ASPECTS OF THE BIOLOGY OF THE CHESTNUT-BACKED SPARROW-LARK (*Eremopterix leucotis*) IN THE LIMPOPO PROVINCE, SOUTH AFRICA

By

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DECLARATION

I declare that **ASPECTS OF THE BIOLOGY OF THE CHESTNUT-BACKED SPARROW-LARK (*Eremopterix leucotis*) 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.

Dikgale M.L. (Mr.) **30 November 2012**

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PREFACE

The fieldwork for this study was carried out from January 2009 to December 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 and their characteristics and taxonomy are discussed. The larks of the world are introduced with special emphasis on the sparrow-larks and in particular the chestnut-backed sparrow-lark. Knowledge gaps about the chestnut-backed sparrow-lark are highlighted and the objectives of the study are described in this chapter. Chapter 2 describes various aspects of the breeding biology of the chestnut-backed sparrow-lark including breeding seasonality, clutch sizes, roles of the sexes during the breeding cycle and breeding success, amongst others. Chapter 3 investigates sexual size dimorphism and geographical variation in southern African populations by measuring and comparing selected biometric parameters of males and females from across the species' range in southern Africa. It also provides a brief description of the timing and pattern of moult and the various vocalizations of the chestnut-backed sparrow-lark. The dissertation concludes with a summary of the results of this study and highlights avenues for future research on the species and the family (Chapter 4).

Chapters 2 and 3 are formatted as research papers which can be submitted for publication with minimum editing. 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 figured are arranged at the end of each chapter.

The results of this study have been presented at a local and a national conference and the details are provided below (* presenting author):

i) **Dikgale, M.L.* and Engelbrecht, G.D.** Breeding biology of the Chestnut-backed Sparrow-lark *Eremopterix leucotis* in the Limpopo Province. Paper read at the Post-Graduate Research Day at the University of Limpopo, South Africa, 16 September 2010.

ii) **Dikgale, M.L. and Engelbrecht, G.D.*** Breeding ecology of the Chestnut-backed Sparrow-lark *Eremopterix leucotis* in the Limpopo Province. Paper read at the joint conference of the Zoological Society of southern Africa (ZSSA) and the Parasitological Society of southern Africa (PARSA) at Stellenbosch University, South Africa, 10 to 13 July 2011.

ABSTRACT

Sparrow-larks form a relatively small genus in the family Alaudidae and comprise only seven species distributed widely throughout Africa and parts of the Eurasian landmass. Sparrow-larks are unique amongst larks in that they are sexually dichromatic and exhibit biparental care. The chestnut-backed sparrow-lark *Eremopterix leucotis* is endemic to Africa with five subspecies recognized based on differences in plumage colouration. The five subspecies are distributed throughout the arid to semi-arid savannas of Africa with two subspecies (*E. l. hoeschi* and *E. l. smithi*) occurring in southern Africa. Despite their widespread occurrence and its interest for research on the evolution of characteristics in the family (e.g. being sexually dichromatic and exhibiting biparental care), very little is known of the biology and ecology of the *Eremopterix* larks. The chestnut-backed sparrow-lark is no exception and most of what we know of the species is based on incidental observations from a few nests. In an attempt to improve our knowledge of this interesting group of species, it was decided to study various aspects of the breeding biology and ecology, moult, vocalizations and geographical variation in the chestnut-backed sparrow-lark.

The breeding biology of the chestnut-backed sparrow-lark was studied at AI3 farm (De Loskop) near Mogwadi in the Limpopo Province of South Africa from January 2008 to December 2010. Data collected during the study included: breeding seasonality, egg and clutch characteristics, duration of the incubation and nestling periods, nest-site characteristics, the roles and relative contribution of the sexes in the breeding cycle, nestling development, diet and nestling provisioning rate, and breeding success. Chestnut-backed sparrow-larks bred mostly during the dry season, which is from April to September in the study area. Nevertheless, the results revealed that breeding is bimodal with a main peak in breeding activity in late summer and autumn (March to April) and a second smaller peak in spring (September to October). The species showed geographical variation in clutch size with a mean of 1.88 eggs recorded in the study area as opposed to 1.00 recorded in the northern parts of its range. Egg dimensions compared well with measurements obtained from the Nest Record Card Scheme of the Animal Demography Unit, University of Cape Town, South Africa. The mean incubation period of 10.33 days recorded in this study compares favourably with that of other *Eremopterix* species

(8–10 days), a genus with some of the shortest incubation periods amongst larks. The mean nestling period of 9.2 days (range: 8–10) in the study area was significantly less than the 10–12 days reported for populations in the northern range of the species, but it compares well with those of other sparrow-larks.

Nest site characteristics, which were quantified within a 1 m^2 quadrant with the nest as the centre, including nest dimensions, were consistent with those reported in the literature. Chestnut-backed sparrow-larks in the study area preferred to nest in areas with a high percentage of bare ground (median = 67.5%) and very little vegetation cover (median = 25%). Most nests faced in a southerly direction compared to nests in the north of the species' range, which face in a north-easterly or easterly direction. The species' preference to face the nests away from the midday sun most probably serves a thermoregulatory function to avoid excessive heat during the warmest parts of the day. Most nests (78.2%) had an apron varying in size from small and insignificant to large and well-developed. The functional significance of the apron remains a matter of conjecture and there was no association between breeding success and presence or absence of the apron. In addition, one pair constructed one nest with and another without an apron, suggesting that individual preference or characteristic is not a determinant factor in the construction of an apron. Both sexes took part in nest construction, incubation and feeding and brooding of nestlings. However, the relative contributions were not entirely symmetrical as males incubated a greater proportion (50.1%) of the time compared to females (43.1%), and the mean and median of male incubation shift lengths were longer than that of females, albeit not statistically significant. However, females made statistically significantly ($P < 0.05$) more nest visits to deliver food compared to males (54.6% vs. 45.5%). The average breeding success, estimated using Mayfield's method, was 16.1% but there were inter-annual differences with the overall breeding success in 2010 being only 8.1% compared to 20.6% of 2008. Known causes of failure included nest depredation, flooding, starvation, nest abandonment and hatching failure.

Statistical analysis of morphometric data of live specimens and museum study skins suggest that, in addition to being sexually dichromatic, chestnut-backed sparrow-larks also exhibit mild sexual size dimorphism. However, there was considerable overlap in these measurements between the sexes and as a result the biological significance of this sexual size dimorphism may be negligible. Nevertheless, the

results show chestnut-backed sparrow-lark males tend to have longer wings and tails compared to females. This may be adaptive with respect to the extended display flights that males perform during the breeding season. Interestingly, the mean mass of breeding females in the study area was significantly more compared to males, whereas the SAFRING database, representing data recorded throughout the year, showed no significant differences in the mean mass between the sexes. The greater mass of breeding females may relate to physiological changes associated with the acquisition of resources and the development of structures and tissues associated with egg-laying and egg-production.

Larks rely heavily on vocalizations to attract mates and advertise territories. Not surprisingly, the study revealed a rich vocal repertoire for the chestnut-backed sparrow-lark. The analysis of the vocalizations shows that chestnut-backed sparrow-larks have a display song performed by males, a sub-song sung by both sexes and various different calls used in different contexts, e.g. flight and alarm calls. The study also presents the first analysis and description of the vocalizations of nestlings. An interesting feature of the vocalizations of the chestnut-backed sparrow-larks was that they performed hetero-specific vocal mimicry, which was incorporated in the sub-song.

Moult is a relatively unknown aspect in the annual cycle of the majority of larks. Chestnut-backed sparrow-larks undergo post-breeding moult, which is an adaptation to reduce the conflict between moult and breeding as both activities have high energy demands. The moult study also showed that they undergo a partial moult in mid-winter, involving the inner-most secondaries and some of the contour feathers.

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.

Table of contents

List of tables

List of figures

An adult male chestnut-backed sparrow-lark

(*Eremopterix leucotis*)

CHAPTER 1

General Introduction

Larks (Alaudidae) tend to be dun-coloured, difficult to find and identify, and reach their greatest diversity in some of the harshest and most austere habitats on Earth, and it is therefore hardly surprising that they are the favourites of few people. However, as a family they exhibit adaptive radiation matched by few other bird families and their superficial similarity belies tremendous variation between different species in population, distribution, behaviour, structure and ecology (Donald 2004). Below follows a brief background to the larks of the world.

1.1. Characteristics, diversity, distribution and systematics of the Alaudidae.

The larks (Alaudidae) are a speciose family of small to medium-sized, cryptically plumaged, primarily terrestrial passerines. The family is distinguished by two unique and primitive features, namely i) a latiplantar, scutellate tarsus, i.e. the posterior surface is flat and covered with prominent scales, as opposed to narrow and smooth as in other passerine families, and ii) a relatively simple syrinx, with only five pairs of syringeal muscles, and a rudimentary pessulus. In general, oscines have between six and eight pairs of syringeal muscles and a well-developed, bony pessulus (de Juana *et al.* 2004).

Other alaudid characters traditionally considered, e.g. gait, diet, length of the outermost primary, length of the hind claw and bill shape, are either too variable within the family as a whole to be diagnostic, or are of a comparatively plastic nature, which are all too likely to have produced superficial similarities with other groups as a result of adaptive convergence (de Juana *et al.* 2004).

The larks have traditionally been regarded as one of the more primitive groups within the Passeriformes with no close relatives. However, DNA-DNA hybridization studies conducted by Sibley & Ahlquist (1990) suggest that, despite the presence of 10 primary feathers in larks, they may be taxonomically closer to the nine-primaried songbirds such as Old World sparrows, wagtails, pipits, accentors, American warblers, New World orioles, tanagers, buntings and finches (Ericson & Johansson 2003). As a result of similarities in the bill structure of these groups, they form a natural grouping known as the superfamily Passeroidea. This view has recently been challenged by Barker *et al.* (2002) who, using conserved nuclear genes, suggested that larks belong within another superfamily, the Sylvioidae. According to Barker *et al.* (2002), the larks' closest living relatives are the largely African family of cisticolid warblers, another group of dun-coloured birds of open environments.

Around 100 species of lark are currently recognized; the exact number depending on whether certain forms are considered as single species or groups of closely related species. Recent studies suggest that several forms that were previously recognized as subspecies should be treated as full species; hence there has been a gradual increase in the number of recognized species in the last two decades (Donald 2004). In this dissertation, the classification system of de Juana *et al.* (2004), who recognize 96 species in 21 genera, is used. Of the 21 genera in the family, all are represented in Africa, Eurasia has 13 and Australasia and the New World support a single genus each.

Pätzold (1994) rightly described Africa as the "lark continent": 78 lark species, over 80%, occur in Africa, with 60 species endemic to the continent. In contrast, Eurasia only boasts 36 species of which 17 are endemic, and the entire New World has only one species, the horned lark (*Eremophila alpestris*), which is also the world's most widespread lark and the only lark to occupy the boreal latitudes. This species' distribution includes North America and the Andean Altiplano in Colombia, Europe and North Africa (de Juana *et al.* 2004). The only other species occurring outside the African-Eurasian distribution are the Australasian bushlark (*Mirafra javanica*) and the Madagascar lark (*Mirafra hova*). The former extends from south-east Asia and the Philippines through Indonesia and New Guinea to Australia, whereas the latter is endemic to Madagascar.

Larks are also well represented on islands that are either close to continents or were previously joined to continents. Islands are colonized by migratory species such as the greater short-toed lark (*Calandrella brachydactyla*) and Thekla lark (*Galerida theklae*), which breed in the Balearic Islands; the greater hoopoe-lark (*Alaemon alaudipes*), bar-tailed lark (*Ammomanes cincture*), black-crowned sparrow-lark (*Eremopterix nigriceps*) and Raso lark (*Alauda razae*), which breed in the Cape Verde Archipelago; and the Eurasian skylark (*Alauda arvensis*), which inhabits the Faroe Islands (Donald 2004).

Lark species richness reaches its pinnacle in the semi-arid and arid regions of the Old World. However, their distribution is not uniform and according to Barnes (2007), five centres of endemism are recognized: i) the Saharo-Sindian region which includes the Sahara and south-west Asia where larks comprise roughly 20% of the avifauna in this region, ii) the Caspian-Mongolian region which holds at least 15 species with seven of them being endemic to this region, iii) the Oriental region contains 23 species, of which ten are endemic to this region, iv) the north-east arid zone of Africa (Kenya, Ethiopia and Somalia), which supports 37 species of which 62% are endemic, and v) the south-west arid zone of Africa (South Africa, Namibia and Botswana) which holds no fewer than 33 species, of which 85% are endemic or near-endemic to this region (White 1961; Moreau 1966; Dean & Hockey 1989; Barnes 2007).

From the above, it is evident that the two arid zone regions of Africa are the two major centres of alaudid endemism. These two regions hold a combined total of 65 species, approximately 83% of the African total and 68% of the larks in the world. The proportions of endemics in these two arid zones are, relative to the area of occurrence, the highest of any bird family in Africa (Dean & Hockey 1989).

Though currently geographically isolated, the two arid zones may previously have been linked by a passage through present day Kenya, Tanzania, Zambia, and Zimbabwe and such a link can be proved by the occurrence of chestnut-backed sparrow-larks (*Eremopterix leucotis*), which span the two centres of lark endemism in Africa. The existence of such a passage can also be confirmed by species such as chestnut-headed sparrow-lark (*Eremopterix signatus*) and Archer's lark (*Heteromirafra archeri*), of the north-eastern zone forming pairs with grey-backed sparrow-lark (*Eremopterix verticalis*) and Rudd's lark (*Heteromirafra ruddi*) of the south-western arid zone, respectively. These species pairs are geographically isolated yet closely related.

Larks are found living in a wide variety of habitats ranging from deserts, to woodlands and high altitude mountainous areas. The only habitat not occupied by larks is essentially closed-canopy forests. The majority of larks inhabit arid and semi-arid areas such as deserts, steppes and savanna habitats receiving between 40mm and 800mm rainfall per annum (Dean & Hockey 1989; Dean & Williams 2004). Within these habitats, they prefer open, structurally simple environments with low vegetation, scattered trees and a large amount of bare ground. These habitats allow larks to forage on foot in search of prey and seeds (de Juana *et al.* 2004). They tolerate climatic conditions ranging from extreme deserts (e.g. greater hoopoe-lark) to very cold conditions (e.g. horned lark). Some species are habitat specialists with very small distribution ranges, e.g. Rudd's lark, Botha's lark (*Spizocorys fringillaris*) and Beesley's lark (*Chersomanes beesleyi*), whereas others exhibit a wide habitat tolerance with exceptionally large distribution ranges, e.g. rufous-naped lark (*Mirafra africana*), chestnut-backed sparrow-lark and flappet lark (*Mirafra rufocinnamomea*).

A recent phylogenetic study by Barnes (2007) revealed that the Alaudidae can be grouped into the following three major clades:

i) Ammomanid larks

This is a group of mainly resident, insectivorous, desert larks although the facultatively nomadic, mainly granivorous and sexually dichromatic *Eremopterix* larks are also included in this clade. They construct open, cup-shaped nests on the ground. Vocal mimicry is unrecorded in ammomanid larks. These larks are restricted to the African and Saharo-Sindian regions. The group includes the genera *Ammomanopsis, Chersomanes, Certhilauda, Alaemon, Ramphocoris, Ammomanes* and *Eremopterix*.

ii) Mirafrid larks

This group includes primarily resident, insectivorous, mostly Afrotropical larks. They construct mainly domed nests and vocal mimicry is well-developed in this group. It includes the genera *Mirafra, Heteromirafra, Corypha, Megalophoneus* and *Calendulauda.*

iii) Alaudid larks

This group's distribution is widespread and comprises Afrotropical, Saharo-Sindian, western Palaearctic and Caspian radiations. These larks are the most adaptable and show a high degree of plasticity in most traits, e.g. they occupy many different habitats, are dietary generalists, are either resident or more frequently facultative nomads or migrants, and construct nests of varying shapes and utilise different display modes when breeding. This clade includes the genera *Alauda, Galerida, Lullula, Spizocorys, Calandrella, Eremophila, Melanocorypha, Eremalauda* and *Alaudula* (Barnes 2007).

Despite having been at the centre of many historic taxonomic debates using traditional morphological characters, recent taxonomic studies combining genetic, behavioural and morphological characters, have revealed considerable and unpredicted diversity and variation in the family (Ryan & Bloomer 1997; Ryan *et al.* 1998; Ryan & Bloomer 1999; Barnes 2007). Despite being some of the best adapted and most numerous birds in some arid and semi-arid regions, the family as a whole remains poorly known (*cf.* de Juana *et al.* 2004). Several species are extremely well studied, e.g. the skylark (*Alauda arvensis*) and the crested lark (*Galerida cristata*) in the Palaearctic region (Donald 2004), but with the exception of a few species, the majority of Afrotropical and Asian species are almost entirely unknown. The nests of some species have never been described and there is a lack of basic biometric data for many species. This leads to difficulties in taxonomic classification and has confounded our understanding of the evolution of biological traits within the family (Barnes 2007).

Several authors have attempted to summarise the biology and ecology of larks (Maclean 1970a, Maclean 1970b; Willoughby 1971; Watkeys 1986; Dean & Hockey 1989; Hunter 1990; Hunter 1991; Tieleman *et al.* 2003c; Tieleman *et al.* 2003a; Dean & Williams 2004). However, most of these studies focussed on several species within a particular biome or region, covered only a specific discipline, e.g. physiology, or are based on studies representing a single breeding event or breeding season. There have been few, detailed studies of individual species spanning more than a single breeding season on the breeding biology and ecology of African larks, hence most of our knowledge of larks is based on incidental observations. Nevertheless, below follows a general discussion of various aspects of the biology and ecology of larks.

1.2. The biology and ecology of larks

1.2.1. Structure

In general, larks are relatively robust, small to medium-sized passerines with moderately long legs and relatively large wings. They range in size from the diminutive *Eremopterix* and *Spizocorys* larks weighing as little as 12 g to more than 75 g in Tibetan larks (*Melanocorypha maxima*).

Larks are generally cryptically coloured with brown and fawn being the dominating colours. These colour combinations are undoubtedly adaptations for a terrestrial life in open terrain. Larks are generally darker above and paler or almost white below. Black and white marks are also a common feature in most larks, occurring on the head, as in thick-billed lark (*Ramphocoris clotbey*) and masked lark (*Spizocorys personata*), or between the neck and breast, as in calandra lark (*Melanocorypha calandra*) and collared lark (*Mirafra collaris*). Larks are adapted to their habitat by having different plumage patterns which allows them to reduce or avoid predation. According to Maclean (1970b), two types of plumage patterns can be identified, namely a generalized and specialized pattern. The generalized pattern is more common than the specialized pattern, and is characterized by a mixture of colours with streak- or spot-shaped markings on a buff background. It is more common in migratory and nomadic species and provides camouflage in most terrains, as compared to the specialized pattern, which is common in more sedentary species and is only effective in matching terrains. The specialized pattern is characterized by a close colour match with the inhabited terrain, which results in southern African larks being divided into reddish species in the red sand dunes of the Kalahari region and greyish species in the grey limestone regions (Maclean 1970b).

There seems to be a correlation between leg length and diet: insectivorous species tend to have longer and stronger legs to chase after prey, while granivorous species that feed on small stationary food items have shorter tarsi (de Juana *et al.* 2004). Recently fledged larks are unable to fly or run, instead moving around by hopping during the first few days after leaving the nest. The toes and front claws are relatively short, whereas the length of the hind-claw shows a great deal of variation in different species. It is rather long, either straight or arched in some species, and short, straight and narrow in others (Donald 2004). According to de Juana *et al.* (2004), there appears to be a relationship between the length of the hind-claw and the extent to which a species runs, i.e. the hind-claw is shorter and stronger in those species that run a lot. On the other hand, Donald (2004) suggests that hind claws are longer in more cursorial species and shorter in species that habitually perch in trees or bushes, a pattern also found in pipits. Larks generally either walk or run and some species prefer to outrun danger rather than to take flight, e.g. the greater hoopoe-lark and Du Pont's lark (*Chersophilus duponti*). The thick-billed lark is unusual as it frequently employs hopping as a means of moving about (Donald 2004). Furthermore, hopping features in the courtship displays of many lark species.

Larks have ten primaries, although the length of the outermost primary is extremely variable amongst species, ranging from almost as long as the adjacent primary (e.g. *Ammomanes* and *Alaemon*) to practically vestigial (e.g. *Melanocorypha* and *Calandrella*). The difference may relate to different migratory habits: a long outermost primary is associated with short, rounded wings, typical of sedentary species, and a short outermost primary leads to a long and pointed wing with a high wing loading that is more suitable for fast, prolonged migratory flight (Donald 2004).

Larks, as well as other primarily cursorial species such as pipits, long-claws and wagtails, have strikingly large innermost secondaries. These secondaries cover all of the primaries when the wing is folded, or they allow at most only the tips of some primaries to be exposed (de Juana *et al.* 2004). These secondaries may fulfil a protective function by serving as a “cloak” for the underlying primaries. Larks live in open, exposed habitats and it is likely that abrasion by e.g. vegetation or wind-blown sand, and UV damage may be high, hence the enlarged secondaries for protection of the remiges.

One of the most striking features of larks is their generally cryptic appearance. This is an adaptation to the open habitats they prefer to inhabit. However, there is sometimes considerable intraspecific variation in the colour of the plumage, e.g. birds in desert environments tend to be paler in colour than birds inhabiting more mesic areas. Furthermore, the amount of dorsal streaking also appears to show a correlation with the extent of plant cover: the darkest and most heavily streaked forms inhabit the most densely vegetated habitats, and those forms with the least streaking inhabit sparsely vegetated habitats (Donald 2004). These intraspecific differences are more pronounced in sedentary species whereas nomadic or migratory species tend to show a more generalized plumage colouration with little regional or even intraspecific variation.

The plumages of larks often include areas of contrasting colouration, e.g. black, white, rufous or yellow. These areas are rarely visible when the bird forages and only becomes visible once the bird displays or is in flight. These markings serve a variety of functions, including inter- and intraspecific communication and as an indicator of individual fitness (de Juana *et al.* 2004). It has been suggested that the sexually dichromatic *Eremopterix* larks have evolved different plumages as these nomadic species exploit transient habitats and the different colours of the sexes facilitate rapid recognition of sexes (Barnes 2007). Despite the relatively bright colouration of male *Eremopterix* larks, the plumage colouration patterns provide disruptive camouflage by breaking up the bird's silhouette.

Juvenile larks tend to have a different plumage compared to adults. It tends to be mottled and usually lacks any contrasting marks. This juvenile plumage is short-lived and the juvenile undergoes a complete post-juvenile moult after 3–7 weeks (Donald 2004). Adults have annually a single, complete post-breeding moult although there are some deviations from this general pattern. For example, some desert larks whose feathers are exposed to rapid wear as a result of wind, sand and radiation, undergo two annual moults (Willoughby 1971).

The most striking variation in the structure of larks is arguably in the shape of the bill (Donald 2004). In this regard, it matches the adaptive radiation undergone by groups such as the vangas (Vangidae) of Madagascar, "Darwin's finches" (Geospizinae) of the Galapagos Islands and the

Hawaiian honeycreepers (Drepanididae). This variation is not only interspecific, but can be observed in different subspecies of some species, and even between the sexes. The variation in the bill structure has allowed larks to colonise and diversify in habitats with limited food resources and in some of the harshest habitats on Earth. The high diversity in the size and shape of the bill reflects a wide array of foraging techniques and diets, and there exists a close relationship between these parameters (Donald 2004). The long, slender-billed groups, e.g. *Certhilauda* and *Chersomanes*, tend to be insectivorous and often use their bills to dig for food items below the surface (Donald 2004; G.D. Engelbrecht, pers. comm.). Species with short, conical bills, e.g. *Mirafra* and *Calendulauda*, usually consume a wide variety of food items, including seeds, vegetable matter and invertebrates. Primarily granivorous species, e.g. *Spizocorys* and *Eremopterix*, are characterised by short, deep bills. It is generally accepted that intersexual differences in bill length are related to the sexes exploiting different ecological niches, thereby avoiding interspecific competition (Willoughby 1971; Dean & Hockey 1989; de Juana *et al.* 2004; Donald *et al.* 2007).

Larks show an interesting range of sexual dimorphism. The majority of Alaudids exhibit considerable sexual dimorphism with males averaging 20–25% larger compared to females for selected biometric parameters such as mass, wing length and length of the bill (de Juana *et al.* 2004). Sexual size dimorphism is most pronounced in the resident, insectivorous ammomanid larks. The genera *Eremopterix* and *Melanocorypha* are unique in the family as these are the only larks that exhibit sexual dichromatism.

1.2.2. Diet

The diet of larks is variable and ranges from almost exclusively granivorous to completely insectivorous. Most larks are, however, omnivorous to a degree and their diet includes invertebrates, seeds and vegetable matter to a greater or lesser degree, which may relate to seasonal availability of certain food items in some instances. For example, some species will preferentially feed on invertebrates during the breeding season in spring or summer and feed on seeds during winter (Cramp 1988, Keith *et al.* 1992). The type of food consumed is in part dependent on the seasons and water dependency of individuals (de Juana *et al.* 2004). Larks also consume grit to aid with the digestion of food. Insectivorous species can fulfil all their water requirements from their diet and by metabolic oxidation of their food, but granivorous species usually have to drink surface water or obtain water from some other source, e.g. the green parts of plants (de Juana *et al.* 2004).

Insectivorous larks feed on such invertebrates as arthropods, termites, ants, beetles, grasshoppers, and spiders. Omnivorous species such as the rufous-naped lark, Karoo lark (*Calendulauda albescens*), dusky lark (*Pinarocorys nigricans*), Gray's lark (*Ammomanopsis grayi*), desert lark (*Ammomanes deserti*), red-capped lark (*Calandrella cinerea*) and crested larks are known to inspect herbivore dung as it contains large quantities of undigested seeds and larvae and adults of coprophagous beetles. Some larks (e.g. greater hoopoe-lark and Raso lark) dig for their food, sometimes to a depth of 60mm (Meinertzhagen 1951; Donald 2004; G.D. Engelbrecht, pers. comm.).

Granivorous species feed mainly on seeds from grasses, shrubs, weeds or cultivated plants, and the seeds may range in size from very tiny seeds to cereal grains (Donald 2004). Larks swallow the seeds whole as they lack the tooth and notch in the upper mandible characteristic of typical seed-eaters such as buntings and finches to extract the kernel from the husk (Donald 2004). Black larks (*Melanocorypha yeltoniensis*) digs tunnels, often with side branches, of up to 20 cm deep in the snow in order to reach seeds (de Juana *et al.* 2004).

As mentioned above, the sexual size dimorphism with regard to bill length exhibited by some larks, e.g. the spike-heeled lark (*Chersomanes albofasciata*) and Raso lark, apparently relates to different sexes exploiting different ecological niches, thereby avoiding competition for the same food resources in areas with limited resources. Male spike-heeled larks feed mainly on beetles while females feed on termites and ants (Willoughby 1971). In Raso larks, males are more granivorous while the females are more insectivorous (Donald *et al.* 2003).

1.2.3. General habits

Larks are typically gregarious and form loose flocks, sometimes numbering several hundred or thousand individuals when on passage or outside the breeding season (de Juana *et al.* 2004). Some species, e.g. the spike-heeled lark, are cooperative breeders and are always found in small groups, while other species never form flocks, occupy year-round territories and are usually only seen as individuals or in pairs, e.g. Friedmann's lark (*Mirafra pulpa*), pink-breasted lark (*Calendulauda poecilosterna*), sabota lark (*Calendulauda sabota*), short-clawed lark (*Certhilauda chuana*) and large-billed lark (*Galerida magnirostris*). Granivorous species are usually nomadic and occur in flocks. The size of a flock is dependent on food availability and they tend to aggregate in areas with abundant seeds. Flocks may include various species of larks as well as species from other families. For example, nomadic black-eared sparrow-larks (*Eremopterix australis*), grey-backed sparrow-larks and Stark's lark (*Spizocorys starkii*) can occur in mixed flocks when conditions are suitable, sometimes joined by other nomadic species such as lark-like buntings (*Emberiza impetuani*) (Dean 2004). During the breeding season, larks are territorial although the size of territories may vary from several hectares in resident insectivorous species, e.g. the short-clawed lark (Engelbrecht 2005) to an area of only a few metres in the immediate vicinity of the nest in the more gregarious species.

Larks exhibit the full range of movement strategies, including long-distance migration, nomadism and residency, in search of food, water or suitable breeding grounds. The type of movements is partially influenced by the nature of the diet and the sociability of a species, e.g. gregarious granivorous larks tend to be more nomadic than resident, solitary insectivorous species. Africa has a preponderance of nomadic larks when compared with Eurasia, which has more migratory species, and this is related to the availability of food (de Juana *et al.* 2004). Migratory species undertake predictable seasonal movements associated with changes in the availability of food or to breed, and this is more predictable in the Eurasian steppes than in the arid and semi-arid regions of Africa where rainfall is patchy and erratic (Dean 2004). For example, the dusky lark is the only Afrotropical lark known to be migratory. It breeds in Central Africa during the dry season and then migrates to the southern and eastern parts of Africa during the wet season (Dean 2005a). Other species such as the monotonous lark (*Mirafra passerina*) and Sclater's lark (*Spizocorys sclateri*) are nomadic and their occurrence in a given area is unpredictable. They may appear in large numbers in suitable habitat in certain areas in some years and then be absent from that area for several years.

The habitats occupied by larks are often rather harsh, but the family shows some remarkable physiological and behavioural adaptations to survive. Desert living larks have been shown to have a lower metabolic rate, a lower rate of evaporative water loss and a greater ability to resorb water from urine and faeces than species living in non-arid areas (Klaassen & Drent 1991; Tieleman *et al*. 2004). Behavioural adaptations to survive in harsh habitats include foraging, singing and displaying during the cooler parts of the day and resting or performing self-maintenance activities such as preening during the heat of the day, perching on raised objects such as rocks or bushes to escape radiated heat from the ground, resting in rodent or lizard burrows, panting, raising or lowering of feathers, etc. (Tieleman *et al.* 2004).

Larks regularly perform dust-bathing and sunning, and not surprisingly for a group adapted to arid environments, there are no records of free-living larks bathing in water (Donald 2004). Larks are one of relatively few groups that regularly include ants in their diet, and it is therefore not surprising that anting as a means of feather maintenance has never been observed in larks (Donald 2004).

Despite all the aforementioned adaptations, severe and prolonged droughts do affect the survival of even the most arid-adapted larks (Safriel 1990; Donald *et al.* 2003). As aridity increases, nestling growth rates, clutch sizes, the number of clutches laid and nest survival rates all decline (Tieleman *et al.* 2002).

1.2.4. Singing and display

In contrast to their rather drab appearance, the exuberant songs and extravagant display flights of most larks has earned them a prominent place in literature and music (Perrins 2003). The possession of a dull plumage for camouflage, as necessitated by the general adaptation to living in open, exposed environments with little cover, as well as to nesting on the ground, may have resulted in larks investing more in song and display flights as a means of advertising individual quality amongst males (Pätzold 1994; Donald 2004).

Lark display flights can take different forms, ranging from a barely discernible, low-level, butterfly-like hovering of the spike-heeled lark, to a simple, steep hyperbolic ascent and descent characteristic of *Certhilauda* larks, to the high, sustained, singing display flights of many *Mirafra* and *Alauda* larks. The ammomanid larks primarily undertake aerial displays involving steep ascents and descents and whistling calls, although they do have a limited vocal repertoire to reinforce aerial displays. The *Eremopterix* larks are the only ammomanid larks with extended aerial displays involving a butterfly-like flight (Keith *et al.* 1992). The alaudid larks use prolonged aerial displays almost exclusively, but a few use brief aerial displays and two S*pizocorys* species use ground-based displays (Barnes 2007). Mirafrid larks principally use one of two forms of display. In the first form, used by most members and particularly those of the genus *Calendulauda*, it involves extended bouts of aerial displays involving simultaneous cruising and singing. Flights are generally performed as a circular display flight, with variation in wing-flapping frequencies producing alternative bouts of circling and hanging in the sky (Barnes 2007). In the second form, species use either perch-based, e.g. the brief wing-fluttering display of the rufous-naped lark*,* or short aerial displays, typically using mechanical wing vibrations to produce a clapping or flapping sound during display, e.g. flappet lark, Cape clapper lark (*Mirafra apiata*) and eastern clapper lark (*Mirafra fasciolata*). In the aforementioned species, mechanical sound production is so well developed that it has largely replaced vocalizations. In the flappet lark, the wing flaps are produced at a frequency double that of normal flight, indicating that the displaying males incur a very high energy cost. This suggests that wing flapping displays are honest indicators of the relative quality of individual males (Ryan & Marshall 2005).

Despite the tremendous energetic costs incurred, larks generally sing in flight. All of the Palearctic and the great majority of African and Asian larks have song flights, although they may be lacking in some species such as *Spizocorys* and some members of the genus *Mirafra* (de Juana *et al.* 2004)*.* Although larks seem to possess an almost endless vocal repertoire, sonogram analyses have shown that their range of vocalizations is relatively limited, but the individual phrases are combined in an enormous variety of ways with little repetition (Donald 2004).

Larks also incorporate imitations of the calls of other birds, and sometimes other sounds, in their repertoire, a feat shared with several other bird families. Vocal mimicry has never been recorded in any member of the ammomanid clade, and although both the alaudid and mirafrid clade have representatives that employ mimicry, it is best developed in the genera *Melanocorypha* and *Calandrella* and some members of the genera *Calendulauda*, e.g. sabota lark and *Mirafra*, e.g. melodious lark (*Mirafra cheniana*) (Barnes 2007)*.*

Finally, apart from the usual territorial and advertising calls of males, larks also have a number of other vocalizations including alarm, threat, feeding and contact calls (de Juana *et al.* 2004).

1.2.5. Breeding

Apart from a few exceptions, the breeding biology of larks can be summarised as follows: i) they are monogamous and territorial, ii) they breed as isolated pairs or in loose colonies, iii) they nest on the ground, iv) nest construction is performed by the female, v) clutch size varies considerably, vi) eggs are incubated by the female only, vii) growth and development is rapid, viii) young are fed by both parents, ix) nest survival is low, and x) the post-fledging dependence period is relatively long (de Juana *et al.* 2004).

The traditional notion is that larks are monogamous, but several recent reports suggest that extra-pair paternity may occur extensively in the family (Donald 2004; Sánchez *et al.* 2004; Hutchinson & Griffith 2008). Apart from extra-pair copulations and polygyny, some species e.g. the spike-heeled lark (Steyn 1988; Tarboton 2001) and Gray's lark (Boix-Hinzen & Boorman 2003; Demasius 2003) occasionally breed co-operatively with "helpers" having been observed feeding chicks.

Larks breed either seasonally or, particularly amongst nomadic species, opportunistically after irregular rain have fallen in semi-arid and arid regions. Breeding in larks is triggered by different environmental conditions for different habitats. In general, larks breed during the wet season or after irregular rains in arid areas when primary production is greatest and invertebrates are more abundant. The dune lark (*Calendulauda erythrochlamys*), is unusual as it has a fixed breeding season that is independent of rain (Boyer 1988). Nomadic and granivorous species such as Stark's lark and grey-backed sparrow-lark move around to areas which have received rain as their breeding is closely coupled to rainfall. For these species, there is a close relationship between the length of the breeding season and the total amount of rainfall (Maclean 1970a). Temperature also influences breeding as it determines the rate at which vegetation develops and as a result affects the length of the breeding period (Lloyd 1999). For example, the south-western Cape in Africa receives winter rain but larks in this region usually start breeding in spring and early summer when temperatures are more amenable to breeding. On the other hand, high temperatures may curtail the season and may lead to a high rate of nest abandonment (Dean 2004).

With the exception of the greater hoopoe-lark, which habitually nests off the ground in small shrubs, larks nest on the ground. Nest construction is usually done by the female, but in a few genera, e.g. *Eremopterix* and *Spizocorys*, both sexes are involved. Nests are either one of two types, namely open, cup-shaped nests usually at the base of vegetation, or domed nests. Ammomanid and alaudid larks all construct open, cup-shaped nests whereas mirafrid larks construct domed nests. However, there are a few exceptions to this general rule in all clades, particularly within the alaudid clade (Barnes 2007).

Many larks construct a rampart or an apron comprised of stones, vegetation or other material around the nest. The function of these ramparts remains obscure but suggestions as to its function include a thermoregulatory function, protection from wind-blown sand and camouflage by disturbing the outline of the nest (Orr 1970; Afik *et al.* 1991; With & Webb 1993). Many species of lark also site their nests so that the entrance direction faces away from the midday sun (de Juana *et al.* 2004). In the southern hemisphere, the nests of some species face in a southern or easterly direction and in the northern hemisphere in a northern and easterly direction (Maclean 1970a; Yanes *et al.* 1997). The siting of nests to exploit certain environmental conditions, e.g. shade or heat, is by no means universal amongst larks and some species orientate their nests entrances randomly (de Juana *et al.* 2004; Engelbrecht 2005).

Clutch sizes are highly variable in larks and range from an obligate one egg per clutch in Sclater's lark to 6–8 eggs in calandra and black larks, but it is generally between two and four eggs (de Juana *et al.* 2004). The number of eggs laid per clutch is also variable within species depending on their habitat and prevailing climatic conditions (Keith *et al.* 1992; Lloyd

1999; Lloyd 2004). In general there appears to be a correlation between increasing aridity and a reduction in clutch size and *vice versa* (Serle *et al*. 1977; Cannings & Threlfall 1981; Morel & Morel 1984). Many species also exhibit intraseasonal variation in clutch size with clutch size being largest at the peak of the breeding season and smallest at the onset and end of the breeding season (de Juana *et al.* 2004; Engelbrecht 2005).

Incubation is usually performed by the female alone, but once again the *Eremopterix* and *Spizocorys* larks are unusual as both sexes share incubation duties. Dual incubation has also been reported for the Australasian bushlark, Malabar lark (*Galerida malabarica*), Sykes's lark (*Galerida deva*), the Oriental skylark (*Alauda gulgula*) and the Spike-heeled Lark (Pätzold 1994; de Juana *et al.* 2004; D.J. van Niekerk, pers. comm.). In some species, males will deliver food to the incubating female, but this is generally rare. In some species, e.g. the pink-billed lark (*Spizocorys conirostris*) and the black-crowned sparrow-lark, incubations starts with the first egg laid but usually it starts with the laying of the penultimate egg in a clutch or upon completion of the clutch. The incubation period is generally short (11–13 days) and ranges from as little as eight days in some species, e.g. black-eared sparrow-lark (Lloyd 1998) to 16 days in others, e.g. short-clawed lark (Engelbrecht 2005).

Lark nestlings are altricial and covered in down, which aids in their camouflage. Both sexes contribute food to nestlings and, as can be expected from a ground-nesting bird, lark nestlings grow very rapidly. Nestlings of nearly all species are able to leave the nest at 6–8 days of age although the norm is 11–13 days. However, they are not able to fly upon fledging and they tend to hide amongst the vegetation for a few days to weeks. The post-fledging dependence period is relatively long and lasts 4–7 weeks for most species.

Larks suffer heavy nest losses with as many as 80–90% of nests lost to predation, flooding and trampling in some species. Estimates of breeding success of various southern African larks range from 15% for the pink-billed lark (Maclean 1970a), 30% for fawn-coloured lark (*Mirafra africanoides*) (Maclean 1970a) and spike-heeled lark (Dean & Keith 1992a), 38% for dune lark (Boyer 1988), 50% for rufous-naped lark (Dean & Keith 1992b) and Gray's lark (Dean & Keith 1992c), 53% for Botha's lark (Allan *et al.* 1983), to 61% for red-capped lark (Winterbottom & Wilson 1959). Given their generally poor breeding success, it is not surprising that replacement broods, i.e. initiation of a new clutch after nest failure, and repeat broods, i.e. initiation of a new clutch after successful fledging of a previous brood, are common amongst larks. The short-clawed lark is known to have as many as five replacement and three repeat broods in a single season (Engelbrecht 2005). Most larks are at least double-brooded, but in recent years there have been an increasing number of records of some species being multi-brooded, e.g. short-clawed lark, Eurasian skylark and Thekla lark (Donald 2004; Engelbrecht 2005). Once again there are exceptions to this and the greater hoopoe-lark is only single brooded (Pätzold 1994). It is difficult to determine if nomadic species are double- or multi-brooded as they do not have a fixed breeding season or site but breed opportunistically in response to rainfall.

From the above, it is evident that despite their superficial similarity, larks exhibit a great deal of variation with regard to many aspects of their natural history. This renders them ideal for studies on their physiological and behavioural adaptations and for comparative studies on the evolution of traits in the family. Despite their suitably for the aforementioned, the majority of larks are poorly known with the nests of some species having never been recorded. Thus, there is a clear need for detailed, scientifically sound research on the biology and ecology of larks, which can serve as a basis for future comparative studies of representatives in the family.

1.3. The sparrow-larks, genus *Eremopterix*

The genus *Eremopterix* is comprised of seven species of relatively small, gregarious, sexually dichromatic larks commonly known as sparrow-larks or finch-larks. The name *Eremopterix* means “desert bird” and is derived from the Greek words “*érimos”* meaning desert and “*ptéryx*” meaning feather or wing. They inhabit open grassland habitats, savannas, shrub-lands and sparsely vegetated desert plains (Keith *et al.* 1992). Sparrow-larks exhibit a range of movement patterns that include resident, nomadic and migratory species (Donald 2004). It is not uncommon for some species to have nomadic, resident and migratory populations in different parts of their range, e.g. chestnut-backed sparrow-lark, black-crowned sparrow-lark, Fischer’s sparrow-lark (*Eremopterix leucopareia*) and perhaps black-eared sparrow-lark (Ryan *et al.* 2004).

Sparrow-larks reach their highest diversity in Africa with five of the seven species being endemic to the continent. The five species endemic to Africa are the chestnut-headed sparrow-lark, Fischer's sparrow-lark, black-eared sparrow-lark, grey-backed sparrow-lark, and chestnut-backed sparrow-lark. The black-crowned sparrow-lark’s distribution range includes the Sahel-Horn of Africa region and the Middle East, as far east as Pakistan and north-west India. The ashy-crowned sparrow-lark (*Eremopterix griseus*) is essentially endemic to the Indian sub-continent. A summary of the distribution and habitat preference of the seven species is presented in Table 1.1.

Sparrow-larks are unusual amongst larks in a number of respects, e.g. exhibiting sexual dichromatism and biparental incubation, the incorporation of spider-web in the nests in some species and their extended display flights. They are the only distinctly sexually dichromatic larks, i.e. the sexes differ in plumage colouration, in the family. Some species in the genera *Ramphocoris*, *Eremophilia, Melanocorypha* and *Pinacorys* exhibit mild sexual dichromatism (Keith *et al.* 1992). Male sparrow-larks are strikingly marked on the head and body in variations of black, white, brown/chestnut and grey, whereas females are rather plain, resembling sparrows. With the exception of the rather unusual looking, and aptly named, black-eared sparrow-lark, males of the other six species have characteristic white ear patches and neck collars.

Sexual dichromatism is believed to arise from sexual selection favouring bright and more visible colours in males and darker and less visible colours in females (Martin & Badyaev 1996). Males that are larger in size or brightly coloured gain more mates through sexual selection when there is male-male competition for females who select mates on the basis of size or colouration (Dunn *et al.* 2001). Brightly coloured individuals are thought to be more at risk of predation and as a result natural selection limits their conspicuousness (Martin & Badyaev 1996). Females are usually more cryptically coloured than males whose colours are variable, and this helps in camouflaging females while they are incubating (Irwin 1994). In some species, e.g. sparrow-larks, where incubation duties are shared amongst the sexes, plumage colouration is of such a nature that it also aids in camouflage by causing disruptive camouflage. Sexual dichromatism is also more common in omnivorous and granivorous species such as sparrow-larks which are nomadic or migratory (de Juana *et al.* 2004). Sparrow-larks breed opportunistically in transient habitats where abundant resources are temporarily available. This requires rapid mate selection and breeding while conditions are optimal. Sexually dichromatic plumage may provide females with cues to rapidly assess mate quality and initiate breeding (Barnes 2007). The risk of being strikingly plumaged, especially when breeding, may be offset by sparrow-larks' habit of breeding in loose colonies (Lloyd 1999).

Secondary sex traits such as sexual dichromatism, believed to be products of sexual selection, are controlled by hormones (Owens & Short 1995). The main sources of the different plumage colours are divided into three categories, namely melanin pigmentation, carotenoid-derived pigmentation and structural colours. Melanin-based dimorphism is associated with sex differences in parental care while structural colours are associated with extra-pair bond paternity and active sexual displays (Owens & Hartley 1998). Carotenoid-derived pigmentations have a dietary source as birds cannot synthesize the carotenoids responsible for their bright yellow, red or orange colours (Brush 1981; Brush 1990). Bright colours, as they are derived from diets, can also serve as signals of an individual's access to superior diets or superior foraging ability (Endler 1980; Hill 1990). Bright colours and other ornamental feathers are advantageous in acquiring mates but have high energy expenditure and as such only high quality males are able to bear such fitness costs (Folstad & Kartner 1992). Bright colours are also a reliable signal of males' genetic resistance to parasites (Hamilton & Zuk 1982; Bortolotti *et al.* 1996).

Another unusual feature of sparrow-larks is that they exhibit symmetrical biparental involvement in all aspects of the breeding cycle, i.e. both sexes assist equally with incubation, and feeding of the nestlings and fledglings (Pätzold 1994). In addition, males of most sparrow-lark species assist at least occasionally with the collection of nest material and nest construction (Pätzold 1994). The only other larks exclusively exhibiting symmetrical biparental care in all aspects of the breeding cycle are members of the genus *Spizocorys* (de Juana *et al.* 2004). Although biparental care has been reported in a few species of larks, e.g. rufous-tailed lark (*Ammomanes phoenicura*), desert lark, Malabar lark and Spike-heeled Lark (de Juana *et al.* 2004; van Niekerk, pers. comm.), it is, however, uncommon and inconsistent within these species. The close accompaniment of a female by a male during this period is often mistakenly interpreted as the male assisting with nest construction. This behaviour actually serves a mate-guarding function to avoid being cuckolded (de Juana *et al.* 2004).

Biparental care is rare in most animal taxa but common in birds, with approximately 50% of bird species having biparental incubation and/or brood care (AlRashidi *et al.* 2010). The relative degree of involvement and parental roles of males versus females often differ amongst pairs within species and amongst species exhibiting biparental care (Clutton-Brock 1991). Two major groups of hypotheses have been proposed to explain biparental care (AlRashidi *et al.* 2010). On the one hand, both parents may be essential for successful rearing of young. Biparental care may be essential if parents breed in habitats where resources are poor or limited, or the physical environment is harsh and challenging (Wilson 1975). Several studies have shown that the extra assistance provided by the one parent (usually the male) provides direct benefits by improving offspring survival, and/or by putting less strain on the female (Gubernick & Teferi 2000; Auer *et al.* 2007; Harrison *et al.* 2009; AlRashidi *et al.* 2010). The other group of hypotheses predict that parents may benefit in future from staying together and sharing care provisioning, e.g. by keeping a partner for future matings and thereby avoiding the costs related to finding and/or attracting a new mate (Black 1996).

Incubation is essential for reproduction in nearly all bird species, because eggs require heat for embryonic development, and the incubating parent can defend the clutch from predators (Ligon 1999; Deeming 2002; AlRashidi *et al.* 2010). However, providing parental care is energetically costly as it not only demands time and energy from the parents, but incubating birds or parents foraging for food for their offspring may render themselves susceptible to predation (Williams 1996; Reid *et al.* 2002a; Szekely *et al.* 2006). Furthermore, biparental incubation may be mandatory for some species, especially ground-nesting species, inhabiting harsh environments such as hot deserts, to prevent eggs from overheating and to ensure viability of the developing embryos (AlRashidi *et al.* 2010). By sharing incubation, the parents reduce the costs of time, energy and predation risk imposed upon them.

Despite parents cooperating to rear their young, there exists a sexual conflict with regard to the apportionment of care. Both males and females are assumed to face a trade-off between investment in current offspring and other competing needs such as self-maintenance and future reproductive opportunities (Roff 1992). Thus, one would generally expect an asymmetry with regard to the relative contribution of each sex in the breeding cycle. In some extreme cases, this may result in some bird species (e.g. Kentish plovers *Charadrius alexandrinus*) shunting parental care to one parent (either male or female) who will have to raise the brood alone (Houston *et al.* 2005). In most species exhibiting biparental care, females are usually involved in all or most parental care duties (nest construction, incubation and feeding of nestlings and fledglings), whereas males are commonly only involved in feeding of young and less frequently in incubation. Nevertheless, males have the potential to influence positively embryo development and success when they participate in incubation (Bailey 1952; Drent 1975; Auer *et al.* 2007). This is achieved by either reducing the rate of heat loss/gain by sitting on the eggs during incubation off-bouts of the female, or by maintaining and sometimes even increasing the egg temperature in species where males invest an equal or greater amount of time on the nest relative to females (Ball 1983; Reid *et al*. 2002b; Hepp *et al*. 2006; Auer *et al.* 2007). The role and extent of the contribution of males in those species where males assist with incubation remains poorly known, as most studies involving biparental care has focussed mostly on food provisioning rates of males, and the relative contribution of males in incubation and nest attentiveness have largely been ignored (Whittingham & Dunn 2001; Auer *et al.* 2007).

Another interesting feature of the nests of several sparrow-lark species is the use of the felt-like webs of *Seothyra* spiders to decorate the rim and apron of their nests (Keith *et al.* 1992; Dean 2005b). Although spider-webs are also occasionally incorporated in the nests of other species, e.g. Stark's, pink-billed and spike-heeled larks, it is regularly found in sparrow-lark nests (Dean 2005b).

Despite their weak flight calls, *Eremopterix* larks are the only ammomanid larks with extended aerial display flights, and all the *Eremopterix* larks tend to "float in the sky with a unique butterfly-like flapping thereby exposing their black underwings" (Keith *et al.* 1992; Donald 2004). Most ammomanid larks have a short, simple ascending-descending type of display flight.

From the above, it is evident that sparrow-larks are unique amongst the Alaudidae in a number of respects. However, the biology and ecology of the majority of the species are poorly known and research on this interesting group will undoubtedly reveal more unique characteristics.

1.4. General background to the chestnut-backed sparrow-lark *Eremopterix leucotis*

The chestnut-backed sparrow-lark is endemic to Africa and occurs widely throughout southern, eastern and north Africa south of the Sahara (Fig. 1.1). Within its range, it inhabits open, sparsely vegetated desert margins, and the arid to semi-arid grassland and savanna regions of Africa (Keith *et al.* 1992). The species is also common in open flats, old lands with short grasses, airfields, recently burnt areas and cultivated lands close to low bushes (Dean 1997; Lloyd 2005a). It has the widest distribution range of the African *Eremopterix* larks and, not surprising, no fewer than five subspecies are recognized on the basis of differences in plumage colouration (Table 1.2). Although the subspecies are largely allopatric, some subspecies have been recorded together in certain areas when environmental conditions are suitable (Irwin 1982; Keith *et al.* 1992). Although generally regarded as nomadic, some populations become resident if suitable conditions prevail while others may be partial migrants with regular seasonal movements (Benson *et al.* 1971; Keith *et al.* 1992).

Chestnut-backed sparrow-larks are primarily granivorous, but they also supplement their diet with invertebrates, particularly during the breeding season (Irwin & Lorber 1983). The species drinks regularly but they are often found well away from water, suggesting they are able to fulfil their water requirements through metabolic oxidation of food or by incorporating more invertebrates in their diet.

The species is usually gregarious in flocks of five to several hundred birds, sometimes in mixed flocks with other sparrow-larks (Keith *et al.* 1992). However, during the breeding season they are usually encountered in pairs, although pairs sometimes nest within metres from each other (Morel & Morel 1984; Keith *et al.* 1992).

Breeding has been recorded in all months of the year (Irwin 1981). Such a prolonged breeding season is typical of nomadic species which breed opportunistically when favourable conditions present themselves (Dean 2004). Nevertheless, breeding appears to peak from the end of the wet season and during the dry season in most regions (Chittenden & Batchelor 1977; Irwin 1982; Irwin & Lorber 1983; Steyn 1988; Skinner 1995; Dean 1997; Lloyd 2005a). The peak breeding season in southern Africa coincides with the period when most grasses have finished producing seeds.

Chestnut-backed sparrow-larks lay 2–3 eggs ($\bar{x}$ = 2.6) per clutch, but there is geographical variation with regard to clutch size in the species (Ryan *et al.* 2004). In the southern parts of the species' range the clutch size averages two, whereas in the northern parts of its range (Senegambia) the clutch size is always one (Serle *et al.* 1977; Morel & Morel 1984). Eggs are laid at daily intervals and incubation commences after completion of the clutch (Chittenden & Batchelor 1977). The incubation duties are shared amongst the sexes but according to Keith *et al.* (1992) the female is mainly responsible for incubation. The incubation period is 11–12 days (Keith *et al.* 1992). Egg shells are removed from the nest soon after hatching. The hatchlings are fed by both parents on a diet consisting of invertebrates and seeds, and females are known to bring more food than males (Morel & Morel 1984). The nestling period is 10–12 days (Morel & Morel 1984). The shorter incubation and nestling periods of chestnut-backed sparrow-larks are possibly adaptations to reduce predation and/or to ensure the nestlings receive the greatest benefit from the optimal but transient conditions that exist after rainfall in arid and semi-arid areas. Such short periods places tremendous energetic demands on parents to find sufficient food to enable the nestlings to grow at or near their physiological maximum (Lack 1968; Tieleman *et al.* 2004). Chestnut-backed sparrow-larks have extended breeding seasons with breeding reported in all months of the year (Lloyd 2005a) and as such it is possible that they may be multiple brooded as suggested by Morel & Morel (1984). However, due to their nomadic habits it is difficult to prove multiple-brooding unequivocally.

1.5. Current study

The current study was initiated by Prof. Engelbrecht in 2008 and I continued with field work in 2009 and 2010. The aim of the present study was to improve our knowledge of various aspects of the natural history of the chestnut-backed sparrow-lark including its breeding biology and ecology, vocalizations, intraspecific and geographical size variation, and the pattern and timing of moult. In this regard, the study will also attempt to shed light on the following three research questions:

> *i) What is the relative contribution and role of males and females during the different stages of the breeding cycle?* Sexual Conflict theory predicts a trade-off between investment in current offspring and other competing needs such as self-maintenance and additional reproductive opportunities. Reproduction has long been viewed as a cooperative exercise between male and female partners. Yet, the evolutionary interests of males and females are often different which leads to sexual conflict. In the majority of cases this leads to an unequal contribution of the partners in the breeding cycle. Sexual conflict has the potential to give rise to variation in behaviour, morphology, breeding systems and the evolution of life-history traits The *Eremopterix* larks falls in a small group of larks which exhibit biparental care in all aspects of the breeding cycle, but whether or not the contributions of males match those of females is as yet unknown.
>
> ii) *In addition to sexual dichromatism, do chestnut-backed sparrow-larks exhibit sexual size dimorphism?* Most lark species exhibit some degree of sexual size dimorphism, usually mass, wing or bill length,

although it is less pronounced in nomadic granivorous species. The prolonged aerial displays of male chestnut-backed sparrow-larks suggest there may be adaptations for sustained aerial display flight.

iii) *Are there differences in the breeding success at different stages of the breeding cycle, e.g. incubation, hatching and nestling periods?* Several studies showed variation in breeding success for different stages of the breeding cycle and this study will attempt to determine if there are differences in the breeding success in different stages and, if so, what the proximal causes for it may be.

In light of the foregoing, the objectives of the study are to:

i) determine the relative contribution of the sexes in the breeding cycle, i.e. in nest construction, incubation, and food delivery,

ii) determine incubation and nestling brooding shift lengths at various stages in the nesting cycle,

iii) determine the fresh egg mass, egg dimensions, egg elongation index, egg volume and egg weight coefficient (K_w),

iv) describe nestling growth and feather development,

v) describe and quantify the diet of nestlings,

vi) estimate the breeding success,

vii) describe the nest site characteristics,

viii) describe the characteristics and dimensions of the nest,

ix) analyse and describe the vocalizations,

x) describe the timing and pattern of moult,

xi) describe the extent of geographic variation and sexual size dimorphism in southern African subspecies of the chestnut-backed sparrow-lark with regard to selected biometric measurements, and

xii) compare the results obtained in this study with selected biometric measurements on the South African Bird Ringing Unit's (SAFRING) database and of selected breeding parameters on the Nest Record Card Scheme (NERCS) database of the Animal Demography Unit, University of Cape Town.

Table 1.1. The seven species of *Eremopterix* larks, their preferred habitat and distribution (Ryan *et al.* 2004).

Scientific name	**Common name**	**Habitat and distribution**
Eremopterix griseus	Ashy-crowned sparrow-lark	Resident inhabitants of scrubs, stony wastelands and cultivated fields in southern Asia, including Pakistan, India and Sri Lanka.
Eremopterix nigriceps	Black-crowned sparrow-lark	Common in arid savannas of Burkina Faso, Cape Verde Islands, Egypt, Eritrea, Ethiopia, and Nigeria. Also occurs sparsely in Eurasia ranging from the Arabian Peninsula to Pakistan and India.
Eremopterix australis	Black-eared sparrow-lark	Widespread in the central Karoo of South Africa and extending into the south western Kalahari. Occurs sparsely in southern Namibia and Namaqualand south of the Orange River, the Western Cape and south-western Free State.
Eremopterix leucotis	Chestnut-backed sparrow-lark	Widespread in the savannas of sub-Saharan Africa from Senegal to Eritrea and north-western Somalia, south through eastern Africa to central and southern Africa.

Scientific name	**Common name**	**Habitat and distribution**
Eremopterix signatus	Chestnut-headed sparrow-lark	Mostly inhabit the tropical and sub-tropical dry shrub-lands, lowland grasslands and hot deserts. Endemic to east Africa where distribution is centred on Somalia, occurring marginally in Kenya.
Eremopterix leucopareia	Fischer's sparrow-lark	Inhabit subtropical and tropical dry, open and lowland grasslands of eastern parts of Africa, Rwanda, central Zaire, northern Zambia and northern Malawi.
Eremopterix verticalis	Grey-backed sparrow-lark	Mostly inhabit the semi-arid plains of Angola from Cabinda south through south-western Zambia and most of the western parts of southern Africa.

Table 1.2. The five subspecies of the chestnut-backed sparrow-lark (*Eremopterix leucotis*), their distribution and a brief description of the male and female of each subspecies (Keith *et al.* 1992).

Subspecies	Distribution	Description	
		Male	Female
E. l. leucotis	South-eastern Sudan, Ethiopia, Eritrea and north-west Somalia.	Black or dark brown shoulders. The mantle and wings are darker than in the males of *E.l. melanocephala*.	Much darker than the females of *E.l. melanocephala.*
E. l. madaraszi	North-eastern Uganda, Kenya, coastal southern Somalia, Tanzania and extreme northern Mozambique.	Richer red above than nominate race and also have larger bills.	Duller, less reddish on the upperparts than females of nominate race; throat to middle of belly is dull black.
E. l. melanocephalus	Senegal and east to central Sudan.	Back brighter and redder than nominate race, mostly white outer wing coverts.	Back is bright chestnut-coloured, breast pale buff with dark brown mottling, dark brown on central belly.

Subspecies	**Distribution**	**Description**	
		Male	**Female**
E. l. smithi	Eastern sections of Botswana, southern and eastern Zimbabwe and north-central and eastern parts of South Africa and central and southern Mozambique. Occurs sparsely and occasionally in Malawi and eastern Zambia.	Paler and tawnier than *E.l. leucotis* and *E.l. madaraszi*, and the shoulders are black.	Dull, chestnut ground colour above. Generally paler than nominate females with black restricted to middle of lower breast and belly.
E. l. hoeschi	Southern Angola and Namibia through to the northern and north-eastern parts of Botswana and north-western Zimbabwe. Occurs sparsely and occasionally in southern Angola and south-western Zambia.	Similar to *E.l. smithi* but male is tawnier above.	Backs are much colder and greyer, under-parts are paler than nominate and *E. l. smithi*.

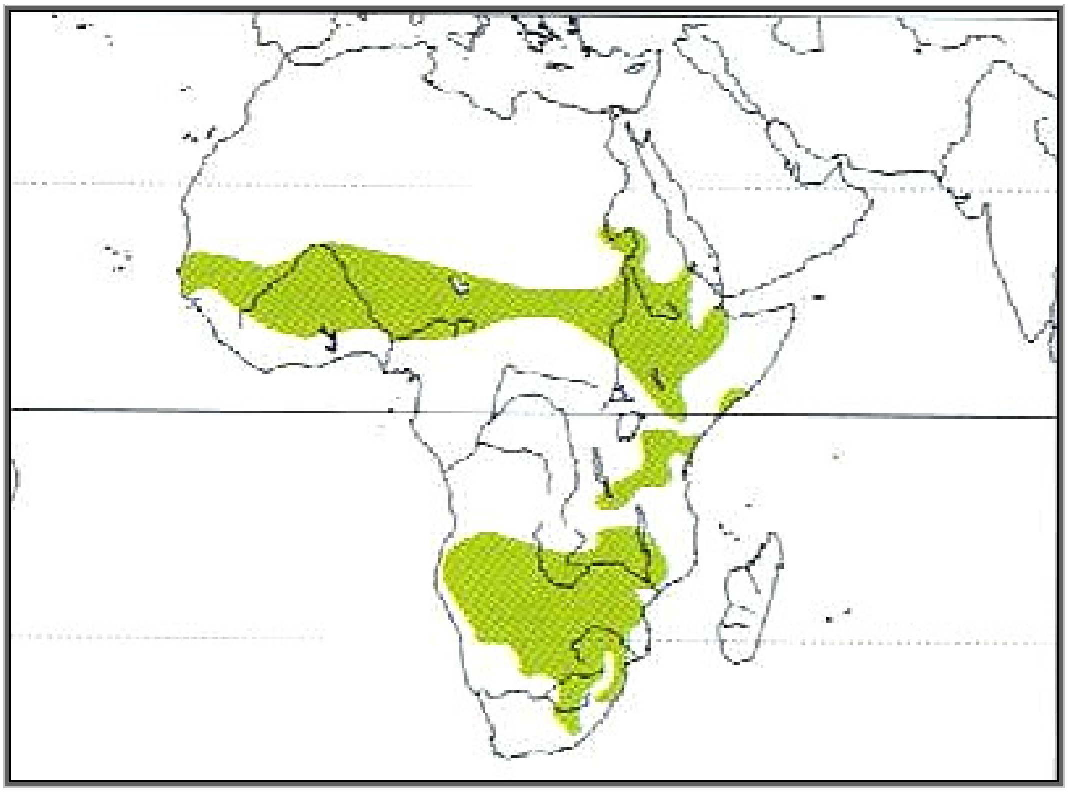

Fig. 1.1. Distribution of the chestnut-backed sparrow-lark (*Eremopterix leucotis*) (Ryan *et al.* 2004).

CHAPTER 2

Breeding biology of the chestnut-backed sparrow-lark *Eremopterix leucotis* in the Limpopo Province, South Africa

2.1. Introduction

The Alaudidae (larks) is a speciose family of small- to medium-sized primarily terrestrial passerines inhabiting arid to semi-arid habitats such as deserts, steppes, savannas and thin scrubs (de Juana *et al.* 2004). Larks are primarily an African group, reaching their highest species richness on the continent, and secondarily a European group (Barnes 2007). The family Alaudidae is comprised of 21 genera with 96 species of larks currently recognized (de Juana *et al.* 2004). There are 78 species occurring in Africa, with 48 species being endemic to sub-Saharan Africa. In contrast, there are only 36 species occurring in Eurasia including 17 endemic species.

Sparrow-larks (*Eremopterix*) represent a relatively small alaudid genus consisting of seven species of which five occur in Africa and two in Eurasia (Table 1.1). Three species occur in southern Africa, namely the grey-backed sparrow-lark (*Eremopterix verticalis*), black-eared sparrow-lark (*Eremopterix australis*) and chestnut-backed sparrow-lark (*Eremopterix leucotis*). Species in the genus *Eremopterix* are unique amongst larks in that they are sexually dichromatic and part of a small group of unrelated larks that exhibit biparental care in all aspects of the breeding cycle, i.e. nest construction, incubation, nestling and post-fledging care (Keith *et al.* 1992). Sparrow-larks are some of the most mobile larks and most species are nomadic or migratory to varying extents. This makes it difficult to study their biology and ecology as their appearance in an area is unpredictable and characterised by rapid settlement and breeding when conditions are favourable. This explains why our knowledge of their biology and ecology is limited and scattered throughout various publications looking only at limited biological and ecological parameters at a time (Steyn 1964; Chittenden & Batchelor 1977; Irwin & Lorber 1983; Morel & Morel 1984). Sparrow-larks are amongst the least known species in the family, with almost nothing known about the breeding biology and seasonality of some species such as the chestnut-headed sparrow-lark (*Eremopterix signatus*), ashy-crowned sparrow-lark (*Eremopterix griseus*) and Fischer's sparrow-lark (*Eremopterix leucopareia*). In Africa, the breeding biology and aspects of the ecology of the two south-western arid zone endemic sparrow-larks, namely the black-eared and grey-backed sparrow-larks, are arguably the best known of the sparrow-larks (Maclean 1970a; Maclean 1970b; Lloyd 1998; Lloyd 1999; Tarboton 2001). Our knowledge of the other species is limited to brief descriptions of various aspects of their breeding biology and behaviour.

The larks are ideal subjects for research on the evolution of various characters, e.g. vocal mimicry, sexual dimorphism and display flights, as the family presents one of the best examples of adaptive radiation on the African continent. However, the generally austere and structurally simple habitats occupied by them, coupled to their drab plumage colouration, may be the reason why they have largely escaped the attention of ornithologists. For example, the biology, ecology and taxonomic relationships of the majority of species in the family are virtually unknown and little more than brief descriptions of nests, eggs or nestlings are known for the majority of species (*cf.* Ryan *et al.* 2004).

Studies on the biology and ecology of species are essential prerequisites for successful biodiversity and habitat management. Dowling (2003) wrote: "knowledge of the breeding characteristics of a species also provides insights into the selection pressures that individuals of that species faced over time. As more data become available on previously unstudied species, it is possible to conduct more rigorous comparative tests to determine which factors are responsible for variations in life history strategies between species and ultimately their persistence in an area". At present, our knowledge of these aspects of lark life history strategies is unfortunately too limited to conduct meaningful comparative studies on the evolution of characters in the family. Furthermore, an understanding of the breeding characteristics of species and their ecological requirements are also necessary for effective management of a species as it allows conservation biologists to more realistically and accurately model risk management (Dowling 2003).

The present study attempts to improve our knowledge of the biology and ecology of the chestnut-backed sparrow-lark in a savanna landscape in the Limpopo Province, South Africa, by studying various aspects of the species' breeding biology. The chestnut-backed sparrow-lark is endemic to Africa and has the widest distribution range of all *Eremopterix* larks (Fig. 1.1). There is a gap in the species' distribution between 12° and 15° south in Malawi, resulting in separation of the northern and southern populations. Given its extensive geographical range, it is not surprising that five subspecies are recognized by Ryan *et al.* (2004) (Table 1.2). Within its range the species inhabits open, sparsely vegetated areas on stony or sandy soils in arid and semi-arid grasslands and savannas (Dean 2005b). The species is also common in habitats with short grass such as old lands, road verges or airfields, recently burnt areas and fallow agricultural fields (Dean 1997; Lloyd 2005a). Although they are primarily nomadic, some populations may become resident if amenable conditions persist while others may be partial migrants with regular seasonal movements (Benson *et al.* 1971; Morel & Morel 1984; Keith *et al.* 1992).

Although the species' distribution is well documented in various regional field guides and atlases (see Ryan *et al.* 2004 and references therein), our knowledge of the species' biology is limited to four short communications of observations of breeding birds (Steyn 1964; Chittenden & Batchelor 1977; Irwin & Lorber 1983; Morel & Morel 1984). Steyn (1964) reports on observations at a single nest and a description of the egg dimensions and nestling development in Matabeleland province, Zimbabwe. Chittenden & Batchelor (1977) described the breeding season, nest orientation, egg dimensions, clutch size and biparental care of the chestnut-backed sparrow-lark from the Eastern Transvaal (now Mpumalanga, South Africa). Irwin &

Lorber (1983) described the breeding seasonality of the chestnut-backed sparrow-larks, preferred habitats and clutch sizes in Zimbabwe. The most detailed study to date on the chestnut-backed sparrow-lark was by Morel & Morel (1984) who described aspects of the breeding biology of chestnut-backed sparrow-lark from Senegambia. Other aspects of the breeding biology e.g. nest site characteristics, breeding success and the relative contribution of the sexes in the breeding cycle still remain unknown. The present study aims to address these shortcomings by collating and supplementing all existing knowledge of the species and by presenting new information about various aspects of the breeding biology of the chestnut-backed sparrow-lark from the southern parts of its range.

2.2. Materials and methods

2.2.1. Study area

The study was conducted at Al3 farm, De Loskop (23°30'S; 29°19'E; 1090m above sea level), in the Limpopo Province, South Africa, hereafter referred to as De Loskop. It is a commercial agricultural farm used mostly for crop (onion and potato) and livestock (cattle) production as well as the manufacturing of compost. It is characterised by a mixture of relatively undisturbed short, open, *Acacia*-dominated scrub, crop fields, fallow lands and a perennial earth dam. Figure 2.1 shows the study area and the surrounding fallow lands and cultivated fields. The vegetation at the study site is described as Makhado Sweet Bushveld (Mucina & Rutherford 2006). It is situated in a summer rainfall region with dry winters (Fig 2.2).

2.2.2. Nest searching and monitoring

Data was collected from January 2008 to December 2010. The site was visited once a week from the beginning of January 2008 to determine when the breeding season commenced. Once the first nests were located, the study area was visited three days per week to collect data and to search for additional signs of breeding activity. Nests were located by searching the study area systematically and using parental cues, e.g. adults carrying nesting materials, food to nestling or faecal sacs. Birds carrying the aforementioned were observed closely to establish the roles and relative contribution of each sex during various stages of the breeding cycle. Nest contents were generally checked at incubation or brooding shift changes. Activity at the nest had little apparent effect on the birds and they either flew in circles above the nest or perched nearby and returned within minutes after the nest site was vacated. Nests found during the construction stage or laying period were monitored on a daily basis to determine the laying interval and to determine the length of the incubation period.

2.2.3. Individual identification

Sparrow-larks are sexually dichromatic and it is therefore possible to distinguish between the sexes and to delineate their roles and relative contributions in the nesting cycle. Nevertheless, a sample of breeding birds were captured at their nests and fitted with SAFRING metal rings and a unique combination of colour-rings to aid in individual identification. This was done to obtain biometric data for the species (see Chapter 3), and to enable individual identification of adults to determine aspects such as possible co-operative breeding, mate fidelity and the number of breeding attempts per season.

2.2.4. Clutch size and egg data

When a nest containing eggs was found, the following data were recorded: clutch size, egg mass (0.01g) using a portable digital scale, the maximum width (EW_{max}) and length (EL_{max}) of the egg measured to the nearest 0.01 mm with digital Vernier callipers. Eggs found within four days of laying ($n = 23$) were considered fresh (FEM). Measurements from these eggs were used to calculate an egg weight co-efficient, K_w, for the species by using the formula of Hoyt (1979): $K_w = \text{mass}/L \times W^2$ where L and W are equivalent to EL_{max} and EW_{max} respectively. The resulting coefficient, $K_w = 0.00052$, was then used to estimate the mass of eggs (EEM) found to be older than four days (n = 43). The EW_{max} and EL_{max} were used to determine the egg elongation index (EEI) and egg volume (EV).

2.2.5. Nestling growth and development

To assist with individual identification of the nestlings, they were marked initially on the thigh with a non-toxic marker pen and with a metal band and two colour bands when they were 7–9 days old.

Nestling growth and development parameters recorded within the first 90 minutes after sunrise, every 1–2 days for the duration of the nestling period, included the following: plumage development, mass measured to the nearest 0.1 g with a portable digital scale, growth of the tarso-metatarsus (hereafter referred to as the tarsus), head length and wing chord all measured to the nearest 0.01 mm. The latter three were recorded with a Vernier calliper as described by de Beer *et al.* (2001).

The growth rate of each nestling was determined by fitting a logistic equation of the form:

$$x\ (t) = A / 1 + \exp\ (-K\ (t - t_i))$$

where x (t) is the mass or length at age t, A is the asymptote of the growth curve, K is the growth rate constant, and t_i is the age at the inflection point of the growth curve. The logistic model is rather inflexible as it is symmetrical around the inflection point, which is fixed at 0.5 of the upper asymptote (Tjørve & Tjørve 2010). The value of x at the inflection point is found at $t = t_i$ and the model thus reduces to:

$$A / (1 + \exp\ (0)) = A/2.$$

Despite this limitation, the logistical model is one of the most useful and often applied models (Tjørve & Tjørve 2010). The t_{10-90}, i.e. the time required to complete growth from 10% to 90% of the asymptote, was also calculated. For a logistic growth curve, this is calculated as:

$$t_{10-90} = 4.394K^{-1}.$$

2.2.6. Roles of the sexes

The roles and relative contribution of each sex during the nesting cycle, the incubation and brooding shift lengths and the rate of prey delivery of males and females to nestlings were monitored for periods ranging from 6–9 hours starting at sunrise. Observations were made either from a hide approximately 30−40 metres away from the nest using a pair of Nikon 10 x 50 binoculars, using a Sony HDR-XR160 digital video camera placed 1−3 m from the nest and recording in “long-play” mode, or using Ecotone H31 Trail cameras placed 1−5 m from the nest. Recording of the incubation shift lengths and the rate of prey delivery was only done on “average” days, i.e. not excessively hot or cold weather, or wet or windy conditions. It was also only recorded for nests with two eggs or nestlings and the rate of prey delivery was only done when nestlings were 3–6 days old.

To determine if there was a difference in the composition of the nestling’s diet brought by males and females, a 400mm Nikon F2.8 telephoto lens and Nikon D300 camera was used to photograph parents delivering food to nestlings at a sample of nests. A pilot study showed that it was generally possible to identify food items as either seed or invertebrates. In many instances it was possible to identify invertebrate prey to order level using the digital images. The following food item categories were recognized: seeds, Orthoptera, Phasmatodea, Isoptera, soft bodied invertebrates (e.g. worms), and unknown items.

2.2.7. Breeding success

Estimation of the breeding success at various stages in the nesting cycle is of importance in determining when nest failures are most likely to occur and to identify possible causes of nest failure. Mayfield’s (1975) method was used to calculate the breeding success independently for the following three stages of the nesting cycle: laying and incubation, hatching, and nestling. These three calculations were then used to estimate the overall breeding success. In addition, a crude breeding success was determined by calculating the percentage of nestlings that fledged successfully from the total number of eggs laid in the nests found during the course of the study.

2.2.8. Nest dimensions and nest site characteristics

Nest dimensions were only recorded in the period three days prior to hatching until three days post-hatching as the results of a pilot study showed that nest dimensions change considerably during the nesting cycle. For example, females may start laying before nest construction is complete and continue to add nest material throughout the incubation period. The nest dimensions may also change appreciably during the development of nestlings as their size increased.

The following nest dimensions (mm) were recorded as described by Hansell (2000): nest width, cup depth, and cup diameter. The nest entrance direction was determined using a Garmin GPS and placed within one of the eight major compass directions. In addition to these measurements, the presence or absence of an apron, its mean width (mm) if present, and the material used in the apron, nest and lining was recorded. Nest site characteristics were described and expressed as the percentage of bare ground/stones, grass, forbs, and debris within a 1 m^2 quadrant using the nest as the centre of the quadrant.

2.2.9. Data analysis

All statistical analyses were performed using either Microsoft Office Excel (2007) or SPSS Version 18 (2009). Descriptive statistics were calculated for all nest and egg dimensions, clutch size data and habitat measurements. To test if habitat characteristics had an effect on nest outcome, a χ^2-test was performed. The Mann-Whitney U test was used to test if nest micro-habitat characteristics had an effect on the nest outcome. This was done by comparing values above and below the median with the nest outcome, i.e. success versus failure. The Mann-Whitney U test was also used to test for differences in the incubation shift lengths of males and females. Growth parameters of nestlings were obtained by calculating the different growth parameters per individual and then to calculate the means of each growth parameter. One-way Analysis of Variance (Anova) was performed to test for differences in the number of nests visits made to deliver food between males and females. A Phi-test was used to determine if there is a difference in the type of food delivered to nestlings by each sex. Statistical significance was concluded at $P < 0.05$ for all tests. 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

A total of 96 nests were found during this study: 29 in 2008, 55 in 2009 and 26 in 2010. Details of nest dimensions, structure, micro-habitat and entrance direction were not recorded at all nests and sample sizes therefore differ for certain parameters.

2.3.1. Seasonality

The onset of the breeding season was preceded by an increase in the number of display flights and flight songs performed by males. This usually occurred from February to March. A summary of the number of nests initiated per month (backdated assuming a mean incubation period of 10.3 days and considering the stage of development of nestlings) for each year is presented in Fig. 2.3. Breeding of the chestnut-backed sparrow-lark in the study area is bimodal, with a main peak in breeding activity at the end of the wet season and beginning of the dry season (i.e. autumn), and a second, smaller peak at the end of the dry season, just before the start of the wet season (i.e. spring).

Chestnut-backed sparrow-larks generally nested in loose aggregations covering approximately 0.2–0.3 ha. However, although the onset of breeding was usually more or less synchronised, some pairs bred in isolation well away from a nesting colony.

2.3.2. Nest construction and dimensions

The majority of nests were placed next to the base of a plant (76.0%; Figs. 2.5, 2.6, 2.7, 2.8, 2.11, 2.12 and 2.13), the remainder placed next to a rock (19.8%; Fig. 2.9), or, rarely, in a hoof print (2.1%) or completely in the open (2.1%; Fig. 2.10). Of the 73 nests placed adjacent to a plant, 63.0% were associated with a grass tuft (Figs. 2.5, 2.6, 2.7, 2.8 and 2.13) and 37% with a forb (Figs. 2.11 and 2.12). The nest construction period, defined as the period between the onset of nest construction and laying of the first egg lasted 1–3 days (n = 8). Nest construction started with the female digging a cup. Subsequently, coarse grass blades were added to the cup. The lining, which consists of finer grass blades, rootlets and sometimes downy feathers from moulting waterfowl, was added last, often continuously throughout the incubation period. Both sexes collected material and participated in the construction of the apron. Spider-silk was incorporated into the apron and to a lesser extend the cup lining in 33.0% of the nests (Fig. 2.5).

The nest dimensions and nest micro-habitat characteristics of 55 nests recorded in this study are presented in Table 2.1 and Fig. 2.4 respectively. The majority of nests (78.2%) had an apron although it varied considerably in size (*cf.* Fig. 2.6 and Fig. 2.8). Material used for the apron in order of frequency were: small stones, sticks, clods of mud, dung, spider silk, grass blades or stems, small flowers, feathers and dried algae. The size of the apron had no significant effect on the outcome of breeding, i.e. success versus failure (χ^2 = 2.49, d.f. 4, P = 0.65). Most nest entrances faced south (78.2% of 55 nests), while the remaining nests faced in a south-westerly (9.1%), south-easterly (9.1%) or north-westerly (1.8%) direction. Two nests (1.8%) were placed completely in the open. The nest micro-habitat analyses show that chestnut-backed sparrow-larks prefer nesting in areas with lots of bare ground with small amounts of cover provided by grass, forbs, stones and rocks (Fig. 2.4). The amount of debris at nests was relatively high ($\bar{x}$ = 15.6% ± 10.8) as most nests were constructed on the floodplain of the perennial earth dam. The debris included sticks and various other plant remains washed up during rain storms or that remained behind when the water started receding towards the end of the wet season. The "other" category also contributed significantly to basal cover at nests ($\bar{x}$ = 24.29 ± 21.46; median = 15) and included mostly cattle dung. There was no significant difference between nest outcome and the presence or absence of an apron (Mann-Whitney U test, $P = 0.68$) or the percentage grass cover (Mann-Whitney U test, $P = 0.75$), forb cover, (Mann-Whitney U test, $P = 0.68$), debris (Mann-Whitney U test, $P = 0.64$), bare ground (Mann-Whitney U test, $P = 0.61$), stones (Mann-Whitney U test, $P = 0.68$) or other material (Mann-Whitney U test, $P = 0.55$).

2.3.3. Egg dimensions and clutch size

The results of measurements taken from 66 eggs are summarized in Table 2.2. Clutch size ranged from 1–2 ($\bar{x}$ = 1.88, mode = 2, median = 2, $n = 88$ nests). Mean clutch size was similar over the three years of the study (2008: 1.87 ± 0.35, n =30; 2009: 1.87 ± 0.34, $n = 39$; 2010: 1.85 ± 0.37, $n = 26$). The mean clutch mass was $\bar{x}$ = 3.55 g ± 0.91 (range: 1.78–4.8) which represents 18.9% of the mean mass of an adult female ($\bar{x}$ = 18.80 g ± 1.04; see Chapter 3). Single- and two-egg clutches represented 10.4% and 21.2% respectively of the mass of an adult female.

2.3.4. Incubation

Eggs were laid within two hours after sunrise at daily intervals with incubation commencing upon clutch completion. Both sexes shared incubation duties. The incubation period, i.e. the period from the laying of the last egg of the clutch to hatching of that egg, was determined to be 10.33 ± 0.49 days (range: 10–11, $n = 12$).

The incubation habits of the chestnut-backed sparrow-larks were monitored over a total of 5480 minutes. During this time, males incubated 50.1% of the time ($\bar{x}$ = 31.18 ± 25.59 minutes, median = 25.0, interquartile range (IQR): 16–42, overall range: 2–123, $n = 88$ incubation bouts), females for 43.1% ($\bar{x}$ = 25.13 ± 22.55 minutes, median = 20.00, IQR: 9.25–26.75, overall range: 2–121, $n = 94$ incubation bouts) and the nest was unattended for 6.8% ($\bar{x}$ = 8.13 ± 8.32 minutes, median = 4, IQR: 2–12, range: 1–27, $n = 46$ unattended periods) of the time. There was no statistically significant difference between the median duration of incubation shift lengths of males and females (Mann-Whitney U test, U = 3484.00, $P = 0.07$). If nests were left unattended, it was mostly between 09:00 and 11:00 in the mornings.

2.3.5. Nestling growth and development

Egg-shells were removed soon after hatching and disposed of away from the nest. Nestlings were brooded for short periods ranging from 2–21 minutes for the first 3–5 days of the nestling period. Both sexes contributed to nest sanitation by initially swallowing faecal sacs until day 3–4 of the nestling period but later flying off with them for disposal away from the nest.

The development of chestnut-backed sparrow-lark nestlings has not been described in detail in the literature and a summary of the main developmental events is therefore presented in Table 2.3. Sufficient data for analysis of growth parameters was obtained from 14 nestlings. Growth was rapid with $K > 0.30$ for all parameters and most growth completed at or around fledging as indicated by the $t_{10\text{-}90}$ values. Asymptotic mass (mean ± S.D.) for nestlings was 11.46 ± 1.48 g or 62.3% of the average mass of adult males and females ($n = 27$ males, 27 females) at De Loskop; growth constant (K; mean ± S.D.) for mass was 0.57 ± 0.19, while the maximum rate of increase in mass occurred at 3.19 ± 0.95 days and most growth ($t_{10\text{-}90}$) was completed at 8.51 ± 2.69 days. Asymptotic tarsus length was 18.83 ± 2.24 mm, or 106.8% of average adult tarsus length from De Loskop ($n = 27$ males, 27 females); growth constant was $K = 0.40 \pm 0.06$ with the maximum rate of increase in tarsus length occurring at 2.26 ± 0.65 days and a $t_{10\text{-}90}$ value of 11.14 ± 1.73 days. Asymptotic head length was 22.64 ± 2.23 mm and the growth constant for head length was 0.33 ± 0.11 with maximum growth rate at 0.03 days; the $t_{10\text{-}90}$ was reached at 14.72 days. Increase in length of the wing chord showed the slowest growth with $K = 0.31 \pm 0.66$ and maximum rate of increase in length at 9.67 ± 3.81 days; asymptotic wing length was 104.99 ± 76.13 mm which represents 124.4% of average adult wing length at De Loskop and $t_{10\text{-}90}$ was achieved at 14.90 ± 2.80 days.

The diet of nestlings, rate of food delivery and the relative contributions of the parents were recorded for a period totalling 3944 minutes at 12 nests with two 3–6 day old nestlings. A food delivery refers to a nest visit during which either one or both nestlings were fed irrespective of how many food items were delivered. During this time a total of 638 food deliveries were made with males making 290 (45.5%) and females 348 (54.6%) nest visits to deliver food. Females made significantly more visits to deliver food (Anova, $F = 4.247$, $P = 0.040$). There was no significant difference in the type of food items delivered by the sexes (Phi test = 0.09, $P = 0.096$). Invertebrates comprised the bulk of the diet of nestlings with at least 50.2% of the food deliveries comprised of invertebrates and at least 34.5% of seeds. In a number of instances (15.4%) it was not possible to accurately determine what the type of food was that was delivered as the delivery was either too quick or the angle of approach of the parents made it impossible to see the food items. Prey loading, i.e. a parent carrying several invertebrate food items in its bill, and prey sharing, i.e. feeding both nestlings during a nest visit, were common.

Towards the latter stages of the nestling period (i.e. from day 6 onwards), nestlings were noticeably more active and continuously jostled in the nest. This placed strain on the nest structure and by the time of fledging, chestnut-back sparrow-larks nests have invariably almost disintegrated. From day 7, nestlings sometimes perched on the nest rim, or even outside the nest, for short periods. Fledging occurred between days 8–10 giving a mean nestling period of 9.20 ± 0.84 days ($n = 10$). Nestlings fledged before they were able to fly but their well-developed legs enabled them to move around. Nestlings tended to hide adjacent to vegetation and were reluctant to move if disturbed. Due to the juveniles' retiring nature, the post-fledging dependence period could not be established.

2.3.5. Breeding success

The Mayfield (1975) breeding success estimate of the chestnut-backed sparrow-larks was calculated using a mean incubation period of 10.33 days and the mean nestling period of 9.20 days as determined in this study. The daily survival rates for the different stages of the nesting cycle as well as the overall breeding success for the three years of this study are presented in Table 2.4. The average breeding success over the three years was estimated to be 16.1%. Of 184 eggs laid in 96 nests, 35 nestlings fledged which gives a crude breeding success estimate of 19.0%. The average number of fledged young per pair was 0.36 ± 0.71. Known causes of nest losses included nest depredation, flooding, failure of eggs to hatch and abandonment of the nest.

Given the brevity of the two breeding peaks, repeat-broods are unlikely. Pairs show mate fidelity over a breeding season and at least two pairs were recorded breeding in autumn and spring. Given the high nest failure rate, replacement broods were common with pairs initiating a new nest usually within two weeks after nest failure.

2.4. Discussion

2.4.1. Seasonality

In common with many nomadic bird species that breed when conditions are favourable, chestnut-backed sparrow-larks have a poorly defined breeding season. According to Irwin (1981) and Lloyd (2005a), breeding has been recorded in all months of the year, although there is a slight peak in breeding activity at the end of the wet season in southern Africa, i.e. autumn. The onset of laying is usually synchronised with several pairs initiating breeding within days of each other and frequently within a relatively small area. This suggests that the population responds to some hitherto unknown cue/s, e.g. temperature, rainfall or the lack there of, food abundance, nesting resources, that conditions are suitable for breeding. During this study, the breeding season was found to be bimodal with a main peak in the onset of laying in autumn (March/April) and a second smaller peak in spring (August to October) (Fig. 2.3). Apart from a few nests initiated in January 2009, this population avoided breeding during the peak wet season and during mid-winter. This pattern suggests that chestnut-backed sparrow-larks may, at least, be double-brooded during a breeding season as suggested by Morel &

Morel (1984). However, double- or multiple-brooding by chestnut-backed sparrow-larks will be difficult to prove due to the species' nomadic behaviour.

2.4.2. Nest construction and dimensions

As reported in the literature (Morel & Morel 1984), both sexes contributed to all aspects of the nesting cycle, including nest construction. This is unusual behaviour amongst the larks as females are solely responsible for nest construction in the majority of larks (Maclean 1985; Boyer 1988; de Juana *et al.* 2004). Although males don't usually assist with nest construction, they do accompany their mates when they collect nesting materials (Keith *et al.* 1992; Tarboton 2001; Engelbrecht 2005). This serves a mate guarding function to prevent other males from mating with the female. Since female passerines are generally receptive for approximately five days prior to laying the first egg until the day prior to laying the last egg in a clutch, it is in a male's interest to guard a female for at least this period to ensure paternity of the offspring. The nest construction period in this study was remarkably brief and lasted 1–3 days, laying sometimes starting with only a few blades of grass in the nest scrape (Fig. 2.13). This is not only considerably shorter than the usual nest construction period of 5–9 days reported for resident lark species (Boyer 1988; Engelbrecht 2005), but is also shorter than the 4–5 days reported for other southern African sparrow-larks (Maclean 1970b; Keith *et al.* 1992). The short nest construction period may reflect an adaptation of a primarily nomadic species that breeds opportunistically when conditions are favourable. Optimum conditions for breeding are of a transient nature, and once these conditions have passed, successful breeding may be jeopardized. Thus, any undue extension of the nesting cycle, e.g. through a prolonged nest construction period, may result in the optimum conditions for breeding becoming sub-optimal with obvious consequences for successful breeding.

The nest site preferences of the De Loskop population were similar to those reported by Morel & Morel (1984) for the species in Senegambia. The results demonstrate a clear preference for nesting in areas dominated by bare ground with limited cover (*cf.* Fig. 2.4). In the present study, this type of habitat was mostly found on the floodplain of the dam or in first-year fallow land. Despite nesting in such open habitats, incubating birds are remarkably well camouflaged when on the nest. Nesting in open areas with poor cover has its advantages as it allows incubating birds to spot potential predators from some distance away. Furthermore, it may also be an anti-predation strategy as many nest predators (e.g. snakes and rodents) prefer to forage in areas with good grass or vegetation cover. As they either breed at the end or before the wet season, nesting in areas with poor cover is not a major draw-back as incubating birds are not usually exposed to heavy rains and/or potential flooding of the nest. However, the results of this study showed no difference between nest outcome and the percentage cover.

The majority of nests found in this study faced in a southerly direction. Similarly, Morel & Morel (1984) found that most nests in the north of the species' range faced in an eastern or north-easterly direction. In both studies, the majority of nests were sited to provide at least some amount of shade during the warmest parts of the day. It is therefore clear that nest siting fulfils a thermoregulatory function to alleviate heat stress during the warmest parts of the day.

The nest dimensions (i.e. nest diameter, cup diameter and cup depth) obtained in the study area were consistent with the dimensions reported for the species and congenerics in the literature (Morel & Morel 1984; Tarboton 2001). An interesting feature of the nests was the presence of an apron at the majority (80.0%) of the nests. An apron is an extension of the nest to form a "platform" or "rampart" which may encircle the nest or, more commonly, form a pathway on the entrance side of the nest. Although the construction of a nest apron is an intriguing feature of the nests of many species of larks, it is by no means restricted to the Alaudidae. Nest aprons have also been recorded in the following families: Turdidae (thrushes), Fringillidae (finches) and Troglodytidae (wrens) (Cramp & Simmons 1988; Afik *et al.* 1991; Maclean 1993; Merola 1995). The material used for aprons varies and, depending on the species, may include pebbles, stones, sticks, dried algae, clods of earth, flowers, and cow dung, with silky spider webs incorporated in some aprons (Ryan *et al.* 2004). Some species appear to show a preference for certain material and use it almost exclusively. For example, the black lark (*Melanocorypha yeltoniensis*) uses the dung of livestock, many North African desert species, e.g. desert lark (*Ammomanes deserti*) uses pebbles almost exclusively, whereas Mediterranean species, e.g. Du Pont's lark (*Chersophilus duponti*) and Thekla lark (*Galerida theklae*) prefer to use sticks (de Juana *et al.* 2004).

Several hypotheses have been proposed to explain the functional significance of aprons. These hypotheses focus on aprons providing nest support, affording protection against adverse weather conditions, fulfilling a thermoregulatory function, being a form of sexual display and providing protection against nest predation (Leader & Yom-Tov 1997). The nest support hypothesis suggests that the nest apron supports the nest and prevents it from sliding off sloping surfaces (Richardson 1965). The weather protection hypothesis proposes that aprons protect nests from wind, rain and dust storms as they anchor nests into their substrate and stabilize the soil in the nest vicinity (Ferguson-Lees 1960; Afik *et al.* 1991). The thermoregulation hypothesis advocates that nest aprons serve as mechanisms to regulate and limit the maximum temperatures inside nests as the majority of species building stone ramparts are desert-dwelling birds where temperatures can be extremely high (Orr 1970; Afik *et al.* 1991). The sexual display hypothesis proposes that nest aprons are constructed as advertisement displays as part of mate selection and pair formation (Ferguson-Lees 1960; Richardson 1965). Finally, the anti-predation hypothesis suggests that aprons allow birds to use elevated areas potentially inaccessible to ground predators and camouflage nests to avoid detection by predators (Etchecopar & Hue 1967). The functional significance of nest aprons in larks has been the subject of debate for a long time. It is generally believed to camouflage the nest by breaking the outline of the nests and thus fulfils an anti-predation function as suggested by Engelbrecht (2005). Another explanation centres on aprons fulfilling a thermoregulatory function (de Juana *et al.* 2004). The results of this study suggest that an apron does not afford any additional protection against predators as there was no association between breeding success and the presence or absence of an apron. Moreover, individual preference or characteristic is not a determinant factor in the construction of an apron, as one pair constructed one nest with and another without an apron. A possible explanation for the construction of an apron is that the substrate may be very hard and difficult to dig a deep cup into, which necessitates construction of an apron in which the nest cup is then constructed. This has been observed for the grey-backed sparrow-lark (de Juana *et al.* 2004). Furthermore, it is possible that the chestnut-backed sparrow-lark's habit of nesting in areas with lots of bare ground may make the nest prone to flooding. Such bare areas will experience considerable run-off that may flood the nest. Although they nest towards the end of the wet season, occasional rain showers are still relatively common in autumn and an apron may serve to reduce run-off by slowing and channelling the flow of water away from the nest.

2.4.3. Clutch sizes and egg dimensions

The mean clutch size of 1.9 found during the present study compares favourably with the mean of 2.0 (*n* = 15) and 1.9 determined respectively by Chittenden & Batchelor (1977) and Serle *et al.* (1977) for southern populations of the species. However, in the northern ranges of the species only one-egged clutches have been reported (Morel & Morel 1984). As a generally nomadic species exploiting favourable areas, a small clutch size is necessary to ensure the nestlings gets the most benefits from the transient, but favourable conditions. Every increase in the clutch size by one egg, means an extra day for the breeding cycle and hence an extra day that nestlings are potentially exposed to nest predation and the possibility that the favourable conditions may be surpassed.

2.4.4. Incubation

Biparental care in all aspects of the breeding cycle, including incubation, is an unusual reproductive strategy amongst larks. It is one of the distinguishing features of the genus *Eremopterix* and is only shared with species in the genus *Spizocorys* (Maclean 1970a; Tarboton 2001). Parental care is a costly exercise as it requires additional investment in time and energy from the parents as they are forced to elevate their own energy and water requirements to provide food for both themselves and their offspring (Tieleman *et al.* 2004). Furthermore, they are also at risk of predation when incubating and feeding offspring (Williams 1996; Reid *et al.* 2002a; Szekely *et al.* 2006). In species with biparental care, this cost is shared between the parents allowing each to take care of itself while brooding and serving as sentries for each other to avoid predation (Székely *et al.* 2006). However, parents also face a trade-off between their current investment and future reproductive opportunities. This may result in some bird species shunting parental care to one parent (either male or female) who will either have to raise the brood alone or perform the bulk of parental care (Osorno & Székely 2004; Houston *et al.* 2005; Székely *et al.* 2006).

Despite being an energetically costly activity, biparental incubation has several potential benefits. Near-constant incubation ensures development of embryos at or near the maximum rate physiologically possible which translates to the shortest possible incubation period. It also relieves some of the stresses of the incubating female by allowing time for foraging and maintaining body condition. In a hot environment, shared incubation may also help parents to reduce heat stress by relieving each other frequently. Constant nest attendance may reduce the chances of being cuckolded or reduce the likelihood of nest predation. Finally, it may also serve to strengthen the pair bond (AlRashidi *et al.* 2010).

The finding that the diurnal contribution to incubation by males is similar to that of the females is rather surprising. Unlike females, male chestnut-backed sparrow-larks do not develop brood patches when breeding (pers. obs.). A brood patch is an area devoid of down and contour feathers on the ventral surface of a bird and is an adaptation to increase the efficiency with which body heat is transferred to eggs (Wiebe & Bortolotti 1993). Brood patch formation is an energetically costly activity and its absence in males is probably due to the fact that in most species, including the chestnut-backed sparrow-lark, the females are responsible for incubating at night. Nevertheless, despite the absence of a brood patch in males of most species, they are able to incubate effectively and can positively influence the development of embryos (Bailey 1952; Drent 1975; Auer *et al.* 2007). Although heat transfer to eggs is likely to be less from males compared to females, males help maintain egg temperatures at optimal ranges (or at least reduce heat loss from eggs) thereby reducing the harmful effects of bad weather; this may result in increased hatching success (Reid *et al*. 2002b; Hepp *et al*. 2006). In fact, a large proportion of incubation on-bouts during the warmer parts of the day are actually spent shading the eggs rather than actively incubating.

The mean incubation period of 10.33 ± 0.49 days recorded during the present study is similar to the 10.5–11.5 days observed by Chittenden & Batchelor (1977). The incubation period of most larks lasts 11–13 days, but *Eremopterix* larks have some of the shortest incubation periods of birds ranging from 8–10 days (Keith *et al.* 1992; de Juana *et al.* 2004; Lloyd 2004). In general, opportunistically breeding species in arid areas tend to have small clutches and short incubation periods (Dean 2004). Once more, this reflects an adaptation to exploit optimum but transient conditions when these are available. Any unnecessary extension of the nesting cycle such as large clutch sizes or prolonged incubation periods may i) result in some parts of the breeding cycle taking place after this window of optimal conditions has passed, or ii) limit opportunities for repeat- or replacement broods if optimum conditions for breeding is extended for longer than expected. This, in turn, may affect breeding success, future reproductive opportunities and the fitness of the offspring (Metcalfe & Monaghan 2001). Given the poor breeding success of the species, it is also possible that the small clutch sizes and short incubation and nestling periods recorded for chestnut-backed sparrow-larks are possibly adaptations to avoid or reduce predation. Rapid incubation and nestling periods will also enable quicker repeat nesting if wet/good conditions extend for longer than expected. Farnsworth & Simons (2001) reported that in birds with large clutch sizes, the eggs are exposed to predation for a longer period of time which may result in reduced breeding success. Although a short nesting cycle reduces the risk of nest predation, short incubation periods require an increase in parental investments (Martin 2002). It is tempting to suggest that the brief incubation period of sparrow-larks may be due to near-constant biparental incubation. However, the genus *Spizocorys*, which also shares incubation between the sexes, has incubation periods of 11–12 days (Tarboton 2001), which is similar to that of species in which only a single parent incubates. Although both sexes are known to incubate in the genus *Spizocorys*, the relative contribution of the sexes during incubation is as yet unknown.

2.4.5. Nestling growth and development

The mean nestling period (9.2 ± 0.84 days) in the study area is less than the nestling period of 10–12 days reported by Morel & Morel (1984). Various measures were taken to avoid premature fledging and it is therefore unlikely that observer interference is responsible for the shorter nestling period recorded in this study. Nevertheless, it is comparable to that of other southern African sparrow-larks, which generally range from 7–10 days (Lloyd 1998). Moreover, it falls within the range of most other larks, which range from 7–14 days (de Juana *et al.* 2004; Donald 2004; Engelbrecht 2005; Maphisa *et al.* 2009). Larks grow very rapidly and are able to walk or run well and even flutter-fly in some instances upon fledging. This allows the brood to disperse, thus reducing the likelihood of an entire brood being lost to predation (Donald 2004; Engelbrecht 2005).

The diet of nestlings was typical of granivorous larks and comprised mostly of invertebrates, supplemented with seeds. The results show that at least 50% of the diet comprised invertebrates but this is likely to be more as unknown food items included a significant part of the diet (15%). Some of these unknown items were likely to have been invertebrates, which will increase the proportion of invertebrates in the diet. Invertebrates form the main dietary component of the majority of lark nestlings as was observed for the short-clawed lark (*Certhilauda chuana*) (Engelbrecht 2005), black-eared sparrow-lark (Maclean 1970b), grey-backed sparrow-lark (Willoughby 1971), red-capped lark (*Calandrella cinerea*) (Winterbottom & Wilson 1959), and Rudd's lark (*Heteromirafra* ruddi) (Maphisa 2004). A protein-rich diet allows for rapid growth and development of tissues and feathers as it provides some essential amino acids that cannot be synthesized by the body (Gill 1995). Moreover, invertebrates may also supply the water requirements of nestlings.

The study revealed that female chestnut-backed sparrow-larks made statistically significantly more nest visits to deliver food to nestlings (54.6% vs. 45.5%) compared to males. This suggests that the relative contribution of the sexes is not entirely symmetrical. Whether this is due to a shift in parental responsibilities remains unknown as yet.

The protein rich diet of invertebrates and seeds fed to the nestlings results in rapid development and growth of nestlings. The results of the growth curve analysis show that most growth of the parameters recorded was completed shortly after hatching. The growth of the tarsus was the fastest of the meristic measurements recorded and most of its growth was completed around the time of fledging (t_{10-90} = 11.1 days). Rapid growth of the tarsus is essential to allow fledglings to be mobile, scamper in the vegetation and also escape potential predators. Recently fledged young are able to move surprisingly fast. The tarsus also has to be well developed to support the mass as the asymptotic mass is also reached at about fledging. Most of the growth of the wing chord is completed shortly after fledging, which confirms observations of recently fledged young being able to flutter-fly short distances within a week after fledging.

2.4.6. Breeding success

Not surprising for larks, breeding success in the study area was very low, averaging 16.1% for the three years during which data was collected (Table 2.4). Bird species with open nests on the ground are known to experience greater predation than enclosed nests or nests placed high above the ground (Ricklefs 1969; Johnson 1991). The breeding success of the chestnut-backed sparrow-lark compares favourably with estimates reported for other southern African sparrow-larks. The low breeding success of the grey-backed sparrow-larks (17%) and black-eared sparrow-larks (31%) are mostly attributed to predation by small mammals including mongooses (Maclean 1970a; Lloyd 1998). The breeding success for a majority of larks is unknown, but for those that are known, the breeding success is generally low. The breeding success ranges from as low as 4% for the Stark's lark (*Spizocorys starki*) (Lloyd 2005b) to as high as 61% for the red-capped lark (Winterbottom & Wilson 1959). Other larks whose breeding success has been estimated include singing bush-lark (*Mirafra cantillans*) (19%); Rudd's lark (30%); spike-heeled lark (*Chersomanes albofasciata*) (22%); short-clawed lark (44%); and Sclater's lark (*Spizocorys sclateri*) (20%), sabota lark (*Calendulauda sabota*) (38%), fawn-coloured lark (*Calendulauda africanoides*) (30%), dune lark (*Calendulauda erythrochlamys*) (28%) and pink-billed lark (*Spizocorys conirostris*) (15%) (Maclean 1970a; Maclean 1970b; Boyer 1988; Mullié & Keith 1991; Keith *et al.* 1992; Lloyd 1998; Engelbrecht 2005; Maphisa *et al.* 2009). From the foregoing, it is evident that the chestnut-backed sparrow-lark's low breeding success compares well with that of other larks.

Although there were no differences in the daily survival rate during the incubation, hatching and nestling periods when all the data was pooled, there were inter-annual differences in the daily survival rates. In 2008 and 2009, the daily survival rate during incubation was slightly higher than during the nestling period (Table 2.4). This is different to many other lark species that generally have a higher daily survival rate during the nestling period. Although the differences in daily survival calculated in this study is small, it may reflect the chestnut-backed sparrow-lark's preference for nesting in areas almost entirely devoid of cover. This, in turn, also makes it unsuitable for some predators, e.g. snakes and rodents that may prefer to forage in areas with at least some degree of cover. More research is required to determine the effect of nest site selection on the daily survival rate of the chestnut-backed sparrow-lark.

In 2010, an unexpected cold spell and unseasonal rainfall in April (*cf.* Fig. 2.2) resulted in abandonment and flooding of several nests during the incubation period. This may account for the poor daily survival rate during the incubation period in 2010 (Table 2.4). The poor hatching rate also suggests that some embryos may have died from exposure. Observations of incubating birds show that they will remain on the nest during an average rainstorm, but will abandon the nest for cover during a torrential downpour. Furthermore, as this cold front and rain coincided with the peak of the main breeding period of the species in the study area, it appears that this resulted in most pairs abandoning the breeding attempt. This may also explain the small number of nests found during April 2010.

The low breeding success rate reported here suggests that repeat (i.e. successive breeding attempts after successfully fledging) and replacement (i.e. successive breeding attempts after nest failure) breeding attempts should be a common phenomenon. Although replacement breeding attempts are relatively common in the family (de Juana *et al.* 2004), comparatively little is known of lark's ability to produce double- or multiple repeat clutches in a single breeding season. Since there have been few long-term or intensive studies on the breeding biology and ecology of larks, its prevalence in the family remains a matter of conjecture. Moreover, double- or multiple repeat breeding attempts will be difficult to prove unequivocally in nomadic species or species exhibiting extensive local movements. However, some recent studies have revealed that double- and perhaps even multiple repeat breeding attempts by larks are perhaps more common than previously expected (de Juana *et al.* 2004; Engelbrecht 2005; Maphisa *et al.* 2009). Species such as the desert lark, bimaculated lark (*Melanocorypha bimaculata*), calandra lark (*Melanocorypha calandra*), and horned lark (*Eremophilia alpestris*) are mostly double-brooded (de Juana *et al.* 2004). Other species such as short-clawed lark can have as many as five breeding attempts (Engelbrecht 2005), whereas four attempts are known for dune (Ryan *et al.* 2004) and Rudd's lark (Maphisa *et al.* 2009).

The fact that NERCS records show that breeding by chestnut-backed sparrow-larks have been reported in all months of the year, suggests that the species must be capable of double- or multiple repeat breeding attempts as suggested by Morel & Morel (1984). This is important for nomadic species which must be able to breed when conditions are favourable. Replacement breeding attempts were relatively common in this study and a new breeding attempt was usually initiated 2–3 weeks after nest failure. During the study, one colour-marked pair was observed breeding in April and again in September. This observation represents breeding during the two peak breeding periods of the chestnut-backed sparrow-lark in the study area and shows that they are at least capable of double-brooding. In addition to this, the abovementioned observation provides the first evidence of mate-fidelity during the breeding season in this species. It remains to be established if this is a common phenomenon. Given the relatively long lag period between nest failure and initiation of a replacement clutch, the brevity of the two breeding periods make it unlikely that double-brooding will be possible during one of the peaks.

2.5. Conclusion

This is the first long-term study of the biology of the chestnut-backed sparrow-lark and one of only a few of species in the family. The results revealed several adaptations of a species to exploit favourable but transient conditions, e.g. extended breeding seasons, short nesting cycles, biparental care and double-brooding. The study also highlighted the importance of conducting long-term studies to account for inter-annual differences in various breeding parameters, e.g. breeding success.

Table 2.1. Nest dimensions (mm) of the chestnut-backed sparrow-lark (*Eremopterix leucotis*) (*n* = 55 nests; except for apron, *n* = 44) at De Loskop, Limpopo Province, South Africa, recorded from January 2008 to December 2010.

	Nest site characteristics	**Mean ± S.D.**	**Range**
Nest Dimensions	Nest diameter	122.56 ± 20.53	81.00–190.00
	Cup diameter	53.40 ± 3.43	45.00–63.00
	Cup depth	27.88 ± 3.95	20.00–37.00
	Apron	30.00 ± 15.50	10.00–85.00

Table 2.2. Clutch size, egg and clutch mass as well as egg dimensions of the chestnut-backed sparrow-lark (*Eremopterix leucotis*) at De Loskop, Limpopo Province, from January 2008 to December 2010. FEM = fresh egg mass (g); EEM = estimated egg mass (g); EW_{max} = maximum width of the egg (mm); EL_{max} = maximum length of the egg (mm); EEI = Egg elongation index; CM = clutch mass (g); EV = egg volume (mm^3).

Parameter	Mean ± S.D.	Range	*n*
Clutch size	1.88 ± 0.33	1.00–2.00	88
FEM	2.02 ± 0.20	1.67–2.40	23
EEM	1.98 ± 0.17	1.66–2.29	43
EW_{max}	13.90 ± 0.45	13.00–15.00	66
EL_{max}	19.87 ± 0.91	18.10–21.90	66
EEI	1.43 ± 0.07	1.25–1.60	66
CM (1-egg)	1.95 ± 0.13	1.78–2.16	8
CM (2-eggs)	3.99 ± 0.35	3.36–4.80	29
EV	3842.83 ± 341.67	3211.00–4927.50	66

Table 2.3. Main developmental events of chestnut-backed sparrow-lark (*Eremopterix leucotis*) nestlings as recorded at De Loskop, Limpopo Province, from January 2008 to December 2010.

Day	**Description**
0	Eyes closed. Skin is a dark, purplish-black colour with tufts of straw-coloured down on all the feather tracts except the ventral feather tract. Primary, secondary and caudal neosoptiles visible. Culmen and nostrils are blackish-horn coloured but the tip of the bill is a paler grey colour. Gape flange is a pale whitish-yellow colour and the inside of the mouth is bright orange with two laterally situated tongue spots at the back of the tongue and one at the distal tip of the tongue. The upper and lower mandibles also have a black spot on each tip.
1	No feather tracts have erupted yet but are visible under the skin.
2	Eyes open slits, tracts clearly visible below the skin. The skin has turned a lighter pinkish-purple colour.
3	Eyes open. All feather tracts erupted. Ventral and capital tract have the least quills erupted.
4	Pin feathers continue to grow.
5	First feathers on the spinal, alar, ventral, crural and femoral tracts start breaking from their sheaths, i.e. are in brush. Occasionally the first secondary flight feathers may be in brush.
6	All tracts, including the capital and caudal but not the remiges and rectrices, have at least some feathers in brush.
7	First primaries and secondaries in brush.
8	Most primaries and secondaries in brush.
9	All primaries and secondaries in brush. First primary and secondary greater coverts in brush.
10	Primaries ± 25–30% in brush

Table 2.4. Inter-annual breeding success of the chestnut-backed sparrow-lark (*Eremopterix leucotis*) at De Loskop, Limpopo Province, from January 2008 to December 2010.

Measure of breeding success	2008	2009	2010	All years
Daily survival during incubation	0.95	0.93	0.85	0.92
Hatching rate	0.92	0.86	0.71	0.92
Daily survival in the nestling period	0.90	0.92	0.95	0.92
Overall breeding success (%)	20.6	17.3	8.1	16.1

Fig. 2.1. A satellite image of the study area (within the black border) at De Loskop (23°30'S; 29°19'E; 1090m above sea level), Limpopo Province, South Africa. (Google 2012; Image date: 01 January 2008).

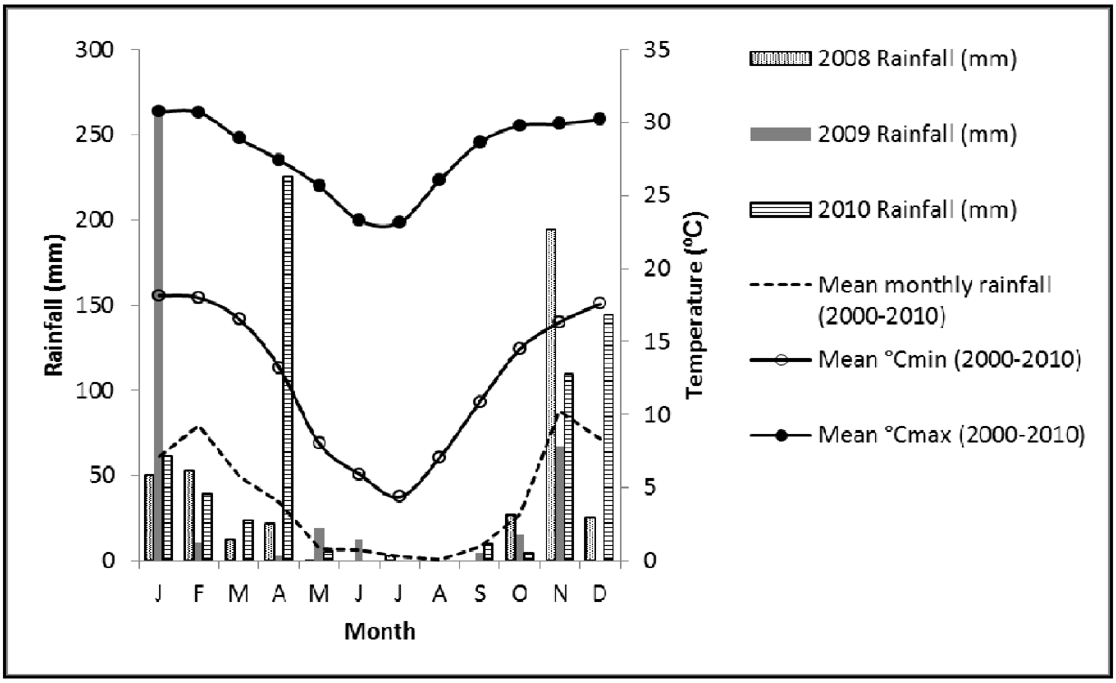

Fig. 2.2. Weather data from the Mara weather station (38km north-east of the study area at De Loskop) for the period January 2008 to December 2010. °Cmin = minimum temperature; °Cmax = maximum temperature). Data courtesy of the South African Weather Service (2010).

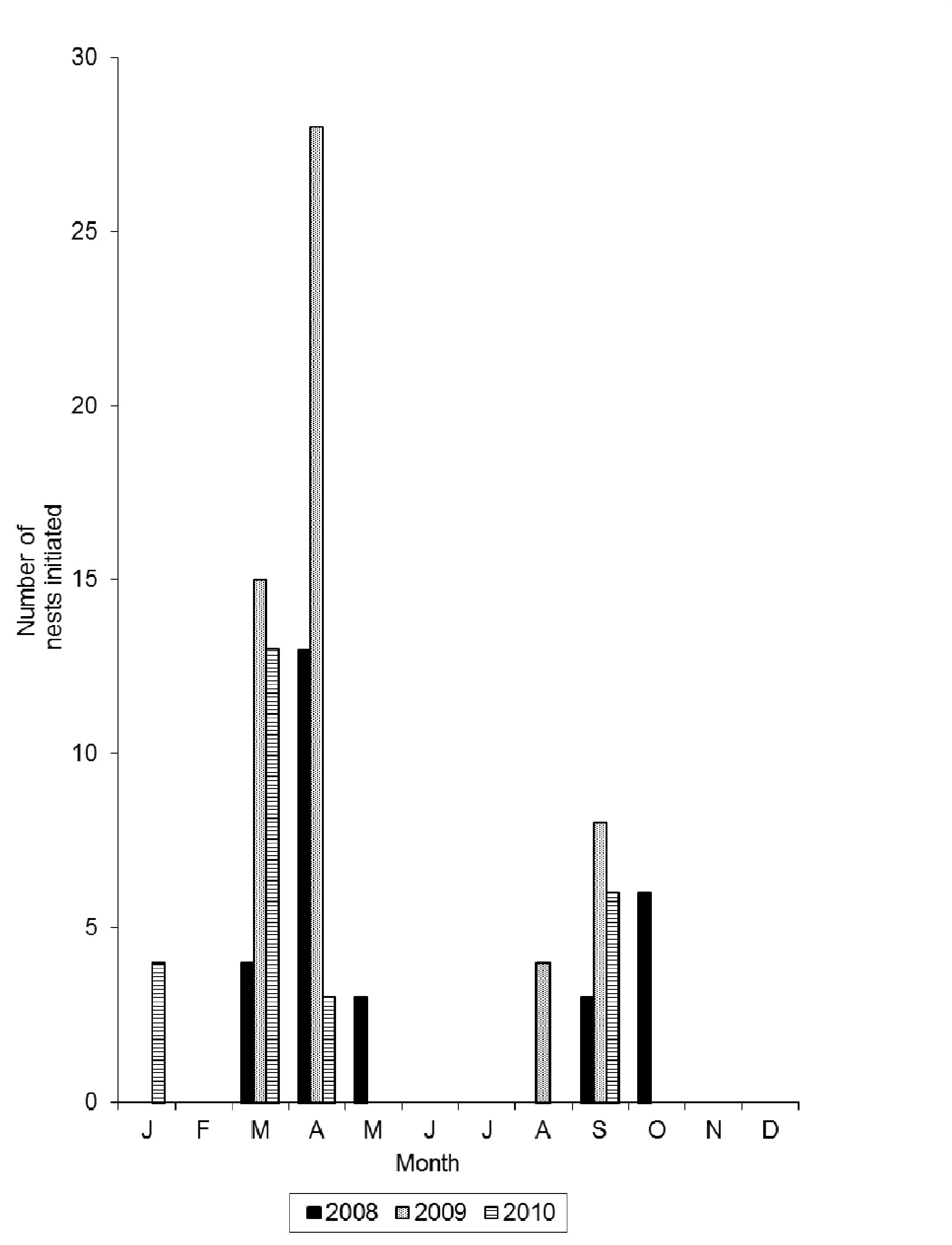

Fig. 2.3. Number of chestnut-backed sparrow-lark (*Eremopterix leucotis*) nests initiated per month from January 2008 to December 2010 at De Loskop, Limpopo Province.

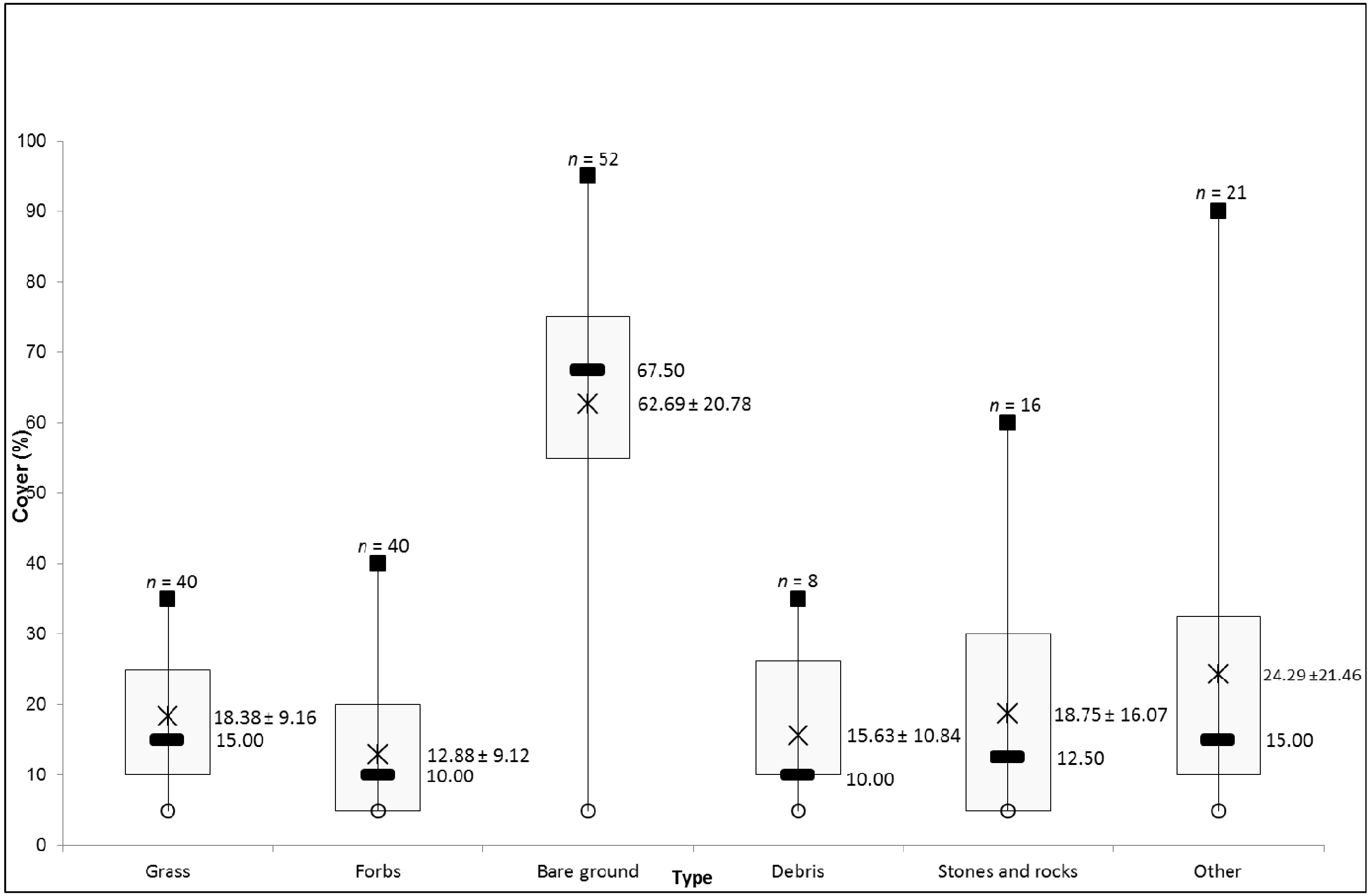

Fig. 2.4. Nest site characteristics of the chestnut-backed sparrow-lark (*Eremopterix leucotis*) at De Loskop, Limpopo Province from January 2008 to December 2010. Filled square and open circle represent the maximum and minimum values, solid bar the median and “x” the mean. The box represents the interquartile range, i.e. middle 50% of the ranked data and is drawn from the first to the third quartile.

Fig. 2.5. Incorporation of spider silk in the chestnut-backed sparrow-lark's (*Eremopterix leucotis*) nest structure (De Loskop, Limpopo Province, March 2009).

Fig. 2.6. Chestnut-backed sparrow-lark's (*Eremopterix leucotis*) nest with a well-developed apron and adjacent to a tuft of grass (De Loskop, Limpopo Province, March 2009).

Fig. 2.7. Chestnut-backed sparrow-lark's (*Eremopterix leucotis*) nest with a small apron and situated next to a tuft of grass (De Loskop, Limpopo Province, April 2009).

Fig. 2.8. Chestnut-backed sparrow-lark's (*Eremopterix leucotis*) nest without an apron and placed next to a tuft of grass (De Loskop, Limpopo Province, March 2010).

Fig. 2.9. Chestnut-backed sparrow-lark's (*Eremopterix leucotis*) nest adjacent to a rock (De Loskop, Limpopo Province, September 2009).

Fig. 2.10. Chestnut-backed sparrow-lark's (*Eremopterix leucotis*) nest completely in the open and not associated with a base structure and without an apron (De Loskop, Limpopo Province, March 2009).

Fig. 2.11. Chestnut-backed sparrow-lark's (*Eremopterix leucotis*) nest at the base of a forb (De Loskop, Limpopo Province, March 2009).

Fig. 2.12. Chestnut-backed sparrow-lark (*Eremopterix leucotis*) nestling in the latter stages of the nestling period, demonstrating the disintegration of the nest structure (De Loskop, Limpopo Province, April 2010).

Fig. 2.13. Chestnut-backed sparrow-larks (*Eremopterix leucotis*) often starts laying well before the nest structure is complete and the sexes continue to deliver nest material to the nest throughout the incubation period (De Loskop, Limpopo Province, March 2010).

CHAPTER 3

Biometrics, moult and vocalizations of the chestnut-backed sparrow-lark *Eremopterix leucotis*

3.1. Introduction

Sparrow-larks (*Eremopterix*) form a relatively small genus in the family Alaudidae and comprise only seven species distributed widely in Africa and sparsely in Eurasia. Sparrow-larks are unique amongst the Alaudidae as they are the only distinctly sexually dichromatic species in the family. Whereas female sparrow-larks have the typical cryptic, drab colouration of larks, males are characterized by being black on the head and ventral plumage, with six of the seven species having white ear patches and collars on the hind neck. Another unusual, but not unique, characteristic of the sparrow-larks is that they exhibit biparental care in all aspects of the breeding cycle. The only other larks exhibiting biparental care are members of the genus *Spizocorys* which includes Stark's lark (*S. starki*), Botha's lark (*S. fringillaris*), pink-billed lark (*S. conirostris*) and Sclater's lark (*S. sclateri*) (de Juana *et al.* 2004). However, *Spizocorys* larks are not sexually dichromatic.

Three *Eremopterix* species occur in southern Africa, namely the black-eared sparrow-lark (*E. australis*), grey-backed sparrow-lark (*E. verticalis*), and chestnut-backed sparrow-lark (*E. leucotis*). The black-eared sparrow-lark is endemic to southern Africa and its distribution is centred in the central Karoo, South Africa. The grey-backed sparrow-lark is a southern African near-endemic with a mostly western distribution in southern Africa, the coastal plain of Angola and the extreme south-west of Zambia. The chestnut-backed sparrow-lark has the largest distribution range of the African *Eremopterix* larks and includes most of the semi-arid savanna regions of sub-Saharan Africa. In the north of its range it occurs in sahelian and soudanian savannas from Senegal and the Gambia in the west to parts of Sudan, Ethiopia, Eritrea and Somalia in the east, extending south to the arid and semi-arid savannas of Kenya and Tanzania. The northern and southern populations of the species are separated by a gap in the species' distribution between approximately 12–15°S. The "southern" subspecies, *E. l. smithi* and *E. l. hoeschi* occurs in short, open grassland and arid to semi-arid savannas of southern Malawi, southern Zambia, southern Angola and southern Africa (Keith *et al.* 1992). Given its widespread distribution, it is not surprising that five subspecies are recognized (see Table 1.2). Once again, the subspecies are recognized on the basis of differences in plumage colouration, but there are also morphological differences between the subspecies. According to Hall & Moreau (1970) and Ryan *et al.* (2004), the two southern subspecies (*E. l. hoeschi* and *E. l. smithi*) are larger than the three northern subspecies (*E. l. leucotis, E. l. melanocephalus* and *E. l. madaraszi*), but unfortunately the authors do not provide any additional details or references.

The majority of ornithological research on African larks to date focussed on resolving taxonomic debates and the description of new species or subspecies. As inhabitants of some of the most austere habitats on earth, larks make interesting subjects for eco-physiological research and several studies have focussed on how they survive in these extreme conditions (Cade *et al.* 1965; Dawson *et al.* 1979; Williams 1996; Williams & Tieleman 2000; Tieleman *et al.* 2002; Tieleman *et al.* 2003a, b, c; Tieleman *et al.* 2004). Compared to the abovementioned types of studies, relatively few studies have focussed on the description of the biology and ecological requirements of larks. Research on the biology and ecology of African larks has focussed mostly on species of conservation concern (Allan 2001; Engelbrecht 2005; Maphisa *et al.* 2009) or species occupying extreme environments (Boyer 1988; Dean 1997). Some of the most common and/or widespread larks in Africa are also the least known in the family and we lack the most basic information, e.g. length of the incubation and nestling periods, biometric data and moult strategies, for the majority of species. Most of our present knowledge of larks is based on anecdotal observations of one or a few nests or breeding events. A few studies spanned a single breeding season and fewer still include two or more breeding seasons. A thorough understanding of a species' biology and ecological requirements is essential for effective management of a species and also for conservation planning. Moreover, Hall & Moreau (1970) in their summary of the Alaudidae states: "The best hope for an advance in classification of the larks lies in an increase of biological information, especially from field workers with opportunities to study related species in all parts of their ranges." Chapter 2 focussed on elucidating aspects of the chestnut-backed sparrow-lark's biology that relate directly to its breeding in southern Africa. This chapter will further our knowledge of the biology of the species by investigating aspects of the species' life history that do not relate directly to breeding, namely, biometric variation, moult and vocalizations.

The specific objectives of this chapter were to record and describe intraspecific morphological variation in the two southern subspecies, *E. l. hoeschi* and *E. l. smithi*, to describe the moult pattern of the southern subspecies, and to analyse and describe the different vocalizations of a population of *E. l. smithi* in South Africa's Limpopo Province. A brief background to each of these objectives follows below.

3.1.1. *Intraspecific morphological variation*

Populations of a species that are separated in space or time may vary in some characteristics. This geographical variation may manifest itself in the phenotype or genotype and can include, amongst others, variation in external morphology (e.g. size, shape, colour), internal morphology (e.g. organ position or size of anatomical structures), physiology (e.g. temperature tolerance, disease resistance, water requirements), biochemistry (e.g. isozymes and blood proteins), physical performance, breeding system (e.g. monogamy, polygamy or co-operative breeding), and/or nuclear DNA and mtDNA markers. Studies of geographic variation have aided the understanding of micro-evolutionary forces, speciation, species concepts, and the nature of species and biodiversity (http://science.jrank.org/pages/48479/Geographic-Variation.html. Accessed 28 April 2011).

Geographical variation or subspecies based on morphological and plumage differences is a common phenomenon in larks. Geographical variation results from phenotypic plasticity, which is a concept describing the changes in adult phenotypes depending on the environment and differences amongst phenotypes resulting from developmental conditions (Tieleman *et al.* 2003b). This is mostly because the geographical distribution of species includes different environments and it is highly unlikely that a single phenotype will exhibit high fitness in all the environmental conditions (Tieleman *et al.* 2003b).

Traditionally, studies of biometric variation in larks have emphasized taxonomic aspects of population differences in selected measurements of a few individuals, usually as an additional aid for the delineation of subspecies based on variation in plumage colouration. Although geographic variation in plumage colouration of larks is well known and reported in the literature, little is known about intraspecific morphological and sexual differences for the majority of species. This is despite the potential value of biometric studies of natural geographical variation as an aid to answer both theoretical and applied questions in avian ecology (Morgan 2004).

Geographical variation with regard to body and bill size is known for several species of larks, the most notable arguably being the sabota lark *Calendulauda sabota*. In this species, populations in the arid western and central parts of the species' range are characterised by a large, awl-shaped bill and large size, whereas populations in the east are characterised by their smaller size and more slender bills. According to Hall & Moreau (1970), the chestnut-backed sparrow-lark also displays geographical size variation with the two southern subspecies being larger than the three northern subspecies. It is uncertain if these differences have a genetic basis or whether it simply reflects clinal variation in a north-south direction. The present study will investigate biometric variation in the two southern subspecies and determine if there are morphological differences between the mostly easterly distributed *E. l. smithi* and the more westerly distributed *E. l. hoeschi* in southern Africa.

Another interesting aspect of morphological variation in larks concerns the occurrence of sexual size dimorphism. Although sexual size dimorphism is evident in most larks, the extent thereof differs amongst species and relates in part to the species' degree of residency and diet (Dean 1997; de Juana *et al.* 2004). For example, resident insectivorous larks display the greatest degree of sexual size dimorphism (particularly with regard to bill length), whereas it is less evident in nomadic and/or granivorous species (de Juana *et al.* 2004). Thus, one would not expect the chestnut-backed sparrow-lark to display significant sexual size dimorphism. This is because adults of the species are essentially granivorous and most populations are either nomadic or at least prone to local movements in response to favourable environmental conditions (de Juana *et al.* 2004). Furthermore, the sexually dichromatic appearance of chestnut-backed sparrow-larks partially offsets the need for sexual size dimorphism as an aid in sexual recognition. It has been suggested that the sexual dichromatism exhibited by the species allows for easy recognition of sexes and rapid settlement and breeding when favourable conditions arise (Barnes 2007). This essentially negates the necessity for marked sexual size dimorphism as males do not have to engage in physical contests for females by fighting or by defending territories. However, males do engage in song flights which are amongst the most energetically demanding forms of sexual selection in the animal kingdom (Donald 2004). One would therefore expect that morphological adaptations to reduce energy expenditure during song flights would be favoured by natural selection. For example, skylark (*Alauda arvensis*) males have a lower wing loading, i.e. the ratio of body weight to wing area, and a larger sternum compared to females (Møller 1991; Lüps *et al.* 1993). Skylark males with a lower wing loading make longer song flights than males with a higher wing loading (Møller 1991). This study will investigate if the chestnut-backed sparrow-lark exhibits, in addition to sexual dichromatism, also sexual size dimorphism.

3.1.2. *Moult*

For birds, the timing of breeding and moult are thought to be some of the most crucial aspects in a bird's annual cycle (Immelmann 1971). According to Barta *et al.* (2006), proper timing is important for three reasons: i) the benefits from these events can vary significantly over the year, e.g. survival of young may depend on when they hatched in the season, ii) performing an action at any given time may significantly influence the animal's future state, which in turn may influence its available actions in future, e.g. when an animal migrates, it changes both its energy reserves and location, which, in turn, influences whether an animal can breed and how successful it may be, and iii) the performance of one activity may exclude the performance of other activities, e.g. breeding and migration at the same time are mutually exclusive.

The timing of breeding is important because of its obvious impact on the bird's breeding success, the considerable energetic costs involved and its impacts on the future survival of the bird. Moult, i.e. the regular replacement of worn plumage by new feathers, is a process that also requires a large input of energy and materials, especially proteins (Maclean 1990). However, it is a necessary process as feathers undergo continuous degradation as a result of abrasion and UV radiation. Reduced feather quality affects flight efficiency and reduces the insulative properties of feathers, thus resulting in increased metabolic costs. A reduction in flight efficiency may also affect a bird's ability to escape from predators. Thus, moulting has advantages in terms of future performance. However, there are also direct costs involved during moulting. Apart from the tremendous energy and protein requirements during moult, flight performance and insulation may be severely affected. The latter is particularly important as it places additional energetic demands on the bird apart from those required for the production of new feathers (Gill 1995). These are some reasons why breeding and moult generally do not overlap in the majority of birds (Maclean 1990; Gill 1995), the ultimate reason being the inherent, genetically programmed circannual rhythms of birds (van Niekerk 2009).

The typical moult pattern of the majority of species involves a complete post-nuptial moult at the end of the breeding season. However, there are many variations on this pattern, particularly amongst species in the tropics. These include a pre-nuptial moult (Brooke 1985), moulting while breeding (Payne 1969; Craig 1983), a complete moult surrounded by a bi-annual breeding season (Wilkinson 1983) or a complete moult following each of the two breeding seasons (Miller 1961; Barta *et al.* 2006). Most larks, however, follow the general pattern of a complete post-nuptial moult (de Juana *et al.* 2004). There are a few exceptions though. A subspecies of the greater short-toed lark (*Calandrella brachydactyla dukhunensis*) undergoes a partial moult affecting the body and upper-wing coverts (de Juana *et al.* 2004). Two complete annual moults have been described for three larks of the Namib Desert in southern Africa, namely Gray's lark (*Ammomanopsis grayi*), Stark's lark and the grey-backed sparrow-lark (Willoughby 1971). The "usual" post-nuptial moult is relatively rapid and takes advantage of the increased food abundance following rains, whereas the second moult is prolonged and continues throughout the dry season. However, it has been suggested that a single, prolonged moult, suspended while breeding is a more likely explanation (de Juana *et al.* 2004). In both the partial and complete moult examples given above, the unusual moult strategy is explained as an adaptation to the rapid wear of plumages that are exposed to wind, sand, vegetation and radiation (de Juana *et al.* 2004). In addition to the adult moult, juvenile larks also undergo a complete post-juvenile moult when about 4–8 weeks old.

The chestnut-backed sparrow-lark breeds mostly towards the end of the wet season and/or during the dry season throughout its range (Ryan *et al.* 2004). However, the species is also an opportunistic breeder and as such breeding has been reported in all months of the year in a given region (Irwin 1981; Ryan *et al.* 2004; Lloyd 2005a). One would therefore expect variation in the onset and duration of both the breeding season and moult in different populations. The only reference to moult in the chestnut-backed sparrow-lark is by van Niekerk (2009) who recorded moult in spring and summer in the

Free State Province, South Africa. The present study will shed light on this crucial aspect of the species' annual cycle by describing the timing and moult strategy from museum specimens as well as data from the study area and the SAFRING database.

3.1.3. *Vocalizations*

Sound is a sequence of mechanical waves of pressure transmitted through media that can be solid, liquid or gas. Waves can be reflected or refracted as a result of moving through media with different physical properties. Sound waves are generally affected by three aspects, namely, the relationship between density and pressure, motion of the medium and viscosity of the medium. The relationship between density and pressure is affected by temperature and determines the speed of sound within the medium. The motion of the medium affects the distance that sound can travel such that if sound travels through gas, it can be transported further than when it travels through liquids and solids. Viscosity is a quantity that describes a fluid's internal resistance to flow and the viscosity of a medium determines the rate at which sound can be attenuated (Kalat 2007).

Bioacoustics refers to a cross-disciplinary science that combines biology and acoustics, and investigates the production of sound, dispersion of sound through media and reception of sound in animals, including humans. It also concerns the organs of hearing and sound production as well as physiological and neurological processes by which sounds are produced and received for communication and echolocation purposes. The collection of sounds produced by insects, amphibians, mammals and birds for communication are of great importance as they can be used and applied in research. Vocalizations are species-specific and as such can be used in taxonomy, systematics and biological studies. They can also be used to measure and monitor the diversity of complex communities in dense vegetation and forests where visual observations are difficult. In birds, vocalization refers to all sounds produced by voice and includes song (e.g. full or primary song and subsong) and calls (e.g. distress, alarm and flight calls) (Krebs & Kroodsma 1980; Catchpole & Slater 1995; Chen & Maher 2006).

Birds have the greatest sound-producing capabilities of all vertebrates (Gill 1995). The variety of sounds emitted by birds reflects adjustments to enhance the information content and the physical transmission of information to listeners (Gill 1995). Sound is produced by forcing air from the lungs through the bronchi to the syrinx, which is the major source of vibratory modulation. Sound from the syrinx then passes through the resonant structures of the trachea, larynx, mouth, and beak. A bird controls the sound it produces by varying the tracheal length, by constricting the larynx or by flaring its throat and beak (Gill 1995).

Bird vocalizations can be divided into the general categories of elements, syllables, phrases, calls, and songs (Fig. 3.1). Elements can be regarded as the elementary sonic units in bird vocalizations (Chen & Maher 2006). A syllable includes one or more elements and is usually a few to a few hundred milliseconds in duration and forms part of a phrase (Chen & Maher 2006). Phrases are short groupings of syllables forming part of a song sequence (Chen & Maher 2006). Different phrases or several repetitions of the same phrase make a song sequence. However a song sequence may also be made by only one phrase (Cramp & Simmons 1977). Calls are generally short, simple sequences of phrases given by either sex and serving mainly to alert and coordinate group behaviour (Cramp & Simmons 1977; Gill 1995; Chen & Maher 2006). Most calls do not vary with the season and, in contrast to song, are not strongly influenced by the state of seasonal development of the sex hormones (Cramp & Simmons 1977). Various calls include distress, flight, warning, feeding, nest and flock calls (Gill 1995). Songs (sometimes called full song or primary song) are long and complex vocalizations often with specific, repeated patterns and are recognizable not only at the specific level but often at group and individual levels (Cramp & Simmons 1977; Gill 1995; Chen & Maher 2006). Song is usually under the control of the sex hormones and is primarily used in territorial and mate attraction/retention contexts, and its utterance is therefore largely confined to the breeding season. Song is an expression of dominance, adulthood and sexual activity (Maclean 1990). A male in song advertises the possession of a site for nesting in suitable habitat where food will not be a limiting factor either immediately or ultimately when there are young (Maclean 1990). Another type of song, subsong, is usually a quiet, extended warbling song, in which fragments of the full song may be heard, often with imitation of other species (Cramp & Simmons 1977). A bird uttering subsong is usually perched low and in an inconspicuous place and, interestingly, the beak may often be closed while singing (Cramp & Simmons 1977).

In addition to these vocal sounds, birds may also make a number of non-vocal sounds, e.g. the wing-clapping displays of some larks, drum-rolling of woodpeckers, tail drumming of snipe and quill-rattling of Indian peafowl (*Pavo cristatus*). In some instances, these non-vocal sounds can be used as a taxonomic tool to distinguish species, e.g. Cape clapper lark (*Mirafra apiata*) and eastern clapper lark (*Mirafra fasciolata*).

Birds generally have 5–14 distinct calls with a variety of overlapping functions (Gill 1995; Baptista & Kroodsma 2001). The functions of calls typically include territorial advertising, attraction of mates, advertising personal characteristics (e.g. species, age, sex, and competence), warning calls (including aggressive and alarm calls) and maintenance of social contact (Gill 1995; Baptista & Kroodsma 2001).

Despite the dull plumage of larks, they are revered as some of the finest songsters amongst birds. It is commonly accepted that the name of the family comes from a Latin corruption of the Celtic word for “great singer” (*al* = great; *awd* = song) (Donald 2004). Amongst passerines, there is usually an inverse relationship between plumage colouration and song development: brightly coloured birds use visual cues to attract mates, whereas dull, drab-coloured birds rely more on song (de Juana *et al.* 2004; Donald 2004). The need for camouflage in the open habitats that larks typically inhabit, has favoured cryptic plumage in the family. This, in turn, has led to a greater investment in song as a means of advertising individual quality amongst territorial males (de

Juana *et al.* 2004). However, the open habitats typically occupied by larks usually have few elevated song posts that would allow songs to be transmitted over long distances and would reduce the likelihood of singers being surprised by terrestrial predators. This may have led to larks developing song flights, despite the considerable energetic costs involved (de Juana *et al.* 2004). Song as a means of advertising has the advantage that it can be "switched on or off" as required, making it safer than permanent visual displays, structures or colours in the open habitats preferred by larks (Baptista & Kroodsma 2001).

The song of larks varies from extremely complex and highly variable to simple mono syllabic notes. For example, the skylark has a repertoire size of 160–460 syllables, excluding the inclusion of imitations of the songs of other birds performed during heterospecific vocal mimicry (Donald 2004). The peculiar spike-heeled lark (*Chersomanes albofasciata*), on the other hand, has a limited vocabulary comprised of a simple dry trill, *trrri-trrri-trrri-trrr,* which appears to serve the dual function of maintaining social contact amongst group members and territorial song (de Juana *et al.* 2004). However, the vocalizations of only a few species have been studied in detail and it is likely that the more simple songs and vocalizations, including that of the Spike-heeled Lark, may be more complex than thought at present.

In those species that have been studied in detail, lark vocalizations usually include at least a display song as well as territorial, alarm, aggressive, distress and flight calls (Cramp 1988; Laiolo *et al.* 2005). An interesting feature of lark vocalizations is the use of heterospecific vocal mimicry by some species to augment an individual's vocal repertoire. Heterospecific vocal mimicry can be described as the copying of the vocalizations of another species of birds or other environmental sounds, and these imitations are then incorporated into a bird's own songs or calls (Kelley *et al.* 2008). Vocal mimicry results from vocal learning, which can be classed into two main categories, namely, copying of conspecifics and copying of heterospecifics or other sounds (Kelley *et al.* 2008). Copying of conspecific sounds refers to copying of the sounds made by the same and/or related species, while copying of heterospecific sounds refers to copying of sounds of species from different species and genera. Vocal mimicry has been reported for several species in the mirafrid and alaudid clades but has as yet not been recorded in the ammomanid clade that includes the sparrow-larks (Barnes 2007).

The vocalizations of sparrow-larks appear somewhat limited although there has been no detailed analysis of the vocalizations of any of the *Eremopterix* larks. The calls that have been described have a sparrow- or finch-like quality comprised of twittering and short notes that are onomatopoetically described as "*chip*", "*tweet*", "*shrimp*", "*shree*" and a mixture of clear whistles or piping notes (Morel & Morel 1984; Ryan *et al.* 2004; Lloyd 2005a). Nevertheless, male display song and a flight call have been described for all *Eremopterix* larks. Other call types that have been described for sparrow-larks include a greeting, alarm, distress and feeding call, as well as the calls made by nestlings and fledglings (Maclean 1970b; Ryan *et al.* 2004). The only vocalizations of the chestnut-backed sparrow-lark that have been described include the male display song and a flight call (Morel & Morel 1984). The onomatopoetic descriptions of the song and calls vary considerably and are open to interpretation. To demonstrate this, a few examples from selected reference works follow: Bates (1934) described a nuptial flight "… accompanied by sharp sounds … like the rattling of dry leaves."; "A sharp rattling little call or song in the breeding season." (Mackworth-Praed & Grant 1962); "Sharp rattling call *chip-chee-w*. Sings beautifully, usually in fluttering flight." (McLachlan & Liversidge 1978); "The song consisted of two series of different notes. The first were husky and rather low, a sort of *cree* of a constant frequency uttered softly 2–4 times, followed by two soft notes *hoo-hoo*, the first note being higher." (Translated from French) (Morel & Morel 1984); "Rattling chirp, *chip-cheew*; song varied and musical, usually in fluttering flight." (Maclean 1985); "Flocks in flight utter a short *chip-chwep*." (Sinclair 1988); "Song complex …and carries only a short distance. Call a short, rattling, not very distinctive *chip-chip*." (Keith *et al.* 1992); "Male song rather monotonous *shrimp zzt zzt zrit*, final note higher pitched; also gives sweet, high-pitched whistles. Flight calls are sharp, high-pitched *chip*, typically in chorus by many birds when flock rises.” (Ryan *et al.* 2004).

From the above it is clear that there is considerable variation with regard to the interpretation of the species’ display song and calls. The present study will analyse the vocalizations of the chestnut-backed sparrow-lark and attempt to provide a more objective description of the various calls of the species.

3.2. Materials and methods

3.2.1. Biometrics

Biometric data of adult chestnut-backed sparrow-larks were obtained from breeding adults trapped at the nest at the study site on the farm De Loskop 205LS (23°30’S; 29°19’E) near Mogwadi, Limpopo Province, South Africa, from the Southern African Bird Ringing Unit (SAFRING) database, and from museum study skins (hereafter study skins) from the following southern African natural history museums: Bloemfontein National Museum, Iziko Museum of Cape Town, Ditsong National Museum of Natural History, Durban Natural Science Museum, East London Museum, and the McGregor Museum in Kimberley.

The following parameters were measured as described by de Beer *et al*. (2001): culmen length (from the base of the bill at the union with the skull to the tip of the culmen), culmen-nare length (from the distal end of the nares to tip of the culmen), bill depth (vertically perpendicular to the nares), bill width (horizontally perpendicular to the nares), length of the tarso-metatarsus (hereafter referred to as the tarsus length, from the notch of the first undivided anterior scute to the notch at the proximal end of the tarsus), wing length (maximum length of the flattened wing chord), and tail length (maximum length of the rectrices). A stopped wing ruler (readable to 1 mm) was used to measure wing length, a plain ruler to measure the tail length (also readable to 1 mm) and digital Vernier callipers were used for all other measurements (readable to 0.1 mm). Birds at the study site were weighed using a Pesola spring scale readable to the nearest 0.5 g. Culmen length was not recorded from museum study skins as this may damage them. Similarly, the SAFRING database is limited and the only parameters that could be included in the analyses were mass and wing length. All specimens were sexed on the basis of plumage colouration. To ensure measurement consistency, all live birds and study skins were only measured by Prof. D. Engelbrecht.

To provide a measure of the sexual size dimorphism, Storer's dimorphism index (DI; Storer 1966) was calculated as DI = 100(f - m)/0.5(f + m), where f and m are the mean values of the analysed parameters in females and males respectively. This index will be positive if the female is larger, that is, if reversed sexual dimorphism is present, and negative if the male is larger.

After checking the data for normality (using Kolmogorov-Smirnov one-sample tests) and homoscedasticity (using Bartlett's test), One-way Analysis of Variance (ANOVA) was used for comparisons between male and female measurements of live specimens and museum study skins as well as between the two subspecies, namely *E. l. hoeschi* and *E. l. smithi*. All statistical analysis for the biometric data was done using SPSS version 18 (SPSS, Inc., Chicago, Illinois).

3.2.2. Moult

Moult was recorded in live specimens in the study area, study skins and by using data of primary moult in the SAFRING database. Due to the difficulty of studying moult in study skins, great care was taken not to damage any of the specimens. The study of moult in the chestnut-backed sparrow-lark is thus essentially limited to a description of the timing of moult and the moult strategy. To describe the timing of moult and obtain basic information about the pattern of moult, study skins were examined using a pair of forceps to lift the feathers. Moult was recorded on the head, dorsal and ventral surface, remiges and rectrices, and the wing coverts. If two or more feathers were moulting in a given area, it was recorded as being in moult.

3.2.3. Vocalizations

Recordings of vocalizations were obtained at the study site mentioned above. Digital recordings were made with the aid of 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: duration or delta time (DT) measured in milliseconds (ms), minimum frequency (LF), maximum frequency (HF), and delta frequency (DF), all measured in kilohertz (kHz). Call data was analysed using Microsoft Office Excel (2007) for Windows.

3.3. Results

3.3.1. Biometrics

Mass and biometric data, summarised in Table 3.1, were recorded from 27 male and 27 female chestnut-backed sparrow-larks captured and released at De Loskop. Although the results revealed there were statistically significant differences between the sexes for mass, head, culmen-nare, wing and tail length, there were considerable overlap of these parameters between the sexes. For example, the difference in the means of these differences are also reflected in of DI < -1 for culmen-nare (DI = -3.54), tail (DI = -2.2), wing (DI = -1.93) and head length (DI = -1.43) and DI > 1 for mass (DI = 4.29). The largest DI value obtained was for mass and the smallest was for the length of the culmen (DI = 0.22). Positive DI values were calculated for mass, culmen length and tarsus (DI = 0.96), showing that females are on average larger than males for these parameters. Negative DI values were obtained for length of the wing, head, tail and culmen-nare lengths.

Excluding the ringing data of chestnut-backed sparrow-larks collected and submitted to SAFRING during the course of this study, the SAFRING database contained data of 66 chestnut-backed sparrow-larks (*n* = 27 males, *n* = 39 females) representing both southern African subspecies (*n* = 46 *E. l.*

hoeschi, n = 20 *E. l. smithi*). To determine if there was a difference in size between *E. l. hoeschi* and *E. l. smithi*, mass (as an indication of overall size) of males and females were analysed separately and the results are presented in Table 3.2. There was no statistically significant difference in the size of the two subspecies (*P* > 0.05). The sample size for wing length was too small for *E. l. smithi* (*n* = 4) and therefore wing length as an indication of size of this subspecies was excluded from the analysis. However, the SAFRING data confirmed a statistically significant difference in the wing length of males and females of the subspecies *E. l. hoeschi* (Anova, F = 13.15, *P* = 0.01) (no data for *E. l. smithi*), but not for mass in either *E. l. hoeschi* (Anova, F = 0.33, *P* = 0.86) or *E. l. smithi* (Anova, F = 0.96, *P* = 0.34) (Table 3.2). The pooled data showed a similar trend between the sexes (Table 3.3).

A total of 67 (*n* = 38 males, *n* = 29 females) museum study skins representing both southern African subspecies were measured and the data analysed. As a result of the state of some of the study skins, sample sizes for the different parameters differ to some extent. Although the sample sizes were small, particularly for *E. l. hoeschi*, there were no significant size differences (*P* > 0.05) between the two southern African subspecies for any of the parameters analysed (Table 3.4). When the data of the two subspecies were pooled, the results showed statistically significant differences in the wing and tail length of male and female chestnut-backed sparrow-larks (Table 3.5). Statistically significant differences in wing length of the sexes were also evident within each subspecies, but for tail length only in *E. l. hoeschi* (Tables 3.6 and 3.7). Once again, there is considerable overlap in the different parameters between the sexes and the relative differences in the mean are small, so these findings should be interpreted with caution.

3.3.2. Moult

None of the breeding adults at De Loskop were moulting during the two breeding seasons in autumn and spring (Chapter 2). This suggests that chestnut-backed sparrow-larks follow the usual lark pattern of not moulting during breeding. The SAFRING database showed birds belonging to the subspecies *E. l. hoeschi* in advanced primary moult in December and early January near Okaputu, Namibia (20°06’58”S; 16°58’30”E). Okaputu falls in a summer rainfall area with the wet season starting in November and lasting until the end of March (World Climate Guide 2012). Thus, given that primary moult is well advanced in December, it suggests that moult commenced at the end of the dry season and start of the wet season. This will fit the pattern of a dry season breeder with a post-nuptial moult starting just prior to the onset of the wet season.

Study skins of birds representing *E. l. smithi* show birds with bleached and abraded, i.e. well worn plumage, from July to September in Zimbabwe, and the North West Province of South Africa. The study skins showed moulting starting towards the end of September in most individuals and completed by early to mid-January. Although there is no information on how long moult lasts in an individual, the moulting “season” lasts 3–4 months. Moult commences on the head and finishes when the last rectrices are replaced. Moult of the rectrices commences when approximately 50–65% of the primaries have been replaced. Specimen 26140 in the Durban Museum of Natural History had a complete body moult on 30 October 1970, by which time primary 6 was half grown and the replacement of the rectrices had just commenced. Furthermore, several specimens had fresh, or were in the process of replacing, the inner three secondaries and some contour feathers in mid-winter, i.e. June and July. The above shows that *E. l. smithi* undergoes a complete post-nuptial moult in summer and a partial moult during which only the inner three secondaries and some contour feathers are replaced in mid-winter.

3.3.3. Vocalizations

The vocalizations of the chestnut-backed sparrow-lark are generally rather soft and do not carry very far. Nevertheless, the vocalizations are extremely complex and variable. The vocalizations recorded were divided into the following types: nestling calls, alarm call, flight call and display song (including a subsong).

3.3.3.1. Nestling calls

These calls can be divided into begging and distress type calls. The begging call is a short, barely audible, tonal *peep* sound (Fig. 3.2). It is made by nestlings upon seeing a parent flying overhead or when parents arrive at the nest. Unattended, older nestlings also give this call from time to time. These calls are difficult to record as they are very soft and the nestlings crouch and remain silent when there is activity near the nest. A summary of the duration, lowest, highest and delta frequency of begging calls is provided in Table 3.8.

Two types of distress calls were made when the nestlings were handled. The first was a loud, harsh *cshhh* burst-type noisy sound of varying length (Table 3.8, Fig. 3.2). The second type was more plaintive and can be described as a drawn out *cruu* or *keeep* call and a shorter *kip* call (Fig. 3.2). The harsh and plaintive calls were sometimes combined into a single call comprised of two to three elements (Fig. 3.2). A summary of the analysis of distress calls is provided in Table 3.8.

3.3.3.2. Adult alarm call

The alarm call can be described as a short, shrill, monotonous, single syllabic, harmonic, "*preeuw*" sound composed of one or two elements (Fig. 3.3). The most common form of an alarm call is characterised by a short, sudden rise in frequency followed by a gradual drop in the frequency. Alarm calls were given by both sexes when breeding birds detect disturbance at or near the nest or fledglings. Alarm calls were almost always given in flight as the birds circle above the nesting area. A summary of the duration and frequency range of alarm calls is presented in Table 3.8.

3.3.3.3. Flight call

The flight call of the chestnut-backed sparrow-lark was a short, sparrow-like *tjirp* sound that is typically composed of a number of syllables and individual elements. The elements displayed rapid frequency modulation over a relative broad frequency range (Table 3.8; Fig. 3.4). In some flight calls, there was a very short gap between syllables. It could not reliably be established if the flight call was unique to an individual.

3.3.3.4. Song

Song was only performed by males and although it is spectrally simpler than the flight call, it is nevertheless complex and included a range of clear whistles, rapid trills, rattling sounds and clicks ranging in duration, speed and frequency (Fig. 3.5). These sounds were configured into various phrases, which may or may not be repeated at various stages during the song bout to form an almost infinite variety of songs. Song was usually given in flight, but occasionally from the ground. Due to the variety of syllables and phrases it was very difficult to analyse the individual elements, syllables or phrases. Song elements and syllables included a broad frequency range from 0.79–7.71 kHz ($n = 440$ phrases).

The chestnut-backed sparrow-lark also had a subsong. Both sexes performed the subsong although it was more common in males. The subsong was always sung from the ground or a perch, usually near the nest. Males were also observed singing the subsong to a female during a courtship display. The subsong was a soft, mixed warble of sounds, which also includes heterospecific mimicry (Fig. 3.6). Heterospecific mimicry included the calls of the desert cisticola (*Cisticola aridula*), neddicky (*C. fulvicapilla*) chestnut-vented tit-babbler (*Parisoma subcaeruleum*), short-clawed lark (*Certhilauda chuana*), pink-billed lark, blacksmith lapwing (*Vanellus armatus*) and Kittlit’z plover (*Charadrius pecuarius*), amongst others.

3.4. Discussion

3.4.1. Biometrics

Sexual dimorphism is a common phenomenon in birds and can manifest itself in plumage colouration, size or ornamental feathers (Price 1984). The majority of studies on sexual dimorphism in birds have focused on the functional significance of sexual size dimorphism of specific groups such as sea birds and raptors (Gonzáles-Solis 2004; Krüger 2005). Comparatively few studies of sexual dimorphism have focussed on the passerines, and of those most have focused on families like the Paridae and Fringillidae (Blondel *et al.* 2002; Badyaev 2005). Chestnut-backed sparrow-larks are unusual amongst larks in that they are sexually dichromatic with males and females having strikingly different plumage colours. Sexual dichromatism is, however, not restricted to the sparrow-larks as some species of the genus *Pinacorys*, *Ramphocorys* and *Eremophilia* exhibit mild dichromatism (Keith *et al.* 1992; de Juana *et al.* 2004). Even though sparrow-larks are the only species in the family *Alaudidae* exhibiting extreme sexual dichromatism, the evolution and functional significance of this dichromatism remains a matter of conjecture (de Juana *et al.* 2004).

The evolution of sexual dimorphism is thought to be influenced by breeding systems and parental care modes (Butcher & Rohwer 1989; Anderson 1994). Chestnut-backed sparrow-larks are monogamous and exhibit biparental care, two characteristics which predispose them to the evolution of sexual dimorphism (Møller 1986; Harvey & Bradbury 1991). Males and females of the chestnut-backed sparrow-larks share all duties during the breeding cycle, i.e. nest construction, incubation and feeding of nestlings (Irwin 1994). Sexual selection is possibly amongst the factors influencing the evolution of sexual dimorphism in chestnut-backed sparrow-larks (Anderson 1994; Badyaev & Hill 1999). It has been suggested that the sexually dichromatic plumage of sparrow-larks enables easy recognition of the sexes upon arrival in an area where favourable conditions exist, thus reducing the need for extensive display flights and/or physical combat between males (Barnes 2007). As sparrow-larks are generally nomadic and opportunistic breeders, it is essential that the entire breeding cycle from mate selection to fledging be kept to a minimum, to ensure that the maximum benefits are derived from the favourable, but transient, conditions for breeding.

Statistical analysis of the data obtained from all three data sets (i.e. live specimens at the study site, SAFRING data and study skins) show that in addition to being sexually dichromatic, chestnut-backed sparrow-larks also exhibit mild sexual size dimorphism for some parameters. The results of the analysis of data from live specimens at the study site show that males average significantly larger ($P < 0.05$) than females for head length, culmen-nare length, and wing and tail length and females tend to be heavier than males. The analysis of SAFRING data confirmed sexual size dimorphism with regard to wing length but not for mass, and the museum skins also showed sexual size dimorphism with regard to wing and tail length. However, there is a large degree of overlap between the sexes for all parameters and the relative difference in mean values of the parameters is small, e.g. 4.4% for mass, 1.4% for head length, 3.6% for culmen-nare length, 1.9% for wing length and 2.2% for tail length.

The mean length of the flight apparatus (i.e. wings and tails) of males are longer compared to females, which may be adaptive with respect to the extensive display flights performed by the males during the breeding season (Keith *et al.* 1992). Similar adaptations have also been observed in Du Pont's lark (*Chersophilus duponti*), where the intensity and rate of display flights appeared to be enhanced by cost-reducing traits such as longer wings and tails (Vögeli *et al.* 2007). However, the significance of the observed sexual size dimorphism for wing and tail length should be interpreted with caution due to the high variation and small mean differences between the sexes of these measurements within all three datasets, i.e. De Loskop, SAFRING and museum study skins. Thus, although the results of the statistical analysis suggest sexual size dimorphism for some parameters in the chestnut-backed sparrow-lark, it may not be biologically significant.

The results revealed that the average mass of males at the study site was statistically significantly less than females, while the average mass of males in the SAFRING database was greater than that of females, albeit not significantly so. Once more, there was considerable overlap in mass between the sexes and it may not be biologically significant. Nevertheless, it should be noted that the De Loskop records represent breeding adults that were captured at the nest, whereas the SAFRING database represent records distributed randomly throughout the year. The difference in the average mass of breeding males and females at De Loskop may reflect the breeding condition of females, rather than a morphological adaptation of males to improve their flight efficiency by a reduction in body size (mass) and possessing longer wing and tail lengths. For example, Hedenström and Møller (1992) found no association between species exhibiting song flights and a reduction in body size. Instead, the greater average mass of breeding females may be related to the build-up of nutrient reserves to be transferred during egg production, as well as physiological changes such as the development of the ovaries and other tissues associated with egg-laying. The demands of egg-laying and breeding place tremendous burdens on breeding birds and therefore they have to be in good physical shape for successful breeding. Nevertheless, a change in body mass during breeding and thereafter is a common phenomenon in birds, particularly in species where only one parent incubates (Newton 1979; Wheeler & Greenwood 1983). Future studies should attempt to record body mass changes of incubating birds during the breeding cycle as well as seasonal variation in body mass.

Sexual size dimorphism is more common in insectivorous larks and is possibly an adaptation to reduce intra-specific competition by exploiting different sub-niches within their territories (Willoughby 1971; Dean & Hockey 1989). The chestnut-backed sparrow-lark is mainly granivorous and exhibits various degrees of local movement depending on the existence of favourable conditions. As they tend to exploit areas where optimal conditions exist, there is very little need for sexual size dimorphism to exploit different niches. The differences in the mean culmen-nare length of the sexes and the relatively high dimorphism index value (DI = -3.54) calculated for birds at De Loskop are therefore not expected. The museum study skins showed no significant differences in this parameter between the sexes and, in fact, females averaged larger than males for this parameter. The results once again show considerable overlap between the sexes for this parameter and it is unlikely to be of any biological significance.

3.4.2. Moult

Moult is of great importance in birds as it replaces old feathers that are constantly abraded and worn due to behavioural activities, exposure to sunshine, feather mites and other environmental stresses (Jenni & Winkler 1994). Reduced feather quality reduces flight ability and may reduce the bird's ability to escape from predators (Smit & Piersma 1989; Holmgren *et al*. 1993; Barta *et al.* 2006). Moult is a relatively unknown aspect of the biology of the majority of birds even though it is one of the most important and energy-demanding periods in their annual cycles (Murton & Westwood 1977; Blem 1980; King 1980; Walsberg 1983; Blem 1990; Newton 2009). Other crucial periods with high energy demands are breeding and migration (Immelmann 1971). Due to their energetic demands, moult and breeding are usually separated in a species' annual cycle (Lindström *et al*. 1993; Klaassen 1995; Murphy 1996; Langston & Rohwer 1996).

Although the moult pattern and strategy of most larks is unknown, the usual pattern seems to be a complete, annual post-breeding moult (Willoughby 1971; Cramp 1988; de Juana *et al.* 2004). However, there are a few exceptions to this general rule. Two complete annual moults have been described for the grey-backed sparrow-lark, Gray's lark and Stark's lark in southern Africa's Namib Desert (de Juana *et al*. 2004). The double moult is explained as an adaptive strategy to rapid wear of their feathers due to exposure to the sun and wind-blown sand in the desert environment (de Juana *et al.* 2004). Herremans & Herremans (1992) also mentioned breeding short-clawed larks (*Certhilauda chuana*) with moulting inner secondaries, which suggests occurrence of a partial moult in this species. The results of this study show that in addition to a complete post-breeding moult in October to mid-January, chestnut-backed sparrow-larks also undergo a partial moult between the autumn and spring breeding seasons, during which only the innermost three secondaries and some contour feathers are replaced. This confirms van Niekerk's (2009) observation of a complete moult in late spring and summer, corresponding to a post-breeding moult, in the Free State Province. Moreover, van Niekerk (2009) suggested the possibility that the species may also moult in mid-winter, a view that is confirmed unequivocally in this study. Larks have very large inner secondaries, which essentially form a “cloak” to cover the other remiges. These feathers serve to reduce abrasion by vegetation and wind-blown sand and also protect the feathers from solar radiation, which can have a significant effect on feather quality and hence flight efficiency. It is energetically more economical to replace only the innermost three feathers than to replace all the remiges.

3.4.3. Vocalizations

Due to the generally monomorphic and cryptic plumage of larks, they rely heavily on song as a means of advertising individual quality to females and other males (Alström 1998; Catchpole & Slater 1995; de Juana *et al.* 2004; Donald 2004). Furthermore, the open, terrestrial habits of larks have necessitated a concomitant development of extensive song flights. Male larks usually sing in flight (occasionally from the ground or a perch), which places tremendous energetic demands on them, but it is an advertisement of individual quality amongst territorial males during breeding (de Juana *et al.* 2004). It is evident from the literature that the vocalizations of sparrow-larks are rather limited and display flights are not particularly noteworthy. This is believed to be due to their sexually dichromatic plumage that allows easy and rapid mate selection when favourable conditions exist. This nullifies the use of extensive display flights and song to attract mates and advertise territories (de Juana *et al.* 2004; Barnes 2007). According to Barnes (2007), the chestnut-backed sparrow-lark belongs to the ammomanid clade, a group of larks that generally lacks extensive display flights, has a limited vocal repertoire and does not perform heterospecific mimicry.

The results of this study showed that contrary to reports in the literature, the chestnut-backed sparrow-lark has an extensive and varied vocal repertoire that includes heterospecific mimicry, and regularly performs extensive display flights. Heterospecific vocal mimicry is a common phenomenon in larks with some species incorporating it into their display flight songs during breeding or using it as a warning call (Cramp 1988; Laiolo *et al.* 2005). Vocal mimicry was, until this study, thought to be limited to species in the alaudid (e.g. *Galerida, Melanocorypha* and *Alauda*) and mirafrid clades (e.g. *Mirafra*) (Dean 1997; Barnes 2007).

Vocal mimicry in chestnut-backed sparrow-larks is incorporated into their subsongs. Heterospecific vocal mimicry presumably serves a function in courtship and mate attraction as males were observed performing the subsong when courting a female or while the female was incubating. Although sparrow-larks are sexually dichromatic, all males look superficially similar and lack secondary sexual characteristics, e.g. long tails or other seasonal adornments, which may serve to advertise the quality of an individual male. Incorporating heterospecific mimicry of a range of species in the courtship display serves to increase the repertoire size of individual males, which may serve as a clue for females during mate selection. Song mimicry has been shown to confer advantages on the singer in a number of species as those males with larger song repertoires are more successful at attracting females (Donald 2004).

Although vocal mimicry is commonly used for breeding purposes in many species of birds, including larks (Laiolo *et al.* 2005), it can also be used to distract predators and intruders (Dobkin 1979; Kaplan 1999; Frith & Frith 2004; Coe 2005; Goodale & Kotagama 2006; Kelley *et al.* 2008), for reduction of aggression at territory boundaries (Baptista & Catchpole 1989) and in territorial displays (Robinson 1974; Curio 1978). During this study a female was recorded performing a subsong near the nest. This was the only occasion where a female was observed performing this activity and it is evidently not common. No evidence of heterospecific vocal mimicry was found in this recording and it is possible that the purpose of the subsong in this instance was to serve a distracting function resulting from activity in the vicinity of the nest. Although singing of a subsong by females is not common, Donald (2004) mentions female skylarks performing a “muted” version of the subsong similar to that of the male during pair formation, mating, nest construction and when predators approach a nest.

3.5. Conclusion

In conclusion, the study showed that, in addition to being sexually dichromatic, there is a tendency for males to have longer wing and tail lengths compared to females. However, there is considerable overlap in these two parameters between the sexes and the differences in means are small. The greater average mass of breeding females in the study area may relate to physiological changes associated with the production and laying of eggs, rather than a reduction in size of males to enhance display flight performance. The study also demonstrated that the species has a particularly rich vocal repertoire that includes heterospecific vocal mimicry. This is the first record of vocal mimicry for the ammomanid clade of larks. The chestnut-backed sparrow-lark also has an interesting moult strategy, which involves a partial moult of the inner secondaries and some contour feathers between the autumn and spring breeding periods. This has been reported in only a few lark species but since only a few moult studies have been conducted in larks, this strategy may ultimately be more common than thought at present.

Table 3.1. Biometrics of adult chestnut-backed sparrow-larks (*Eremopterix leucotis smithii)* from De Loskop, Limpopo Province caught between January 2008 and December 2010. All measurements are in mm except mass (g).

	♂ (*n* = 27)	**♀ (*n* = 27)**	***P***
	Mean ± S.D., range	**Mean ± S.D., range**	
Mass	18.00 ± 0.85, 16.50–19.50	18.79 ± 1.04, 17.00–21.50	0.00
Head	28.94 ± 0.41, 28.10–30.00	28.53 ± 0.58, 27.00–29.40	0.00
Culmen	13.86 ± 0.48, 12.70–14.70	13.89 ± 0.62, 12.40–15.30	0.78
Culmen-nare	8.90 ± 0.43, 7.60–9.80	8.59 ± 0.36, 7.90–9.00	0.00
Tarsus	17.66 ± 0.49, 17.00–18.90	17.83 ± 0.74, 16.20–19.30	0.33
Wing	85.26 ± 1.61, 82.00–87.00	83.63 ± 1.47, 80.00–87.00	0.00
Tail	46.89 ± 1.58, 44.00–50.00	45.87 ± 1.21, 43.00–48.00	0.01

Table 3.2. Mean, standard deviation and range of the mass (g) and wing length (mm) of males and females of the two southern African subspecies of the chestnut-backed sparrow-lark (*Eremopterix leucotis hoeschi* and *E. l. smithi*) in the SAFRING database. Wing length was not included in the analysis for *E. l. smithi* as the sample size was too small (*n* = 1 male and *n* = 3 females).

		E. l. hoeschi	***E. l. smithi***	***P***
		Mean ± S.D., range (n)	**Mean ± S.D., range (n)**	
♂	**Mass**	18.75 ± 1.00, 17.00–21.00 (18)	18.87 ± 3.40, 12.00–24.50 (9)	0.89
	Wing	84.29 ± 2.17, 82.00–89.00 (17)		
♀	**Mass**	18.68 ± 1.47, 16.00–22.00 (28)	17.75 ± 1.51, 15.10–20.00 (11)	0.09
	Wing	82.12 ± 1.75, 79.00–86.00 (26)		

Table 3.3. Pooled results of the analysis of mass (g) and wing length (mm) of both subspecies of the chestnut-backed sparrow-lark (*Eremopterix leucotis hoeschi* and *E. l. smithi*) in the SAFRING database.

	♂ (*n* = 27)	**♀ (*n* = 39)**	***P***
	Mean ± S.D., range	**Mean ± S.D., range**	
Mass	18.79 ± 2.05, 12.00–24.50	18.42 ± 1.52, 15.10–22.00	0.40
Wing	84.44 ± 2.20, 82.00–89.00	82.17 ± 1.79, 79.00–86.00	0.00

Table 3.4. Mean, standard deviation and range of selected biometric parameters of male and female museum study skins of the two southern African subspecies of the chestnut-backed sparrow-lark (*Eremopterix leucotis hoeschi* and *E. l. smithi*). All measurements recored in mm.

		E. l. hoeschi	***E. l. smithi***	***P***
		Mean ± S.D., range (n)	**Mean ± S.D., range (n)**	
♂	**Culmen**	12.80 ± 0.52, 11.70–13.60 (11)	12.44 ± 0.59, 11.30–13.60 (27)	0.09
	Culmen-nare	8.65 ± 0.55, 8.00–9.60 (11)	8.54 ± 0.44, 7.90–9.20 (27)	0.56
	Tarsus	17.90 ± 0.48, 17.00–18.70 (10)	18.17 ± 0.94, 16.90–20.20 (27)	0.38
	Wing	83.55 ± 2.73, 80.00–87.00 (11)	82.44 ± 2.50, 77.00–87.00 (27)	0.24
	Tail	47.45 ± 2.58, 44.00–52.00 (11)	45.89 ± 2.08, 41.00–49.00 (27)	0.06
♀	**Culmen**	12.78 ± 0.56, 12.00–13.40 (6)	12.53 ± 0.58, 11.80–13.60 (21)	0.35
	Culmen-nare	9.04 ± 0.45, 8.60–9.85 (6)	8.60 ± 0.48, 7.30–9.20 (21)	0.06
	Tarsus	17.94 ±0.86, 16.60–19.00 (5)	17.85 ± 0.62, 17.00–19.00 (21)	0.80

	E. l. hoeschi Mean ± S.D., range (n)	*E. l. smithi* Mean ± S.D., range (n)	*P*
Wing	79.50 ± 1.38, 77.00–81.00 (6)	80.61 ± 1.92, 78.00–85.00 (23)	0.20
Tail	44.00 ± 2.10, 40.00–46.00 (6)	44.98 ± 2.06, 42.00–49.00 (23)	0.31

Table 3.5. Results of the analysis of selected biometric parameters (mm) of museum study skins of the two southern African subspecies of the chestnut-backed sparrow-lark (*Eremopterix leucotis hoeschi and E. l. smithi*) combined.

	♂	♀	***P***
	Mean ± S.D., range (n)	**Mean ± S.D., range (n)**	
Culmen	12.55 ± 0.59, 11.30–13.60 (38)	12.59 ± 0.57, 11.80–13.60 (27)	0.80
Culmen-nare	8.57 ± 0.47, 7.90–9.60 (38)	8.70 ± 0.50, 7.30–9.85 (27)	0.30
Tarsus	18.09 ± 0.85, 16.90–20.20 (37)	17.87 ± 0.65, 16.60–19.00 (26)	0.26
Wing	82.76 ± 2.58, 77.00–87.00 (38)	80.38 ± 1.86, 77.00–85.00 (29)	0.00
Tail	46.34 ± 2.32, 41.00–52.00 (38)	44.78 ± 2.06, 40.00–49.00 (29)	0.01

Table 3.6. Biometrics of *Eremopterix leucotis hoeschi* museum skins. All measurements in mm.

	♂	♀	***P***
	Mean ± S.D., range (n)	**Mean ± S.D., range (n)**	
Culmen	12.74 ± 0.69, 11.00–13.60 (11)	12.78 ± 0.56,12.00–13.40 (6)	0.89
Culmen-nare	8.65 ± 0.55, 8.00–9.60 (11)	9.04 ± 0.45, 8.60–9.85 (6)	0.15
Tarsus	17.89 ± 0.48, 17.00–18.70 (10)	17.94 ± 0.86, 16.60–19.00 (5)	0.89
Wing	83.55 ± 2.73, 80.00–87.00 (11)	79.50 ± 1.38, 77.00–81.00 (6)	0.00
Tail	47.45 ± 2.58, 44.00–52.00 (11)	44.00 ± 2.09, 40.00–46.00 (6)	0.01

Table 3.7. Biometrics of *Eremopterix leucotis smithi* museum study skins. CL = Culmen length, CN = culmen-nare length, TL = tarsus length, and TL_2 = tail. All measurements in mm.

	♂	♀	***P***
	Mean ± S.D., range (n)	**Mean ± S.D., range (n)**	
Culmen	12.44 ± 0.59, 11.30–13.60 (27)	12.53 ± 0.58, 11.80–13.60 (21)	0.620
Culmen-nare	8.54 ± 0.44, 7.90–9.20 (27)	8.60 ± 0.48, 7.30–9.20 (21)	0.67
Tarsus	18.17 ± 0.94, 16.90–20.20 (27)	17.85 ± 0.62, 17.00–19.00 (21)	0.19
Wing	82.44 ± 2.50, 77.00–87.00 (27)	80.61 ± 1.92, 78.00–85.00 (23)	0.01
Tail	45.89 ± 2.08, 41.00–49.00 (27)	44.54 ± 2.92, 35.00–49.00 (23)	0.06

Table 3.8. Summary of mean, standard deviation and range of the duration and frequencies of the various nestling, alarm and flight calls of adult chestnut-backed sparrow-larks (*Eremopterix leucotis*) recorded at De Loskop, Limpopo Province, South Africa between January 2008 and December 2010.

Call type	*n*	Duration (s)	Low frequency (kHz)	High frequency (kHz)	Delta frequency (kHz)
Nestling					
Begging	4	0.04 ± 0.01, 0.04–0.05	3.14 ± 0.16, 2.96–3.31	4.96 ± 0.06, 4.88–5.01	1.82 ± 0.21, 1.56–2.06
Distress					
i) Harsh	6	0.24 ± 0.10, 0.10–0.40	1.77 ± 0.57, 1.27–2.82	3.91 ± 0.68, 3.30–5.00	2.14 ± 0.23, 1.83–2.5
ii) Plaintive	10	0.11 ± 0.08, 0.03–0.30	3.02 ± 0.22, 2.70–3.40	3.87 ± 0.48, 3.34–4.89	0.84 ± 0.48, 0.36–1.97
iii) Harsh-plaintive	7	0.27 ± 0.05, 0.21–0.32	2.67 ± 0.55, 2.07–3.24	4.73 ± 0.22, 4.45–5.02	2.06 ± 0.70, 1.32–2.95
Adult					
Alarm	99	0.21 ± 0.03, 0.11–0.27	2.17 ± 0.38, 1.33–3.13	5.33 ± 0.50, 4.28–6.54	3.16 ± 0.71, 1.56–4.66
Flight	255	0.15 ±0 .05, 0.08–0.44	2.53 ± 0.37, 1.54–3.84	5.14 ± 0.53, 3.59–6.28	2.61 ± 0.53, 1.29–4.19

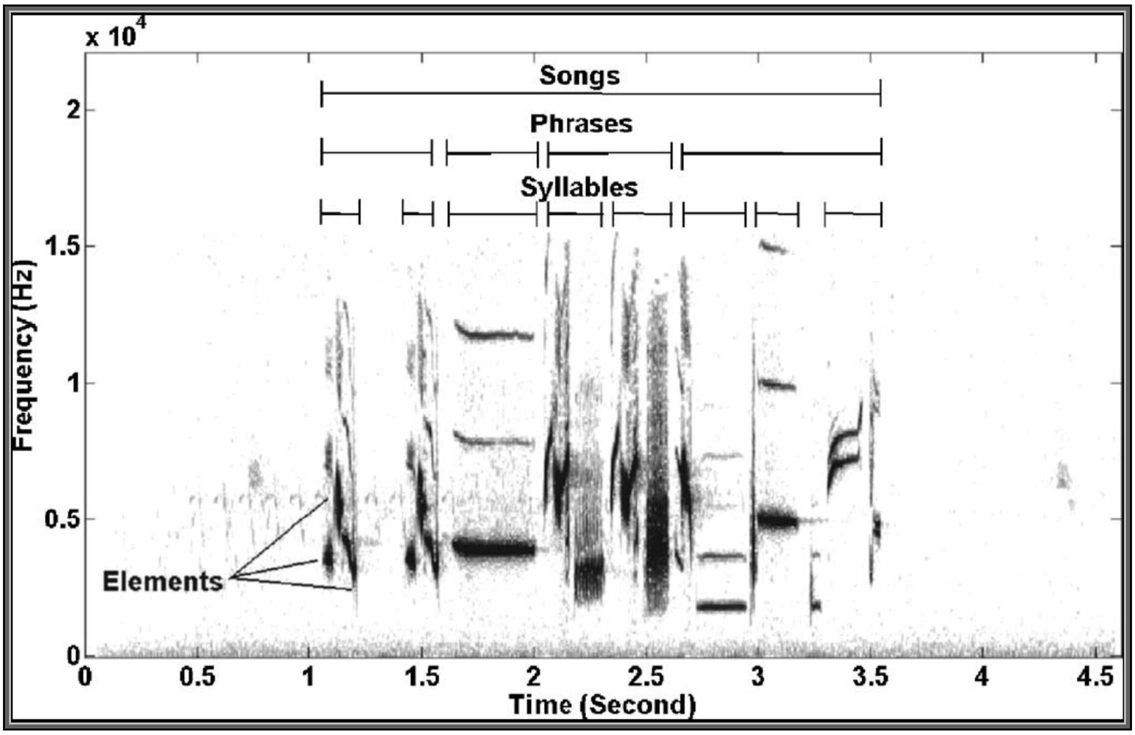

Fig. 3.1. Descriptive hierarchy of bird vocalizations. From Chen & Maher (2006).

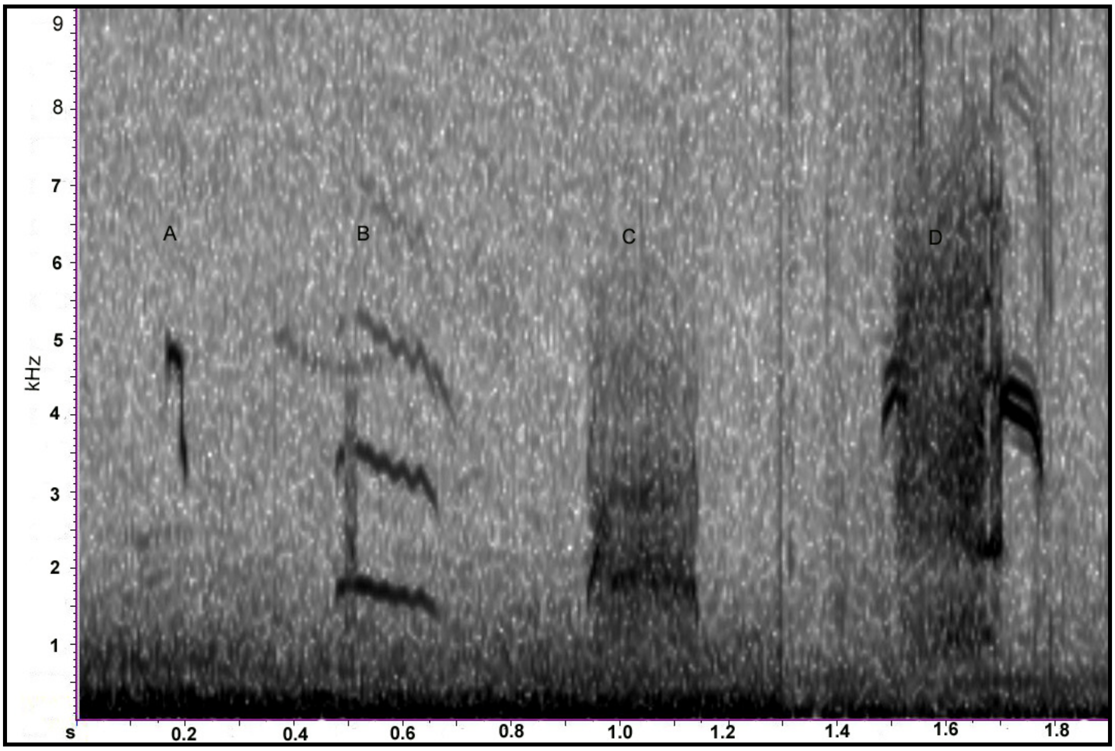

Fig. 3.2. Various calls of chestnut-backed sparrow-lark (*Eremopterix leucotis*) nestling calls recorded at De Loskop, Limpopo Province, South Africa between January 2008 and December 2010. A = begging call, B = plaintive distress call, C = harsh distress call and D = the harsh-plaintive distress call.

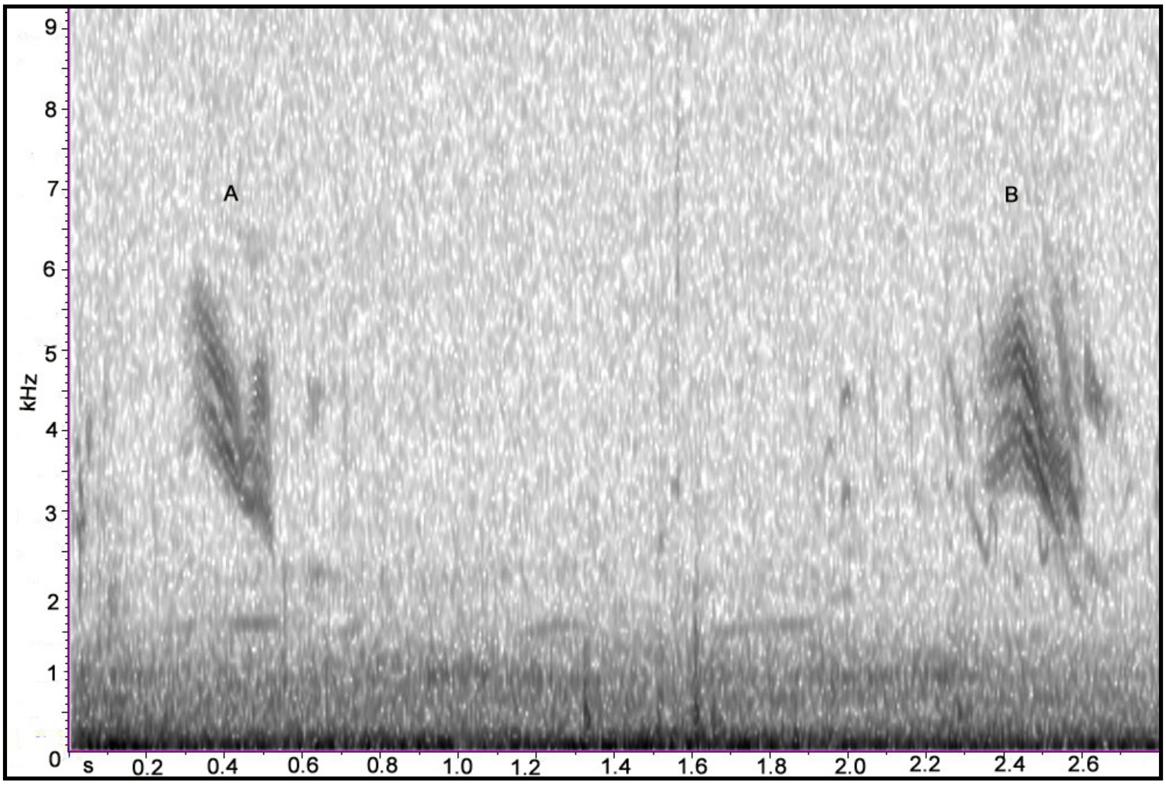

Fig. 3.3. Alarm calls of chestnut-backed sparrow-lark (*Eremopterix leucotis*) recorded at De Loskop, Limpopo Province, South Africa between January 2008 and December 2010. A = alarm call characterised by a sudden drop and then a slight rise in frequency, B = the more common alarm call characterised by a short, sudden rise in frequency followed by a gradual drop in frequency.

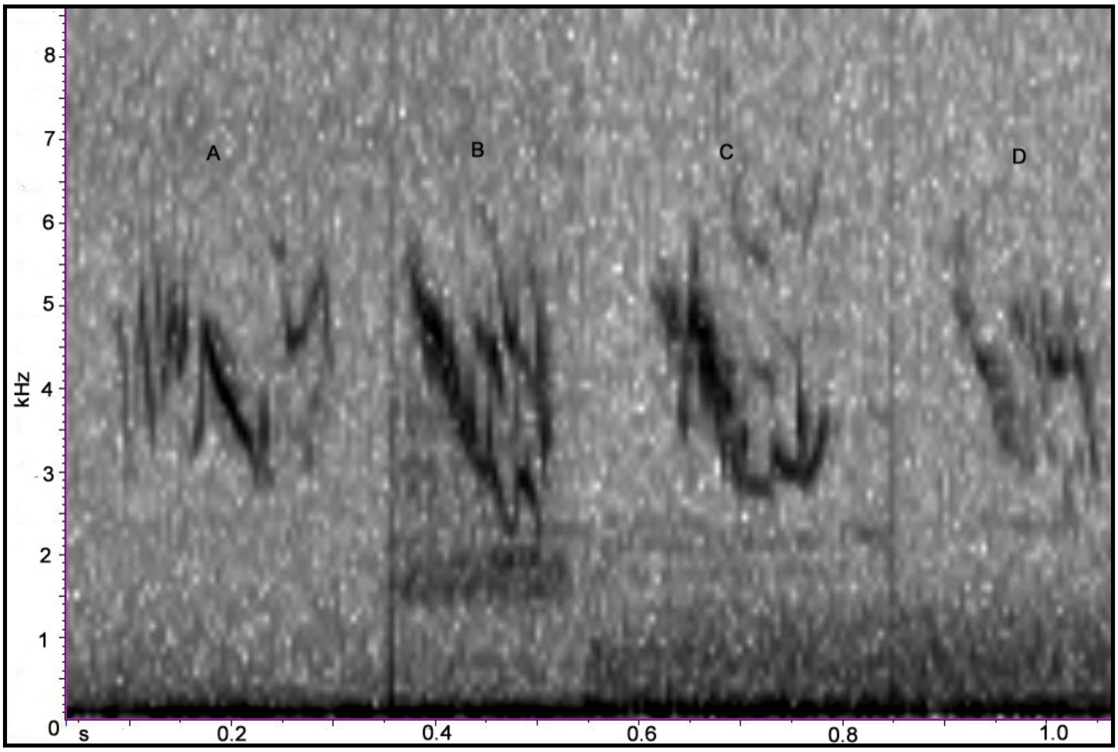

Fig. 3.4. Four examples of flight calls of the chestnut-backed sparrow-lark (*Eremopterix leucotis*) recorded at De Loskop, Limpopo Province, South Africa between January 2008 and December 2010.

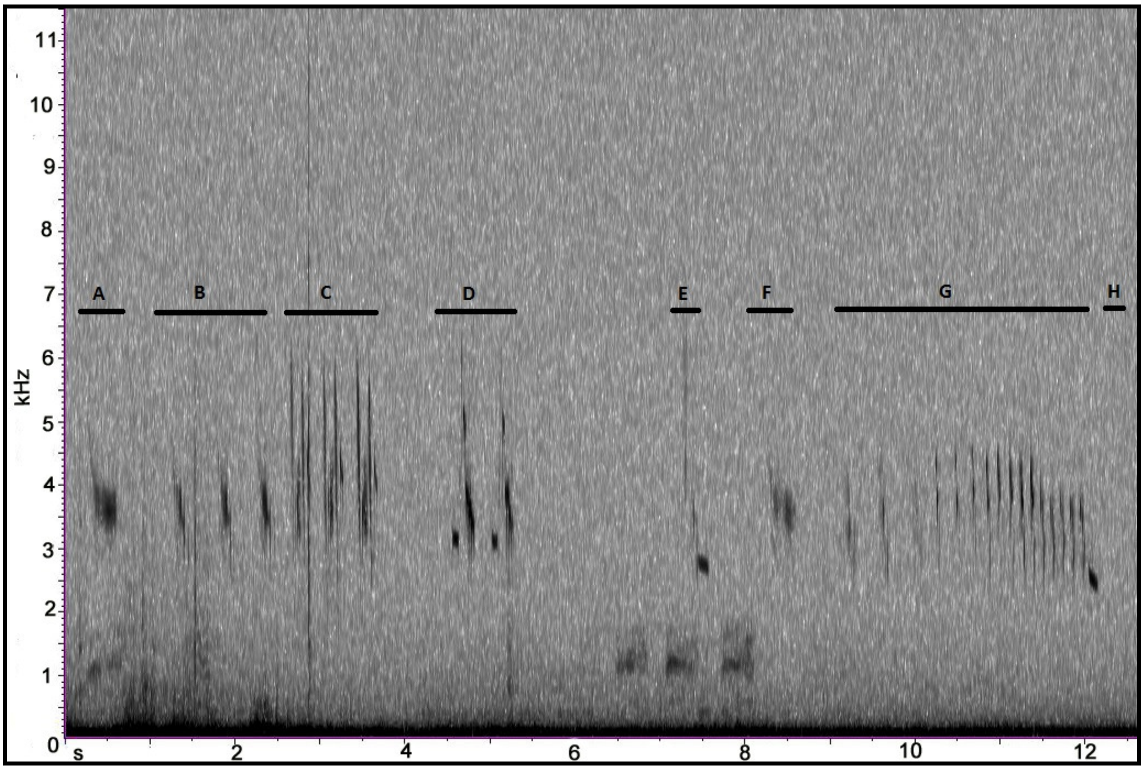

Fig. 3.5. A sonogram of a part of the display song of a male chestnut-backed sparrow-lark (*Eremopterix leucotis*) recorded at De Loskop, Limpopo Province, South Africa on 23 March 2009, showing the various clicks and rattling phrases. A = short whistle comprised of a single syllable, B = three regularly spaced elements producing a “click” sound, C = three regularly spaced, rattling syllables comprised of several elements showing rapid frequency modulation, D = a short phrase comprised of two syllables, each comprised of two “click” elements with different frequencies, E = a single, relatively low pitched “click” element, F = a single “click-like” syllable comprised of two elements, G = a “trill” phrase comprised of several individual elements which gradually increase in speed and decreasing in frequency, terminating in H = a single, relatively low frequency single “click” element.

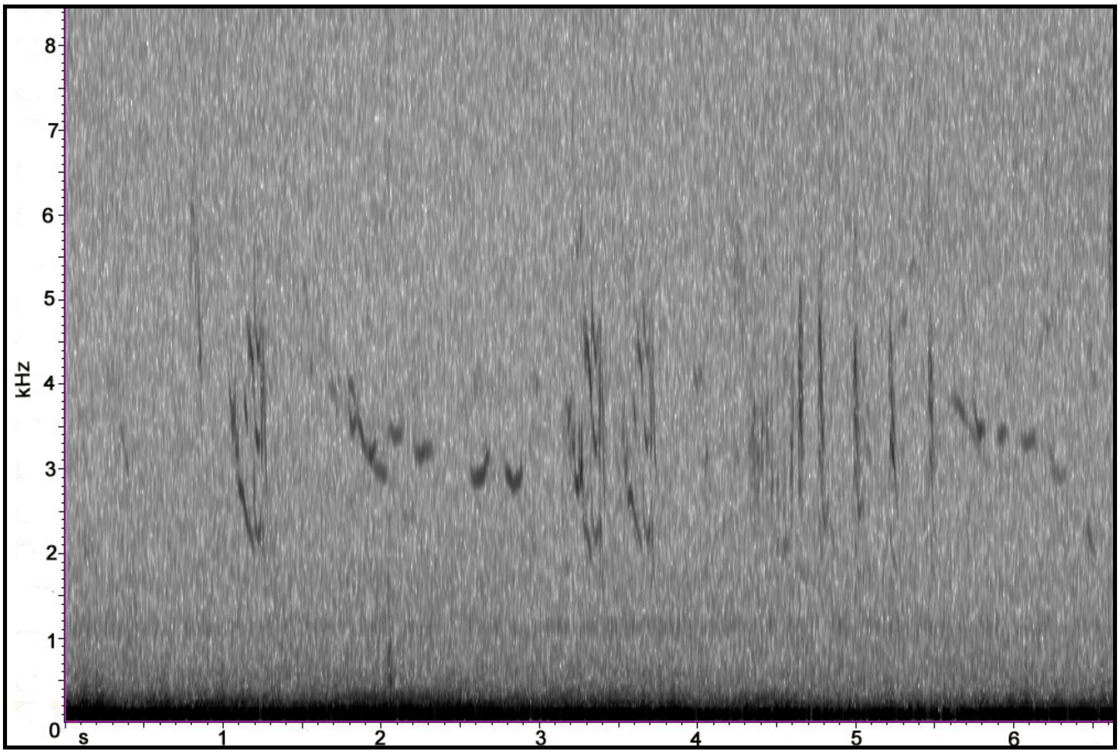

Fig. 3.6. Sonogram of the subsong which also includes heterospecific mimicry of the chestnut-backed sparrow-lark (*Eremopterix leucotis*) recorded on 15 April 2010 at De Loskop, Limpopo Province, South Africa. Note the range of notes and the repetition of certain elements and syllables.

CHAPTER 4

Conclusion

The study succeeded in describing various previously unknown aspects of the ecology and breeding biology of chestnut-backed sparrow-larks. It also highlighted the need for further research on the species and members of the family.

Some of the major findings of this study is highlighted below. The breeding season at De Loskop is bimodal, i.e. breeding takes place in autumn and spring, with no breeding recorded during the winter months.

The study demonstrated the need for long-term studies of the biology of species in order to get a better understanding of the spatial and temporal factors affecting breeding. For example, the results showed how breeding success can differ between years and how stochastic events can drastically affect the results of a study.

The results confirm the findings of a growing number of studies which demonstrate that larks generally have poor breeding success.

Biparental care appears to be symmetrical during incubation, but females make significantly more visits to the nest to deliver food compared to males.

The study is the first to show unequivocally that chestnut-backed sparrow-larks are double-brooded and that replacement clutches are common.

Chestnut-backed sparrow-larks show mate fidelity during both peaks of the breeding season and in successive broods.

Chestnut-backed sparrow-larks are not only sexually dichromatic but they also show a mild degree of sexual size dimorphism with regard to wing and tail length with males tending to have longer wing and tail lengths. The results also showed that breeding females are on average heavier than males which is related to physiological changes associated with egg-production and – laying.

They have a rich repertoire of vocalizations that includeheterospecific vocal mimicry, a feature hitherto unrecorded in any of the sparrow-larks or in the ammomanid clade of larks to which it belongs.

The study confirmed Van Niekerk's (2009) notion that in addition to a complete post-breeding moult, they undergo a partial moult of some contour feathers and the innermost secondaries between the two breeding 'seasons' in mid-winter.

The results of the study have also highlighted avenues for future research. A brief description and recommendations follow.

- Investigate geographical size variation and the extent of sexual dimorphism in populations/subspecies across the species' entire distribution range,
- Elucidating the demography of the species. This will require intensive ringing to determine the population size and movement patterns. There had been relatively few sightings of colour-marked individuals, which suggests the population is either very large, or there is extensive movement to and from the De Loskop study site.
- Determine the sex ratio of nestlings and use genetic analysis to test paternity of the offspring. Field observations suggest that extra-pair paternity may be possible.
- Compare breeding strategies and success of different populations. The area within which the study was conducted is an agricultural farm that has undergone several anthropogenic changes. It is important to conduct a similar study in a more natural environment to determine if there are differences in the breeding success.
- The low breeding success estimated in the study area can be attributed to a number of factors, including predation. A study aimed at identifying

causes of nest failure at different stages of the breeding cycle should be conducted as the current study showed differences in survival rates during the incubation, hatching and nestling periods in some years, as well as inter-annual differences in the breeding success.

- Expand the study on the relative contribution of males and females to include different stages of the incubation and nestling periods as well as different times of the day.
- Parental provisioning should also be investigated further to determine if there are differences in parental investment between one- and two-egg clutches.

To conclude, the current study shed valuable light on the ecology and breeding biology of the chestnut-backed sparrow-lark. 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 can form an integral part of other intra- and interspecific comparative studies.

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