ASPECTS OF THE BIOLOGY OF THE PINK-BILLED LARK (*Spizocorys conirostris*) IN THE LIMPOPO PROVINCE, SOUTH AFRICA

by

Mathonsi Mandlenkosi Habile Thabo

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DECLARATION

I declare that **ASPECTS OF THE BIOLOGY OF THE PINK-BILLED LARK (*Spizocorys conirostris*) IN THE LIMPOPO PROVINCE, SOUTH AFRICA** is my own work and that all the sources used or quoted have been indicated and acknowledged by means of complete references and that this work has not been submitted for any other degree at any other institution.

Mathonsi Mandlenkosi Habile Thabo **25 June 2013**

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Signature

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PREFACE

The fieldwork for this study was carried out from October 2008 to October 2010, under the supervision of Professor D. Engelbrecht of the Department of Biodiversity at the University of Limpopo. Professor Engelbrecht kindly agreed to provide me with raw breeding data of the same population collected during 2008. This study represents original work by the author and where work of other authors has been used; they are duly acknowledged in the text and listed as references.

Chapter 1 is a general introduction to the family Alaudidae in which their characteristics and taxonomy are discussed. This is followed by a brief overview of the general biology and ecology of larks of the world in general, followed by a more specific emphasis on the genus *Spizocorys*, and finally the Pink-billed Lark. In this section, gaps in the available knowledge of Pink-billed Larks are highlighted. This chapter culminates in the aim and objectives of this study. In Chapter 2 the various aspects of the breeding biology of the Pink-billed Lark are reported. This includes, amongst others, aspects such as breeding seasonality, clutch sizes, roles of the sexes during the breeding cycle and breeding success. Chapter 3 provides the results of a morphometric study of museum study skins from across the species range. This includes an analysis of sexual size dimorphism and geographical variation of the different subspecies. This chapter also provides a brief description of the timing and pattern of moult and the various vocalizations of the Pink-billed Lark. Chapter 4 concludes the dissertation with a summary of the results of this study and highlights avenues for future research on the species and the family.

The format of Chapters 2 and 3 takes the form of research papers that can be submitted for publication with minimum editing. Chapter 2 has been published in the Journal of African Zoology (see below). Chapter 3 is in preparation for submission to a peer-reviewed journal. As such, there is some repetition in the introductory paragraphs and concluding remarks of chapters 2, 3 and 4. To give this manuscript a degree of uniformity, the literature cited in all chapters has been formatted according to the manuscript requirements of the Journal of African Zoology, and a reference list appears at the end of the dissertation. Tables and figures are arranged at the end of each chapter.

The results of this study (Chapter 2) have been published in the Journal of African Zoology and have been presented at a local and two national conferences. The details are:

i) **Engelbrecht D. and Mathonsi M.H.T.** (2012) Breeding ecology of the Pink-billed Lark, *Spizocorys conirostris*, in an agricultural landscape in South Africa. *African Zoology* **46(1):** 26- 34.

ii) **Mathonsi, M.H.T. and Engelbrecht, G.D.** Breeding biology of the Pink-billed Lark *Spizocorys conirostris* in the Limpopo Province. Paper read at the Post-Graduate Research Day at the University of Limpopo, South Africa, 16 September 2010.

iii) **Mathonsi M.H.T. and Engelbrecht G.D.** Is there a difference in the relative contribution of male and female Pink-billed Larks (*Spizocorys conirostris*) during the nesting cycle? Joint ZSSA & PARSA Conference, Stellenbosch, South Africa, July 2011.

ABSTRACT

The genus *Spizocorys* comprise a group of six small, gregarious larks inhabiting grasslands, and arid and semi-arid savannah, dwarf shrublands and gravel plains of southern Africa. They are unique amongst larks in that they are sexually monomorphic and exhibit biparental care. The Pink-billed Lark *Spizocorys conirostris* is endemic to southern Africa with six subspecies recognized based on differences in plumage colouration. The six subspecies are distributed throughout southern Africa with the darker, more rufous and heavily streaked populations occurring in the mesic east and paler, lightly streaked individuals occupying the more arid western and north-western parts of the species range. Despite their widespread occurrence and the growing interest for research on the evolution of characteristics in the family Alaudidae, very little is known about the general biology and ecology of the *Spizocorys* larks. Most published information on Pink-billed Larks are based on incidental observations and there has been no detailed study on any aspect of this species biology or ecology. In order to contribute to the improvement of our current knowledge of this interesting group of species, it was decided to study various aspects of the breeding biology and ecology, morphometrics, moult, vocalizations and intraspecific geographical variation in the Pink-billed Lark.

The breeding ecology of the Pink-billed Lark was studied at Al3 farm (De Loskop) near Mogwadi in the Limpopo Province, South Africa, from October 2008 to October 2010. The study site is a commercial agricultural farm used mainly for production of crops, e.g. tomatoes, onions and potatoes, and to a lesser extent for free range livestock (cattle) production. The results are compared with data in Birdlife South Africa's Nest Record Card Scheme (NERCS).

Fifty-three nests were found during the course of this study. Nesting was observed between February and May, with peak activity in April and May. Only three nests were found outside this period. Analysis of the NERCS records from across the species' range revealed an extended breeding season for the species with breeding recorded in all months of the year, albeit with a slight peak in April to July. Analysis of NERCS records revealed geographical variation in the onset of breeding.

The results of the analysis of nest micro-habitat features supports the view that "it appears to need good cover always" but contrasts with the opinion that "the

nest is usually poorly concealed" as stated in literature. The percentage grass and forb cover at nests in the present study averaged 68% with debris such as moribund vegetation increasing the amount of cover to 84%. Another interesting anomaly between the present study and that reported in the literature is in the preferred base structure. In literature it was found that the majority of nests (93%) were placed at the base of a grass tuft and the remainder against shrubs. In this study, small herbaceous shrubs were the preferred base plants (62%) followed by grass. Analysis of nest orientation data showed that nest entrance directions are not uniformly distributed, i.e. there is a bias towards a preferred entrance direction, namely south (Raleigh's Uniformity Test, $Z = 43.21$, $P < 0.001$). The preferred nest orientation in this study was south (60%), south-west (24%) or south-east (16%).

Egg mass and dimensions showed no regional variation but there was evidence of geographical variation in clutch size. There was no significant difference ($P \geq 0.05$) in the rate of food delivery by males and females, but the results suggest there may be inter-sexual differences in the type of food delivered to nestlings. Invertebrates comprised two-thirds of the diet of nestlings while seed made up the remainder. The growth and development of nestlings are described for the first time. The incubation period was 12 days and the nestlings fledged after 10–13 days. Breeding success, determined using Mayfield's method, was very low, averaging 12.8% over the two years of this study. Known causes of failure included nest predation, flooding, starvation, nest abandonment and failure to hatch.

Statistical analysis of morphometric data of live specimens and museum study skins suggest that sexual size dimorphism was only statistically significant for two parameters, namely wing and tail length. Males tend to have longer wings and tails compared to females which may be an adaptive advantage for their extended display flights. The results of the analysis of intraspecific geographic variation revealed a statistically significant difference in wing length between the nominate race and those of the other southern African subspecies combined.

Apart from a single individual moulting the innermost secondaries during the breeding season, no other evidence of moult was recorded in breeding birds. Inspection of museum study skins showed that they undergo a partial moult before the onset of the breeding season, involving the inner-most secondaries and some of

the contour feathers. Pink-billed Larks undergo post-breeding moult in spring, which is an adaptation to reduce the conflict between moult and breeding as both activities have high energy demands. Furthermore, males will undergo pre-breeding moult have fresh flight feathers at the onset of the breeding season which would be an advantage for the demands incurred by aerial display flights.

The study revealed a rich vocal repertoire for the Pink-billed Lark. The vocalizations analysed and described for the first time include the flight song of males, contact, alarm, flight calls, aggressive, ground, territorial call and nestling begging calls.

The results of this study shed valuable light on the natural history of this species and contributed significantly to ornithology and our growing understanding of the biology and ecology of the family. The results can also form a basis for future inter- and intraspecific comparative studies. The study illustrates the importance of undertaking long term studies of species to account for inter-annual differences in various ecological parameters.

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CHAPTER 1

General introduction

One of the focal points of avian life history studies is a thorough understanding of the causes and consequences of variation in reproductive strategies of birds (Auer *et al.* 2007). According to Auer *et al.* (2007), acquiring and maintaining detailed knowledge of the breeding biology of species is the key to understanding the variations in avian reproductive strategies. This knowledge provides critical natural history data that describes patterns of variation within avian communities, helps to facilitate the generation of new hypotheses and allows us to test the validity of existing ones.

The larks (Alaudidae) represent a family of approximately 96 species (de Juana *et al*. 2004). The family is largely confined to the Old World, reaching its greatest species diversity in Africa with 81% of the species occurring on the continent and 63% being endemic to Africa. The variation in life history characteristics exhibited by larks, e.g. sexual dimorphism, variation in the type of display flights and patterns of parental care, the use of heterospecific vocal mimicry, and the varying degrees of movement such as nomadism or residency, make the family ideal for comparative studies on the evolution of life history strategies.

Although larks have always been at the centre of taxonomic and, more recently, phylogenetic debate (Meinertzhagen 1951; Macdonald 1953; Lawson 1961; Winterbottom 1962; Clancey 1966; Clancey 1972; Clancey 1993; Ericson and Johansson 2003; Beresford *et al.* 2005; Barnes 2007), the family has largely escaped the interest of field biologists and there is a general lack of biological or ecological information for the majority of larks. A few species, particularly some of conservation concern, e.g Razo Lark *Alauda razae,* Rudd's Lark *Heteromirafra ruddi* and Short-clawed Lark *Certhilauda chuana,* and/or those inhabiting extreme environments, e.g. Dune Lark *Calendulauda erythrochlamys* and Greater Hoopoe-lark *Alaemon alaudipes*, have received attention from conservation biologists or physiologists and rates amongst the best known species in the family. However, the honour of the best studied lark must be given to the Skylark *Alauda arvensis* (see Donald 2004). For the majority of larks however, basic biological and ecological data such as diet, duration of the incubation and nestling periods and breeding success is lacking. In fact, the nests and eggs of some species have never even been described, e.g. Indochinese Bushlark *Mirafra erythrocephala,* Kordofan Lark *Mirafra cordofanica,* Williams's Lark *Mirafra williamsi,* Rusty Lark *Mirafra* rufa, Friedmann's Lark *Mirafra pulpa*, Ash's Lark *Mirafra ashi*, Degodi Lark *Mirafra degodiensis*, Foxy Lark *Calendulauda alopex*, Blanford's Lark *Calandrella blanfordi*, Erlanger's Lark *Calandrella erlangeri* and Masked Lark *Spizocorys personata* (*cf.* de Juana *et al.* 2004). Our generally poor knowledge of the biology and ecological requirements of larks has confounded our understanding of the evolution of variation in life history strategies within this interesting family. In the section that follows, a brief overview of lark taxonomy is provided and the reader is also introduced to some aspects of the biology, ecology and life history characteristics of larks.

1.1. The Alaudidae

1.1.1. What is a lark?

The family Alaudidae (larks) is a well-defined group of small to medium-sized, cryptically plumaged, primarily terrestrial, ground-nesting songbirds. They are distinguished by two unique tarsal and syringeal features. Firstly, they possess a latiplantar, scutellate tarsus, i.e. the posterior surface is flat and covered with prominent scales, in contrast to the narrow and smooth tarsus found in other passerine families. Secondly they possess a structurally relatively simple syrinx comprised of only five pairs of syringeal muscles and a rudimentary pessulus compared to the 6–8 pairs of syringeal muscles and a well-developed, bony pessulus of other passerines (de Juana *et al.* 2004). These two anatomical features aside, larks are arguably best known for their generally cryptic plumage and their amazing song and display flights. Their dun colouration confounds identification resulting in them often being overlooked or ignored by birdwatchers and even scientists. However, their song and display flights compensate for their drab livery and have been celebrated by poets and writers for centuries (Beer 1995).

1.1.2. Taxonomy of larks

The Alaudidae is a monophyletic family, i.e. they share derived characteristics, with no close living relatives (de Juana *et al.* 2004). The combination of their unique tarsus and syrinx makes the family such a distinct entity that no genera in the Alaudidae have ever been placed in another family. However, since the introduction of the binomial classification system by Linnaeus, lark taxonomy has been in a constantly fluctuating state. There is considerable morphological and plumage colouration variation within the family and even intraspecifically, which complicates the delineation of genera using traditional morphological characters (Winterbottom 1962).

Larks were long placed at or near the beginning of the passerines, just after the sub-oscines and before the swallows (Sheldon and Gill 1996; Patterson 2002; Ericson and Johansson 2003; Barker *et al.* 2002; 2004). This was largely due to Mayr and Amadon’s (1951) contention that the pessulus and tarsal features of larks were primitive and not derived features. However, recent evidence suggests that although larks have ten primaries, they may be taxonomically closer to passerines possessing nine primaries such as canaries and buntings as a result of similarities in bill structure (Sibley and Ahlquist 1990; Keith *et al.* 1992). This notion is supported by the reduction or vestigiality of the outermost primary in many lark species. Even after extensive higher order phylogenetic studies the exact position of the Alaudidae remained inconclusive (Sibley and Ahlquist 1990; Sibley and Monroe 1990; Sheldon and Gill 1996; Barker *et al.* 2002, 2004). However, several recent phylogenetic studies confirm the larks as a distinct lineage in the Sylvioidea clade with it closest sister group, surprisingly, the morphologically and ecologically dissimilar parrotbills and bearded tits (Panuridae) of Eurasia (Ericson and Johansson 2003; Alström *et al.* 2006; Fuchs *et al.* 2006; Johansson *et al.* 2008).

The results of a phylogenetic study of the Alaudidae by Barnes (2007) showed that they can be divided into three main clades: an ammomanid clade, a mirafrid clade and an alaudid clade (Table 1.1). The ammomanid larks show a close southern African affinity and include the genera *Chersomanes*, the Long-billed Lark complex (*Certhilauda*) and *Ammomanes* (*Ammomanopsis*) *grayi*, but also the hoopoe-larks (*Alaemon*) of northern and north-eastern Africa. A second grouping in this clade includes a Saharo-Sindian radiation which comprises of *Ramphocoris clotbey*, *Ammomanes cincturus*, and *Ammomanes deserti*, sister to the Afro-Sindian sparrow-lark (*Eremopterix*) clade (Barnes 2007). Interestingly, the Malagasy endemic *Mirafra hova* was found to be a basal member of *Eremopterix*. The mirafrid clade is not well resolved yet but includes a relatively diverse assemblage and Barnes (2007) suggested it be comprised of the genera *Calendulauda, Heteromirafra, Corypha* and *Megalophoneus.* The alaudid clade comprises a merger of eight traditionally classified genera which can be divided into two groups. The first group includes the genera *Alauda, Galerida, Lullula* and the Afrotropical genus *Spizocorys*, whereas the second group, albeit poorly resolved, comprises the genera *Eremalauda*, *Eremophila*, *Calandrella*, Alaudula and *Melanocorypha* (Barnes 2007).

1.1.3. The distribution of larks

Throughout their global range, larks tend to inhabit open, structurally simple habitat with lots of bare ground and mean annual precipitation of less than 100 mm to approximately 800 mm (de Juana *et al.* 2004). This is typically found in deserts, semi-arid woodland and scrubland, steppes, savannahs and high altitude mountainous regions (Dean and Hockey 1989; Dean and Williams 2004). In fact, the only major habitat type really avoided by larks is closed-canopy forest (Donald 2004).

The family is represented on all continents except Antarctica. The Alaudidae is primarily an African family with 78 (81%) of the 96 species recognized by de Juana *et al.* (2004) occurring in Africa. Furthermore, 60 (62.5%) species are endemic to the continent (de Juana *et al.* 2004). This is in contrast with Eurasia which has 36 species and only 16 endemics, and the Americas (Horned Lark *Eremophila alpestris*) and Australasia (Australasian Bushlark *Mirafra javanica*) each have only a single representative of the family. Even within Africa, the distribution is somewhat skewed with two major centres of lark endemism, namely the south-west (26 endemic species) and north-east arid zones (23 endemic species). Together these two zones contain nearly 70% of all African larks. The diversity in these two areas may be due to three factors: i) a long natural history of open habitats which allowed for adaptive radiation within these habitats, ii) a high diversity in topography, soil type, vegetation and climate patterns which created a mosaic of different open habitats within a relatively small area, and iii) the austere habitats larks inhabit are occupied by relatively few songbirds which may have reduced competition and allowed larks to radiate and occupy all available niches (Donald 2004).

Although not nearly as prolific as the abovementioned two zones, Eurasia also has two zones which stand out for their high levels of lark endemism. The Caspian-Mongolian deserts support 15 species with six species endemic to this area. The Oriental region in southern Eurasia contains 23 lark species which include 10 endemics. The southern Africa sub-region (as defined zoo-geographically), boasts a rich diversity of larks and includes 31 species with no fewer than 16 endemics and 10 near-endemics (Table 1.2).

1.1.4. Song and display flights

Larks have well developed advertising songs and display flights, with many species performing sustained song flights (Keith *et al*. 1992; de Juana *et al*. 2004). With the exception of male *Eremopterix* larks, members of the family are generally dull, drab coloured birds which in most cases rely on song and display flights to attract mates and deter rival males. This combination of a sober plumage and complex song is not uncommon amongst passerines (de Juana *et al.* 2004). In many other passerine families, the sexes rely on visual attraction of mates by sexual dichromatism or dimorphism in certain traits, e.g. the colour, length and type of plumage (Webster *et. al.* 2008). Their sustained song flights may have evolved secondarily as the generally open, structurally simple habitats they usually inhabit may lack suitable song perches (de Juana *et al.* 2004). This in turn may have resulted in males developing elaborate and/or sustained song flights. Sustained aerial display flights appear to be the ancestral state within the Alaudidae (Barnes 2007).

The song of larks is extremely complex, exhibit strong variation over short distances and often includes imitations of other bird species, i.e. heterospecific vocal mimicry (Donald 2004). For example, the individual repertoire size of Skylarks varies from about 160 to more than 460 syllables (Donald 2004). Males sing either in flight, while perched or on the ground. Their songs serve i) as a form of sexual advertising prior to and during the breeding season, ii) to notify rival males that the territory is occupied, iii) for individual identification of the sexes and iv) for disclosure of location of both sexes (Gill 1990; Donald 2004). Their apparently large investment in energy for song and display flights is compensated for by a lack of brightly coloured plumage displays (de Juana *et al*. 2004; Donald 2004). Furthermore, their drab plumage which results in excellent camouflage in the austere habitats they generally inhabit means that larks probably have to invest less energy in predator evasion (de Juana *et al*. 2004).

1.1.5. Plumage and morphological aspects

Larks are cryptically plumaged with a drab, dun-coloured appearance. Their plumage is mostly brownish or buff, but ranges from light tan and even yellow to a deep orange colouration which is often cryptic and matches the colour of the substrate in their respective habitats (Dean *et al*. 1992). This leads to larks often exhibiting small scale geographical differences in plumage colouration which has led to the recognition of several subspecies for wide-ranging species, e.g. Sabota Lark *Calendulauda sabota* and Spike-heeled Lark *Chersomanes albofasciata*.

Their cryptic plumage serves them well in the open habitats they inhabit as it provides good camouflage and therefore reduced visibility to predators. Two types of plumage patterns are exhibited in larks: generalized plumage and specialized plumage (Maclean 1970a). The generalized plumage pattern provides camouflage in most terrains and is more commonly found in migratory and nomadic species. It is characterised by a mixture of colours with streak-shaped or spot-shaped feathers on a buff background. The specialized plumage pattern, in contrast, is commonly found in sedentary species and is only effective in habitats with a matching substrate. In this regard, Maclean (1970a) divided southern African larks into reddish species in the red sand dunes of the Kalahari region and greyish species in the grey limestone regions.

Although larks have 10 primaries, the outermost primary is often much reduced in some species, for example *Melanocorypha* and *Calandrella*. It has been hypothesized that species with a long outermost primary are more sedentary while long-distance migrants are characterized by reduced outermost primaries (de Juana *et al.* 2004). A characteristic feature of larks and other primarily terrestrial passerines such as pipits and wagtails (Motacillidae) is their greatly enlarged innermost secondaries (S7-S9). These feathers are longer than the primaries and outer secondaries, effectively forming a cloak over the underlying flight feathers. The open habitats that larks inhabit result in a high degree of wear on the feathers as a result of abrasion by windblown sand and contact with vegetation, as well as bleaching caused by damaging UV rays of the sun (de Juana *et al.* 2004). The innermost secondaries serve no particular function in flight, but in the folded wing the outer primaries are tucked underneath these feathers thereby providing protection to the flight feathers. The high degree of wear and tear these innermost secondaries are exposed to, result in some species, or at least some populations of species, undergoing two annual moults, sometimes only involving the innermost secondaries (de Juana *et al.* 2004; Dikgale 2012).

Larks vary in size from approximately 15 g, e.g. *Spizocorys* and *Eremopterix* larks, to 75 g, e.g. the Tibetan Lark *Melanocorypha maxima* (Keith *et al.* 1992; de

Juana *et al.* 2004). They are rather robustly built with a long wing span and moderately long legs. This has adapted them to be able to manoeuvre rapidly and skilfully along the ground, either by walking or running, including the capability to hop around quickly while still in juvenile stages (de Juana *et al.* 2004).

Larks exhibit two kinds of sexual dimorphism, namely sexual dichromatism and sexual size dimorphism. The majority of larks are sexually monochromatic, although the seven species of *Eremopterix* larks are strongly dichromatic and several other species exhibit mild forms of sexual dichromatism, e.g. White-winged Lark *Melanocorypha leucoptera* and Horned Lark *Eremophila alpestris*. Sexual size dimorphism is a more common phenomenon, especially amongst the resident and sedentary insectivorous larks and is expressed mostly as differences in wing, tail, tarsus and, in particular, bill length. Bill shape and length varies between species and sometimes intra-specifically between sexes and can be a good indication of feeding ecology. For example, Razo Larks show sexual dimorphism in bill length. In this species, the male’s bill is 20% longer than the female’s and Donald *et al.* (2007) showed that males and females exploit different food resources. The sexes actually exhibit foraging as though they are different species (Donald *et al.* 2007). This form of dimorphism enables Razo Larks to utilize the limited food sources in the Cape Verde Archipelago Islands more efficiently. It is hypothesized that the difference in bill length allows the utilization of different niches, thereby reducing intra- and inter-specific competition (Willoughby 1971; Dean and Hockey 1989). This is supported by pronounced sexual size dimorphism in resident insectivorous species such as Spike-heeled Lark *Chersomanes albofasciata* and Short-clawed Lark *Certhilauda chuana*, and it is almost absent in migratory or nomadic granivorous species such as *Eremopterix* and *Spizocorys* larks.

Perhaps the most striking feature of lark morphology is the tremendous diversity in bill size and shape. Few other passerine families can match the adaptive radiation in bill morphology exhibited by larks. The size and shape of bird bills have provided biologists with some of the most interesting material with which to study evolutionary processes (Symonds and Tattersall 2010). Conventional bills are viewed to have evolved in relation to foraging. Various studies of the Darwin's finches in the Galapagos Islands highlight how inter- and intraspecific differences and changes in beak morphology are related to ecological competition (Grant and Grant 2006), dietary type (Lack 1947a) and environmental change (Grant and Grant 1994). The feeding habits of a species commonly determines bill shape and length in larks, such that species that have long, slender, and often de-curved bills, e.g. the Greater Hoopoe-lark, Spike-heeled lark and *Certhilauda* spp., are generally insectivorous larks and feed mainly on invertebrates, whilst species that possess short, robust, and conical bills, e.g. *Eremopterix*, *Spizocorys* and *Calandrella* spp. are granivorous larks and feed mainly on seeds (Keith *et al.* 1992).

1.1.6. Diet

The diets of larks range from almost entirely granivorous to almost entirely insectivorous. However, most larks are generally catholic in the choice of diet and their diet includes at least a degree of variation within this continuum (Maclean 1970b; Kopij 2005). Feeding habits are in actual fact dependant on i) location (the availability of resources such as abundance of seed and/or invertebrates), ii) morphology (bill and leg length such that insectivorous species generally have longer legs and bills compared to the short, conical bills and shorter legs of granivorous species), and iii) season as winters rarely produce invertebrates in abundance (de Juana *et al.* 2004). Furthermore, granivorous species also tend to drink water regularly, albeit not necessarily every day, whereas insectivorous larks fulfil their water requirements through their diet (Cramp 1988; Keith *et al.* 1992; de Juana *et al.* 2004).

The diet of insectivorous larks comprises mainly invertebrates such as arthropods, termites, ants, beetles, grasshoppers, and spiders. The granivorous species' diets consist mainly of seeds of grasses, shrubs, weeds or cultivated plants, and range in size from very small to the size of cereal grains, e.g. sorghum. All species seem to swallow small stones/grit to aid with digestion.

An interesting feature of lark biology is interspecific sexual differences in the diet of many species. The expression of sexual dimorphism in some morphological features, e.g. bill length, is manifested in small but significant differences in the diets of the sexes. This is particularly evident amongst insectivorous larks, e.g. Razo Lark and Spike-heeled Lark (Willoughby 1971; Dean and Hockey 1989; Donald *et al.* 2007). For example, male Razo Larks are mainly granivorous while females are mainly insectivorous. The Spike-heeled Lark (*Chersomanes albofasciata*) is another example. A study by Willoughby (1971) showed that males preferentially feed on beetles (Coleoptera) and females prefer termites (Isoptera) and ants (Hymenoptera).

1.1.7. Breeding

Although the breeding biology and ecology of the majority of larks is poorly known, some general patterns are emerging from those species that have been studied so far. These include larks being mainly monogamous and territorial, they breed either as isolated pairs or in loose colonies, they nest on the ground, females are solely responsible for nest construction and incubation duties (except the genera *Spizocorys* and *Eremopterix*), clutch sizes are usually small but varies considerably, nestling growth and development is extremely fast, breeding success is generally poor and post-fledging dependence lasts relatively long (de Juana *et al.* 2004). For all the aforementioned, there are notable exceptions but these will not be dealt with in this dissertation.

1.2. An overview of the genus *Spizocorys*, with specific reference to the Pink-billed Lark *Spizocorys conirostris*

Despite the widespread distribution of African larks and the fact that nearly two thirds of the species in the family are endemic to Africa, very little is known about the biology and ecology of the majority of species. Thus, information on the breeding biology of the Alaudidae would greatly improve our understanding of the family and make significant advances in understanding not only of variation in the life histories of larks, but also of other bird species. The proposed study will attempt to fill this void by studying various aspects of the biology and ecology of a southern African near-endemic, the Pink-billed Lark.

1.2.1. The genus Spizocorys

The genus *Spizocorys* comprise a group of six small, gregarious larks inhabiting grasslands, and arid and semi-arid savannah, dwarf shrublands and gravel plains of southern Africa and the Horn of Africa (Keith *et al.* 1992). With the exception of Stark's *Spizocorys starki* and Pink-billed Lark, the other *Spizocorys* larks have very small global ranges. One species, Botha's Lark *Spizocorys fringillaris*, is listed as Endangered by the IUCN (IUCN 2012). Four species are found in southern Africa and two species are restricted to the Horn of Africa. A summary of the main identification features, distribution and habitat preference of the six species are provided in Table 1.3.

The genus *Spizocorys* represents an unusual group of larks. Firstly, it is one of only a small group of larks exhibiting biparental care in all aspects of the breeding cycle, the other being larks of the genus *Eremopterix*. Both sexes contribute to nest construction, incubation, brooding and feeding of nestlings and fledglings. In most larks the female is solely responsible for nest construction and incubation duties, although males will assist with feeding nestlings and fledglings (de Juana *et al.* 2004). However, males have the potential to positively influence embryo development and hatching success when they participate in incubation (Auer *et al.* 2007) and it is therefore surprising that it is not a more common phenomenon in the Alaudidae. Secondly, the genus *Spizocorys* is unique amongst larks as they are the only sexually monochromatic larks known to commence with incubation upon laying of the first egg, resulting in a staggered, asynchronous hatching pattern (Maclean 1970a; Keith *et al.* 1992). The only other lark known to commence with incubation upon laying of the first egg is the sexually dichromatic Black-crowned Sparrow-lark

Eremopterix nigriceps. The majority of larks commence with incubation upon clutch completion or with laying of the penultimate egg in the clutch (de Juana *et al.* 2004; Donald 2004). *Spizocorys* larks therefore seem to represent an intermediate form between sexual monomorphism and uniparental breeding on the one side and sexual dichromatism and biparental breeding on the other side. Thus, knowledge of the breeding biology of these larks may shed light on the evolution of parental care and sexual dimorphism in the family.

1.2.2. The Pink-billed Lark

The Pink-billed Lark is a common, albeit localised, inhabitant of the semi-arid to relatively high rainfall regions in the grassland, Kalahari, Nama Karoo and savanna biomes of southern Africa (Dean 2005). Within this range, they generally occupy open, short grassland, burnt fields, Kalahari sandveld, fallow fields and recently harvested croplands (Dean 1997). They are also found on the edges of pans or floodplains with short grass, particularly in north-eastern Botswana and south-western Zambia. It is usually considered to be a nomadic species, although some populations appear to be resident or show only very localised movements (Dean 2005). A map illustrating the species distribution is presented in Fig. 1.1.

Given its extensive distribution range, it is not surprising that six subspecies are currently recognized for the Pink-billed Lark (de Juana *et al.* 2004). Their recognition is largely based on plumage colouration with darker, more rufous and heavily streaked populations occurring in the mesic east and paler, lightly streaked individuals occupying the more arid western and north-western parts of the species range. This phenotypic variation in colouration along an aridity gradient is a common phenomenon in many southern African birds, including some other lark species, e.g. Spike-heeled and Sabota Lark *Calendulauda sabota* and is known as Gloger's Rule. A brief summary of the key diagnostic features and distribution of the six currently recognized subspecies of the Pink-billed Lark are presented in Table 1.4.

Despite its widespread distribution in southern Africa, most of our present knowledge of the species is based on a single study of a nomadic population in the arid west of the species range by Maclean (1970b). This author provided baseline data such as nest structure and nest site characteristics, egg dimensions, clutch size, the duration of the incubation and nestling periods, the role of the sexes in certain aspects of breeding and breeding success. Since Maclean's (1970b) study, our knowledge of the species has all but stagnated and the only noteworthy contributions to our knowledge of the species is based on some incidental observations of various aspects of the species' life history by Maclean (1970a), Herholdt and Grobler (1987), Lloyd (1999) and Tarboton (2011).

The movements of the Pink-billed Lark are complex and poorly understood (Maclean 1970a; Herholdt and Grobler 1987). Populations from the semi-arid western parts of southern Africa are nomadic and seem to move in response to local rainfall patterns (Dean 1997). On the other hand, populations from the more mesic eastern parts of its range appear to be resident as long as conditions remain favourable, e.g. availability of surface water and short, open, grassy habitat (de Juana *et al.* 2004).

Breeding in the arid west is usually opportunistic in response to rainfall, hence breeding records span all months of the year (Tarboton 2011). However, breeding of populations in the more mesic parts of the region is seasonal, commencing in late spring (October/November) and terminating in July, but with a slight peak between April and July (Dean 1997; de Juana *et al.* 2004; Tarboton 2011). The species does not appear to defend permanent territories as they form flocks in the non-breeding season. The species is apparently monogamous and nests solitary although breeding may take place in loose aggregations with some nests fairly closely spaced (Maclean 1970b).

The incubation period ranges from 11 to 13 days and commences with the first laid egg (Maclean 1970b). Although both sexes contribute to incubation duties and feeding of nestlings, the extent of the contribution of each sex and the diet of nestlings is unknown. Little is known about nestling development except that young leave the nest at about 10 days of age (Maclean 1907b). Most of the other aspects of breeding, e.g. growth and plumage development of nestlings, breeding success, diet of nestlings etc. remain unknown. The proposed study will aim to shed light on these and various other aspects of the breeding biology of a sedentary population of the Pink-billed Lark. This will not only improve our knowledge of the species, but will contribute to the growing understanding and knowledge of the biology and ecology of a poorly known family.

1.3. The purpose of this study

In light of the foregoing, the following aim and objectives were set for this study.

1.3.1. Aim

To improve our knowledge of the general biology and ecology of the species, with special reference to its breeding ecology, and relate it to our existing knowledge of other African larks. To fulfil this aim, the following specific objectives were set.

1.3.2. Objectives

1.3.2.1 Determine the roles and relative contribution of the sexes in the breeding cycle.

1.3.2.2 Describe the various egg parameters, including the fresh egg mass (g), egg dimensions (mm), egg elongation index, egg volume and the egg weight coefficient (K_w).

1.3.2.3 Describe the growth and development of nestlings and fit their growth data to a logistical growth curve model.

1.3.2.4 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.

1.3.2.5 Analyse and describe the various vocalizations of the species.

1.3.2.6 Determine the diet and relative composition of the diet of nestlings.

1.3.2.7 Describe the nest dimensions and structure and the nest site characteristics within a 1 m^2 quadrant using the nest as the centre of the quadrant.

1.3.2.8 Analyse morphometric data of male and female Pink-billed Larks collected during fieldwork. The sample size will be supplemented by studying museum skins of the species sourced from various southern African natural history museums.

1.3.2.9 Compare the breeding characteristics of the Pink-billed Lark with published information on other species in the family.

Table 1.1. The three phylogenetic clades in the Alaudidae according to Barnes (2007).

Ammomanid	**Alaudid**	**Mirafrid**
Alaemon	*Alauda*	*Calendulauda*
Ammomanopsis	*Galerida*	*Heteromirafra*
Chersomanes	*Lullula*	*Corypha*
Certhilauda	*Spizocorys*	*Mirafra*
Ramphocoris	*Calandrella*	
Ammomanes	*Eremophila*	
Eremoptrix	*Melanocorypha*	
	Eremalauda	
	Alaudula	

Table 1.2. A summary of the status and vegetation types occupied by southern African larks.

Common name	Scientific name	Endemism	IUCN status	Biome/s
Red-capped Lark	*Calandrella cinerea*	Not Endemic	Not threatened	Grassland/Cropland
Large-billed Lark	*Galerida magnirostris*	Endemic	Not threatened	Grassland/Arid scrubland
Dusky Lark	*Pinarocoys nigricans*	Not Endemic	Not threatened	Woodland/Savannah
Spike-heeled Lark	*Chersomanes albofasciata*	Near Endemic	Not threatened	Grassland/Karoo/Savannah
Sabota Lark	*Calendulauda sabota*	Near Endemic	Not threatened	Savannah/Nama-Karoo
Fawn-coloured Lark	*Calendulauda africanoides*	Near Endemic	Not threatened	Kalahari Shrub/Savannah
Karoo Lark	*Calendulauda albescens*	Not Endemic	Not threatened	Karoo/Coastal shrublands
Dune Lark	*Calendulauda erythrochlamys*	Endemic	Not threatened	Desert dunes
Barlow’s Lark	*Calendulauda barlowi*	Endemic	Not threatened	Arid shrublands/Vegetated dunes
Red Lark	*Calendulauda burra*	Endemic	Vulnerable	Nama-Karoo/Shrub covered sand dunes
Monotonous Lark	*Mirafra passerina*	Near Endemic	Not threatened	Thornveld/Mopane woodland

Common name	Scientific name	Endemism	IUCN status	Biome/s
Melodious Lark	*Mirafra cheniana*	Endemic	Near Threatened	Grassland
Rufous-naped Lark	*Mirafra africana*	Not Endemic	Not Threatened	Grassland/Savannah
Flappet Lark	*Mirafra rufocinnamomea*	Not Endemic	Not threatened	Savannah/Woodland
Eastern Clapper Lark	*Mirafra fasciolata*	Near Endemic	Not threatened	Grassland/Savannah
Cape Clapper Lark	*Mirafra apiata*	Endemic	Not threatened	Karoo shrub/Coastal fynbos
Short-clawed Lark	*Certhilauda chuana*	Endemic	Not threatened	Semi-arid thornveld/Dry acacia savannah
Eastern Long-billed Lark	*Certhilauda semitorquata*	Endemic	Not threatened	Grassland/Rocky slopes
Karoo Long-billed Lark	*Certhilauda subcoronata*	Endemic	Not threatened	Grassland/Karoo shrub
Benguela Long-billed Lark	*Certhilauda benguelensis*	Near Endemic	Not threatened	Plains/Arid hill slopes
Cape Long-billed Lark	*Certhilauda curvirostris*	Endemic	Not threatened	Coastal shrub/Vegetated dunes/Croplands

Common name	Scientific name	Endemism	IUCN status	Biome/s
Agulhas Long-billed Lark	*Certhilauda brevirostris*	Not Endemic	Near Threatened	Karoo shrub/Coastal fynbos/Cropland
Pink-billed Lark	*Spizocorys conirostris*	Near Endemic	Not threatened	Grassland/Pasture/Desert scrub
Botha's Lark	*Spizocorys fringillaris*	Endemic	Endangered	Grassland
Sclater's Lark	*Spizocorys sclateri*	Endemic	Near Threatened	Nama-Karoo shrubland
Stark's Lark	*Spizocorys starki*	Near Endemic	Not Threatened	Arid savannah and grassland
Rudd's Lark	*Heteromirafra ruddi*	Endemic	Vulnerable	Grassland
Gray's Lark	*Ammomanopsis grayi*	Near Endemic	Not Threatened	Inland sandy habitats/Coastal gravel plains
Black-eared Sparrow-Lark	*Eremopterix australis*	Not Endemic	Not Threatened	Grassland/Karoo shrubland
Chestnut-backed Sparrow-Lark	*Eremopterix leucotis*	Not Endemic	Not Threatened	Savanna/Recently burnt areas
Grey-backed Sparrow-Lark	*Eremopterix verticalis*	Not Endemic	Not Threatened	Karoo/Grassland/Arid savannah

Table 1.3. The six species of *Spizocorys* larks, their key identification features, distribution and habitat preferences.

Common name	Scientific name	Key identification features	Distribution	Habitat preference
Pink-billed Lark	*Spizocorys conirostris*	Length 12-13 cm, mass 12-17 g. A small stocky Lark with a short, stout pink bill. The chin and throat are white, the breast is rufous-buff, streaked dark brown, and the belly and undertail coverts are rufous-buff.	Near endemic extends from patches in western Zambia to Namibia, Botswana and South Africa	open, short grassland (often recently burnt), Kalahari sand dunes with dense grass cover and fallow fields and croplands shortly after harvesting
Botha's Lark	*Spizocorys fringillaris*	Length 13-14 cm, mass 16-21 g. A small lark with a pink bill. The upper parts, breast and flanks are heavily streaked blackish, and the belly and under-tail coverts are white.	Endemic Restricted distribution centred on south Mpumalanga and the eastern Free State.	Well-grazed upland grasslands, Moist Clay Highveld Grassland. During breeding, it prefers short, dense, severely grazed natural grassland on plateaux and upper hill slopes, avoiding rocky areas, taller grass in bottomlands, vleis, croplands and planted pastures.

Common name	Scientific name	Key identification features	Distribution	Habitat preference
Stark's Lark	*Spizocorys starki*	Length 13-14 cm, mass 14-23 g. A small, pale lark. Adult: The upper parts are pale brown with dark brown streaks. The lores, eyebrows, and underparts are whitish; the breast has a few brown speckles. The bill is pale and fairly heavy. The eyes are brown and the legs and feet are pinkish white.	Near-endemic south-western Angola through Namibia to the Northern Cape and south-western Botswana	Sparse, arid to semi-arid grasslands and shrublands; gravelly and stony surfaces are preferred.
Sclater's Lark	*Spizocorys sclateri*	Length 13-14 cm, mass 17-21 g. Adult: A small compact large with a large, awl-shaped bill. At close range a characteristic "tear-drop" mark is visible below the eye. The eyes are brown and feet are pinkish white.	Endemic to South Africa and the extreme south of Namibia.	Sparse, semi-arid and arid gravelly or stony plains of the Karoo and shrublands of southern Namibia.

Common name	Scientific name	Key identification features	Distribution	Habitat preference
Obbia Lark	*Spizocorys obbiensis*	Length 12cm, mass 12-16g. Small lark with a stout bill. Prominent supercilium, dark eye-stripe, moustacial and malar stripes. Whitish below, with regular blackish streaks along flanks and on breast.	South eastern Somalia	Large, fixed and vegetated coastal dune habitat.
Masked Lark	*Spizocorys personata*	Length 14-15 cm A dark lark with a diagnostic black face mask and yellow or pink bill. The belly is cinnamon, and the breast grey-brown.	Ethiopia and Kenya	Subtropical or tropical dry shrubland and subtropical or tropical dry lowland grassland.

Table 1.4. The six subspecies of the Pink-billed Lark *Spizocorys conirostris,* their key diagnostic features and distribution.

Sub-species	**Location**	**Variation**
Spizocorys conirostris conirostris (Sundevall 1850) and *S. c. griseovinacea* (Clancey 1972)	North-west Province, Mpumalanga, KwaZulu-Natal, Free State and the Eastern Cape and north-western parts of Lesotho	Drab, mostly brownish or buffish plumage
S. c. barlowi (Roberts 1942)	Northern Cape Province, southern Botswana and southern Namibia	Paler under parts, whitish belly and features less streaking above
S. c. damarensis (Roberts 1922)	Paler on the under parts and is less streaked	North-western Namibia and north-western Botswana.
S. c. crypta (Irwin 1957)	North-eastern Botswana at the Makgadikgadi Pans and Lake Dow.	Exhibits greyish feather edges with whitish tips, finely streaked appearance while the upper parts are paler.
S. c. makawai (Traylor 1962)	Western Zambia in Liuwa and the Mutala Plains.	Brownish appearances above with buff pinkish feather edges, under parts are pinkish-chestnut in colour.
S. c. harti (Benson 1964)	Western Zambia region in Liuwa and the Mutala Plains	Paler above and below with pale grey upper part feathers.

Fig.1.1. Distribution of the African endemic Pink-billed Lark *Spizocorys conirostris.*

CHAPTER 2

Breeding ecology of the Pink-billed Lark, *Spizocorys conirostris* in an agricultural landscape, South Africa

2.1. INTRODUCTION

The larks (Alaudidae) represent a family of approximately 96 species, largely confined to the Old World reaching its greatest species diversity in Africa (de Juana *et al.* 2004). The variation in life history characteristics exhibited by larks, e.g. sexual dimorphism, variation in the type of display flights, use of heterospecific vocal mimicry, and the varying degrees of movement such as nomadism or residency, make the family ideal for comparative studies on the evolution of life history strategies. However, apart from a few species that are well studied, poor knowledge of the biology and ecological requirements of larks has confounded our understanding of the evolution of variation in life history strategies in the family.

The Pink-billed Lark, *Spizocorys conirostris,* is a common inhabitant of the semi-arid to relatively high rainfall regions in grassland, Kalahari, Nama Karoo and savannah of southern Africa (Dean 2005). It is usually considered a nomadic species, although some populations appear to be resident or show only very localised movements (Dean 2005). In common with other *Spizocorys* larks, the sexes are monomorphic and, unusually for larks, both sexes of *Spizocorys* larks participate in all aspects of the breeding cycle, i.e. nest construction, incubation and care of the nestlings and fledglings (de Juana *et al.* 2004). The combination of sexually monomorphic plumage and biparental breeding of *Spizocorys* larks appears to be unique amongst larks as the only other larks known to share incubation duties are the sexually dichromatic *Eremopterix* larks. Moreover, *Spizocorys* larks generally have small clutch sizes ranging from a single egg in Sclater's Lark *Spizocorys sclateri* to two in the other genera. Another unusual feature of the *Spizocorys* lark breeding biology is that the onset of incubation consistently commences with laying of the first egg (Maclean 1970a), an unusual feature amongst the larks. Despite its widespread distribution in southern Africa, most of our present knowledge of the species is based on a baseline study by Maclean (1970a, 1970b) on a nomadic population in a pristine, natural environment in the arid west of the species range.

The aim of this study was to augment our existing knowledge of the species by obtaining data on the breeding ecology of a resident population in an agricultural environment from the more mesic eastern parts of the species' range. The specific objectives of the study were to i) fill existing information gaps in our knowledge of the breeding ecology of the species, ii) compare breeding strategies of a resident eastern population with a nomadic western population, and iii) analyse data for the species in the Birdlife South Africa Nest Record Card Scheme (NERCS) and to compare it with the results of the present field study and Maclean's (1970a, 1970b) studies.

2.2. METHODS

The study was conducted on the farm De Loskop 205 LS (23°30' S, 29°19' E) near Mogwadi in the Limpopo Province, South Africa. It is a commercial farm involved in the production of potatoes, onions, tomatoes and livestock. The vegetation at the study site is described as Makhado Sweet Bushveld (Mucina and Rutherford 2006) and the area 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. It is situated in a summer rainfall region with a mean annual precipitation of 350–550 mm and a wet season extending from November to January (Mucina and Rurtherford 2006).

Field studies were conducted from October 2008 to October 2010. Data were collected 2–5 times per week for periods ranging from 2–12 hours. Parental roles and relative contributions were determined by fitting a sample of breeding pairs with numbered SAFRING metal rings and a unique combination of coloured plastic rings. Birds were sexed by means of the presence of a brood patch in breeding females and the absence thereof in males.

Nests were located by systematic searching and using parental behaviour cues. Nest and cup diameter, cup depth and width of the apron (if present) at the entrance to the nest directly opposite the base structure were recorded to the nearest millimetre as described by Hansell (2000)**.** The nest micro-habitat structure was recorded by visually estimating the percentage cover of i) grass, ii) forbs, iii) bare ground, iv) debris and v) other material, e.g. dung or rocks, within a 1 m^2 quadrant of the nest, using the nest as the centre of the quadrant. Nest orientation was determined with the aid of a handheld GPS and by considering the nest entrance as the area directly opposite the base structure against which the nest was constructed, e.g. a grass tuft. To test if nest entrance directions were biased towards a particular direction, Rayleigh's test of uniformity was used with the ORIANA version 2 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.

When a nest was found during nest construction or the laying period, it was visited daily to determine when incubation commenced. Once incubation commenced, nests were monitored every 2–3 days until day 10, when nests were once more visited daily to accurately determine the length of the incubation period. To reduce observer disturbance at nests which may have an effect on the breeding success of the population, the following precautions were taken: i) contact with the nest or nest contents were limited as much as possible and avoided during the nest construction and/or laying period, ii) where possible the nests were approached from different angles to inspect contents or measure the young so as to avoid creating a footpath to the nest, iii) nests were only inspected in the first 90 minutes after sunrise in order to avoid exposing the eggs or nestlings to excessively high or low temperatures, iv) no data was collected in adverse weather conditions, e.g. rain, and v) no measurements were recorded if nestlings were in the final stages of the nestling period to avoid premature fledging of nestlings. This approach is similar to the protocol followed by Engelbrecht (2008) who found no difference in the breeding success at nests with limited observer disturbance compared to nests where various measurements were recorded throughout the nesting cycle.

Eggs were weighed and the maximum length (l) and maximum width (w) of the eggs were recorded at a sample of nests. Fresh egg mass (FEM) was taken as the mass of an egg measured within four days of laying. For eggs four days and older, egg mass was estimated (EEM) from their dimensions, using a weight coefficient K_W as described by Hoyt (1979). The EEM was used to assess female investment in each clutch, by expressing egg mass and total clutch mass as a percentage of the mean adult mass. Data relating to clutch size and the onset of breeding in the NERCS database were analysed and compared with data of De Loskop to determine if there are regional or seasonal differences in these parameters.

Growth and development of individually marked nestlings were recorded within the first 90 minutes after sunrise every 1–2 days. Nestling development was described with regard to plumage development and growth. For growth, mass (g), length of the wing chord, head and tarsal length were recorded as described by de Beer *et al.* (2001). The growth rate of each nestling was determined by fitting the growth curve by a logistic equation (Ricklefs 1967, 1968). The $t_{10\text{-}90}$, 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 $t_{10\text{-}90} = 4.394 / K$.

The diet of nestlings, provisioning rate and the relative contribution of each parent was determined by photographing (Nikon D300 and 400 mm, f2.8

telephoto lens) colour-marked birds from a hide placed 10–15 metres away delivering food to nestlings and recording the time and sex of the bird. The images obtained allowed for easy distinction between seeds and invertebrates and for the relative accurate identification of invertebrates to order level. All data were collected from sunrise until 12:00 when the nestlings were 3–6 days old. To avoid skewed results due to shyness of one or both parents or due to the presence of an observer, data recording only commenced once both parents have delivered at least one prey item.

Overall breeding success and daily survival rates for the egg-laying, incubation, hatching and nestling periods were calculated using Mayfield's (1975) method. To facilitate comparison of breeding success estimates of this study and that by Maclean (1970a), I also calculated a crude overall breeding success estimate according to the method used by Maclean (1970a). This intuitive method is based on an expression of the proportion of offspring fledged from the total number of eggs laid. It is a very crude estimate as not all nests are found at the same stage of the nesting cycle. For example, some nests are only found late in the nestling stage whereas other are destroyed during laying. It is highly unlikely that a nest destroyed during the laying stage will ever be found, and chances are good that a nest found in the latter stages of the nestling period is likely to fledge young. This is because a nest is more likely to be found in the nestling stage when parental activity, e.g. feeding and nest defence, is greater. Furthermore, if two nests fail but one was active for double the time of the other, it was still more successful than the nest that failed at an earlier stage. In essence, this means that successful nests are more likely to be found than unsuccessful nests and it is important to correct for this fact in estimates of the breeding success in a population. The Mayfield (1975) breeding success estimator eliminates this bias by calculating the daily nest survival rate, i.e. the proportion of nests that did not fail on a given day, while the nests were under observation. The overall number of nest-days of observation is referred to as exposure days.

Egg and nestling masses were measured using an Ohaus Scout Pro portable digital scale (Pine Brook, NJ) with a precision of 0.01g. All measurements were recorded using Omni-Tech digital Vernier callipers (Livonia, MI) with a precision of 0.1mm. All statistical analyses of data were performed using Microsoft Excel for Windows and SPSS ver. 18 (2009). Means are presented ± S.D., with the exception of daily nest-survival rates which are presented as ± S.E. and calculated as the binomial standard error for a sample (Zar 1999).

2.3. RESULTS

2.3.1. Breeding seasonality

The breeding season of Pink-billed Larks at De Loskop peaked at the end of the wet season (March to May) in both years (See Fig. 2.1). Only three nests were recorded outside of this period: a single nest was found on 15th February 2009 and another two nests were found in February 2010.

2.3.2. Nests and nest site characteristics

Fifty-three active nests were found during the study period: 28 in 2009 and 25 in 2010. With the exception of three nests located in a fallow field, all the nests were situated on the floodplain of the earth dam. The nest construction period, i.e. the period from when nest construction commenced until the first egg was laid, was reliably established to take one (n = 2), two (n = 2) and three days (n = 1). The nest was a fairly deep scrape in the ground, lined with fine grass blades, rootlets, small flowers of *Sutera caerulea*, downy and contour feathers of moulting waterfowl and animal hair. The majority of nests (60.4%) had an apron of varying size ($\bar{x}$ = 31.2 mm ± 9.8 S.D., range 15–70 mm) constructed of coarser material than the nest structure and lining. It included small sticks up to 150 mm in length, grass blades, animal dung, roots, clods of earth or small stones, feathers and small flowers. A summary of the dimensions and micro-habitat characteristics of nests in the study area is presented in Table 2.1. Some images of nests illustrating the foregoing are presented in Figs. 2.2–2.5.

Most nests (62.3%, $n = 33$) were situated at the base of forbs (*S. caerulea* and *Xanthium strumarium*), with the remainder placed next to a grass tuft (32.1%, $n = 17$) or a cow pat (5.7%, $n = 3$). Analysis of nest orientation data showed that nest entrance directions are not uniformly distributed, i.e. there is a bias towards a preferred entrance direction, namely south (Raleigh's Uniformity Test, $Z = 43.21$, $P < 0.001$). The majority of nests faced south (60%) while the rest faced either south-west (24%) or south-east (16%). The high mean vector length of $r = 0.93$ suggests that the data is tightly concentrated around the mean vector ($\mu = 187.35° \pm 21.89°$). There was no significant difference between breeding outcome (i.e. success vs. failure) and the presence or absence of an apron (Mann-Whitney U test, $U = 99.5$, $P = 0.65$), the percentage grass cover (Mann-Whitney U test, $U = 294.5$, $P = 0.75$), forbs (Mann-Whitney U test, $U = 266.5$, $P = 0.68$), bare ground (Mann-Whitney U test, $U = 262.0$, $P = 0.61$), debris (Mann-Whitney U test, $U = 170.5$, $P = 0.64$) or other material at the nest (Mann-Whitney U test, $U = 36.0$, $P = 0.47$). In 2010 nests with a greater percentage cover experienced significantly more nest losses compared to nests where forb cover was less (Mann-Whitney U test, $U = 24.0$, $P < 0.05$). Apart from the percentage forb cover, there was no association between breeding outcome and any of the nest site characteristics between 2009 and 2010.

2.3.3. Clutch size, egg dimensions and incubation

Eggs were laid early in the morning at daily intervals. Clutch size in the study area ranged from 1–2 ($\bar{x} = 1.7 \pm 0.5$ S.D., mode and median = 2, $n = 53$). Although there were inter-annual differences in clutch size (2009: $\bar{x} = 1.8 \pm 0.4$ S.D.; 2010: $\bar{x} = 1.6 \pm 0.5$ S.D.), these were not significant (Fisher's Exact Test, $P = 0.07$).

Egg dimensions, fresh egg mass (FEM), estimated egg mass (EEM) and egg volume (EV) of Pink-billed Larks in the study area are presented in Table 2.2. The mean EEM of $\bar{x} = 1.7$ g ± 0.1 S.D. in the study area represents 10.2% ± 0.8 S.D. (range 9.1–12.1%, $n = 42$) of the mean mass of adult females at De Loskop ($\bar{x} = 16.6 \pm 1.0$ S.D., range 15.0–19.0, $n = 18$; G.D. Engelbrecht, unpubl. data). The mean clutch mass was $\bar{x} = 2.8$ g ± 0.8 S.D. (range 1.7–3.9 g, $n = 26$), representing 16.6% of the average mass of adult females. The mean EEM of two-egg clutches were $\bar{x}$ = 3.4 g ± 0.3 S.D. (range 3.0–3.9 g, *n* = 16) which represent 20.3% of the average mass of an adult female.

Incubation commenced upon laying of the first egg and the incubation period, i.e. the interval between the laying of the last egg of a clutch and the hatching of that egg, was accurately determined as 12 days (*n* = 2). Nestlings hatched asynchronously and invariably within two hours after sunrise. Egg-shells were removed soon after hatching and dropped at least 20m from the nest. Nestlings were brooded by both parents for periods ranging from 3–43 minutes for the first 3–5 days after hatching, but brooding bouts tended to be longer in inclement weather or were even performed when nestlings were seven days old during such conditions. Both parents assisted with nest sanitation by either swallowing faecal sacs at the nest for the first four days or later flying off with it.

2.3.4. Nestling growth and development, diet and the nestling period

Newly hatched nestlings were blind and mostly naked except for some sparse straw-coloured down on the capital, spinal, alar and femoral feather tracts. The skin was initially dark grey with a pink undertone on the dorsal surface and flesh coloured on the ventral surface which became darker over the next few days. The culmen was horn-coloured and the gape flange was pale yellow. The inside of the mouth of newly hatched nestlings was pale pinkish-orange which changed to bright yellow over the course of the next two days. Nestlings had three tongue spots; two lateral spots at the back of the tongue and one at the distal tip of the tongue, as well as one spot at the tip of each mandible. The eyes started to open when the nestlings were two days old and were fully open on day 3. The first feather tracks erupted when the nestlings were three days old and by day 4 all tracks had erupted. After six days most feather tracks with the exception of the flight feathers were in brush. The primaries and primary coverts were the last to emerge from their sheaths and this happened at age 7–8 days. The nestlings were fully feathered at 9–10 days of age. The mean growth parameters for increase in mass, head length, tarsus and the wing chord and the $t_{10–90}$, are presented in Table 2.3. The mean nestling period was $\bar{x}$ = 11.4 days ± 1.2 S.D. (range 10–13 days, n = 13). Despite the asynchronous hatching pattern, nestlings invariably fledged on the same day. Fledged young could not fly but were able to jump or flutter a few centimetres at a time. Three days after fledging they were able to fly short distances of 1–2 metres. Fledglings tend to remain hidden amongst the vegetation. We were unable to accurately determine the post-nestling dependence period.

The diet of nestlings, provisioning rates and relative contributions of males and females as observed at five nests with two nestlings each for a period totalling 900 minutes of observations of 3–6 day old nestlings are presented in Table 2.4. We recorded 184 food deliveries ($\bar{x}$ = 12.3 visits/hour) with males contributing slightly more (54.3%) than females (45.7%), although this difference was not statistically significant (ANOVA, $P \geq 0.05$). The nestlings were fed a diet of seed and invertebrates with invertebrates comprising the bulk of the diet of nestlings (67.9%). Identifiable prey items included grasshoppers and locusts (Orthoptera), stick insects (Phasmatodea), termites (Isoptera), moths, butterflies and their larvae (Lepidoptera). The sexes delivered similar percentages of the different food items, although only males were recorded delivering phasmatodeans and females brought more unidentifiable food items (Table 2.4). Unidentified items were invertebrates but they were generally too small or too processed, e.g. head or appendages removed, and hence difficult to identify. Unknown items included instances where it could not reliably be established what type of food was delivered as the angle of approach to the nest by the parents did not allow for a visual of the food. Prey loading, i.e. carrying more than one prey item, by the parents is a common phenomenon with up to four prey items brought at a time. Parents also often shared food between nestlings during delivery. When nestlings were left unattended, they lay silently and motionless only moving when the parents arrived to feed them.

2.3.5. Breeding success

Of 91 eggs laid in 53 nests, 61 hatched and 35 nestlings fledged successfully, giving a crude breeding success rate of 38.5%. The daily survival rate for the different stages in the breeding cycle as well as the overall breeding success are presented independently for the 2009, 2010 and the two breeding seasons combined in Table 2.5. The average number of fledged young per pair was $\bar{x}$ = 0.7 ± 0.9 S.D. (range 0–2, *n* = 53). Known causes of nest failure included depredation (unknown agent/s), nest abandonment and trampling. We found no evidence of replacement or repeat-brooding attempts by pairs at the study site during the study period.

2.4. DISCUSSION

The results of the present study of the breeding ecology of a population of Pink-billed Larks in an agricultural environment confirm some of the aspects of their breeding, e.g. biparental care in all aspects of their breeding, the duration of the incubation and nestling periods and a generally poor breeding success. This study has also revealed new information for the species and larks in general.

Although the De Loskop population is resident and can be found all year round at the study site, breeding was only recorded within a relatively narrow period from February to May, i.e. towards the end of the wet season and the early stages of the dry season. Analysis of the NERCS records from across the species' range revealed an extended breeding season for the species with breeding recorded in all months of the year, albeit with a slight peak in April to July. Such circum-annual breeding is typical of species which breeds opportunistically after rain. However, closer inspection of the NERCS records shows geographical variation in the onset of breeding. The April–July peak reported by Tarboton (2011) corresponds to populations inhabiting the savannah biome and represents the subspecies *S. c. barlowi*. The breeding season of resident or sedentary populations from the more mesic central and southern parts of the species' range, starts with the onset of the wet season (November), and peaks in February, then followed by a gradual decline in breeding until May.

These populations inhabit the grassland biome and represent the nominate race *S. c. conirostris*. Thus, the NERCS data suggest that apart from a slight overlap of the two breeding seasons in April and May, grassland populations breed during the wet season whereas savannah populations breed during the dry season. When to start breeding is one of the most critical factors determining the reproductive performance of birds. Birds therefore breed when conditions are most favourable for maximizing their breeding success. The interplay of photoperiod, rainfall and temperature are regarded as the major factors determining the onset of breeding (Immelman 1971; Lloyd 1999; Dawson *et al.* 2001; Barrientos *et al.* 2007). It is possible that savannah populations curtail breeding during the summer months (wet season) when high daily ambient temperatures may make breeding difficult. Grassland populations, on the other hand, breed during the wet season when conditions for breeding are generally most suitable and primary production and invertebrate biomass is at its peak. They may also avoid breeding in winter as the low ambient temperatures may make breeding risky. Several lark species from southern Africa's western and northern regions avoid breeding in mid-summer when ambient temperatures are at a peak (*cf.* Hockey *et al.* 2005).

The onset of breeding of the De Loskop population appears to be intermediate between the grassland and savannah populations. The De Loskop population belongs to the nominate race *S. c. conirostris* whose distribution is essentially restricted to the highveld grasslands of eastern southern Africa. However, the study site falls within the savannah biome at an altitude of approximately 1100 masl. It is therefore conceivable that the high ambient summer temperatures associated with the savannah biome, coupled with the low ambient temperature at a relatively high altitude in the dry season, may constrain breeding to a relatively narrow period over the transition from the wet to the dry season.

Details of nest construction, nest dimensions, materials used and the presence of an apron at the majority of nests (60% in this study) is similar to that reported by Maclean (1970a, 1970b) and Tarboton (2011). The mean nest construction period of 1.8 days (range 1–3 days) in this study may at first appear to be considerably shorter than the 4–9 days reported for other larks (Boyer 1988; Engelbrecht 2005; Maphisa *et al.* 2009) and of Maclean’s (1970a) “just over four days” estimate. However, the brevity of the nest construction period was the result of laying commencing well before the nest structure was completed. Nevertheless, both sexes continued to add material to the structure and lining of the nest throughout the incubation period, a common phenomenon in many larks species (de Juana *et al.* 2004).

The brief nest construction period is typical of species which breed opportunistically when favourable conditions present themselves. Such favourable conditions are usually of a transient nature and once the optimal conditions for breeding have passed, successful breeding becomes risky. This is supported by the more or less synchronised onset of breeding with several pairs usually starting to lay within a short period and nesting together in a loose aggregation. Thus, it appears as if there is a hitherto unknown clue/s that stimulates breeding in the population. Another plausible explanation may be found in the apparently relatively brief breeding season of this population during the two years of this study. Any unnecessary extension of the nesting cycle, e.g. prolonged nest construction periods, large clutch sizes, long incubation or nestling periods etc., may jeopardise the chances of a repeat- or replacement breeding attempt in the same season. Although repeat- or replacement breeding attempts have not been recorded in this species yet, it has been recorded in other larks and would be theoretically possible (Engelbrecht 2005; Dikgale 2012).

Analysis of the nest micro-habitat features supports Maclean’s (1970b) view that “it appears to need good cover always” but contrasts with Tarboton’s (2011) opinion that “the nest is usually poorly concealed”. The percentage grass and forb cover at nests in the present study averaged 68% with debris such as moribund vegetation increasing the amount of cover to 84%. The debris was often incorporated into the apron that effectively served to disrupt the outline of the nest. Given the amount of cover, nests were usually well concealed and difficult to locate. Another interesting anomaly between the present study and that of Maclean (1970b) is in the preferred base structure. Maclean (1970b) found that the majority of nests (93%) were placed at the base of a grass tuft and the remainder against shrubs. In this study, small herbaceous shrubs were the preferred base plants (62%) followed by grass.

According to Maclean (1970b) and Tarboton (2011), most Pink-billed Lark nests face either south or east. Of the 55 nests recorded by Maclean (1970b), 49% faced east, 13% south-east and only a single nest faced south. Some of the winter nests reported by Maclean (1970b) were completely exposed (20%) and some nests even faced north (7%) and north-east (9%), evidently serving a thermoregulatory function. In contrast, the preferred nest orientation in this study was south (60%), south-west (24%) or south-east (16%). While it is clear that nest orientation has a thermoregulatory function, other local environmental factors, e.g. wind, cover, season etc., may also be important determinants of nest orientation on a local landscape level.

The description and dimensions of eggs and the length of the incubation period in the study area is similar to that given by Maclean (1970a). According to the literature, the clutch size range from 1–3 (Maclean 1970a; Keith *et al.* 1992; de Juana *et al.* 2004; Dean 2005; Tarboton 2011), but there is a single record of a four-egg clutch in the NERCS database (P. Ferreira, Phillipstown, Northern Cape Province, 3 March 1994). This is clearly unusually large for the species and in fact for the genus *Spizocorys* whose clutch sizes tend to be small (Donald 2004). The possibility exists that this record may be a case of intra-specific nest parasitism (e.g. egg-dumping by a female that lost her nest or true cuckoldry) or perhaps misidentification. Observations of birds at the breeding grounds reveal considerable intra-specific antagonistic behaviour, most commonly manifested as chasing but also culminating in physical attack on rare occasions. Moreover, video footage at nests has shown that conspecifics do sometimes wander close to active nests which make intra-specific brood parasitism a distinct possibility.

The mean clutch size within the study area compares well with clutch size estimates from across the species' range calculated using NERCS data ($\bar{x}$ = 1.9 ± 0.5 S.D., range 1–4, mode and median = 2, *n* = 126). The relatively small mean clutch size may reflect an adaptation of an opportunistically breeding species suffering high nest losses. Since each egg represents an additional nest day, the overall nesting period can be reduced by producing small clutches, thereby creating opportunities for repeat- and replacement breeding attempts during a relatively short optimal breeding period. This may be illustrated best by Sclater's Lark which consistently only lays a single, large egg. It has been suggested that the large egg results in hatching of a relatively large and advanced nestling which grows rapidly as it receives all the food (Steyn and Myburgh 1989). Furthermore, Lack's (1947b) hypothesis predicts that the clutch size is adjusted by natural selection to the maximum number of nestlings the parents can feed. Species living in unpredictable environments may therefore adjust their clutch size downwards as a precautionary measure in case food supply will be limited during the nesting cycle. This will apply to nomadic species such as Pink-billed Larks.

Analysis of NERCS data failed to show significant differences in clutch size for months of the year (Kruskal-Wallis Test, $X^2 = 15.0$, $P = 0.18$), but there was evidence of geographical variation in clutch size (Kruskal-Wallis Test, $X^2 = 11.5$, $P < 0.01$). Although the sample size for the Eastern Cape was relatively small, the mean and median clutch size of birds in the Eastern Cape ($\bar{x} = 1.6 \pm 0.6$ S.D., median = 1.5, $n = 18$) was smaller than those from the central ($\bar{x} = 1.9 \pm 0.5$ S.D., median = 2.0, $n = 41$) and western ($\bar{x} = 2.0 \pm 0.3$ S.D., median = 2.0, $n = 57$) regions.

The incubation period of 12 days matches the 11–13 days reported by Maclean (1970b) and falls within the range reported for most lark species (de Juana *et al.* 2004). If one considers that uniparental incubation by the female is the norm in most lark species, then it is clear that the near-continuous biparental incubation of the Pink-billed Lark does not provide any gains in terms of shortening the nesting cycle. It is interesting to note that the genera *Spizocorys* and *Eremopterix* (sparrow-larks) are the only African larks known to exhibit biparental incubation. Members of both genera are primarily granivorous and breed opportunistically when favourable conditions exist. This requires rapid mate selection and onset of breeding when favourable conditions exist in order to exploit the optimal but transient conditions. Sexually dichromatic plumage in sparrow-larks is believed to facilitate rapid mate selection and recognition when favourable conditions for breeding arise (Barnes 2007), but this may not apply to the sexually monomorphic *Spizocorys* larks. The constant chasing of rivals observed on the breeding grounds is typically the visual manifestation of mate-guarding to ensure paternity of the offspring. It may also serve to repel potential brood parasites. Given that intra-specific nest parasitism is a possibility in this species, continuous biparental incubation may have evolved as an anti-cuckoldry strategy. Furthermore, the unusual asynchronous hatching strategy of the pink-billed and other *Spizocorys* larks may have evolved to further minimize risks to unincubated eggs, e.g. protection against predation or cuckoldry, rather than a brood reduction strategy as they breed opportunistically when conditions are optimal. However, this hypothesis can only be tested by performing paternity testing of the offspring.

Typical for larks, nestling growth and development is rapid, the nestling period is rather short, and nestlings leave the nest before they are able to fly. Comparative data for nestling growth in African larks are scarce but analysis of the growth parameters show that at around the time of fledging, the mass, tarsus and wing length approach that of adults. The rapid growth and development of the tarsus allows fledglings to move around after fledging. This is typical of the young of many ground-nesting birds that develop bipedal locomotion well before they are able to fly (Beason 1995). The $t_{10–90}$ value for wing length shows that most of the growth is completed shortly after fledging, which is consistent with observations of 15–16 day old fledglings' ability to flutter-fly short distances.

The food delivery analysis revealed that invertebrates comprise the bulk of nestling's diet (68%) while seed constitutes the rest. Most larks feed their young exclusively on invertebrates the few exceptions being the primarily granivorous larks that, in addition to invertebrates, also include vegetable matter in the diet (de Juana *et al.* 2004). A primarily insectivorous diet provides the young with a rich supply of water and protein, and hence amino acids that the body cannot synthesize, which is essential for rapid growth of feathers and tissues (Gill 1990).

Whether the observed differences in the food items delivered to nestlings by males and females reflect individual or sexual preferences would be an interesting avenue for future research.

Being open, ground-nesting species, larks suffer very high nest depredation rates (de Juana *et al.* 2004, Donald 2004). Breeding success estimates of less than 30% for larks is the rule rather than the exception (*cf.* Maclean 1970b; Boyer 1988; Keith *et al.* 1992; Suárez and Manrique 1992; Dean and Williams 2004; Donald 2004; Hockey *et al.* 2005; Maphisa *et al.* 2009). Nevertheless, the overall breeding success of 12.8% calculated in this study seems strikingly low but is remarkably similar to Maclean's (1970b) estimate of 14.7% for the Pink-billed Lark. This is despite the two studies being conducted in completely different environments: the one in a pristine natural environment and the other in a transformed agricultural environment. However, Maclean (1970b) simply expressed breeding success as the percentage of eggs that produced fledglings. Using this approach, the breeding success in this study was considerably higher at 38%. This discrepancy in the breeding success estimates (crude vs Mayfield) demonstrates why the Mayfield (1975) method and other methods based on "repeated visits" are superior to methods using the proportion of fledglings from the number of eggs laid. As mentioned above, nests that fail early in the nesting cycle are likely to be missed in calculations of the nesting success, and nests are more likely to be found during the nestling period and are likely to fledge young. These two factors tend to inflate the breeding success and could explain the discrepancy of 12.8% using Mayfield's (1975) approach and 38% using the apparent nest success based on fledged offspring. The daily survival rate in the nestling period was higher compared to the daily survival rate in the incubation period. This is due to nests Given such a poor breeding success, one would expect replacement broods to be a common phenomenon, yet we have never found any evidence of a replacement- or repeat brooding attempt at the study site. It is also possible that replacement- or repeat broods may be undertaken in a different area.

Daily nest survival was greater during the nestling period in both years. This same phenomenon is evident if Maclean's (1970b) data are examined closely. Several factors may explain the differential nest survival as observed in this study. Firstly, if predation is non-random and poorly concealed nests suffer early predation, a trend of decreasing predation and hence increased daily nest survival over the nesting period is expected (Martin *et al.* 2000). Secondly, the dietary preference of a nest predator can result in different predation rates, e.g. the common egg-eater *Dasypeltis scabra* specialises in eating birds' eggs (Broadley 1962; Gartner and Greene 2008). Thirdly, the species' more or less synchronised onset of breeding and its habit of nesting in loose aggregations may attract potential nest predators to the increased activity in the nesting area. As nests are usually scattered over a relatively small area, it is highly likely that any successful predation event may result in the nest predator seeking additional "rewards" in the area. The pattern of nest losses observed in the study fit this pattern, as nest losses seemed to be clustered with up to five nests lost in a single day.

There were also inter-annual differences in the breeding success, most notably in the lower daily nest survival rate during the incubation period in 2010. The 2010 breeding season was different to the 2009 season in several ways, e.g. a later onset of breeding, it was considerably colder and wetter when breeding commenced and there was a significantly greater amount of forb cover at nests. This inter-annual variation in some breeding parameters highlights the importance of collecting breeding ecology data preferably spanning two or more breeding seasons.

In conclusion, the present study has shed valuable information on the breeding biology and ecology of the Pink-billed Lark specifically, but also of larks in general. Although some of the results concur with published information on the species, it has also highlighted several anomalies and avenues for future research on the life history of the Pink-billed Lark. The study has also demonstrated the value of using additional resources such as the NERCS database to obtain a better understanding of the spatial and temporal variation in breeding parameters of a species.

Table 2.1. Dimensions (mm) and micro-habitat characteristics (% cover, ± S.D., range) of Pink-billed Lark nests at De Loskop.

Nest characteristic	Parameter	Mean ± SD, range
Dimensions	Nest diameter (*n* = 23)	106.7 ± 27.5, 53.0–140.0
	Cup diameter (*n* = 44)	52.2 ± 3.2, 43.0–58.0
	Cup depth (*n* = 44)	31.6 ± 2.7, 26.0–37.0
Micro-habitat (*n* = 28)	Grass (*n* = 50)	36.0 ± 17.2, 15.0–80.0
	Forbs (*n* = 50)	31.8 ± 16.0, 5.0–75.0
	Bare ground (*n* = 50)	18.8 ± 8.3, 5.0–40.0
	Debris (*n* = 50)	16.1 ± 12.4, 0–40.0
	Other (*n* = 50)	7.4 ± 9.5, 0.0–25.0

Table 2.2. Mean fresh egg mass (FEM), egg dimensions (L = maximum length; W = maximum width), estimated fresh egg mass (EEM) and egg volume (EV) for Pink-billed Larks in the study area (De Loskop) and from across the species' range using NERCS data.

De Loskop (*n* = 42)	
Parameter	Mean ± S.D., range
FEM (g) (*n* = 20)	1.7 ± 0.1, 1.5–1.9
L (mm)	18.4 ± 0.9, 16.9–19.8
W (mm)	13.5 ± 0.3, 13.0–14.1
EEM (g)	1.7 ± 0.1, 1.5–2.0
EV (mm^3)	3 342.1 ± 239.8, 3 007.1– 3 936.4

Table 2.3. Means of the parameters of the logistic growth curve for the increase in mass and growth of the head, tarsus and wing length of Pink-billed Lark nestlings (n = 7).

	A	K	t	$t_{10–90}$
Mass	11.63	0.45	4.40	9.82
Head length	25.53	0.20	1.17	21.49
Tarsus length	19.80	0.36	2.90	12.16
Wing length	76.70	0.30	8.86	14.52

Table 2.4. The number of food items delivered to 3–6 day old Pink-billed Lark nestlings at five nests (*n* = 900 minutes). Percentages in parentheses.

Food item	Male	Female	Total
Seed	30 (30)	25 (29.8)	55 (29.9)
Isoptera	37 (37)	24 (28.6)	61 (33.2)
Phasmatodea	8 (8)	0 (0)	8 (4.3)
Orthoptera	10 (10)	9 (10.7)	19 (10.3)
Unidentified	14 (14)	23 (27.3)	37 (20.1)
Unknown	1 (1)	3 (3.6)	4 (2.2)
Total	100 (100)	84 (100)	184 (100)

Table 2.5. Daily survival rates (DSR) (± S.E.) and overall breeding success (%) for the laying, incubation (12.0 days, *n* = 2), hatching and nestling (11.4 days, *n* = 13) periods for the Pink-billed Lark.

Measure of nest success	2009	2010	Overall
DSR during laying and incubation	0.92 ± 0.11	0.88 ± 0.10	0.90 ± 0.07
Hatching rate	0.79 ± 0.79	0.88± 0.33	0.88 ± 0.19
DSR during the nestling period	0.94 ± 0.08	0.95 ± 0.11	0.94 ± 0.06
Overall breeding success	14.4	10.6	12.8

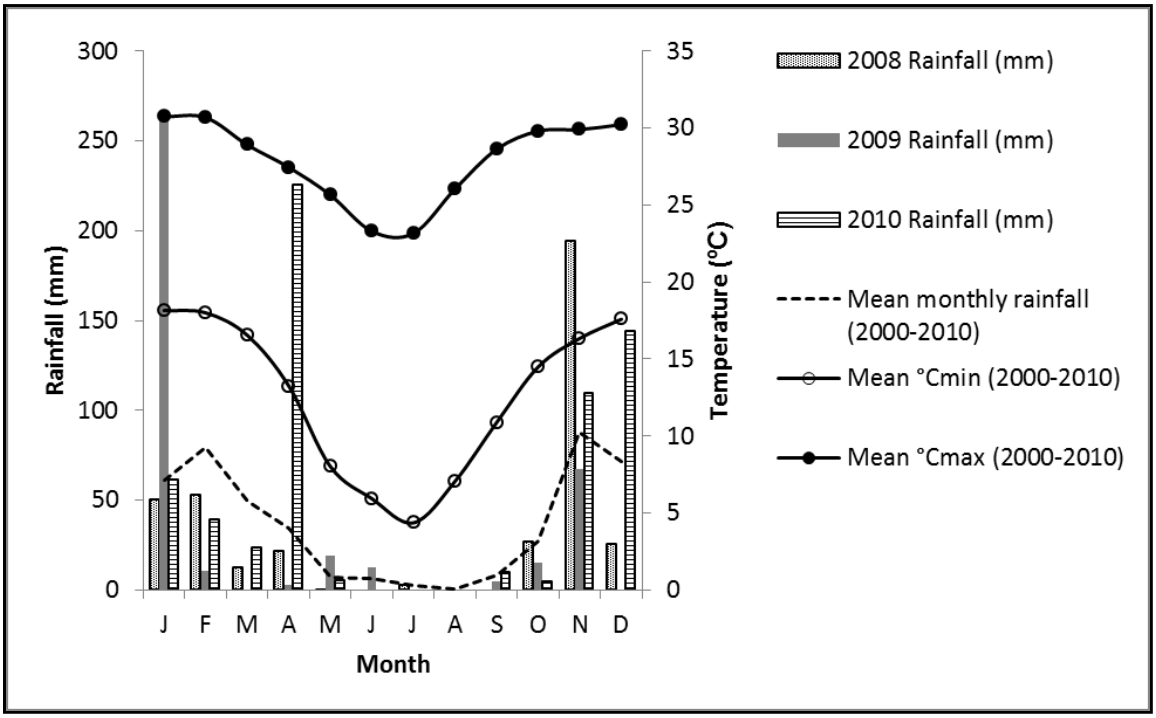

Fig. 2.1. Weather data from the Mara weather station (38km north-east of the study area at De Loskop) for the period January 2008 to December 2010. °Cmin = minimum temperature; °Cmax = maximum temperature). Data courtesy of the South African Weather Service (2010).

Fig. 2.2. Pink-billed Lark *Spizocorys conirostris* nest at the base of a forb and with a well-developed apron constructed of dung and sticks (De Loskop, Limpopo Province, May 2011).

Fig. 2.3. Pink-billed Lark *Spizocorys conirostris* nest at the base of a forb and with a well-developed apron constructed mainly of grass (De Loskop, Limpopo Province, May 2011).

Fig. 2.4. Pink-billed Lark *Spizocorys conirostris* nest without an apron (De Loskop, Limpopo Province, May 2011).

Fig. 2.5. Pink-billed Larks *Spizocorys conirostris* sometimes start laying well before the nest is complete. In this instance incubation had started before any lining had been added by the pair (De Loskop, Limpopo Province, May 2011).

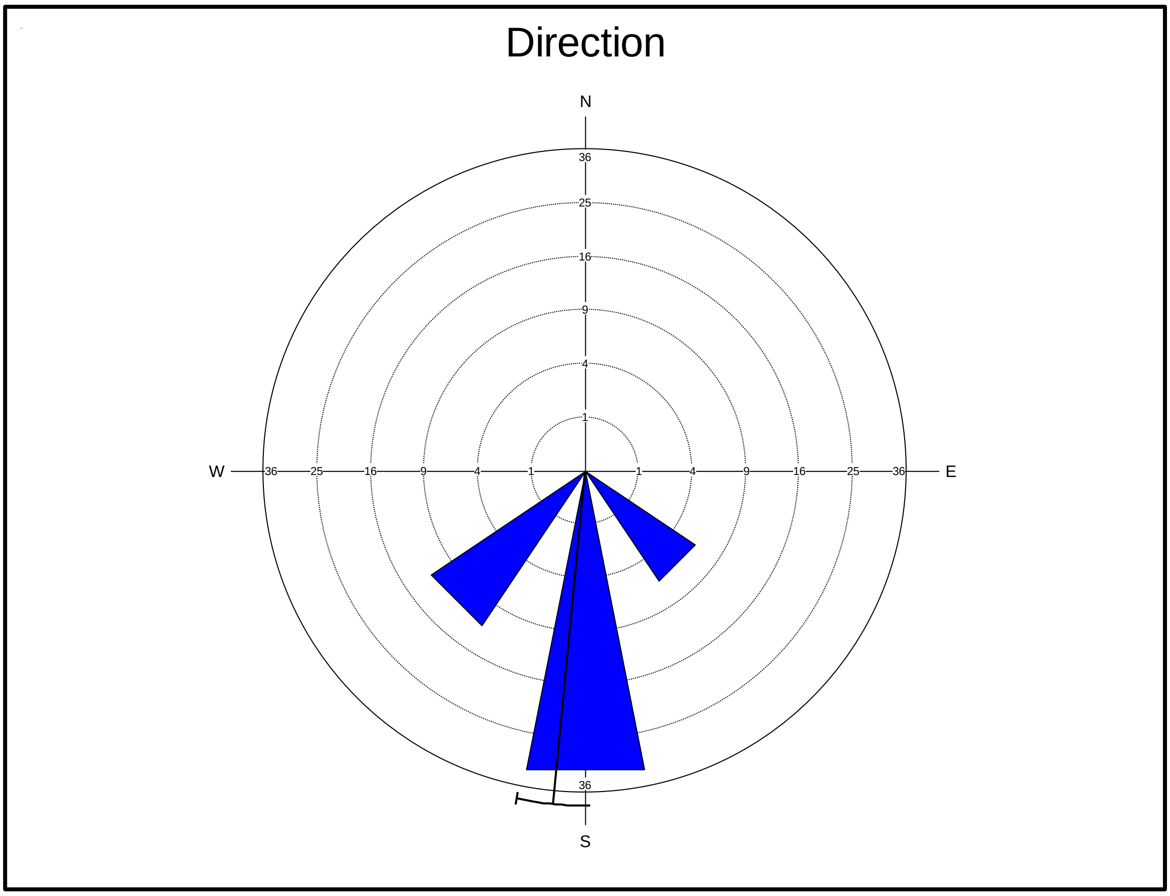

Fig. 2.6. A compass rose summary of the preferred nest entrance directions of the Pink-billed Lark *Spizocorys conirostris* at De Loskop, Limpopo Province between October 2008 and October 2010, based on the eight principal compass directions.

CHAPTER 3

Morphometrics, moult and vocalizations of the Pink-billed Lark *Spizocorys conirostris*

3.1. Introduction

The Pink-billed Lark is near-endemic to the southern African subcontinent, extending marginally into Angola and south-western Zambia (de Juana *et al.* 2004; Dean 2005; Mills 2006). It favours short, open grassy areas or the edges of pans and floodplains in the grassland, Nama-Karoo and savannah biomes. It is a shy and unobtrusive species which often goes undetected even in suitable habitat. This is reflected by its relatively low reporting rate of 5.7% during the first Southern African Bird Atlas Period (SABAP1) (Dean 1997). Populations in the central Highveld grasslands of South Africa appear to be resident whereas populations inhabiting the semi-arid and arid parts of its range appear to be nomadic (Dean 1997).

There is a general paucity of information about the Pink-billed Lark. Two studies stand out as having made significant contributions to our understanding of the species: Clancey (1972) studied geographical variation in plumage colouration and Maclean (1970a) studied the breeding biology of a nomadic population in the Kalahari Desert. Apart from these two studies, the only other notable contributions were a few short notes on various aspects of the species life history by Maclean (1970b). The results of Maclean's (1970a) study were compared with the results of this study (Chapter 2) and will not be dealt with in this chapter.

Clancey's (1972) work on geographic variation in plumage colouration revealed a fair degree of variation in populations across its range and culminated in the recognition of no fewer than eight subspecies. These are *Spizocorys conirostris conirostris, S. c. makawai, S. c. harti, S. c. damarensis, S. c. crypta, S. c. barlowi, S. c. transiens* and *S. c. griseovinacea.* However, Keith *et al.* (1992) does not recognize

S. c. griseovinacea and de Juana *et al.* (2004) and Dean (2005) both considered *S. c. transiens* and *S. c. griseovinacea* as indistinct from the nominate race. The nominate race *S. c. conirostris* is widely distributed in mesic grasslands of the Highveld and eastern Nama-Karoo. *Spizocorys c. barlowi* occurs in the semi-arid and arid Kalahari grasslands and savannah as well as the edges of the Nama-Karoo in the Northern Cape Province of South Africa, southern Namibia and southern and central Botswana. *Spizocorys c. damarensis* and *S. c. crypta* are found along the edges of saline pans in Ovamboland and Etosha in Namibia and the Makgadigadi pan complex and Lake Dow in north-eastern Botswana respectively. The two Zambian races are floodplain inhabitants of the Liuwa and Mutala Plains (*S. c. makawai*) and the Matabele Plains (*S c. harti*). The variation in plumage colouration is, however, clinal along an aridity gradient. The darker, heavily streaked races occupy the mesic central and southern parts of its range and the paler, faintly streaked races inhabit the more arid western and northern parts of the species' range, a correlation known as Gloger's Rule. Many southern African birds with distribution ranges extending across mesic and arid regions support Gloger's Rule, e.g. Sabota Lark, Spike-heeled Lark, Kalahari Scrub-robin *Cercotrichas paena* and Tractrac Chat *Cercomela tractrac*.

Although geographical plumage variation is well studied in the Pink-billed Lark, little is known about intra-specific geographical variation in morphometric parameters in this species. Analysis of morphometric data has the potential to help answer both theoretical and applied questions in avian ecology and should form part of any ornithological study on the biology of a species (Morgan 2004; Alonso and Arizaga 2006). For example, morphometric data allow us to: i) describe and identify species; ii) distinguish discrete populations in relation to their geographical areas of origin; iii) attribute age and sex to individuals, iv) provide insights into predation risk or migratory behaviour; and v) determine the degree of variation in sexual size dimorphism (SSD) between sexes (Alonso and Arizaga 2006; Mallet 2007).

The paucity of basic information on the Pink-billed Lark is demonstrated well by morphometric data presented by Keith *et al.* (1992). For example, their data is based on a sample of only 18 males and 17 females of unknown provenance. Since their publication, there have been no new contributions to increase the sample sizes for morphometric data. Such a lack of basic biological data is not unusual for southern African birds and as long ago as three decades ago, Craig (1983) urged ringers to publish their morphometric data to address this shortcoming.

Intraspecific morphological variation in larks is usually expressed as SSD and/or sexual dichromatism. The former is evident in most resident and insectivorous larks and to a lesser extent in some nomadic and/or granivorous species (de Juana *et al.* 2004). Sexual dichromatism is the variation in plumage colouration between sexes and is present in only a few species of larks, most notably the sparrow-larks of the genus *Eremopterix*. It is believed that sexual dichromatism partially offsets the need for SSD, as it allows for easy recognition of sexes and rapid settlement and breeding at the beginning of the breeding season and/or when conditions become favourable (Barnes 2007).

Another aspect of avian biology which needs to be addressed is our current state of knowledge of the moult pattern of southern African birds. Although moult is one of the three major events in the annual cycles of birds, the other being breeding and migration, it has been much less studied than these two aspects (Jenni and Winkler 1994; Kjellén 1994; Newton 2008). This is partly because of a general lack of appreciation of its relevance to the annual cycle and population processes, and its potential role in conservation-driven research (Newton, 2009). At present, there is nothing known about the timing or moult pattern of the Pink-billed Lark. The present study will aim to address this caveat by reporting on moult recorded in museum specimens.

The unobtrusive nature of the Pink-billed Lark makes it difficult to identify and hence it is likely that it is under-reported throughout its range. However, it has characteristic flight and display vocalizations which, in turn, may facilitate identification (Dean 2005). Thus, knowledge of the full range of vocalizations of the species may assist in its identification which, in turn, may contribute to a better understanding of the demographics of this species. Bird vocalizations are generally rather diverse and include songs, which range from full or primary song to sub-song, and also various other calls such as alarm, begging, territorial, distress, flight, warning, feeding and flock calls, amongst others (Krebs and Kroodsma 1980; Gill 1990; Catchpole and Slater 1995; Chen and Maheer 2006).

The vocal repertoire of birds can be divided into five categories, namely elements, syllables, phrases, calls and songs. Elements are deemed the simplest form of vocalizations and are often referred to as elementary units (Chen and Maher 2006). A syllable is slightly more complex as it consists of two or more elements which usually last for the duration of a few hundred milliseconds. Syllables are the building blocks of phrases and this too collectively forms part of a song sequence (Chen and Maher 2006). Calls are basically short, simple sequences of phrases. Calls are given by either sex and mainly serve to alert and to coordinate group behaviour (Cramp and Simmons 1977; Gill 1990; Chen and Maher 2006). Multiple phrases, whether variable or repetitive, form a song sequence. However, one phrase can constitute a song sequence (Chen and Maher 2006). Songs are long and complex vocalizations that contain specific and repeated patterns and are recognizable at species, group and individual levels respectively (Cramp and Simmons 1977; Gill 1990; Chen and Maher 2006).

In light of the foregoing, the aim of this study was to improve our understanding of aspects of the biology and behaviour of the Pink-billed Lark to supplement the knowledge gained on the species breeding biology in Chapter 2. The specific objectives of this chapter were to:

i. Investigate intra-specific geographical variation in selected biometric parameters using different databases,
ii. Determine if the Pink-billed Lark exhibits SSD,
iii. Provide a description of the onset and pattern of moult in the species, and
iv. To analyse and describe the vocalizations of a resident population in South Africa’s Limpopo Province.

3.2. Methods

3.2.1. Morphometrics

For analysis of intraspecific geographic variation and to determine if the species exhibits SSD for selected morphological parameters, museum study skins of Pink-billed Larks were requested from the following South African natural history museums: Ditsong National Museum of Natural History (Pretoria), East London Museum (East London), Iziko South African Museum (Cape Town), McGregor Museum (Kimberley), Durban Natural Science Museum (Durban) and the National Museum (Bloemfontein). The data was supplemented with data collected from specimens captured during the course of the study. It should be noted that data from the museum study skins and data collected during the course of fieldwork in this study were treated as separate databases. This is due to specimen shrinkage occurring during drying of museum study skins which can amount to differences in values of 2–5% (Kuczynski *et al.* 2003).

Live specimens were captured at the study site on the farm AL3 De Loskop (23°30'S, 29°19'E) (hereafter De Loskop) near Mogwadi in the Limpopo Province, South Africa. The study site is situated at the northern edge of the Polokwane Plateau at an altitude of 1100 masl. It falls within the Makhado Sweet Bushveld vegetation type (Mucina and Rutherford 2006) and is characterised by a mixture of relatively undisturbed short, open, *Acacia* dominated scrub, fallow lands, cultivated fields and an earth dam. De Loskop is situated in a summer rainfall region with a mean annual precipitation of 478 mm and a wet season extending from November to January (SA Weather Service 2010).

Specimens were captured at or near the nest using either mist-nets or a walk-in trap placed over the nest. Captured birds were individually banded with numbered SAFRING metal bands and a combination of coloured plastic leg bands to aid in individual identification which was required for other aspects of the study (see Chapter 2). Each captured individual was weighed to the nearest 0.1 g using an Ohaus Scout Pro portable digital scale. The following parameters were measured as described by de Beer *et al.* (2001): head length (living specimens only), culmen length (measured from the base of the bill at the union with the skull to the tip of the Culmen, living specimens only), 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), tarsus length (length of the tarso-metatarsus is measured from the notch of the first undivided anterior scute to the notch at the proximal end of the tarsus), wing length (is measured as the maximum length of the flattened wing chord), tail length (maximum length of the rectrices). Digital Vernier callipers were used for all the measurements (readable to 0.1 mm) except tail length and the length of the wing chord. Tail length was measured with a standard ruler (readable to 1 mm) and wing length was recorded using a standard stopped wing ruler (also readable to 1 mm) typically used by bird ringers. Living specimens were sexed on the basis of the presence of a brood patch in breeding females and its absence in males. For museum skins, sexing was based on information provided on the specimen’s tag.

Morphometric data were first checked for normality using Kolmogorov-Smirnov one-sample tests. To determine if the species exhibits SSD, the non-parametric Mann-Whitney U test was used to test for significant differences between sexes for the measured parameters. For intra-specific geographic variation the median test was used. In all instances, the significance level was $P < 0.05$. All statistical analysis for the biometric data was done using SPSS version 18 (SPSS, Inc., Chicago, Illinois)

3.2.2. Moult

Breeding and moult generally do not overlap in the majority of birds (Maclean 1990; Gill 1990) and like most passerines, larks undergo a complete post-breeding moult although there are a few exceptions (de Juana *et al.* 2004). As such, very limited moult data was collected from live specimens during the course of this study. Despite their value to shed light on some crucial aspects of species life history, the fragility of museum study skins also presents challenges to studying moult. The fragility of the museum specimens were taken into consideration as great care was taken to ensure minimal or no damage was incurred when the study skins were examined. A pair of forceps was used to gently lift the feathers for examination. Moulting was recorded on the head region, on the dorsal and the ventral surfaces, on the remiges and rectrices and on the wing coverts. If two or more moulting feathers were observed in a given area, then that area was considered to be in moult. Moult data from the study skins were supplemented by primary moult data in the SAFRING database as recorded by bird ringers.

3.2.3. Vocalizations

Digital recordings of vocalizations were made with a Marantz PMD670 Professional digital recorder and a Sennheiser ME66 directional microphone. Sonograms were analysed using the Raven 1.3 software package (Bioacoustics Research Program 2008). An estimate of quantitative variation in vocalizations was made by measuring the following variables for each call:

i. The number of notes in a phrase or call,
ii. Duration or delta time (DT) of the phrase or call measured in milliseconds (ms),
iii. Lowest frequency (LF) of the phrase or call measured in kilohertz (kHz),
iv. Highest frequency (HF) of the phrase or call measured in kHz.

Call data was analysed using Microsoft Office Excel (2007) for Windows.

3.3. Results

3.3.1. Morphometrics

Mass and morphometric data of forty-seven (n = 18 males, n = 29 females) adult Pink-billed larks captured during the course of this study are presented in Table 3.1. Pink-billed larks at De Loskop exhibited statistically significant ($P < 0.05$) SSD for wing and tail length but not for any of the other parameters recorded (Table 3.1). However, there was some overlap between the sexes for wing and tail length. In general, females tended to be larger than males except for parameters relating to the flight apparatus.

A total of 152 (*n* = 96 males, *n* = 58 females) museum study skins representing the four southern African subspecies were measured and the data analysed. Since the sample sizes for *S. c. barlowi* (*n* = 9 male, *n* = 4 female), *S. c. damarensis* (*n* = 7 male, *n* = 5 female) and *S. c. crypta* (*n* = 1 male, *n* = 1 female) were all small, data for these three subspecies were pooled for analyses of geographic variation for morphometric data. A summary of the results of the analyses of morphometric data of male and female study skins are presented in Tables 3.2 and 3.3 respectively. Since the data of most of the parameters did not conform to a normal distribution (Kolmogorov-Smirnoff test, $P < 0.05$), the non-parametric Mann-Whitney U test was used to determine if there are geographic differences between the nominate race and the other three southern African races for the parameters measured. Although the results showed weak statistically significant differences in wing length between the nominate race and the other races ($P = 0.030$ for males and $P = 0.043$ for females), it should be interpreted with caution as the sample sizes were small for the pooled subspecies and there was also considerable overlap in values. For analysis of SSD in study skins, no distinction was made between the subspecies and a summary of the morphometric data is presented in Table 3.4. The results of SSD analysis of study skins support the results of the De Loskop population which also indicated that the Pink-billed Lark is sexually dimorphic for wing and tail length (Median test: Wing $X^2 = 28.11$, $P < 0.001$; Tail $X^2 = 18.45$, $P < 0.001$).

3.3.2. Moult

Moult data collected during the course of this study suggest that Pink-billed Larks at De Loskop subscribe to the general passerine pattern of avoiding moulting during the breeding season. Apart from a female (SAFRING number: AR30093) moulting the innermost secondary on 20 March 2013, no actively moulting birds were recorded during the breeding season at De Loskop. Another female (SAFRING number: AB48203) was in the early stages of moulting the capital tract feathers on

16 May 2010. However, this female had a regressing brood patch suggesting that she had completed breeding at the time. Two females (AP60551 and AP60607) were in the early stages of primary moult in early August 2012, with the latter undergoing a complete moult of contour feathers at the time.

A similar pattern was observed with the museum study skins and records in the SAFRING database. Primary moult was nearly completed in November in two study skins (Durban Natural Science Museum #18331: Lake Dow, Botswana; Ditsong National Museum of Natural History #30762: Tierputs, Botswana). Three records in the SAFRING database (GA59029, GA59031 and GA59032), all from the Kimberley district, Northern Cape Province, South Africa were in advanced primary moult in October. Furthermore, most specimens collected between November and January were in fresh, recently moulted plumage. Several specimens had fresh, or were in the process of replacing, the innermost three secondaries and some contour feathers in mid-winter, i.e. June and July. Although the moult data is limited, it appears as if the Pink-billed Lark undergoes a partial post-breeding moult during which the inner secondaries and some contour feathers are replaced during winter, followed by a complete moult starting in early spring and which is completed in about November.

3.3.3. Vocalizations

Seven different vocalizations were identified. Brief descriptions of each call follow and a summary of the duration, lowest and highest frequency and the number of notes of calls are presented in Table 3.5.

i. Nestling distress call: These calls were often made by nestlings upon the arrival of either parent at the nest. Nestlings also made these calls upon catching sight of a parent flying overhead. The latter can be a long or a short spike call (Fig. 3.1). Two variations of this call type can be distinguished: distress and begging calls. Begging calls can be either a harsh screech or a high pitched *“peep”* call. Nestling calls are among the most difficult to record as they are often very soft and nestlings tend to remain silent when they sense activity near the nest.

ii. Ground calls: A mix warble of different clicking, *"tseep"* and pulsed calls when birds are foraging on the ground. These are generally rather soft calls and very difficult to record. It is possible that these calls may be a sub-song, i.e. a muted version of full song (Fig. 3.2).
iii. Aggressive call: This is a very rapid *"tsk"* call comprised of pulsed notes (Fig. 3.3). This call is heard during aggressive encounters such as chasing of rivals in flight, or when attacking conspecifics approaching too close to an active nest.
iv. Alarm call: This can be described as a pulsed one- or two note call (Fig. 3.4). Alarm calls are characterised by a fluctuation in frequency: they typically have a short, sudden rise in frequency followed by a gradual drop in frequency. Alarm calls are made by both sexes mostly while in flight as they circle around the area of concern, e.g. when a disturbance at or near the nest or fledglings is detected.
v. Contact call: A raspy, three- to nine-note call usually called when the adults are foraging near the nest or when flying near the nest (Fig. 3.5).
vi. Flight song: Two types of flight song were identified. It forms part of a territorial display flight. One is a single, rapid pulsed call. The other is also a rapid pulsed call, but comprise of two notes; a short one followed by a longer, descending phrase (Fig. 3.6).
vii. Flight call: Flight calls were high pitched phrases comprised of 2-24 notes. It appears as if each individual has a unique "signature" call (Fig. 3.7).

3.4. Discussion

3.4.1. Morphometrics

Sexual dimorphism is a common phenomenon in the Alaudidae (De Juana *et al.* 2004). It may take the form of SSD as in many insectivorous larks or sexual dichromatism as in the genus *Eremopterix* and to a lesser extent in other lark genera such as *Eremophila, Pinacorys* and *Ramphocorys* (Keith *et al.* 1992; de Juana *et al.* 2004; Arnqvist and Rowe 2005). The Pink-billed Lark is primarily granivorous and it is therefore unlikely to exhibit strong SSD. This is because seeds are generally abundant and there is very little need for SSD to exploit different niches as with, for example, insectivorous species. However, the results of this study revealed that the species exhibits statistically significant SSD with regard to wing and tail length, with males averaging larger than females for these parameters. Males at De Loskop also tend to be smaller than females for most of the parameters recorded (Table 3.1).

It is interesting to note that the two parameters which showed significant SSD are related to flight. A longer wing and tail length, and generally smaller body dimensions may confer adaptive advantages to males during display flights. For example, Vögeli *et al.* (2007) observed that the intensity and rate of display flights of Du Pont's lark *Chersophilus duponti* appeared to be enhanced by cost-reducing traits such as longer wings and tails. Nevertheless, the significance of the observed sexual size dimorphism for wing and tail length should be interpreted with caution due to the high degree of overlap and small mean differences between the sexes for these measurements. Thus, although the results revealed statistically significant differences for these parameters, the biological significance of such a small difference may be questionable.

Although not statistically significant, the results revealed that females tend to be heavier than males. Once more, there is considerable overlap in these measurements and these results should also be interpreted with caution. It is possible that the greater mass of females may be an artefact of sampling as most females were actively breeding when mass and morphometric data were recorded. Actively breeding females are likely to be heavier than non-breeding females as they experience a build-up of nutrient reserves which are used for egg production, and experience physiological changes such as the development of the ovaries and other tissues associated with egg-laying (Newton 1979; Wheeler and Greenwood 1983). Breeding places tremendous energetic demands on particularly female birds and they have to be in good physical shape for successful breeding. In a study by Dikgale (2012) on Chestnut-backed Sparrowlarks *Eremopterix leucotis* at De Loskop, breeding females were also found to be generally heavier than males and non-breeding females.

The results of the analysis of intraspecific geographic variation revealed a statistically significant difference in wing length between the nominate race and those of the other southern African subspecies combined. Unfortunately the sample sizes for the subspecies *S. c. damarensis*, *S. c. crypta* and *S. c. barlowi* are too small to make valid inferences regarding the possible adaptive significance of the longer wing length of the nominate race compared to the slightly shorter wing length of the other subspecies. A more detailed morphometric study of intraspecific geographic variation of the Pink-billed Lark will certainly be an exciting avenue for future research.

3.4.2. Moult

Moult is an energetically very expensive activity and most passerines defer moult so that it does not coincide with other demanding activities such as breeding or migration (Jenni and Winkler, 1994). Moult is energetically costly in terms of the synthesis of feathers, a reduction in flight performance during replacement of the remiges and tectrices, and lowered insulation capacity of plumage during moult of contour feathers (Dietz *et al*., 1992; Murphy, 1996; Chai and Dudley, 1999). Results of the analysis of the timing and pattern of moult of the Pink-billed Lark in the present study certainly seem to support this general notion. Apart from a single individual moulting the innermost secondaries during the breeding season, no other evidence of moult was recorded in breeding birds in this study, nor was it observed in museum study skins. However, many of the live specimens and museum study skins had fresh innermost secondaries. A rapid partial moult, involving only the three innermost secondaries, has been recorded in several lark species and usually occurs during breeding (Herremans and Herremans 1992; de Juana *et al.* 2004; Dikgale 2012). Larks have strikingly large inner secondaries which act as a “cloak” to protect the underlying secondaries and primaries from abrasion by various substrates and bleaching by UV rays. By only replacing the innermost secondaries, larks avoid the high energetic costs of a complete moult, yet gain the benefits of fresh plumage.

The breeding season of Pink-billed Larks extend well into May and even July (see Chapter 2) which coincides with the austral winter months. Thus, a complete post-breeding moult starting in winter may place excessive demands on birds, specifically with regard to their insulation abilities. It is therefore understandable that it would be more beneficial to delay the onset of a complete moult until spring when conditions become more favourable and to approach the breeding season with fresh plumage. This scheduling of the main moult to a pre-breeding moult, rather than a post-breeding moult, has the additional advantage that both sexes will have fresh - and perhaps brighter – plumage, which may suggest a link between sexual selection and the timing of moult in the Pink-billed Lark. Furthermore, males will have fresh flight feathers at the onset of the breeding season which would be an advantage for the demands incurred by aerial display flights. Although the aforementioned interpretations of the moult patterns recorded in the present study is based on a small sample, it highlights the importance of a comprehensive understanding of the timing and pattern of moult to elucidate adaptations to different ecological characteristics of a species.

3.4.3. Vocalizations

In general, there is an inverse relationship between plumage colouration and song development (Donald 2004). It has been suggested that the dun, cryptic colouration of larks is an adaptation for the generally austere, open habitats that these mainly ground-living species inhabit. As such, larks invest heavily in song and display flights as signals of fitness and some species have a rich vocal repertoire. Larks are revered as some of the finest songsters in the bird world (Donald 2004; De Juana *et al.* 2004). Although there is an extensive body of literature on avian vocalizations encompassing fields such as behaviour, evolution, neuroscience and psychology to name but a few (Slater 2003), relatively little is known about the full vocal repertoire of the majority of larks. This is despite the potential value that knowledge of the range of vocalizations of cryptic species such as larks may add to bird monitoring programmes.

According to the literature, Pink-billed Larks have a display song described as “short, whistled elements” (De Juana *et al.* 2004), contact, alarm and flight calls (Maclean 1970a; 1993). This study is the first to analyse these vocalizations and also report on previously unrecorded nestling, aggressive, ground and territorial calls.

The nestling distress call is typical of many nestlings as it is usually rather harsh and loud. Similar sounding screech calls are made by nestlings of other species nesting in open habitats, e.g. cisticolas (*Cisticola* spp.), pipit (*Anthus*) and African Quailfinch (*Ortygospiza atricollis*). Its aim is to startle or deter a potential predator.

The aggressive calls recorded during this study are similar to those produced by other lark species during aggressive encounters (Engelbrecht, pers. comm.). Due to the difficulty in recording aggressive calls, these calls are under reported in the description of the vocal repertoire of larks, and therefore these recordings are of particular value for future research on vocalizations.

Ground calls represent a subdued mixture of various notes and calls and since they are usually performed on the ground and in the presence of another individual, this type of call may represent a version of sub-song. Unlike flight song which is usually exclusively performed by males, females of various species are known to include sub-song in their vocal repertoire (Donald 2004; Dikgale 2012).

The flight song is so distinctive and characteristic of the species, that it is surprising that it appears to not have been described in the literature yet. This call is associated with a display flight and is often interspersed with flight calls. The only reference to a flight song of Pink-billed Lark describes it as “short, sweet whistled elements”. This description is open to interpretation but no calls resembling this description were recorded in this study. Instead, the display flight song starts with a rapid, pulsed call lasting about one second and which sounds like a pencil rapidly being dragged over a comb. This is followed by alternating flight calls and song. The flight song is arguably the most reliable indicator of the presence of the species and knowledge of it is of particular value in bird monitoring programmes.

The results of the analyses of flight calls suggest that each individual has a unique “signature” flight call. The other calls, e.g. contact, alarm, ground and aggressive are typical for the population and show relatively little intraspecific variation. The Pink-billed Lark forages in loose aggregations or flocks, and a “universal language” for calls such as alarm calls would be advantageous in a flock when a predator is around. By the same token, some form of individual recognition as was observed with flight calls would also be advantageous for pairs. If a male and female are attuned to each other’s call, it would be easy to locate a mate in a flock.

In conclusion, this study has made a major contribution to our understanding of various aspects of the biology and ecology of the Pink-billed Lark. The results revealed cryptic sexual size dimorphism of the flight apparatus which suggests that this may be an adaptive advantage to males during display flights. Analysis of the timing and pattern of moult revealed an interesting strategy which appears to deviate from the usual lark pattern. The pre-breeding moult may be an adaptation to avoid loss of insulation capabilities associated with moulting of contour feathers during winter as a result of cessation of the breeding season at or near the onset of winter. The Pink-billed Lark was shown to possess a rich vocal repertoire and several hitherto have not been described vocalizations are reported here for the first time. An interesting finding is the apparent individual distinctiveness of flight calls which may facilitate finding a mate when flying as a flock.

Table 3.1. Mean, standard deviation and range of the mass (g) and selected morphometric measurements (mm) of adult Pink-billed larks *Spizocorys conirostris* from De Loskop, Limpopo Province caught between April 2009 and April 2013. Sample sizes in parentheses.

	Males	Females	*P*
Mass	15.80 ± 0.83, 14.00–17.00 (18)	16.25 ± 1.08, 14.66–19.00 (29)	0.141
Head length	28.06 ± 0.57, 27.1–29.00 (18)	27.91 ± 0.60, 26.80–29.08 (29)	0.401
Culmen length	13.37 ± 0.50, 12.70–14.50 (18)	13.45 ± 0.56, 12.38–14.60 (29)	0.658
Culmen-nare	8.46 ± 0.31, 7.87–9.10 (17)	8.56 ± 0.54, 7.00–9.90 (27)	0.503
Bill depth	6.01 ± 0.24, 5.60–6.55 (16)	5.98 ± 0.15, 5.60–6.34 (27)	0.636
Bill width	5.04 ± 0.31, 4.60–5.50 (10)	5.00 ± 0.21, 4.60–5.30 (13)	0.718
Tarsus length	18.85 ± 0.71, 17.66–20.10 (18)	19.01 ± 0.76, 17.40–20.60 (29)	0.479
Wing length*	77.19 ± 1.51, 75.00–80.00 (18)	74.24 ± 1.88, 71.00–78.00 (29)	<0.001
Tail length*	42.72 ± 1.96, 39.00–45.00 (18)	39.61 ± 1.59, 37.00–43.00 (28)	<0.001

*Statistically significant: $P < 0.05$

Table 3.2. Morphometric data of study skins of males of the nominate race of the Pink-billed Lark *Spizocorys conirostris conirostris* compared with the three other southern African subspecies (*S. c. damarensis, S. c. barlowi and S. c. crypta*) combined. Results are presented as mean ± S.D., range, (*n*). Significance level is $P < 0.05$).

	S. c. conirostris	Pooled subspecies	*P*
Culmen-nare	8.32 ± 0.64, 6.90–11.50 (n=79)	8.32 ± 0.41, 7.80–11.50 (13)	0.844
Bill depth	6.23 ± 0.38, 5.40–7.60 (n=77)	6.39 ± 0.41, 5.80–7.60 (13)	0.146
Bill width	5.28 ± 0.36, 4.80–6.10 (n=78)	5.23 ± 0.25, 5.00–6.10 (13)	0.931
Tarsus length	19.63 ± 0.76, 18.10–22.40 (n=78)	19.69 ± 0.90, 18.00–22.40 (16)	0.698
Wing length	76.91 ± 1.94, 72.00–82.00 (n=79)	75.24 ± 3.11, 67.00–82.00 (17)	0.030*
Tail length*	43.77 ± 2.23, 38.00–50.00 (n=79)	42.94 ± 3.15, 38.00–50.00 (17)	0.211

Table 3.3. Morphometric data of study skins of females of the nominate race of the Pink-billed Lark *Spizocorys conirostris conirostris* compared with the three other southern African subspecies (*S. c. damarensis, S. c. barlowi and S. c. crypta*) combined. Results are presented as mean ± S.D., range, (*n*). Significance level is $P < 0.05$).

	S. c. conirostris	Pooled subspecies	*P*
Culmen-nare	8.15 ± 0.56, 7.00–9.10 (n=44)	8.10 ± 0.71, 6.90–9.10 (n=10)	0.663
Bill depth	6.24 ± 0.39, 5.80–7.30 (n=43)	6.42 ± 0.54, 5.85–7.10 (n=10)	0.448
Bill width	5.19 ± 0.27, 4.60–5.90 (n=44)	5.19 ± 0.44, 4.80–6.00 (n=10)	0.206
Tarsus length	19.58 ± 0.74, 18.10–21.00 (n=44)	19.73 ± 0.90, 18.10–21.00 (n=10)	0.525
Wing length*	73.83 ± 2.39, 69.00–79.00 (n=45)	72.10 ± 2.28, 69.00–76.00 (n=10)	0.043*
Tail length	40.82 ± 1.98, 37.00–46.00 (n=45)	40.85 ± 3.80, 36.00–46.00 (n=10)	0.808

Table 3.4. Mean, standard deviation and range of selected morphometric measurements (mm) of museum study skins of adult Pink-billed larks *Spizocorys conirostris* from southern African. Sample sizes in parentheses.

	Males	Females	*P*
Culmen-nare	8.32 ± 0.61, 6.90–11.50 (92)	8.14 ± 0.58, 6.90–9.10 (54)	0.503
Bill depth	6.25 ± 0.39, 5.40–7.60 (90)	6.28 ± 0.42, 5.80–7.30 (53)	0.636
Bill width	5.28 ± 0.35, 4.80–6.10 (91)	5.19 ± 0.30, 4.60–6.00 (54)	0.718
Tarsus length	19.64 ± 0.78, 18.00–22.40 (91)	19.61 ± 0.76, 18.10–21.00 (54)	0.479
Wing length	76.61 ± 2.27, 67.00–82.00 (96)	73.52 ± 2.44, 69.00–79.00 (56)	<0.001
Tail length	43.63 ± 2.42, 38.00–50.00 (96)	40.83 ± 2.37, 36.00–46.00 (55)	<0.001

Table 3.5. Summary of mean, standard deviation and range of the duration and frequencies of the various vocalizations of Pink-billed Larks *Spizocorys conirostris* at De Loskop, Limpopo Province, South Africa, recorded between April 2010 and April 2012. Ground and aggressive calls were not included in the analysis as their notes are too variable for analysis. Duration (s) = the duration of a note, F_{min} = minimum frequency (kHz) and F_{max} = maximum frequency (kHz) and # = number of notes per vocalization.

Call type	Duration	F_{min}	F_{max}	#
Nestling distress *n* = 89	0.24 ± 0.12 0.04–0.49	4123.90 ± 655.69 2245.10–5086.70	5444.94 ± 890.07 2877.50–6607.10	1
Alarm *n* = 61	0.32 ± 0.10 0.08–0.74	3296.20 ± 0.12 2861.70–3687.60	5723.30 ± 490.90 4003.50–6647.90	2 ± 0.90 1.00–8.00
Contact *n* = 12	0.50 ± 0.20 0.30–0.80	2641.10 ± 859.60 135.50–3183.70	4245.30 ± 757.50 3912.40–6520.60	5 ± 2.60 3.00–9.00
Territorial *n* = 43	0.50 ± 0.10 0.30–0.70	3413.80 ± 2914.10–3839.00	4720.70 ± 792.80 4019.30–6199.70	1.30 ± 0.40 1.00–2.00
Flight *n* = 105	0.70 ± 0.40 0.20–2.10	3018.80 ± 204.40 2485.90–3655.70	4823.90 ± 300.20 4065.90–5714.00	7.40 ± 4.50 2.00–24.00

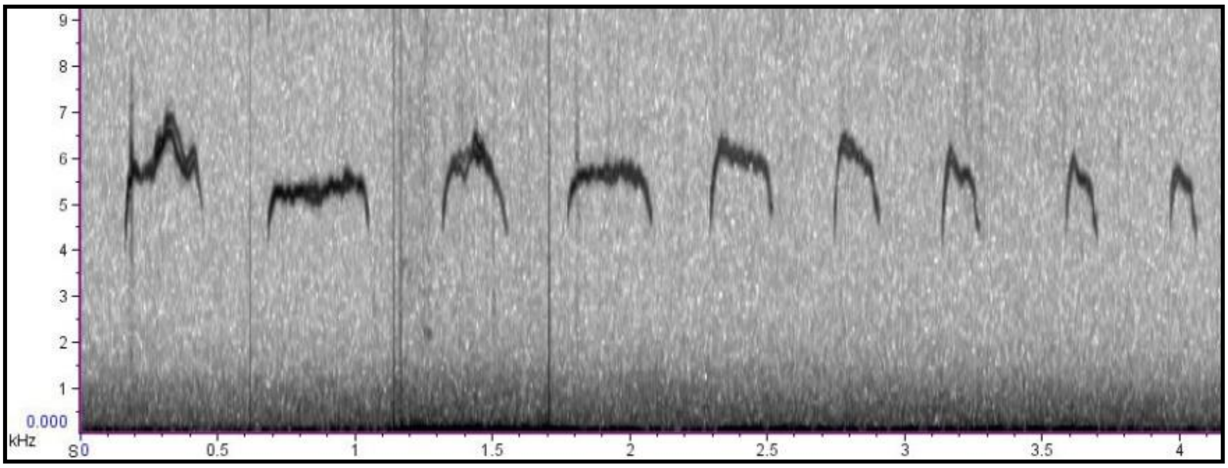

Fig. 3.1. Nestling distress calls of Pink-backed Larks *Spizocorys conirostris* recorded at De Loskop, Limpopo Province, South Africa between April 2010 and April 2012.

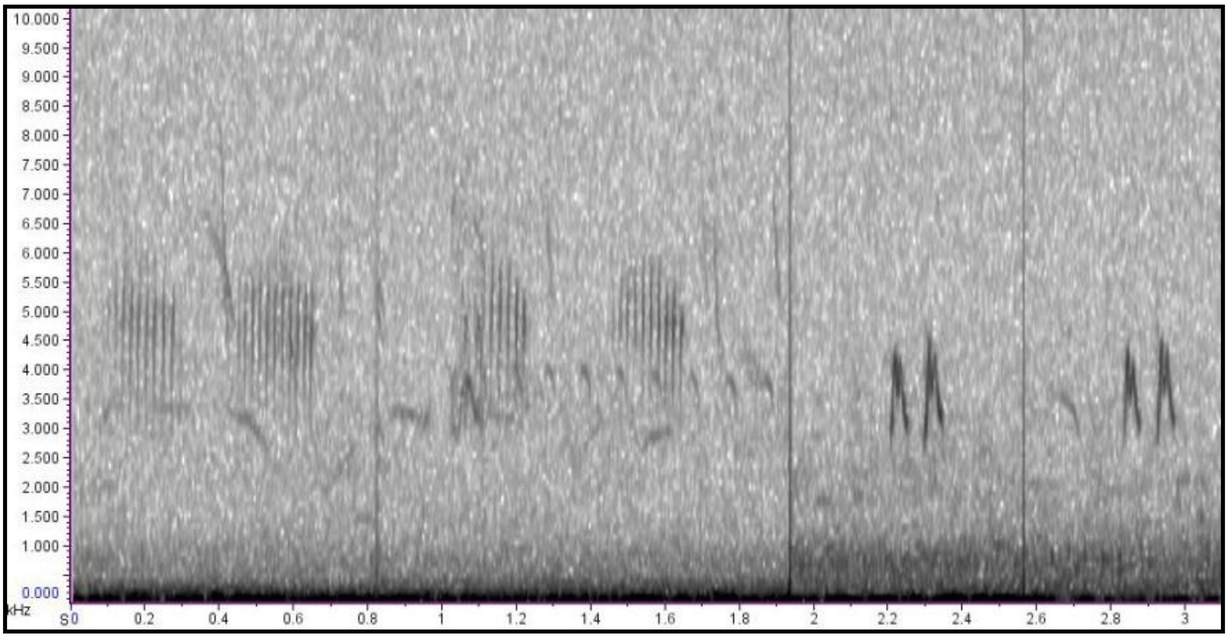

Fig. 3.2. Various ground calls of Pink-backed Larks *Spizocorys conirostris* recorded at De Loskop, Limpopo Province, South Africa between April 2010 and April 2012.

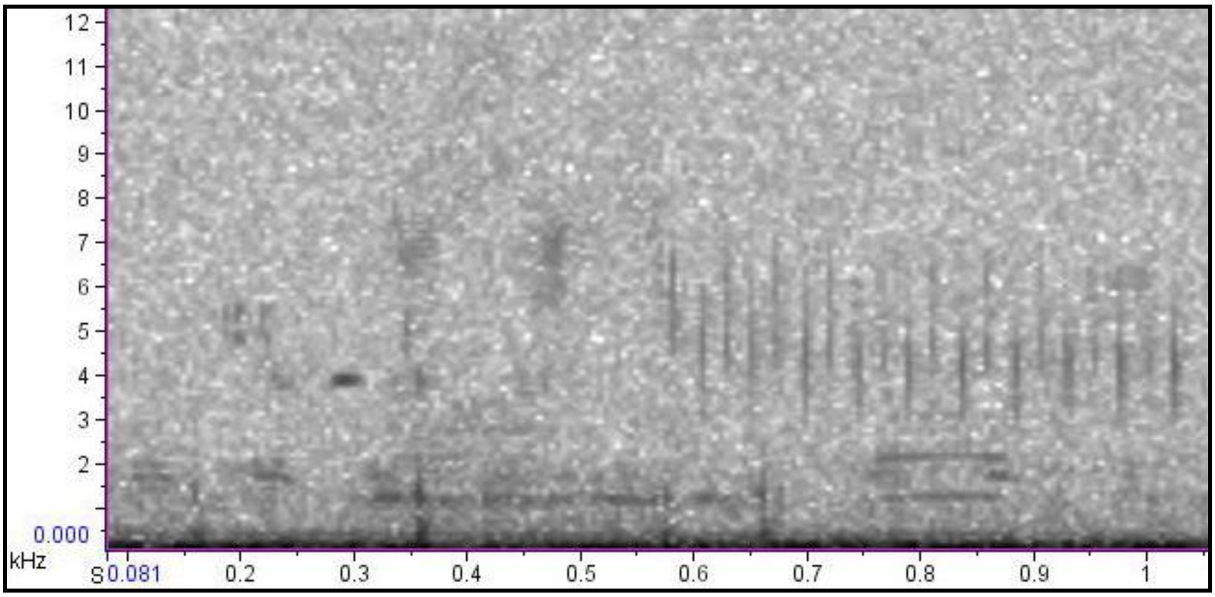

Fig. 3.3. An example of an aggressive call of Pink-backed Larks *Spizocorys conirostris* recorded at De Loskop, Limpopo Province, South Africa between April 2010 and April 2012.

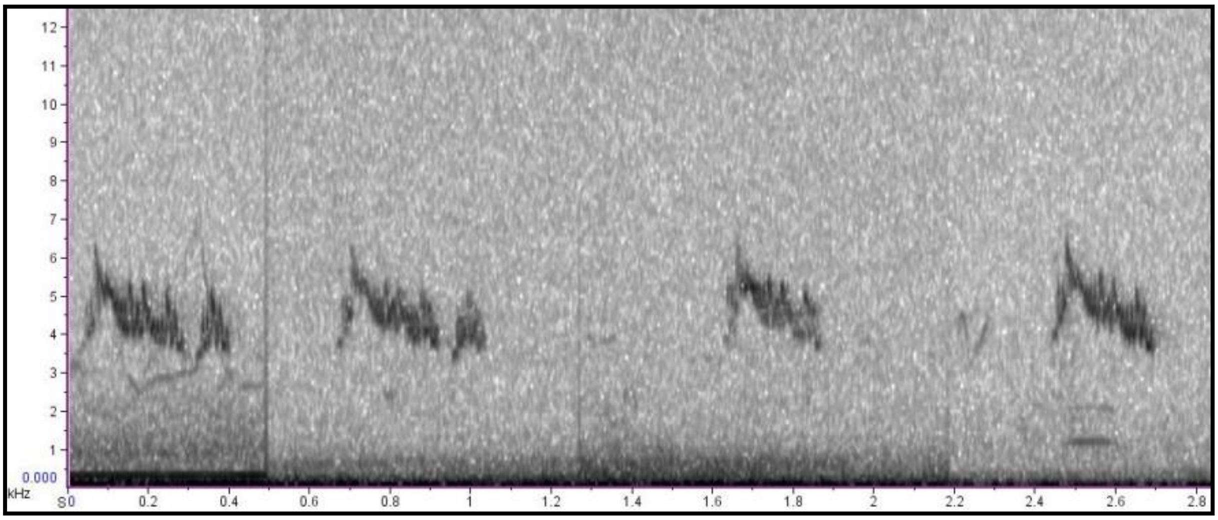

Fig. 3.4. Alarm call of Pink-backed Larks *Spizocorys conirostris* recorded at De Loskop, Limpopo Province, South Africa between April 2010 and April 2012.

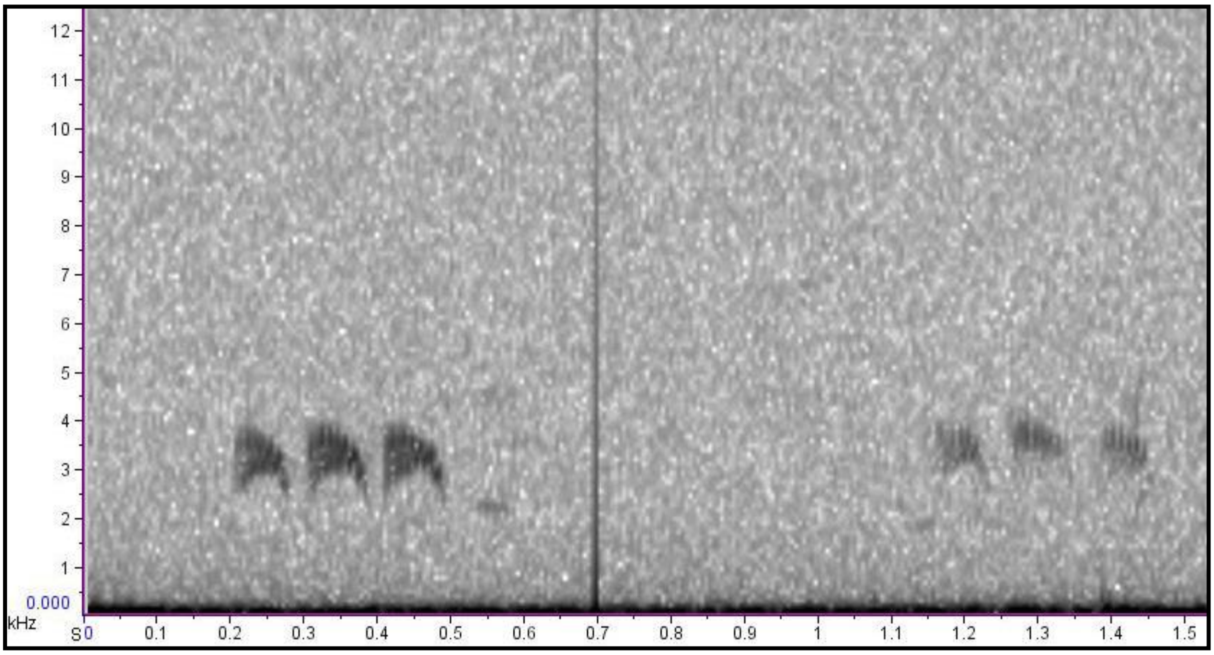

Fig. 3.5. Contact call of Pink-backed Larks *Spizocorys conirostris* recorded at De Loskop, Limpopo Province, South Africa between April 2010 and April 2012.

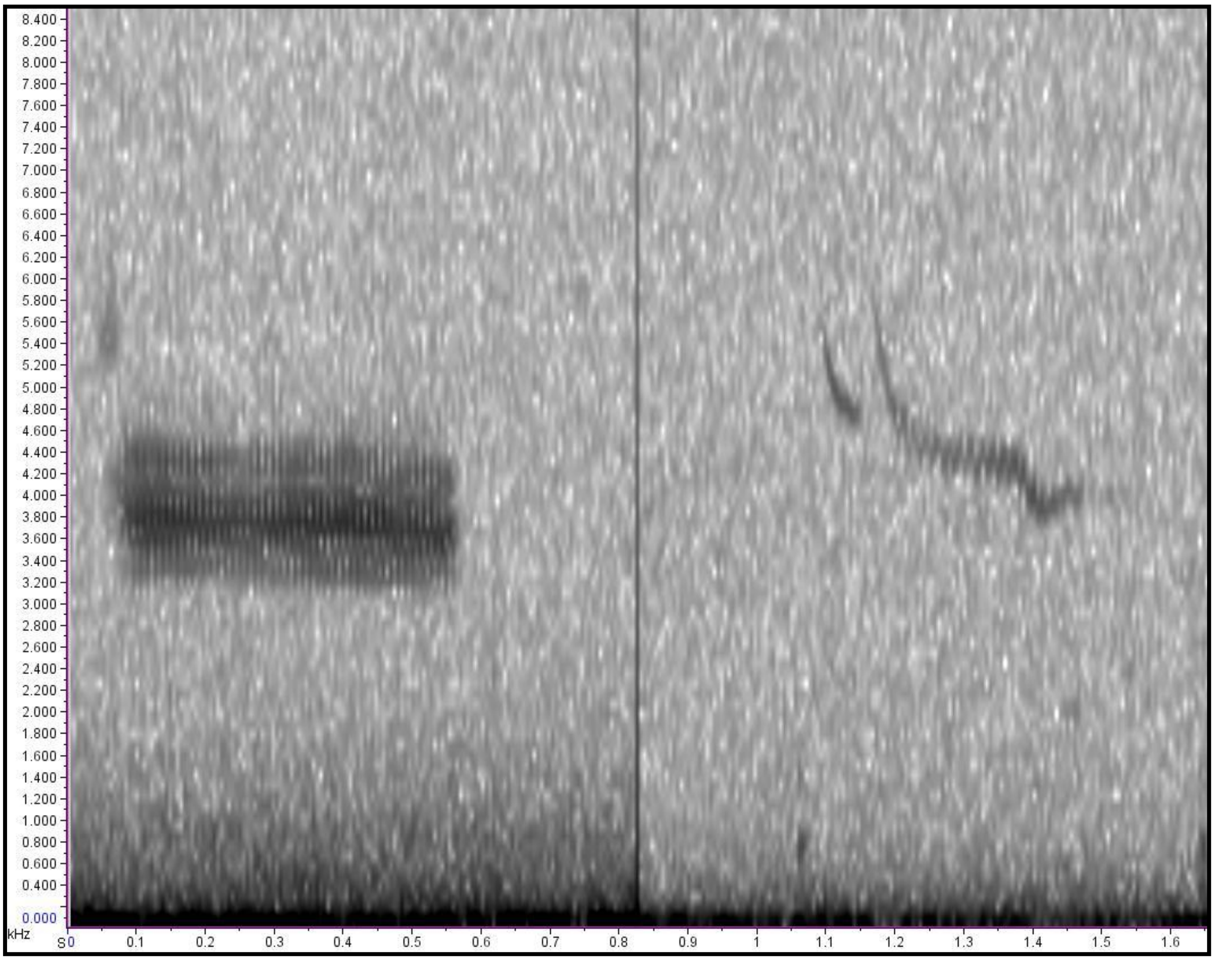

Fig. 3.6. Display flight song of Pink-backed Larks *Spizocorys conirostris* recorded at De Loskop, Limpopo Province, South Africa between April 2010 and April 2012.

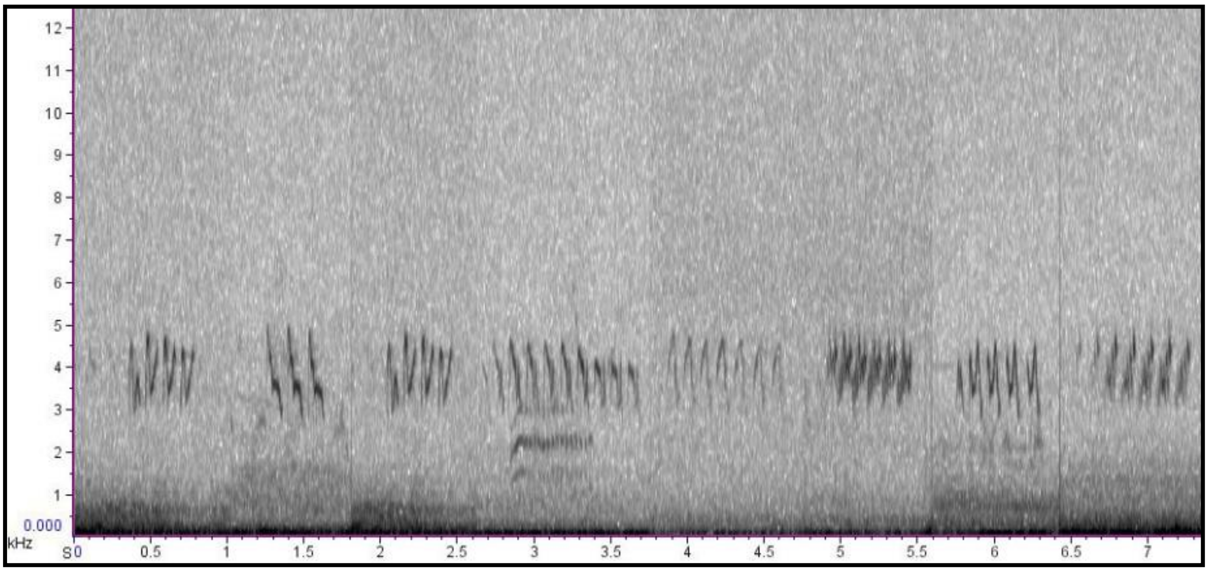

Fig. 3.7. “Signature” flight calls of eight individuals of Pink-backed Larks *Spizocorys conirostris* recorded at De Loskop, Limpopo Province, South Africa between April 2010 and April 2012.

CHAPTER 4

Conclusion

This project represents the first detailed study of the biology and ecology of the Pink-billed Lark. As such it has made a major contribution to our knowledge of this species and the family in general. As the life history strategies of this fascinating passerine family are unravelled through detailed studies such as these, it opens doors for other avenues of research, ultimately contributing to the scientific discipline of ornithology. As more and more species become better known, it is possible to carry out comparative studies on the evolution of various characteristics in the family.

The study has also demonstrated that various on-line databases, e.g. NERCS and SAFRING, represent a mostly untapped source of data which can contribute significantly to our knowledge of birds without the necessity of huge travel and/or equipment expenses. For example, a desktop study of NERCS data revealed possible geographical variation in clutch size and temporal variation in the onset of breeding in different populations of the Pink-billed Lark.

The study highlighted the need for long-term studies of breeding ecology of birds. Long-term studies give a broader perspective into the various factors that can affect breeding success and minimise the effect of stochastic factors on the results of a study. Thus, the longer and more detailed a study is, the more consistent the results of that study will be.

Some of the major and interesting findings of this study are briefly given below. The De Loskop population is resident and can be found all year round at the study site. However, breeding in this population was only recorded from February to May, which was towards the end of the wet season and in the early stages of the dry season. This appears to be intermediate between the grassland and savannah populations as revealed by analyses of NERCS data.

The genera *Spizocorys* and *Eremopterix* (sparrow-larks) are the only African larks known to exhibit biparental incubation. This study confirms biparental care in all aspects of the breeding cycle of the Pink-billed Lark and also showed that parental care is essentially symmetrical, i.e. parental care is shared equally, at least during the middle stages of the nestling period. However, there appears to be sexual differences in the type of food delivered to nestlings.

Breeding success was very low in this study, but is nevertheless similar to the estimate calculated in a population in the Kalahari Desert. There were slight differences between years which highlights the importance of collecting breeding ecology data preferably spanning two or more breeding seasons.

The study revealed cryptic sexual size dimorphism of the flight apparatus which suggests that this may be an adaptive advantage to males during display flights. The results also revealed that females were slightly heavier than the males during the breeding season. This may be related to the physiological changes that females undergo in order to accommodate the production and the laying of eggs.

In the analysis of the timing and pattern of moult, it was revealed that an interesting strategy was employed by the Pink-billed Lark. This strategy appears to deviate from the usual lark pattern. The pre-breeding moult may be an adaptation to avoid loss of insulation capabilities associated with moulting of contour feathers during winter as a result of cessation of the breeding season at or near the onset of winter.

The Pink-billed Lark was shown to possess a rich vocal repertoire and several hitherto new types of vocalizations were reported here for the first time. An interesting finding is the apparent individual distinctiveness of flight calls which may facilitate finding a mate when flying as a flock.

Although some of the results concur with published information on the species, it has also highlighted several anomalies and avenues for future research on the life history of the Pink-billed Lark. A brief description and recommendations follow.

- A more detailed morphometric study of intraspecific geographic variation of the Pink-billed Lark will certainly be an exciting avenue for future research.
- A study aimed at identifying causes of nest failure at different stages of the breeding cycle should be conducted.

- Whether the observed differences in the type of food items delivered to nestlings by males and females reflect individual or sexual preferences would be an interesting avenue for future research.
- A more detailed study of the relative contributions of males and females in different stages of the nesting cycle, e.g. the incubation and nestlings periods, will provide important clues as to the extent of biparental care.
- The interpretations of the moult patterns recorded in the present study is based on a small sample. A study on a larger sample size representing all subspecies would contribute greatly to the understanding of moult patterns.
- Nest entrance direction was briefly touched on in this study. An in-depth study into the significance of the nest entrance direction in relation to breeding behaviour would shed valuable light on the behavioural patterns exhibited by larks during the breeding seasons

In conclusion, the present study has shed valuable information on the breeding biology and ecology of the Pink-billed Lark specifically, but also of larks in general. It made a significant contribution to our growing understanding of the ecology and breeding biology of the family Alaudidae, and to ornithology in general. The results from this study will form an integral part of other intra- and interspecific comparative studies.

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