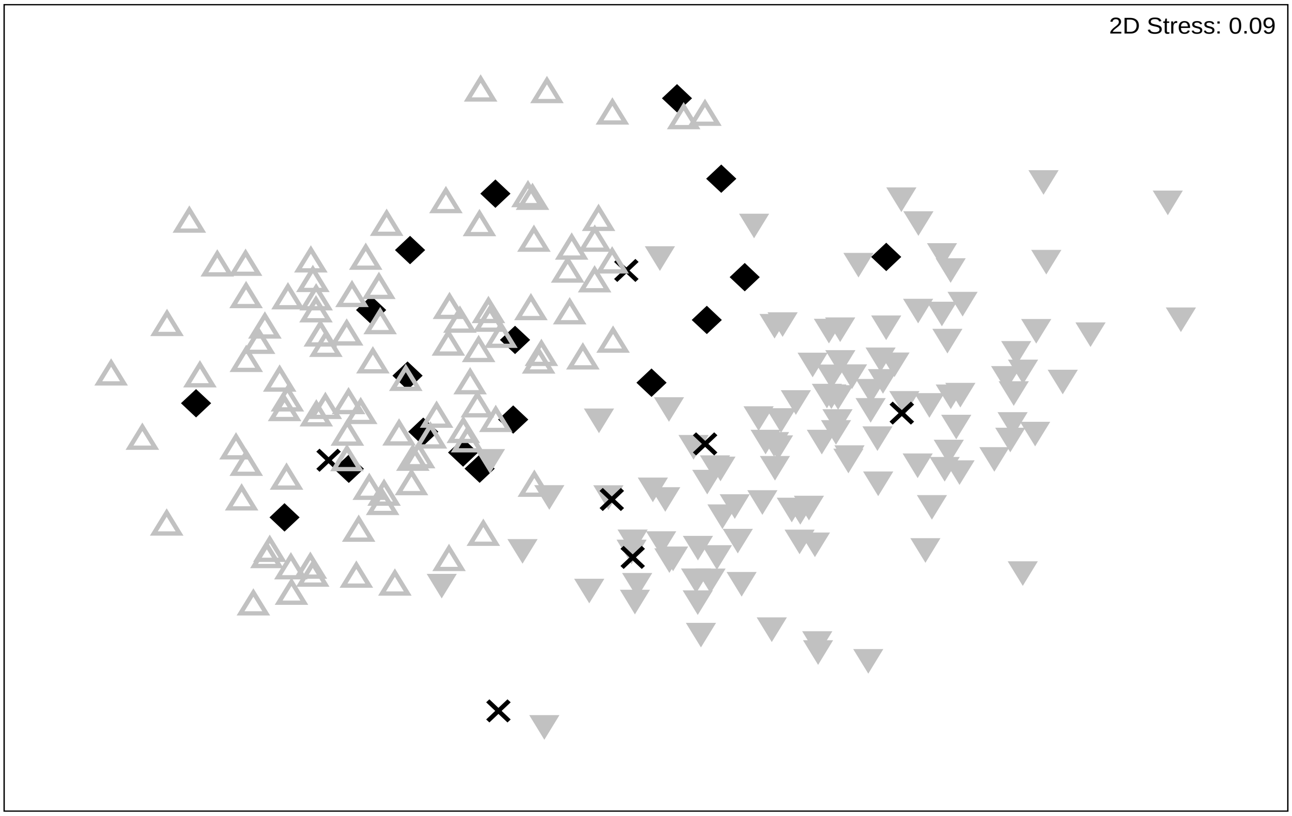

Figure 4.3. Multidimensional scaling ordination of male data for geographical variation of the Sabota Lark *Calendulauda sabota* across its range. Thick-billed group (▲), slender-billed group (∆), *C. s. waibeli* (**x**), *C. s. ansorgei* (♦). Resemblance was D1 Euclidean distance.

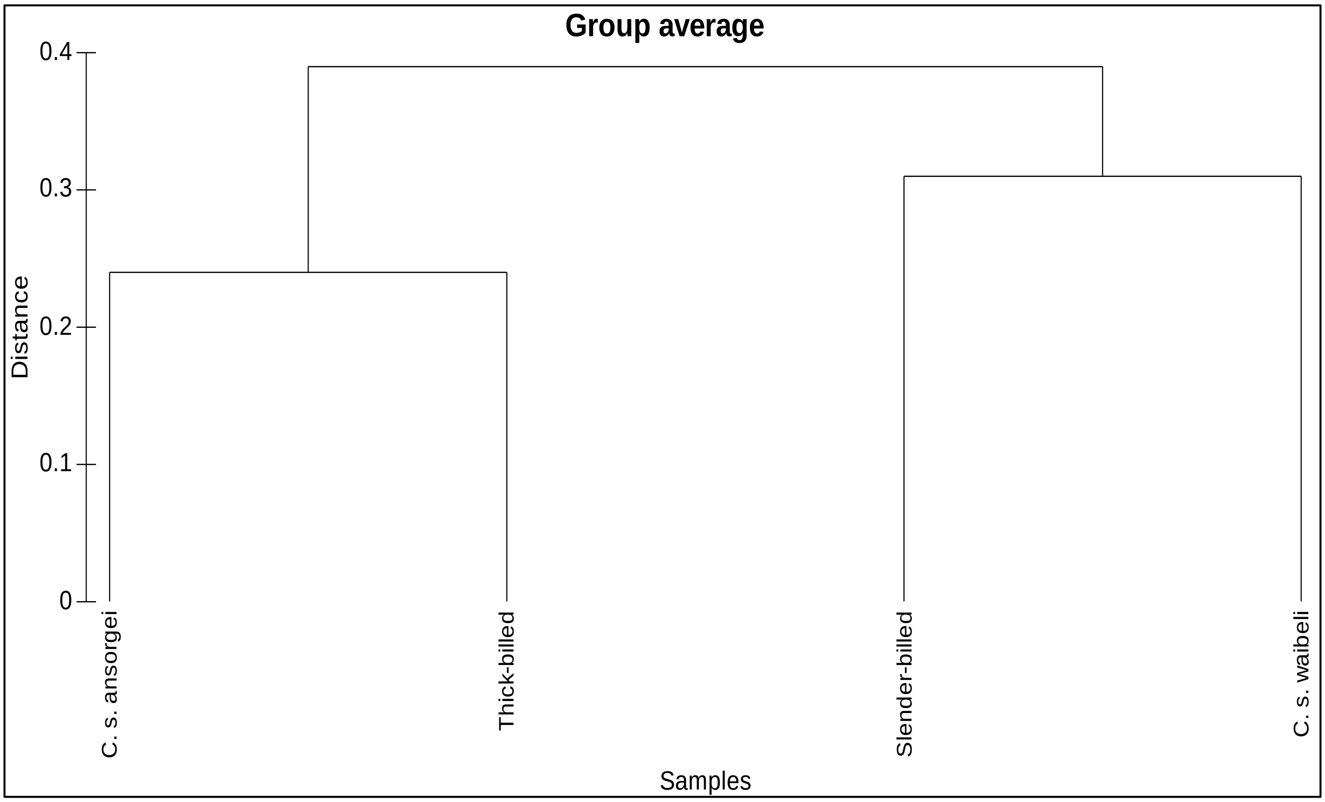

Figure 4.4. The calculated average distance showing the relation between the formed groups of the Sabota Lark *Calendulauda sabota*.

CHAPTER 5

As one of the most widespread larks in southern Africa, the Sabota Lark *Calendulauda sabota* is an ideal candidate species to study geographical variation in various biological and ecological parameters, e.g. latitudinal variation and the effect of different rainfall regimes on various biological and ecological parameters. Unfortunately our scant knowledge of even the most basic breeding parameters, e.g. duration of the incubation period, precluded studies investigating such aspects. In an attempt to address this shortcoming, I conducted the first detailed scientific study of the breeding biology and ecology of the Sabota Lark. The results not only improved our knowledge of the species, and the family Alaudidae, substantially, but it also challenged longstanding ideas about various aspects of its natural history and taxonomy.

Chapter 2 showed the value and challenges of using citizen science data to obtain some basic information about the biology of poorly known and difficult to study species. Data was obtained from various databases administered by the Animal Demographic Unit at the University of Cape Town, as well as the National Museum in Bloemfontein to investigate aspects such as breeding seasonality, breeding biology, diet, geographic variation and biometrics of the species from across its range. The results of this desktop study were used as a base to design a field-based study on the breeding ecology of the Sabota Lark.

Chapter 3 presents the results of a two-year long field study of the breeding biology of the species. This is one of only a handful of African larks which have been studied intensively and as such a wealth of new data was generated which significantly improved our knowledge of this species and the family in general.

Chapter 4 investigated geographic size variation in subspecies of the Sabota Lark. This research was based on data collected from museum study skins and represented all the currently recognized subspecies in southern Africa. Multivariate statistics was used for the first time in this species to determine the relationships of southern African subspecies using biometric data. The results challenged the current taxonomy but lend support to an earlier suggestion by Hall & Moreau (1970) but which did not get much support from other taxonomists at the time.

A summary of the major contributions this study has made follows below.

- Both NERCS data and the results of the field study show that the Sabota Lark breeds in the wet season.
- There is geographic variation in the onset and peaks of the breeding season in the mesic east and arid west of the subcontinent.
- Typical of many lark species, males only assisted females during the nestling period, but unusually for larks, males assisted with brooding nestlings. This usually took the form of shading nestlings, but there was one instance where a male actually brooded nestlings by entering the nest and transferring heat.
- Double-brooding was reported for the first time and replacement clutches were common.
- In common with many other ground-nesting species, the Sabota Lark also had a poor breeding success.
- Video-monitoring of nests revealed some of the predators of Sabota Larks and factors which may lead to nest failure or abandonment. It was also one of the first studies to use video-monitoring to describe the roles and relative contributions of the sexes in the nesting cycle.
- The results showed that there is limited sexual dimorphism in this species and that it is not consistent throughout the species' range. The results also revealed that wing and tail length are the most important parameters contributing towards the similarities within and dissimilarities between the sexes.
- The multivariate analysis suggests that the species can be divided into four groups, namely a thick-billed group, a slender-billed group with *C. s. waibeli* and *C. s. ansorgei* representing their own groups as they share characteristics with both the other two groups.

Based on the findings of this study, the following recommendations are made and future research opportunities are highlighted.

- Citizen science data has the potential to improve our knowledge of poorly known and difficult to study species. Managers of citizen science projects should do more to encourage people to contribute to these databases. The NERCS data is potentially very valuable but since the early 1990's there had been virtually no submissions to this database. This project should be revived and ways should be sought to encourage people to submit data. It is also suggested that field researchers should submit their data to the project.
- Video-monitoring of nests have the potential to make a major contribution to our understanding of animal behaviour. The use of video cameras should be encouraged and should ideally include 24 hour video-surveillance to get a better understanding of parental roles and their relative contributions as well as other activities taking place at the nest e.g. predation
- Future studies should attempt to determine the proximal causes of breeding failure in the Sabota Lark and other ground nesting species. This should include different micro-habitats and geographic localities.
- The results of this study showed sexual size dimorphism for different parameters in different subspecies. This should be investigated in more detail to determine if it is an artefact of sample size or if there is an ecological explanation for this.
- To confirm the possible groupings of the eight subspecies of the Sabota Lark, it is suggested that more biometric data be collected representing all the subspecies and ideally genetic analysis should be done to confirm the suggested groupings obtained in this study.
- Stomach contents should be collected from across the species range to determine if the species exhibits seasonal and geographical variation in relation to its diet.

To conclude, the current study has made a major contribution to our knowledge of the Sabota Lark, but also has raised some interesting questions and opened avenues for future research on this interesting species and the family Alaudidae in general.

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