

THE DIET AND FEEDING BEHAVIOR OF THE RED-CAPPED LARK, *Calandrella cinerea*
IN KEDONG RANCH, NAIVASHA, KENYA.

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DECLARATION BY THE CANDIDATE

This thesis is my original work and has not been presented for a degree in any other university or any other award.

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DEDICATION

This thesis is dedicated to my parents Julia Moisso Mwangi and Joseph Mwangi Kagiri without whom this work would never have begun, countlessly made great sacrifices to bring me up, see me through school and mould me to the person I am today. I in a special way dedicate it to my father who has always been there for me, a great inspiration and exceptionally strong in some very difficult situations. I also dedicate it to my husband Justus Musau Kikuvi and our two children Chris Mwaka and Joan Moisso for their prayers, inspiration, appreciation, patience, understanding and great support throughout the study period. Finally, I dedicate this work to my sisters (Regina Masenga, Felistas Mamroso, and Ann Wanjiku) and to all those who are determined to make great sacrifices & take a step of faith to exemplarily succeed and pursue excellence in all their undertakings despite the numerous difficult situations and challenges encountered.

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Abstract

The study was conducted at Kedong area in Naivasha, Kenya from March to August, 2016 with the aim of assessing the diet and feeding behaviour of the Red-capped Lark and how it is influenced by factors of insect prey abundance/diversity and seasonality. Quantitative data on feeding behavior was obtained through focal animal sampling and nest observations. The densities of foraging substrates were estimated. Insects were sampled through pitfall traps, sweep-nets and butterfly traps. A total of 868 observations on food items consumed by the adult Red-capped Larks were undertaken. The Red-capped Lark predominantly consumed animal nutrients (insects belonging to orders Coleoptera, Orthoptera, Lepidoptera, and Hymenoptera) which were supplemented by grass seeds from two grass species; *Eragrostis tenuifolia* and *Harpachne schimperi*. Picking and gulping were the most employed food capture and handling technique respectively for both seasons. A one-way ANOVA test confirmed that mean feeding and search rates between seasons did not vary significantly. During breeding period, mean rates for feeding, searching for food, walking, and resting and preening in the morning, mid-morning and evening significantly varied except for scanning and courtship display. For non-breeding period, mean rates for all other activities apart from courtship display varied significantly for the time periods. The nestling diet comprised of insect larvae, grasshoppers, butterflies/moths, ants and beetles. Insect larvae were the most frequent item delivered, accounting for 51.9% of the nestling diet. A Welch student's t-test showed that there were no significant differences in mean delivery rates of different prey items provided by male and female parents. However, there were significant difference in the mean delivery rates of insect larvae, grasshoppers and butterflies/moths delivered to nestlings of different ages per day. There were significant differences in the Shannon Weiner diversity (H') indices for insect prey species collected in open grassland, Acacia woodland and *Tarconathus*-Acacia woodland. However, there was no significant difference in insect prey abundance for the vegetation types between seasons. A positive correlation between availability and utilization of insect prey items by the bird was established. Given that knowledge on the diet and feeding behaviour of the Red-capped Lark is limited, this study provided key insights on its diet and factors that influence its feeding behavior.

CHAPTER ONE: INTRODUCTION AND LITERATURE REVIEW

1.1 Background

Knowledge and information on ecology of bird species is of great value to conservationists/researchers, hence avian foraging ecology has been intensively studied since the beginning of 1980s. However, although many tropical birds have become a representative of avian adaptations worldwide, few studies have been conducted on the ecology of these birds (Yatuha and Dranzoa, 2009). As a result, knowledge on foraging ecology of many tropical birds is still incomplete (Mansor and MohdSah, 2012). Tropical birds have diverse life history traits that are considered important in testing evolutionary and ecological theory (Stutchbury and Morton, 2008). Further studies on tropical birds have therefore been recommended to shed more light on the theory as well as on avian ecology to ensure successful efforts in conserving the bird species (Davis, 1977; Clancy, 2011). Feeding behaviour is one of the most critical aspects of avian ecology with some key areas to focus on including food availability/utilization, food capture/handling techniques (that vary between species and individuals) time allocation to feeding activities. These are important in understanding feeding behaviour and factors influencing time allocation by birds (Barros *et al.*, 2014). For instance, the way in which birds use a habitat to forage may be influenced by factors such as vulnerability to predators and food availability (Wishart and Seal, 1980).

Studying feeding behaviour and some specific predator-prey interactions that shape foraging niches is hence critical in avian studies to allow prediction of impacts of biodiversity loss, as well as deepen understanding on preconditions of maintaining avian biodiversity (Rosenberg, 1993; Spafford and Lortie, 2013). Many tropical grassland bird species rely greatly on insect species as a food source hence insect prey availability is a key limiting factor for avian reproduction and survival (Stojnic *et al.*, 2012; Wellicome *et al.*, 2013). For example, abundance and diversity of insect food source may influence breeding behaviour as parental adults strive to maximize their breeding success. Factors that have been attributed to these differences include vegetation type and seasonality (Dugger *et al.*, 2004; Jahn *et al.*, 2010). Across the globe, habitat degradation and loss due to anthropogenic activities have contributed to decline in population of grassland birds and their insect food source (Kearns and Oliveras, 2009). In addition, factors that

influence distribution of insects at multiple scales make them an increasingly group of interest to researchers (Cheli *et al.*, 2010; Verdu *et al.*, 2011). This study aimed at assessing the diet and feeding behavior of the Red-capped Lark, and how it's influenced by factors of seasonality and insect prey abundance/diversity. Quantitative data on adult feeding behavior was obtained through direct field visual observations (focal animal sampling) and observation of parents' food provisioning behaviour at the nest done using a spotting scope while inside a hide. The foraging substrates of the Red-capped Lark were assessed and their density established. Insects were sampled through pitfall traps, sweep-nets and butterfly traps. The study revealed that some aspects of diet and feeding behaviour of the Red-capped Lark were influenced by seasonality, insect prey species abundance/diversity and time of day.

1.2 Literature review

1.2.1 The ecology of the Red-capped Lark

The Red-capped lark is a tropical passerine bird that in Kenya occurs abundantly in dry/warm tropical grasslands (1200 m above sea level) and wet/cool montane grasslands (2600 m above sea level) (Ndithia *et al.*, 2017b). This gregarious bird species belonging to the family *Alaudidae* also occurs in other parts of Africa (extends from South-west Kenya, Tanzania, Uganda, Southern Democratic Republic of Congo, Angola, Botswana, Malawi, Namibia, and Mozambique to Southern Africa) (Hockey *et al.*, 2005; Birdlife International, 2016). The Red-capped Lark has streaked grey to brown upper parts, an upright stance, an estimated height of 14-15 cm and is easily identified by a rufous cap, red shoulders and white under-parts (males have a redder plumage and a longer crest). The bird relies on insects as a major source of food especially during the breeding season. It mainly breeds at the onset of rains (Grizard *et al.*, 2015), with breeding coinciding with rainfall peaks in the months of March/May and September/December. Birds tend to pair-up and build ground-level open-cup nests that are placed next to a grass tuft or scrub (Ndithia *et al.*, 2017a). Some of the materials that birds use to construct nests include finer plant fibres, dry grass and animal dung. In most cases, the female lays two eggs per clutch in the nest which she incubates solely with the male feeding her at the nest. Eggs hatch synchronously 12 days after incubation begins and both parents feed the nestlings until they leave the nest after about 9-10 days (personal observation). When they are not actively breeding, Red-capped Larks form flocks of 10-20 birds.



Figure 1: A ringed territorial Red-capped lark male showing leg bands on both legs to identify individual birds

The diet composition of the Red-capped lark include mantids, Hemiptera(bugs), wasps, termites, Lepidoptera (moths, butterflies and their larvae), Coleoptera (beetles), Pentatomidae (stinkbugs, Margarodes (scale insects), Orthoptera (grasshoppers), Curculionidae (weevils) and snails (Hockey *et al.*, 2005). Substrates that form food niche of the Red-capped Lark include large mammal dung, soil moulds and grass substrate (personal observation).

Knowledge on habitat use of the Red-capped Lark that now inhabits some of the highly threatened Kenyan grasslands remains limited (Gottschalk *et al.*, 2007). With many grasslands becoming threatened biomes (due to land use changes leading to habitat loss/fragmentation, conversion of habitats to land for socio-economic development, poor management of grassland habitats, unnatural grazing regimes and environmental degradation), changes in tropical grassland ecosystems have resulted to declining populations of many tropical grassland birds. The degradation and loss of the grassland habitats have had negative impact on bird populations with human impacts affecting birds in the habitats intensifying in the recent years. This makes it critical for knowledge on behaviour and habitat requirements of avian grassland species be applied to ensure their conservation and, prediction of how past/future changes in seasonal food availability could influence their survival and population growth.

1.2.2 Red-capped Lark and factors influencing their abundance in a habitat

Although the Red-capped Lark is evaluated as a species of “Least Concern” by the International Union for Conservation of Nature (IUCN), the population is now considered to be approaching the thresholds for “Vulnerable” under the population size criterion (Birdlife International, 2016). The grassland habitats of the bird in Kenya are threatened. Rajpar and Zakaria (2011) assert that due to their habitat requirements, birds tend to have correlation with their habitats. For example, seasonality and insect prey abundance are factors that may influence the abundance of birds in a given habitat (Jahn *et al.*, 2010). Given that the Red-capped Lark relies on insects and grass seeds as food source, factors that influence insect prey abundance are likely to be critical for its survival and reproduction.

In ecosystems, nutrient flow and energy through the various trophic levels of the food chains are controlled by insects, making them crucial components of food chains and nutrient cycles (Siemann *et al.*, 1999; Dunn *et al.*, 2011). However, in recent decades, there have been rapid decline in diversity of insect species due to anthropogenic activities (Benton *et al.*, 2002). These activities have become key threats to insect biodiversity and survival of bird species that feed on them (Dugger *et al.*, 2004). Some studies in relation to food availability and foraging behaviour of bird species have reported a strong seasonal variation in abundance of main insect prey and feeding behaviour. Although arthropod taxa differ in their response to rainfall, the abundance of arthropods that are a key food resource for numerous tropical birds is often positively linked to rainfall (Jahn *et al.*, 2010). For many tropical birds, rainfall is associated with breeding cycles, abundance of insect food source and community diversity (Gibbs, 2007; Rompré *et al.*, 2007; Williams and Middleton, 2008).

Apart from rainfall, the population density of insects in a habitat is influenced by extremely high/low temperatures (Wardle and Barker, 1997). This may in turn affect the avian foraging behaviour especially during non-breeding and breeding seasons (Stouffer *et al.*, 2013). For instance, since insect abundance is expected to be lower during the non-breeding season, search times for insect prey by birds are predicted to be longer (Jahn *et al.*, 2010). This is because the dry season is characterized by a dramatic decline in rainfall and availability of insect prey. The influence of seasonal availability of insect food source on the foraging behaviour of tropical birds needs to be investigated by researchers and more studies that deepen an understanding of

when/how food limits avian reproductive output hence need to be undertaken. This is very important in understanding how past/future shifts in seasonal food availability could influence the life (history) cycle and population growth of avian species (Dunn *et al.*, 2011).

The structural complexity of the environment in a particular area is related to the behaviour of organisms that inhabit the area as well as the abundance/diversity of species (Mcnert and Rypstra, 2000). Vegetation type that occurs in an area contributes to this complexity given that vegetation provides insects with habitats and act as a source of food for the herbivorous species (Khadijah *et al.*, 2013). As a result, there exists a relationship between plant species composition in different vegetation types and insect abundance /diversity. According to Haddad *et al* (2001) and Knops *et al* (1999), an increase in number of plant species in natural ecosystems results to higher insect species abundance and richness. However, in grassland ecosystems, insect species diversity and abundance may vary with vegetation types. Due to this variation, the question of to which extent the plant species composition, richness or diversity influences insect species diversity and abundance has been raised in ecological studies.

1.2.3 Insect prey availability and avian feeding behaviour

Availability of food resources and foraging behaviour are some of the key factors that influence diet selection in birds (Rosenberg, 1993). Since food availability is a key limiting factor for avian survival and reproduction, birds that greatly depend on insect food source often rely on a short period of food abundance to feed their young (Wellicome *et al.*, 2013). Pedro *et al* (2013) confirmed that the bimodal breeding season of the Coal-crested finches (*Charitospiza eucosma*) may have been influenced by two annual peaks of food (insect) resource abundance. This can be attributed to the fact that the abundance of a given prey influences its availability to the predator. For example, birds ensure that their reproduction matches the abundance (food peak) of their main prey to ensure there is sufficient food for the young ones (Garcia-Navas and Sanz, 2011).

In avian studies, there is need for a deeper understanding of some specific predator-prey interactions that are critical in shaping foraging niches (Rosenberg, 1993). For instance, Benton *et al* (2002) asserts that a general decline in insect abundance may result to a decline in the population of bird species that rely on insects as food items (Bengt, 1996). Given that individual birds may differ in their food intake at any given time, the average diet of a given bird population

is likely to change throughout the year (Anna *et al.*, 2014). One of the factors that has been attributed to this is the availability of a given prey species. This is seen in many species where individuals specialize in devouring one type of prey at one time but switches to another when the first one is unavailable. The individuals may then move on to others until insect activity decreases. Similarly, birds tend to form "search images" hence learn to find particular abundant (although often camouflaged) prey and specialize in them as long as they remain available. This means that the diet of a given population may shift dramatically as increasing numbers of individuals form new search images.

A relationship between insect species abundance and the feeding behaviour of birds that prey on them exists. Joern and Laws (2013) in a study to examine the arthropod species diversity in grasslands confirmed that diversity plays a key role in predator-prey interactions. Such relationships that exist between insect abundance/distribution and avian feeding behaviour make avian studies in relation to insect food source very important in understanding the ecology of grassland bird species (Dunn *et al.*, 2011).

1.2.4 Avian diet, feeding behaviour and micro-habitats/substrate

For bird species, the foraging behaviour is significantly influenced by the type of feeding substrate it depends on for food (Mansor and MohdSah, 2012). A foraging substrate is the micro-habitat from which birds derive their food items hence forms food niche for birds. Due to the fact that insects tend to actively avoid areas with birds that feed on them, birds are likely to search for prey on preferred micro-habitats hence develop numerous specialized niches. For instance, specialized bird species that are trophically similar may differ in the type of foraging substrate they prefer (Holmes and Robinson, 1988). This may be influenced by the type of insect prey found in the substrate that a bird feeds on. Focusing on foraging substrates explores how birds utilize different food niches to adapt to the habitat since the partitioning of food resources is important for the survival of avian species. Knowledge on foraging ecology of tropical birds has become fundamental in providing an understanding of the ways in which species in a habitat partition their resources (Schulze *et al.*, 2000).

1.2.5 Time allocation by birds to feeding activities

The proportion of time allocated to feeding activities by birds provides some insight into feeding behaviour (Lu and Zheng, 2009). Since food can limit the survival and level of reproductive success in a species, including birds, the amount of time allocated to various activities while feeding is very important (Wishart and Seal, 1980). These activities may include resting, preening, scanning, walking and courtship displays. For example, studies on avian feeding behaviour have confirmed that one critical activity engaged in by birds while feeding is scanning for predators. This is because failure to be vigilant may result to death by predation (Bertram, 1978). On the other hand, allocation of too much time for vigilance may lead to reduced feeding time and starvation (Sullivan, 1990). This makes the allocation of time to feeding activities by individual birds critical for their survival. This means that it may become necessary for small insectivorous birds that are experiencing food limitation to have a large proportion of their time allocated to feeding as compared to other activities. Another factor that may influence the proportion of time an individual bird allocates to feeding is food availability and parental responsibility (Osterblom and Olsson, 2002). Studies on foraging behaviour in relation to the proportion of time allocated to activities can hence provide details of time-budget for birds (Lu and Zheng, 2009).

1.2.6 Food provisioning behaviour of parental birds at the nest

Availability of food affects the reproductive cycle of birds (Akinpelu and Oyedipe, 2004). As a result, their foraging behaviour may vary with the non-breeding and breeding seasons when weather conditions also vary (Felicity *et al.*, 2014). Some of the factors that influence avian foraging behaviour in relation to insect prey during the two seasons include the variation in prey abundance/supply as well as the investment of adult parents in the survival of the young. For instance, Robb *et al* (2008) states that food supply is widely regarded as one of the most fundamental factors that influences breeding investment in birds. In this case, the abundance and diversity of insect prey in a habitat influences breeding behaviour as adults strive to maximize their breeding success. For birds that prefer to breed during the wet season, breeding often coincides with the time period when arthropod abundance is highest. This can be attributed to the fact that the arthropods are a critical food source for the young and provide additional food resources for the adults (Stouffer *et al.*, 2013). For example, Schulze *et al* (2000) in his study on

the behaviour, diet and breeding biology of double-toothed kites (*Harpagus bidentatus*) in Guatemala reported that throughout the nestling period, the proportion of insects comprising the nestling diet continued to increase as females intensified their hunting effort and brought food to the nestlings.

According to the breeding currency hypothesis, insectivorous bird species tend to exploit large/soft-bodied prey during the breeding season as compared to the non-breeding season when they shift to small/ hard-bodied prey. This is because the soft-bodied prey is important for feeding the young. A study on the foraging behaviour of the Cerulean warblers (*Setophaga cerulean*) during the breeding and the non-breeding seasons reported that i) areas of higher prey abundance were preferred more by birds as compared to those with lower prey abundance ii) more than 50% of nest visits made by parent birds involved the delivery of large prey items iii) larvae comprised 69 % of identifiable large prey delivered to nestlings iv) adult birds captured 7% more large prey during the breeding season as compared to the non-breeding season (Felicity *et al.*, 2014). Such studies have confirmed a strong link between insect prey availability and the adult provisioning behaviour at the nest.

Previous research studies on avian foraging behaviour have shown that prey quality influences how birds adjust their feeding behaviour. For example, a study on the foraging behaviour of the Mediterranean blue tits (*Cyanistes caeruleus*) indicated that prey choice decisions may have been affected by the quality of food supply (Garcia-Navas & Sanz, 2011). Factors that contribute to the food peak (such as abundance/diversity of insect food source and seasonality) are therefore important for the parental adults. This is because food items that play a decisive role in the nestling diet of some bird species may only be available during a relatively brief period (wet season), demanding that birds reproduce when great need for food by the young matches the time when preferred food items for nestlings (such as caterpillars) are most abundant (Jahn *et al.*, 2010). In addition, the male and female parent birds may show variation in the provisioning behaviour at the nest (Mänd *et al.*, 2013). Studying the provisioning behaviour of parent birds at the nest can shed light on the adult provisioning behaviour at the nest.

1.3 Justification

Grassland birds have ecological/economic significance since they influence the functions of ecosystems and support human welfare (Barros *et al.*, 2014). As the negative impacts of anthropogenic activities continue to intensify in and around their habitats, some of the key threats to their survival include the decline in bird populations and loss of breeding habitats (Dunn *et al.*, 2011; Diniz, 2011). There is therefore great need to fill the huge knowledge gap that still exists in relation to the ecology of many tropical birds, including the study species. Further ecological studies are necessary in understanding how birds adapt to their habitats and the inter-specific interactions they have with other species (Davis, 1977; Benton *et al.*, 2002; Clancy, 2011). The diverse life history traits of tropical birds offer researchers unique opportunities to test the evolutionary and ecological theory (Stutchbury and Morton, 2008). Furthermore, passerines (such as the study species) are diverse and successful species hence offer a variety of adaptations in avian species to be studied. The knowledge gaps that exist in relation to the ecology of the Red-capped Lark include;

- i) Knowledge on its diet and feeding behaviour remains incomplete since no research work on feeding behaviour in the study area has previously been conducted.
- ii) Knowledge on taxonomic classification (family, genus, species) , diversity and abundance of its insect prey species at the Kedong grassland area is limited
- iii) Research work on how seasonality influences diet and feeding behaviour in the study area has not yet been conducted.

Due to these gaps, there is poor understanding of how this grassland bird is adapted to its habitat and how factors such as food availability and seasonality affect its survival. This makes the study very important in filling these knowledge gaps; deepening an understanding of when and how food limits avian reproductive output; and predicting how past/future changes in seasonal food availability could influence the phenology and population growth of avian species. The major objective of the study was to assess the diet and feeding behaviour of the Red-capped Lark at Kedong grassland area with key focus on how factors of seasonality and insect prey abundance/diversity influence the behaviour.

The long-term impact of the study findings on conservation include : i) deepening an understanding of habitat requirements of the Red-capped lark and other grassland birds in the

study area ii) assisting the Kedong ranch management to integrate a comprehensive grassland bird management plan in the overall management plan of the ranch iii) predicting potential impacts of avian biodiversity losses iv) deepening an understanding of preconditions of maintaining avian biodiversity. The need to address the problem of current/future species loss and habitat degradation as the effects of anthropogenic activities intensify makes an ecological study on the species very critical. Findings from the ecological study will be integrated in the conservation plans of the study area to ensure effective management of the grassland bird species.

1.4 Research Questions

- i. What was the diet of the Red-capped Lark?
- ii. Does the abundance and diversity of insect prey types vary with vegetation type and season?
- iii. What was the insect prey type fed to nestlings by the parental adults?

1.5 Objectives of the Study

Overall objective

The goal of this study was to assess the diet and feeding behaviour of the Red-capped Lark and how it is influenced by factors of insect prey abundance/diversity and seasonality.

Specific objectives

- i. To determine the diet of the Red-capped Lark
- ii. To determine the diversity and abundance of insect prey types of the Red-capped Lark
- iii. To describe the provisioning behaviour of the adult parent birds at the nest

1.6 Hypotheses

- i. Diet and feeding behaviour may not be influenced by seasonality and availability of insect prey type
- ii. The abundance and diversity of insect prey type may not vary with vegetation type and season
- iii. There may be no difference in type and number of insect prey type fed to nestlings by the parent birds.

CHAPTER TWO: STUDY AREA, MATERIALS AND METHODS

2.1 Study area

2.1.1 Location

The study was conducted in Kedong ranch ($0^{\circ}53' 37''S$, $36^{\circ} 23' 54''E$) located on the floor of the Eastern Rift Valley in Naivasha, a town approximately 90 kilometres North West of Nairobi. It is sandwiched between two conservation areas (Hell's gate and Longonot National Parks). The savannah grassland ecosystem is inhabited by various species of wildlife and is exposed to intensive grazing by herds of wildlife and livestock. The open grassland area in the ranch has a high population of resident Red-Capped Larks, making the grassland habitat suitable for this study.

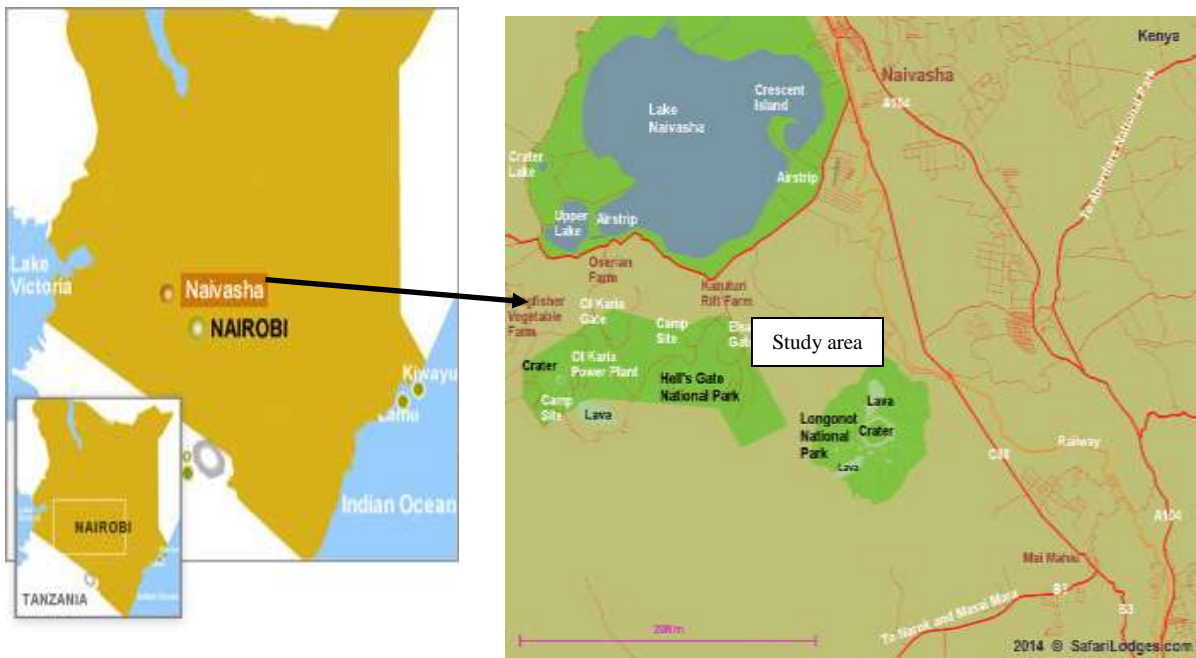


Figure 2: A composite map showing location of the study area

2.1.2 Conservation status of the study area

The study area is in Naivasha, an area of high conservation priority due to its great significance in conservation of avian species and other biodiversity. Birdlife International lists Lake Naivasha (adjacent to the study area) as an Important Bird Area (IBA)(Bennun and Njoroge, 2001). In addition, Lake Naivasha is listed as a Ramsar wetland of international importance.

2.1.3 Soil and topography

The study area lies at an elevation of 2077 m above sea level. The soils are calcareous, loam friable stony and loam clay in nature. The nature of these soils has been attributed to factors such as volcanic activity witnessed in the past, extensive relief variation and underlying bedrocks. The soils hence developed from volcanic and lacustrine deposits (Torrión, 2002).

2.1.4 Climate

The area has a tropical savannah climate which is characterized by one distinct and one less distinct rainy period. The area hence has a bimodal rainfall pattern (Figure 3). The long rainy season occurs in March-May while the short rainy season in (October-November), with two intervening dry seasons (Bhandari, 2005). Naivasha has been designated as an agro-ecological zone IV (semi-arid to semi-humid) with an annual rainfall of 600-1100 mm (FAO, 1996). The annual average temperature is 25.0° C while the average low temperature is 9.4° C.

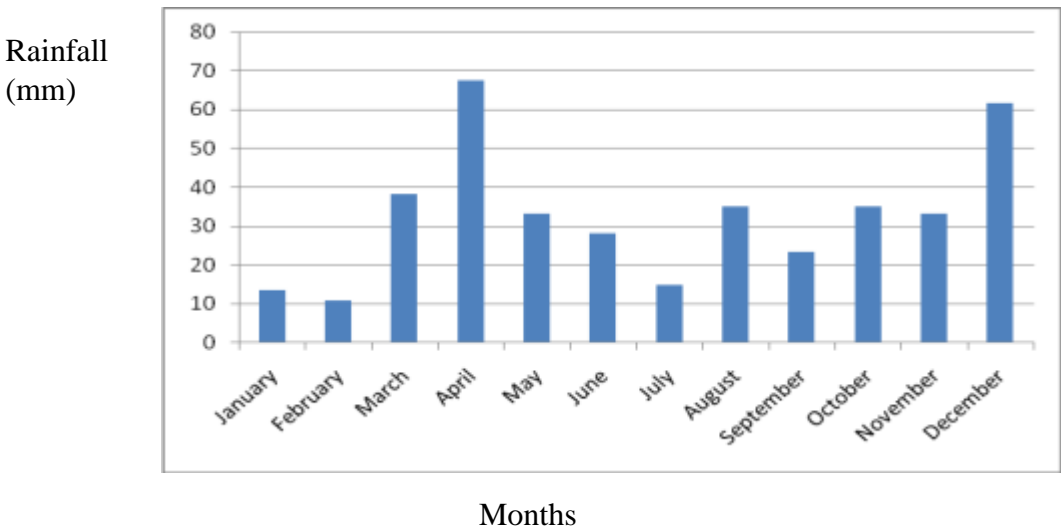


Figure 3: Mean monthly rainfall for the study area (2011-2013) (Ndithia *et al.*, 2017a)

2.1.5 Flora

Some of the indigenous *Acacia* trees found in the area include *Acacia drepanolobium*, *A. gerrardii*, and *A. xanthopholea*. Other common tree species include *Acocanthera schimperi* and *Euphorbia candelabrum*. The *Tarconanthus camphoratus* forms a common bush while the common grass species present include *Pennisetum spp*, *Themeda triandra*, *Eragrostis tenuifolia*, *Chloris virgata*, *Cynodon nlemfuensis (var.nlemfuensis)*, *Harpachne schimperi* and *Pennisetum mezianum*. *Felicia muricata* and *Indigofera bogdanii* are the two species of forbs found in the study area. Although the study area comprised open grassland, the acacia- woodland and *Tarconanthus camphorates*-acacia woodland were the two main vegetation types that occurred along the edges of the open grassland. The characteristic of the vegetation type influences the habitat of wildlife species, including the study species (Red-capped Lark).

2.1.6 Fauna

Some of the resident terrestrial bird species found in Kedong ranch include the Red-capped Lark (*Calandrella cinerea*) (study species), Rufous-naped Lark (*Mirafra Africana*), Grassland pipit (*Anthus cinnamomeus*), Cattle egret (*Bubulcus ibis*), Pectoral patch cisticola (*Cisticola brunnescens*), Ant-eater Chat (*Myrmecocichla aethiops*), Kori Bastard (*Ardeotis kori*), African Goshawk (*Accipiter tachiro*), Near-Threatened Grey-crested Helmeted shrike (*Prionops poliophus*) and African Fish Eagle (*Haliaeetus vocifer*).

Apart from the birds, other wildlife species found in the area include the Grant's gazelle (*Nanger granti*), Thomson's gazelle (*Eudorcas thomsonii*), Grevy zebra (*Equus grevyi*), Maasai giraffe (*Giraffa tippelskirchi*), Cape buffalo (*Syncerus caffer*), Eland (*Taurotragus oryx*), Bat-eared fox (*Otocyon megalotis*) and Spotted hyena (*Crocuta crocuta*). Some of the threatened bird species found in the area include the endangered Grey-crested Helmeted-shrike (*Prionops poliophus*), Little Grebe (*Tachybaptus ruficollis*), Lesser Flamingo (*Phoeniconaias minor*), Red-knobbed Coot (*Fulica cristata*), and African Spoonbill (*Platalea alba*).

2.1.7 Socio-economic activities

Some of the key socio-economic activities undertaken in the study area and its environs include intensive cattle ranching, wildlife and biodiversity conservation, pastoralism, horticultural farming, power production (geothermal), fishing, business and trade. High value residential properties have led to loss of wildlife habitats in the area due to increased demand for land. Commercial flower/horticultural crop farming are common in the area with flower farming generating huge revenue earnings (Harper *et al.*, 2011). This has made agriculture one of the key socio-economic activities that contribute to land-use changes that have negative impact on wildlife habitats. In private ranches (such as the study area), large herds of grazing cattle and wildlife contribute to changes that modify the grassland habitat for birds through grass habitat structure alteration. Human activities in the conservation area adjacent to the study area (Hell's Gate National Park) have also intensified due to geothermal electricity generation that supports about 18.9% of the country's national power supply (WWF, 2011). These developments are a key threat to conservation and survival of Red-capped Lark population in Kedong area.

2.2 Materials and methods

2.2.1 Research design

Conclusive research design was used with data collected aimed at testing specific hypothesis and examining how variables relate. A large sample of observations on adult birds was expected to be obtained through focal animal sampling where focal birds were randomly selected for sampling adult behavior (Akinpelu and Oyedipe, 2004). Systematic sampling was used to select sampling plots in each of three vegetation types (open grassland and adjacent woodlands (Acacia woodland and *Tarconanthus camphoratus*-Acacia woodland). The study area was first divided

into equal grids of 100m x 100m. To select the 100m x 100m plots to be used for sampling, systematic sampling was done by first establishing parallel transects perpendicular to a baseline across the study area. The distance between transects was set at 200m hence a total of 3 transects were established in the whole study area. Sampling plots for insect prey and foraging substrates were then selected at an interval of 100m.

In the three vegetation types (open grassland, Acacia woodland and *Tarconanthus camphoratus*-Acacia woodland identified in the study area), pitfall sampling was done in 5 randomly selected units of 20 m x 20 m within the larger 100m x 100m plots selected for sampling. In the selected plots for sampling within the grassland, sweep net sampling was done along a 10m transect.

2.2.2 Assessment of foraging substrates (Dung substrate and soil moulds)

The foraging substrates that form micro-habitats where the Red-capped Lark obtained its food included large herbivore dung piles and fresh soil moulds/heaps. To sample the substrates, the study area was first divided into equal grids of 100m x 100m (Nkwabi *et al.*, 2010). To select the 100m x 100m plots to be used for sampling, systematic sampling was done by first establishing parallel transects perpendicular to a baseline across the study area. The distance between transects was set at 200m hence a total of 3 transects were established in the whole study area. Sampling plots were then selected at an interval of 100m (Okolie *et al.*, 2015). This gave a total of 5 plots along each of the 3 transects hence a total of 15 plots were identified for sampling.

In these plots selected within the open grassland, the total number of fresh dung piles and soil moulds per each sampling plot were counted. The data was used to establish the density of the substrates in plots and the whole study area. For the analysis, each plot was considered to be a replicate. A total of 10 samples were obtained.

2.2.3 Herbaceous layer sampling to assess grass substrate

To sample the grass substrate in the study area that was homogenous, the 100m x 100m plots (selected through systematic sampling) were divided into 25 equal units measuring 20m x 20m. One unit in each plot was selected (through random sampling) for herbaceous layer sampling. This gave a total of 15 units for sampling.

In each unit, a 10m transect was established 5m from each plot boundary to minimize the edge effects (Zhu *et al.*, 2012). Quadrats of 1m x 1m were placed at an interval of 2 m along the

transect, giving a total of 3 quadrats per each 10m transect established per unit. The total number of grass clumps per quadrat was counted. Plant cover was also estimated and the height of the grass in each of the four corners of the quadrat and the middle measured using a metre rule. The total number of grass clumps counted per quadrat was used to estimate the grass density in the plots and the entire study area during breeding and non-breeding periods. A total of 10 samples were obtained.

2.2.4 Focal animal sampling to assess diet and feeding behaviour

Data on feeding behavior recorded was obtained from as many birds as possible using the focal animal observation technique (Martin and Bateson, 1988; Nhlane, 1992; Akinpelu and Oyedipe, 2004). Foraging birds were observed from about 50 m away using a telescope (30 X). Observations were made under good weather conditions, avoiding bad weather conditions (when drizzling or raining) (Murphy, 1987; Schulze *et al.*, 2000). Feeding behavior observations were conducted in the morning (0700-1100 hrs) and late afternoon (1600-1800 hrs) when birds were most actively feeding (Felicity *et al.*, 2014). To find the focal bird, the observer walked slowly (approx. 4km/h) across the study area and every third that was actively feeding identified as the focal bird. The bird was first observed for 10 seconds without recording any data. This time period minimized the likelihood of recording only the conspicuous behavior, and also ensured that the bird resumed normal activity patterns in the presence of the observer (Block, 1991).

Observations of birds while feeding were made for 15 minutes per individual. Timed data on behavior (per minute) was collected. A stop-watch was used to time the duration of activities per minute. Each focal individual was observed for 15 minutes (consisting of one minute observations with 30 seconds intervals in between the observations). This amounted to about 10 minutes of feeding behavior observation sessions (each session of one minute) per focal bird. The number of times each feeding behavior (pecking, scanning, walking, searching and preening) was observed per minute was recorded. The activities were defined as provided by Fitzpatrick and Bouchez (1998) as follows;

1. Feeding- Each distinct jab or peck at the foraging substrate
2. Scanning- bird looked up/ raised its beak clear of substrate and within 10° of horizontal level
3. Searching- movements leading up to sighting of food or food concealing substrate. Searching ended when food item was sighted and attacked

4. Preening- use of the beak by a bird to strip or pick through the feathers
5. Walking- forward progression of an individual using legs
6. Food capture techniques- (i) picking- birds walk on the ground and pick prey along the route; ii) run-picking-picking of insect prey preceded by a short sprint).
7. Food handling techniques- (i) gulping- swallowing of prey without noticeable manipulation other than the bird holding the food briefly using the bill; ii) tearing and gulping-dissecting food items into smaller pieces followed by swallowing) (Remsen and Robinson,1990).

Observations began as soon as the focal bird began foraging. When focal individual stopped foraging or was lost from sight before 30 seconds (of the one minute observation) elapsed, data was not considered for analysis. When the focal bird stopped foraging or was lost from sight, another individual adult bird within the flock was selected as the focal bird in order to complete the observation period (De Melo and Guiherme, 2016). Data were obtained on behaviours (feeding, scanning, walking, searching, preening, courtship display), food capture and handling techniques, time of feeding, food type and type of foraging substrate selected for food capture. Each distinct jab or peck at the foraging substrate was considered to represent a feeding hence number of pecks per minute accurately represented feeding rates (Davis, 1977). Behavioral event data was used to determine frequency of each behavior every one minute a bird was observed. This allowed for the calculation of rates per minute. The records were treated as independent in the analysis (Fitzpatrick and Bouchez, 1998). To avoid re-sampling the same bird, the observer moved 150 m from a location before the sampling of the next bird began (Munoz and Colorado, 2012). A total of 1250 independent observations were made (486 observations (for 82 birds) during breeding period (March-May and June to July) and 764 observations (for 94 birds) during non-breeding period (June and August).

2.2.5 Parent feeding behaviour at the nest

During breeding season, observations using a telescope were made to assess the parent provisioning behavior at the nest. To ensure close observation and reduced observer effects, observations of birds were made while inside a hide (about 15-20m from the nest) using a spotting scope (30 X) (Marques, 2004). The hide comprised of a metal frame covered with a green material and tree twigs on the sides. This avoided biased results since close presence may influence the avian nest behavior especially in relation to parental birds (Yatuha & Dranzoa,

2009). Breeding activity was monitored daily and when nests in the process of construction were found, GPS coordinates of their location were marked and a nest code assigned. This allowed for later monitoring so that observations could be made after nestlings hatched. Observation periods were from dawn to dusk, except in instances of unfavorable weather (Schulze *et al.*, 2000), which in the study area was characterized by drizzling, strong wind or heavy rainfall. Observations started at 0700hrs and ended at 1800hrs. The variation in the activity of parent birds at the nest was documented and the prey items identified. During the nest behaviour observations, the following was recorded; nest code(unique to each nest for identification and monitoring), time of each feeding session/feeding times, age of the nestlings, duration of feeding in the nest, food type and identity of parent birds (where possible). The collected data were used to describe the parental behavior patterns and allowed for calculation of prey delivery rates.

Observations on nest behavior (to obtain data on prey delivery rates and diet) were completed for a total of 163 hours. During the study period, 11 nests were observed for 11 hours of the day (from 7.00 am-6.00pm), while another 7 nests were observed for the time periods 7.00-8.00am; 9.00-10.00am; 11.00am-12.00pm; 1.00pm-2.00pm; 3.00-4.00pm; 5.00-6.00pm. Since the nestlings of the Red-capped Lark often fledge from the age of 9-10 days, observations were undertaken on nests with nestlings of between 1-10 days old. Observations were made on nestlings of the following age classes: Day 2(2 nests), Day 3(4 nests), Day 4(2 nests), Day 5(1 nest), Day 6(2 nests), Day 7(2 nests), Day 8(2 nests) and Day 10(1 nest). All nests had two nestlings.

2.2.6 Assessment of insect prey species

2.2.6.1 Pitfall sampling

In the three vegetation types (open grassland, Acacia woodland and *Tarconanthus camphoratus*-Acacia woodland identified in the study area), pitfall sampling was done in 5 randomly selected units of 20 m x 20 m within the larger 100m x 100m plots selected for sampling. The transects were placed 5m from the plot boundaries to minimize edge effects In each unit, pitfall traps that were 950 cm³ (7cm diameter, 10cm depth) consisting circular plastic containers were placed 3m apart along 10m transects to sample the insects (Nemec *et al.*, 2014). Each transect hence had 3 pitfalls placed along it. The traps were filled with a solution of water, detergent and a little alcohol then placed in the soil to a depth of approximately 10cm with the opening being level

with the ground surface. All traps were checked and contents of each trap emptied at the end of each sampling period then preserved in an ethanol solution. The specimens were then sorted and identified to the family, genus and species level. Their total numbers were recorded. The data were used to determine insect prey species richness and abundance in the three different vegetation types where insects were sampled. During the data analysis, units in each habitat type were considered to be replicates. A total of 10 pitfall trap samples were collected during the study period.

2.2.6.2 Sweep net sampling

In the selected plots for sampling within the grassland, one transect measuring 10m was established for sweep net sampling. The transect was placed at least 1 m away from the plot boundary to reduce edge effects (Zhu *et al.*, 2012). To ensure samples in each plot were representative, the researcher walked slowly and one sweep taken every 2 metres for a total of 5 sweeps/transect (Haddad *et al.*, 2001; Spafford and Lortie, 2013). The net was continuously swung rapidly 0.1 to 3m above the ground in a figure of eight pattern from side to side to avoid escape of the captured insects. Insect specimens were collected only under favorable conditions (sunny days with minimal cloud cover and calm or no wind) (Zhu *et al.*, 2012). Sampling was done between 0900 and 1200hrs (Jerrentrup *et al.*, 2014). The contents were preserved in bottles containing 70% ethanol. Butterflies collected were preserved in envelopes for later pinning. Records were made on the number of various species of insects collected and data used to determine the insect species richness and abundance in the open grassland vegetation. A total of 10 sweep net samples were collected.

2.2.6.3 Butterfly sampling

Since sweep net sampling to sample butterflies could not be done in the woodlands (Acacia woodland and *Tarconanthus camphoratus*-Acacia woodland) adjacent to the open grassland habitat of the Red-capped Lark, butterfly traps were used to sample butterflies in the three vegetation types. Sampling was done in the 5 randomly selected units of 20 m x20 m. The Van Someren-Rydon (VSR) trap was used (Freitas *et al.*, 2014), with bait (fermented mixture of ripe bananas and pineapples) placed inside and one trap set in each unit (Jew *et al.*, 2015). Butterflies collected were later preserved in envelopes for later pinning. The specimens were identified and data used to determine species richness and abundance of butterflies in the three different vegetation types. A total of 10 samples were collected.

2.2.7 Data analysis

Data were tested for normality using the R-QQ plot for normality and Shapiro-Wilk Test. Comparison was made on means for samples obtained from a normal distribution. Statistical tests were performed using R- program version 3.2.1 and PAST software. A one-way ANOVA test was used to examine between-nest variation in prey composition, adult behaviour patterns and prey delivery rates. Multiple comparison test (Tukey HSD) was used to make multiple comparisons for mean rates in adult behavior recorded in the morning (7.00-9.00 am), mid-morning (9.01 am-11.00am) and evening (4.00-6.00pm). Chi-square tests were done to infer differences in behavior between breeding and non-breeding periods. A Welch Student's t-test was conducted to examine differences in food provision by male and female parents to nestlings and selection for foraging substrates for food capture by birds. To compare food availability with utilization, the mean weekly consumption for food was correlated to the mean weekly captures of insect prey. Insect prey diversity in various vegetation types (open grassland, Acacia-woodland and *Tarconanthus camphoratus*-acacia woodland) was estimated using Shannon-Weiner diversity indices (H'). In all the statistical tests conducted, the level of significance was always set at $\alpha < 0.05$. The mean values were reported as means \pm SE.

CHAPTER THREE: RESULTS

3.1 Diet of the Red-capped Lark, availability and utilization of food items

3.1.1 Insect, availability and utilization

For avian species that feed on insects, diet composition and availability of insect prey often relates to the abundance of potential prey items in the habitat where it searches for food. The study revealed that the diet of the Red-capped Lark comprised both insect food and grass seeds. However, insect diet was predominant. The insect diet comprised of insects in the orders Coleoptera, Orthoptera, Lepidoptera, and Hymenoptera. During the breeding period, 63.2% (n = 221 observations) of diet was insect food and 36.8% (n = 131) plant food (grass seeds). Similarly, during the non-breeding period, 81.5% (n = 421) of diet was insect food and 18.5% (n = 95) grass seeds (Figure 4).

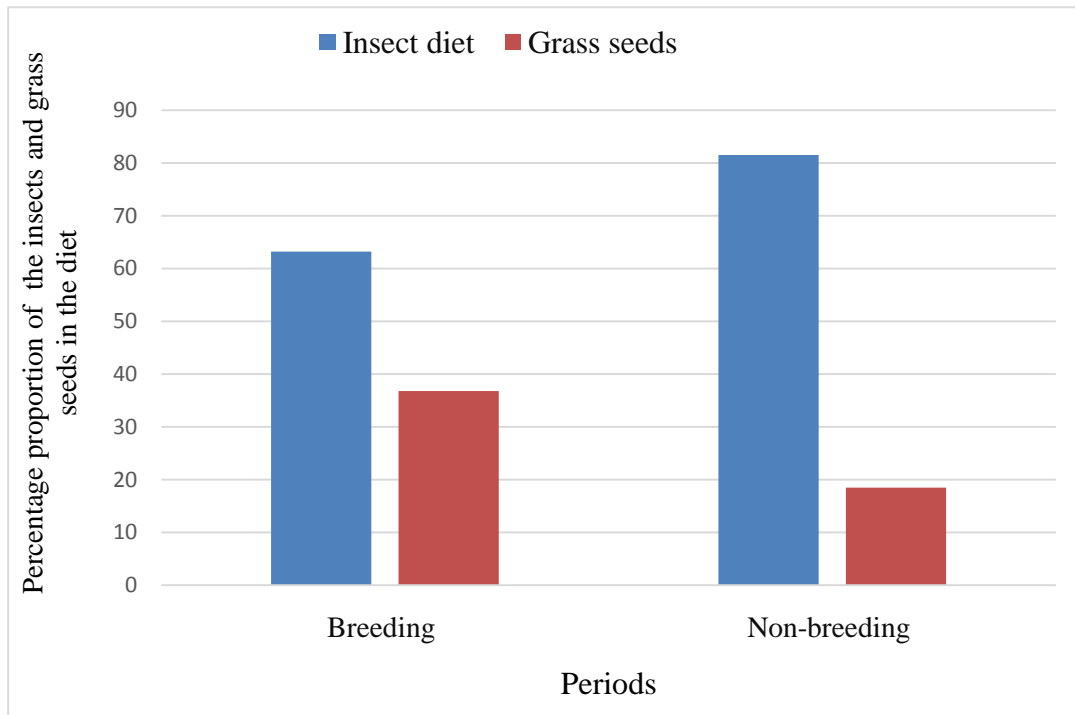


Figure 4: Composition of insect and plant diet for the Red-capped Lark during breeding and non-breeding periods

The various grass species found and identified in the open grassland habitat area of the Red-capped Lark included *Eragrostis tenuifolia*, *Chloris virgata*, *Cynodon nlemfuensis* (*var.nlemfuensis*), *Themeda triandra*, *Harpachne schimperi* and *Pennisetum mezianum*. Out of these 6 grass species, the Red-capped Lark was observed feeding on seeds from only two grass species; *Eragrostis tenuifolia* and *Harpachne schimperi*. The consumption of grass seeds during breeding period (36.8 % of diet; n = 131 feeding observations) was significantly higher than during non-breeding period (18.5 % of diet; n = 95 feeding observations) ($\chi^2_{0.05, 1} = 3.95$, $p < 0.05$).

Examination of the relationship between availability of prey items and utilization by adult Red-capped Larks was done by correlating mean weekly consumption of prey items by sampled adult birds with mean weekly captures of prey items in the open grassland habitat. The Pearson's correlation coefficients revealed that there was a positive relationship between availability and utilization of prey items. There was a significant positive correlation for insects in the orders Lepidoptera ($r^2 = 0.57$, $p < 0.05$) but none for the orders Coleoptera ($r^2 = 0.19$, $p > 0.05$), Orthoptera ($r^2 = 0.01$, $p > 0.05$), and Hymenoptera ($r^2 = 0.09$, $p > 0.05$).

A total of 754 individuals {belonging to 27 different insect taxa and 7 orders (Orthoptera, Coleoptera, Lepidoptera, Hymenoptera, Hemiptera, Diptera and Araneae)} were collected from the open grassland habitat of the Red-capped Lark during the breeding period. Insects in the order Orthoptera (36.3 % of total number collected), Hymenoptera (18.3% of total), Lepidoptera (17.1 % of total) and Coleoptera (6.8 % of total) were the most abundant. Insects in the order Diptera were the least abundant (1.9 % of total number collected (Appendix 1). A total of 221 feeding observations involving insect prey consumed by the Red-capped Lark were completed during the breeding period. The insect prey preferences by birds were calculated by converting observations of positively identified items into the proportion of the total feeding observations made. Insects in the order Orthoptera (21.9% of diet), Lepidoptera (20 % of diet) and Coleoptera (12% of diet) comprised the largest proportion of the insect diet. Insects in the order Hymenoptera (7% of diet) accounted for the lowest proportion (Figure 5). The results confirmed that insects in the orders Orthoptera, Hymenoptera and Coleoptera that were found to be most abundant in the open grassland habitat of the Red-capped Lark comprised its insect diet.

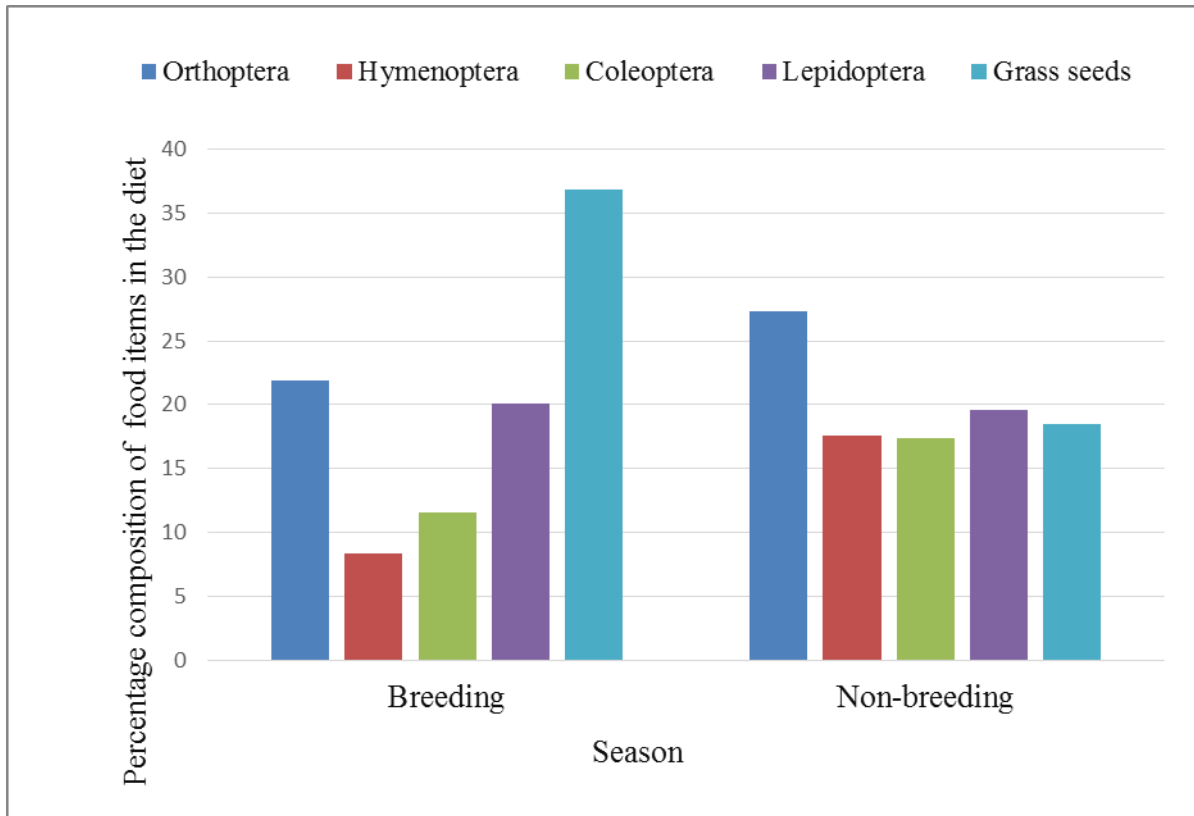


Figure 5: Dietary preferences of the Red-capped Lark during breeding and non-breeding periods

A total of 418 individuals {belonging to 16 different insect taxa and 7 orders (Orthoptera, Coleoptera, Lepidoptera, Hymenoptera, Hemiptera, Diptera and Araneae)} were collected and identified in the open grassland habitat of the Red-capped Lark during the non-breeding period (Appendix 4). The most abundant were insects in the order Orthoptera (42.5% of total), Lepidoptera (38.9 %) and Hymenoptera (12.4 %). The least abundant were insects in the orders Hemiptera (0.95 %) and Araneae (0.95 %). A total number of 421 observations on insect food items consumed by the Red-capped Lark were completed with the most frequently consumed insects being those in the orders Orthoptera (28.4 % of diet composition), Lepidoptera (18.02 %) Coleoptera (17.4%) and Hymenoptera (17.6%) (Figure 5). Insects that were found to be the most abundant in its open grassland habitat accounted for the largest proportion of the Red-capped Lark’s insect diet.

Apart from the open grassland habitat of the Red-capped Lark, insects were also sampled in the Acacia and *Tarconathus*-Acacia woodlands that were adjacent to the habitat. During the study period, 1,430 individual insects {belonging to 7 insect orders (Orthoptera, Coleoptera, Lepidoptera, Hymenoptera, Hemiptera, Diptera and Araneae)} were collected and identified from the open grassland, Acacia-woodland and *Tarconathus*-Acacia woodland. There were 869 insects sampled during the breeding period and 561 insects during the non-breeding period.

Given that the open grassland was the habitat of the Red-capped Lark, a Chi-square test to examine differences in insect prey abundance between breeding and non-breeding periods confirmed that there was no significant difference in abundance of insects between seasons ($\chi^2_{0.05,1} = 49.17, p > 0.05$).

During the breeding period, insect prey species abundance was significantly higher in the open grassland (n = 754) compared to Acacia-woodland (n = 55) and *Tarconathus*-Acacia woodland (n = 60) ($\chi^2_{0.05,2} = 507.16, p < 0.05$). In the Acacia woodland, insects collected belonged to 12 different insect taxa and 6 orders (Orthoptera, Coleoptera, Lepidoptera, Hymenoptera, Diptera and Araneae) (Appendix 2). In the *Tarconathus*-Acacia woodland, insects collected belonged to 11 different insect taxa and 6 orders (Orthoptera, Coleoptera, Lepidoptera, Hymenoptera, Diptera and Araneae) (Appendix 3).

The diversity indices of insect species for the open-grassland, Acacia-woodland and *Tarconathus*-Acacia woodland) were estimated. Although the insect species diversity index ($H' = 2.308$) for the open grassland was the highest as compared to that of Acacia woodland ($H' = 2.102$) and *Tarconathus*-Acacia woodland ($H' = 1.89$), there was no significant difference in the diversities. A Hutcheson t-test to examine the differences revealed that there was no significant difference in diversities between the open grassland and the Acacia woodland (t = 0.56, df = 63, p > 0.05), open grassland and *Tarconathus*-Acacia woodland (t = 1.13, df = 67, p > 0.05) and Acacia-woodland and *Tarconathus*-Acacia woodland (t = 0.41, df = 117, p > 0.05).

During the non-breeding period, insect prey species abundance was significantly higher for open grassland (n = 418) compared to Acacia-woodland (n = 64) and *Tarconathus*-Acacia woodland (n = 79) ($\chi^2_{0.05, 2} = 231.23$, $p < 0.05$). Insects collected in the Acacia woodland belonged to 13 different insect taxa and 6 orders (Orthoptera, Coleoptera, Lepidoptera, Hymenoptera, Diptera and Araneae) (Appendix 5). In the *Tarconathus*-Acacia woodland, insects collected belonged to 8 different insect taxa and 5 orders (Orthoptera, Coleoptera, Hymenoptera, Diptera and Araneae) were identified (Appendix 6).

The estimated species diversity index for the Acacia woodland ($H' = 2.294$) was the highest as compared to open grassland ($H' = 1.544$) and *Tarconathus*-Acacia woodland ($H' = 1.566$). A Hutcheson t-test indicated that there was significant difference in diversities between open grassland and the Acacia woodland ($t = 2.17$, $df = 72$, $p < 0.05$), as well as between Acacia-woodland and *Tarconathus*-Acacia woodland ($t = 4.09$, $df = 126$, $p < 0.05$). However, there was no significant difference in diversities for open grassland and *Tarconathus*-Acacia woodland ($t = 0.08$, $df = 93$, $p > 0.05$).

3.1.2 Jaccard's coefficient similarity of insect sampled in different habitats during breeding and non-breeding periods

Jaccard's indices using the formula $CCJ = c / S_1 + S_2 - C$ (where; C - number of species the two communities have in common; S_1 - the total number of species found in community 1 ; S_2 is the total number of species found in community 2) were calculated to compare similarity in insect species collected in the open grassland, *Tarconathus*-Acacia woodland and Acacia woodland during the breeding and non-breeding periods. The estimated similarity values between the periods for the habitats indicated that there was minimal similarity (0.35) for the open grassland (habitat of the Red-capped Lark) and *Tarconathus*-Acacia woodland (0.58). However, there was high overlap (0.92) for the Acacia-woodland for the two periods.

Within seasons, the estimated similarity values for different vegetation types showed that there was minimal community overlap between insect species that were sampled (values were less than 0.5) (Table 1). Similarity was higher during non-breeding period than during breeding period. It was highest for insect species collected in the *Tarconathus*-Acacia and Acacia woodlands during the non-breeding period (0.61).

Table 1: Jaccard's similarity indices for insects sampled in open grassland, *Tarconathus*-Acacia woodland and Acacia woodland during breeding and non-breeding periods

Vegetation types	<i>Tarconathus</i> -Acacia vs. Acacia woodland	Open grassland vs. Acacia woodland	Open grassland vs. <i>Tarconathus</i> -Acacia woodland
Jaccard's coefficient(breeding)	0.43	0.39	0.37
Jaccard's coeffic(non-breeding)	0.61	0.45	0.41

3.1.3 The foraging substrates of the Red-capped Lark and their selection for food capture

Apart from the grass substrate, mammal dung piles and fresh soil moulds were other two foraging substrates selected for food capture by the individuals. In the grassland habitat of the Red-capped Lark, fresh soil moulds were often small piles of fresh soil around holes that were dug overnight by mammals from where birds obtained ants/termites. The mean densities of the foraging substrates (grass, soil moulds and dung) in the open grassland habitat of the bird were estimated for 100m x 100m plots sampled during breeding and non-breeding periods (Figure 6).

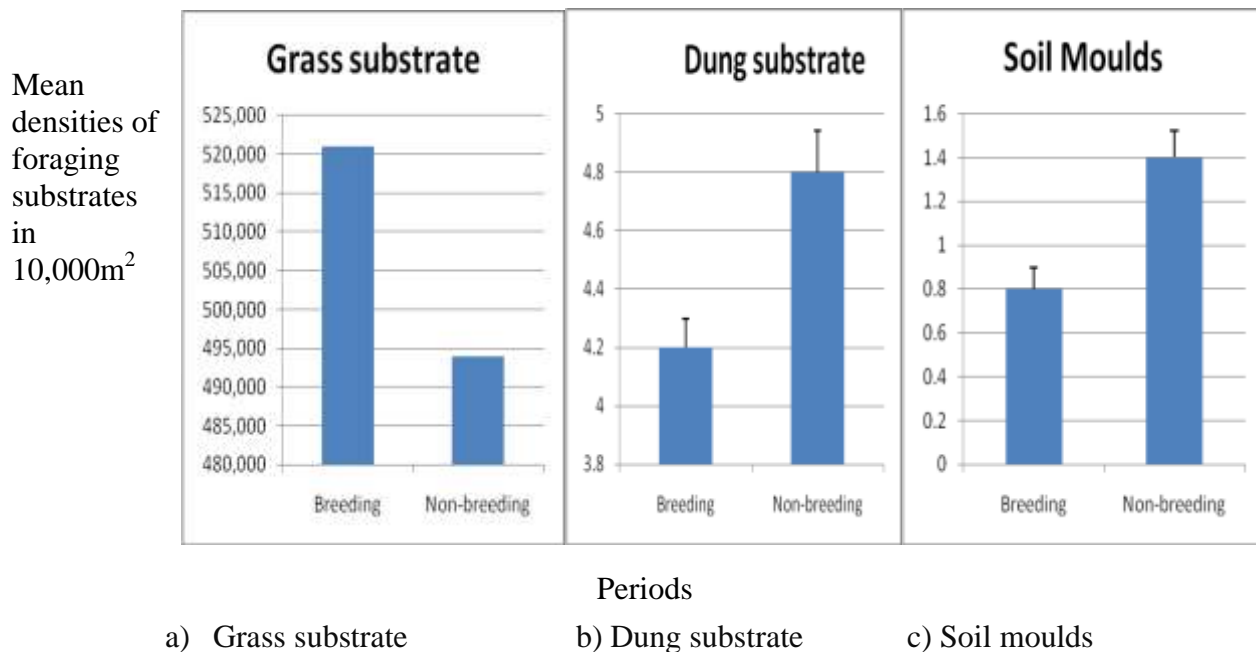


Figure 6: Mean densities of the different foraging substrates of the Red-capped Lark in the sampled 100x100m plots (10,000 m² area) during breeding and non-breeding periods

The foraging substrate most selected by birds for food capture during breeding and non-breeding periods was the grass substrate, followed by the dung substrate and soil moulds.

Individual birds were observed for a total of 10 observations (1 minute per observation) hence mean rates per the 10 observations that birds selected a foraging substrate for food capture were calculated. During the breeding period, there was significant difference in mean rates that birds selected the grass substrate, dung substrate and soil moulds ($F_{0.05, 2, 243} = 352.8, p < 0.05$) for food capture (Figure 7). Similarly for the non-breeding period, there was significant difference in mean rates that birds selected the grass substrate, dung substrate and soil moulds ($F_{0.05, 2, 279} = 257.1 p < 0.05$).

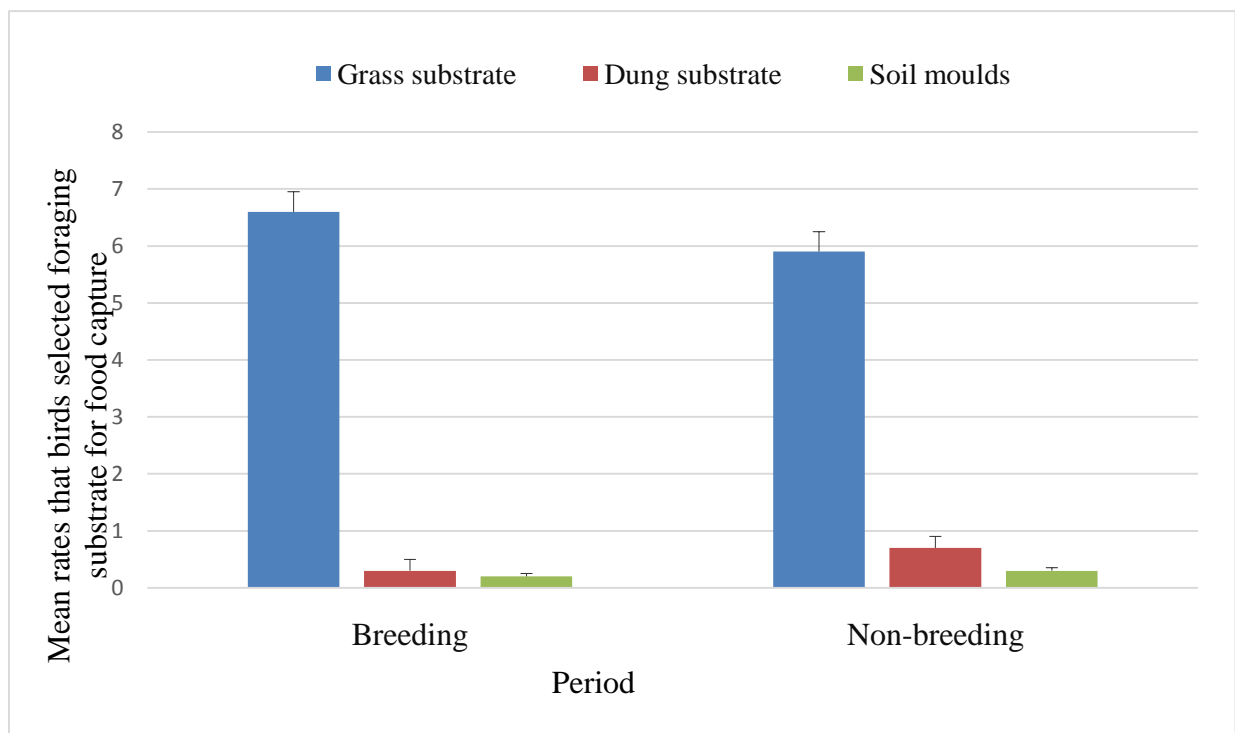


Figure 7: Mean rates \pm SE that birds selected foraging substrates for food capture (n = 82 birds for breeding and n = 94 birds for nonbreeding)

3.2 Food capture and handling techniques

The Red-capped Lark employed active foraging while searching for food on the ground. It was observed that the two food capture techniques that were employed by the bird were picking (birds walking on the ground and picking prey while walking) and run-picking (picking of food that was preceded by a short sprint). Picking was the most common food capture technique for both breeding and non-breeding periods.

During the breeding period, there was significant difference in the mean rates that birds employed picking (5.5 ± 0.25) as compared to run-picking (0.02 ± 0.02) (Figure 8) (paired t-test; $t_{0.05, 2, 82} = 20.94, p < 0.05$). During the non-breeding period, there was significant difference in the mean rates that birds employed picking (5.3 ± 0.23) as compared to the run-picking (0.1 ± 0.02) (Figure 8) ($t_{0.05, 2, 94} = 23.35, p < 0.05$). For the feeding observations involving picking, food items fed on by the birds were often grass seeds, butterflies/moths, insect larvae and grasshoppers while those involving run-picking were grass seeds, grasshoppers and butterfly/moths.

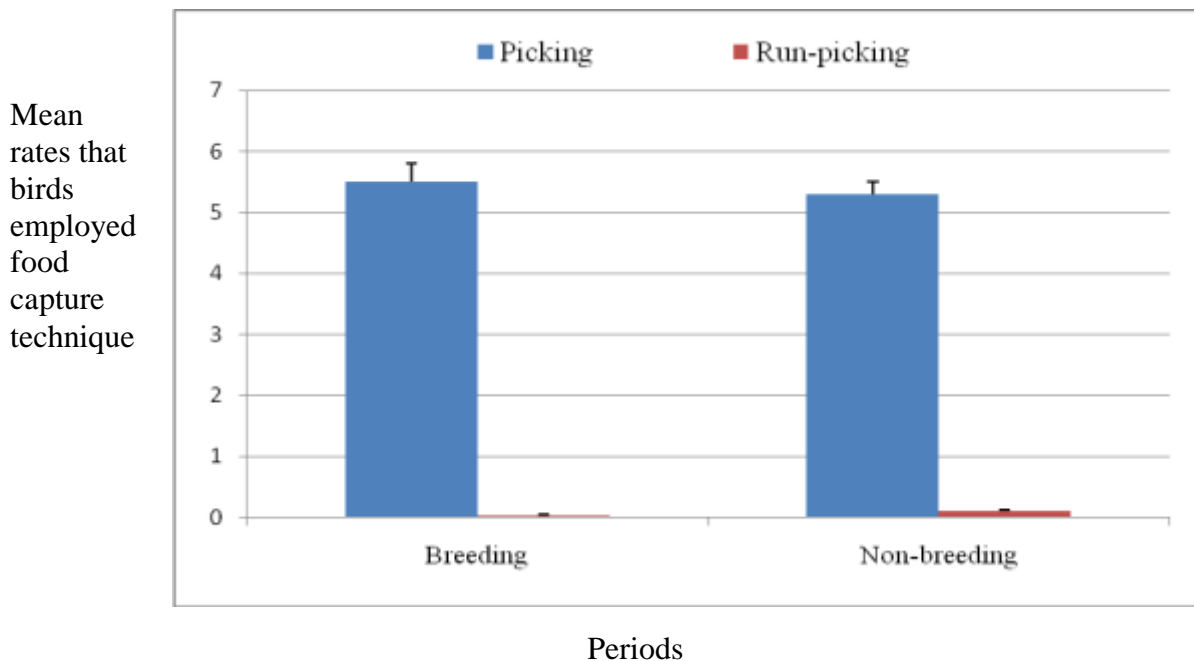


Figure 8: Mean rates \pm SE that birds employed food capture techniques (n = 82 birds for breeding and n = 94 birds for nonbreeding)

Tearing and gulping (dissection of food into smaller pieces followed by swallowing) and gulping (swallowing upon capture without manipulation other than food being held briefly using the bill) were the two food handling techniques used by the birds. However, gulping was observed to be the most common food handling technique employed.

During the breeding period, there was significant difference in the mean rates that birds employed gulping as compared to tearing and gulping ($t_{0.05, 2, 82} = 11.95, p < 0.05$) (Figure 9). Gulping was employed to handle food for the 88.2 % of feeding bouts observed while tearing & gulping accounted for 11.8 % of the feeding bouts.

For the non-breeding period, there was significant difference in the mean rates that birds employed gulping as compared to tearing and gulping ($t_{0.05, 2, 94} = 8.31, p < 0.05$) (Figure 9). Gulping was employed for 69.6 % of feeding bouts compared to tearing & gulping which accounted for 30.4 % of the feeding bouts. The food items consumed by gulping were grass seeds, insect larvae, grasshoppers and butterflies/moths while those by tearing and gulping were mostly the grasshoppers, beetles, butterflies/moths and insect larvae.

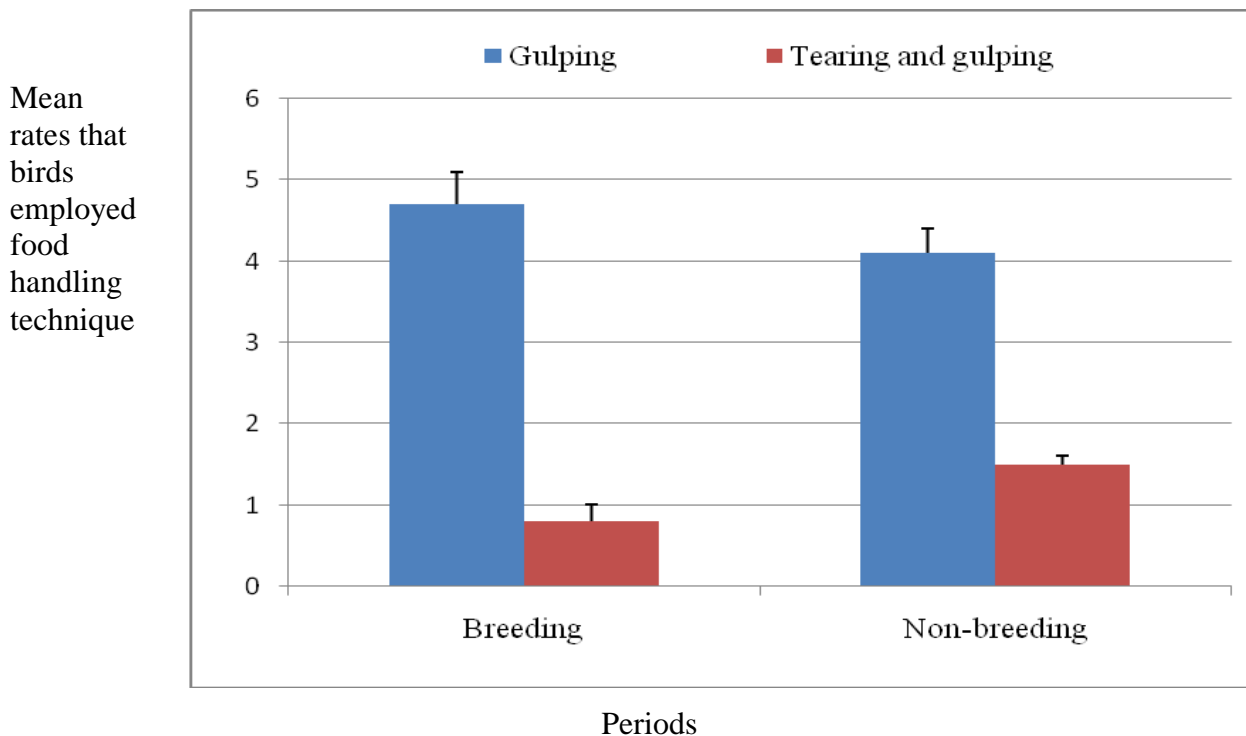


Figure 9: Mean rates \pm SE that birds employed food handling techniques (n = 82 birds for breeding and n = 94 birds for nonbreeding)

3.3 Feeding behaviour and diurnal time-activity budget

The feeding behaviour and diurnal time activity budget of the Red-capped Lark were influenced by factors of seasonality and time of the day. The birds partitioned behaviour between walking, resting, vigilance (scanning), reproductive (courtship) behaviour and self-maintenance behaviour (preening). The diurnal time-budget between 7.00-11.00 am and 4.00-6.00 pm was dominated by the feeding activity (Figure 10). Feeding was the most dominant activity during the breeding and non-breeding periods.

A one way ANOVA to compare differences in rates for feeding ($F_{0.05,1,1214} = 1.2, p > 0.05$), search for food ($F_{0.05,1,1214} = 1.04, p > 0.05$), walking ($F_{0.05,1,1248} = 0.88, p > 0.05$), preening ($F_{0.05,1,1247} = 3.13, p > 0.05$) and resting ($F_{0.05,1,1248} = 1.12, p > 0.05$) between breeding and non-breeding periods revealed that the rates did not vary significantly. However, there were significant differences for scanning rates ($F_{0.05,1,1248} = 7.1, p < 0.05$) (Figure 10).

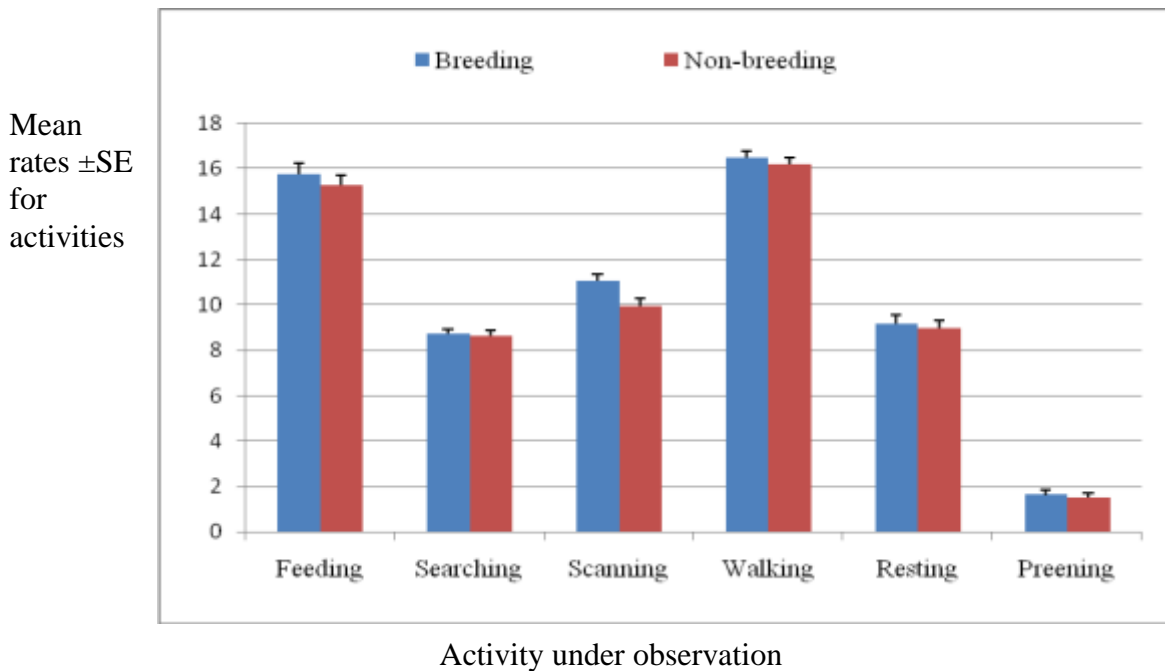


Figure 10: Mean rates \pm SE /min for activities during breeding and non-breeding periods

Apart from seasonality, the mean proportion of time allocated to different activities varied with the time of the day (the three observations time periods were morning, 7.00 - 9.00am, mid-morning, 9.00-11.00 am and evening, 4.00 - 6.00 pm). During the breeding period, feeding was the predominant activity in the morning and evening (Figure 11).

To test for differences in mean rates for activities undertaken by birds during the three time periods of the day, a one way ANOVA test on rates for activities was conducted. As compared to the other activities, feeding and searching for food were the two key activities related to feeding behaviour hence a post hoc Tukey HSD pair-wise comparison for mean feeding and searching rates was also conducted.

Findings confirmed that during the breeding period, there was significant difference in mean rates for feeding ($F_{0.05, 2, 375} = 12.07$, $p < 0.05$) with rates being significantly higher in the morning than in mid-morning, significantly lower in the morning than evening and significantly higher in the evening than in mid-morning (post hoc Tukey HSD, $p < 0.05$).

There was significant difference in the mean search rates ($F_{0.05, 2, 375} = 6.77$, $p < 0.05$) with rates for evening being significantly higher than for morning and mid-morning (Tukey HSD, $p < 0.05$). However, the search rates for mid-morning were not significantly higher than for morning (Tukey HSD, $p > 0.05$).

There was significance difference in mean rates for resting ($F_{0.05, 2, 375} = 7.38$, $p < 0.05$), preening ($F_{0.05, 2, 375} = 7.64$, $p > 0.05$) and walking ($F_{0.05, 2, 375} = 8.43$, $p < 0.05$) during the three observation time periods. However, there was no significant difference in the mean rates for scanning ($F_{0.05, 2, 375} = 1.22$, $p > 0.05$) and courtship ($F_{0.05, 2, 375} = 0.99$, $p > 0.05$) for morning, mid-morning and evening.

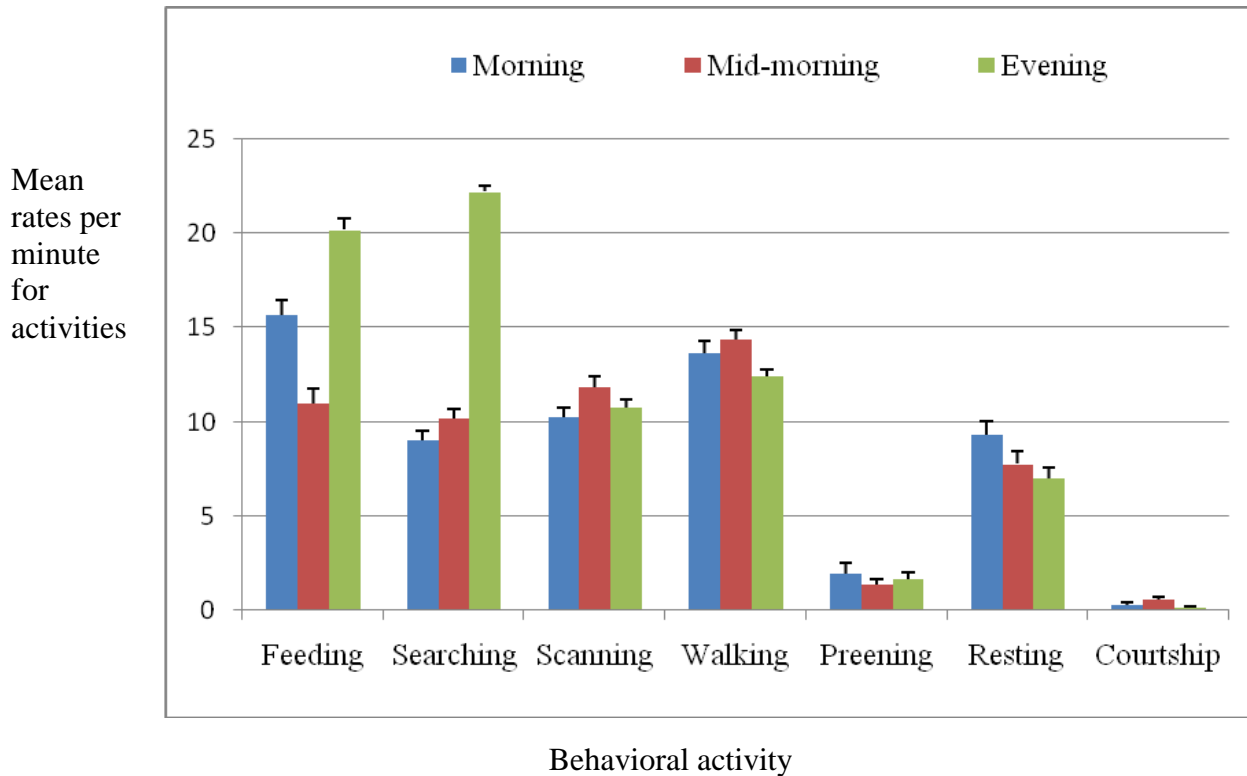


Figure 11: Diurnal time-activity budget for the Red-capped Lark in the morning, mid-morning and evening during the breeding period

For the non-breeding period, the highest amount of time per minute spent in the morning and evening was allocated to feeding (Figure 12). A one-way ANOVA test confirmed that there was significant difference in rates for feeding ($F_{0.05, 2, 582} = 16.24, p < 0.05$) for the three time periods. The mean feeding rates were significantly higher in the morning than mid-morning and significantly higher in the evening than in the mid-morning (post hoc Tukey HSD, $p < 0.05$).

There was significant difference in mean rates for searching for food ($F_{0.05, 2, 582} = 4.36, p < 0.05$) with mean rates not significantly higher for morning than evening, and higher for mid-morning (post hoc Tukey HSD, $p > 0.05$).

There was significant difference in rates for scanning ($F_{0.05, 2, 582} = 7.9, p < 0.05$), walking ($F_{0.05, 2, 582} = 6.05, p < 0.05$), preening ($F_{0.05, 2, 582} = 6.37, p < 0.05$) and resting ($F_{0.05, 2, 582} = 5.44, p < 0.05$) during the different periods. However, there was no significant difference in mean rates for courtship behaviour for the three time blocks ($F_{0.05, 2, 582} = 0.13, p > 0.05$).

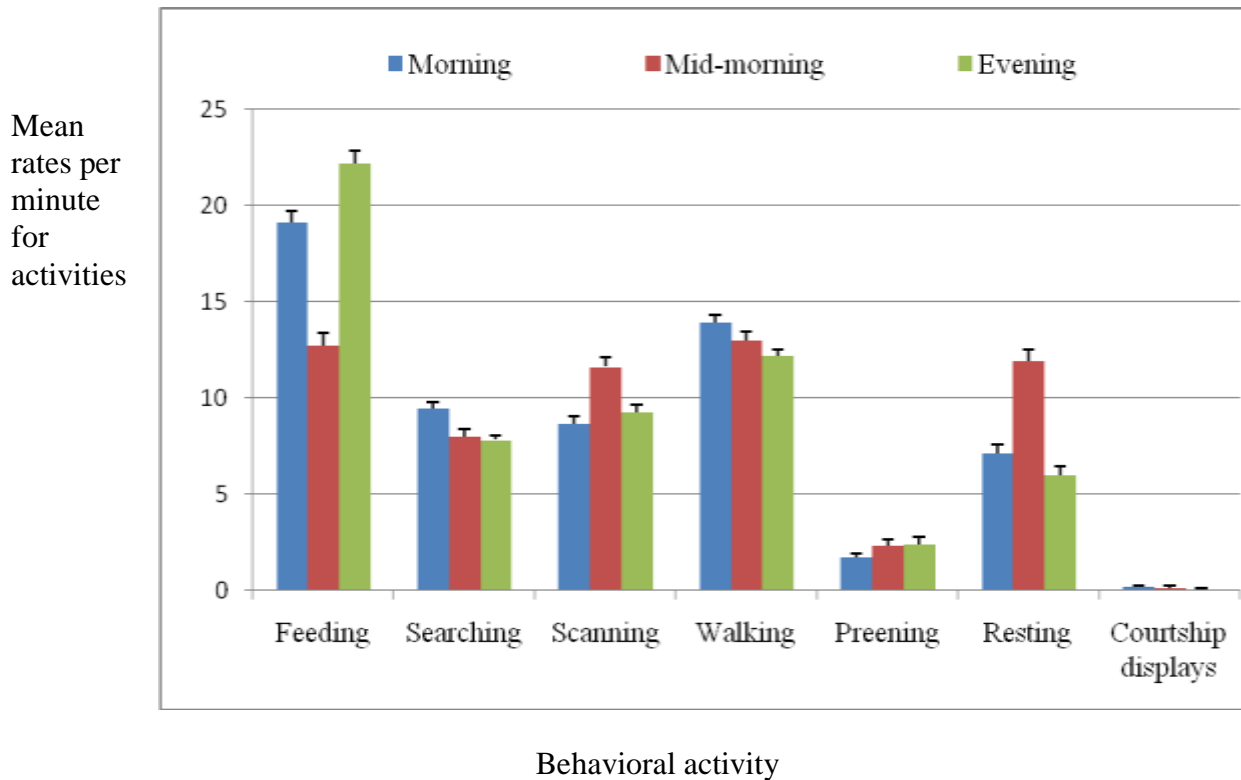


Figure 12: Diurnal time-activity budget for the Red-capped Lark in the morning, mid-morning and evening during the non-breeding period

3.4 Adult food provisioning behaviour at the nest

A total of 772 feeding observations on 18 nests were undertaken. Nests that were observed had 2 nestlings at different age classes {(Day 1(2 nests), Day 2 (2 nests), Day 3 (4 nests), Day 4 (2 nests), Day 5 (1 nest), Day 6 (2 nests), Day 7 (2 nests), Day 8 (2 nests) and Day 10 (1 nest) days old)}.

Data collected on nest behavior when birds were breeding during both wet and dry seasons were combined and analysis conducted based on the varying ages of the nestlings and different hours of the day (7.00 am - 6.00 pm). The results revealed that both parent birds provided a variety of food items to the nestlings which included insect larvae (caterpillars and larvae), grasshoppers, butterflies/moths, beetles and ants.

3.4.1 Nestling diet composition

Data obtained confirmed that insect larvae and grasshoppers were the main prey items brought by the parents to the nestlings. These two constituted more than two thirds of the total diet composition (81 % of the nestling diet) while the butterfly/moths, ants and beetles constituted only 19 % of the total diet composition. The percentage proportion of each prey item in the nestling diet was calculated. Results showed that parent birds primarily provided nestlings with more insect larvae (n = 401; 51.9 % of total prey in the nestling diet) than with grasshoppers (n = 225; 29.1 % of total), butterfly/moths (n = 120; 15.54 %), ants (n = 19; 2.46 %) and beetles (n = 7; 0.9 % of total) (Figure 13).

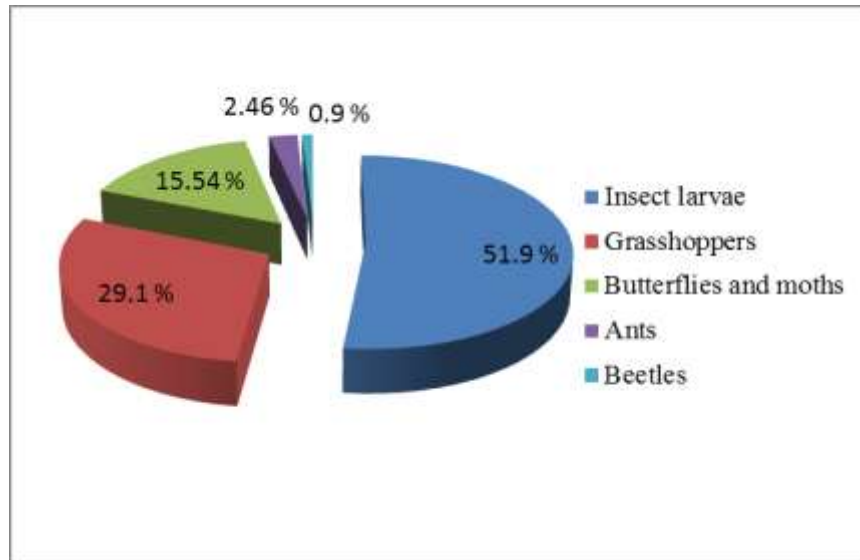


Figure 13: Percentage proportion of different food items in the nestling diet (n = 18 nests)

Although most of the times the parent birds delivered a single prey item, there were instances when the parents delivered two prey items at the same time. This was often two items of grasshopper, butterfly and insect larvae). Of the total 21 observations when parents brought two items, 13 observations were by males and 8 by females. Despite this variation, there was no significant difference in the number of feeding observations that the male and female birds delivered two prey items ($\chi^2_{0.05, 1} = 0.6, p > 0.05$). Parent birds were observed delivering an insect larvae & grasshopper (n = 9 for males, n = 5 for females), insect larvae & butterfly/moth (n = 1 for males, n = 1 for females), 2 grasshoppers (n = 1 for males, n = 1 for females) and, grasshopper & butterfly (n = 2 for males, n = 1 for females).

The mean delivery rates of insect larvae provided to nestlings per nest/day was 22.7 ± 4.4 , 16.0 ± 2.4 grasshoppers, 7.2 ± 2.0 butterflies/moths, 1.9 ± 0.4 ants and 0.4 ± 0.2 beetles (Figure 14). There were significant differences in the mean delivery rates of these prey items provided to nestlings for different nests per day ($F_{0.05,4,75} = 21.22$, $p < 0.05$). A post hoc Tukey HSD showed that there were significant differences in mean delivery rates of all other prey items ($p < 0.05$) except between grasshoppers and butterflies/moths ($p > 0.05$).

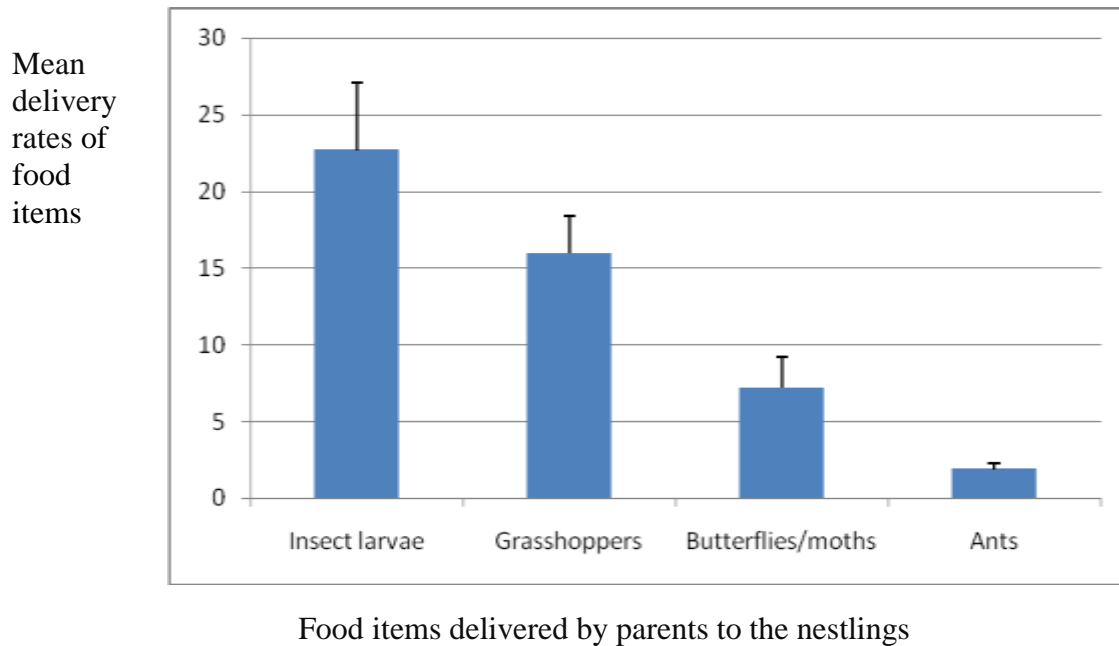


Figure 14: Mean delivery rates of different food items provided to nestlings per nest/day (n= number of nests observed; n = 18 nests)

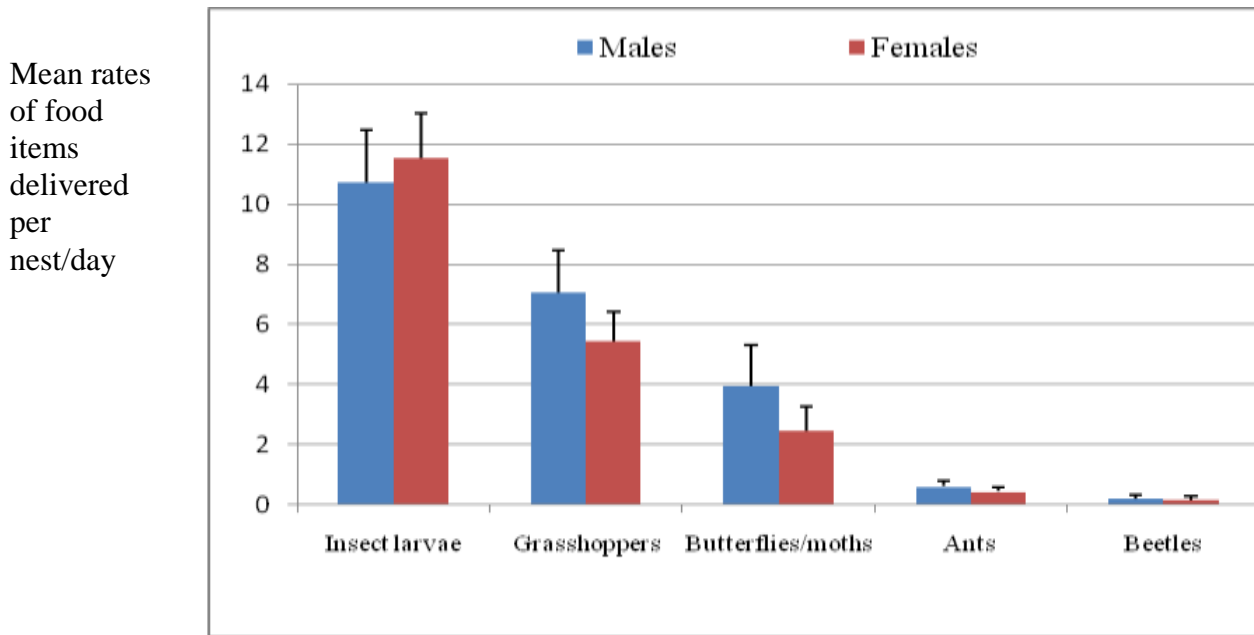
3.4.2 Insect prey delivery by male and female parent birds at the nest

Males and female parents differed in the number of insect larvae, grasshoppers, butterflies/moths, ants and beetles they delivered to nestlings of varying ages. The males did not significantly provide more prey items (n = 406 feeding observations) than females (n = 366 observations) ($\chi^2_{0.05,1} = 1.03$, $p > 0.3$).

To analyze the parental provisioning behavior of the male and female parent birds, information for each sex was pooled and repeated measures ANOVA conducted. There were no significant differences in the mean delivery rates of all prey items delivered by females ($F_{0.05,10,44} = 0.67$, $p > 0.05$) and males ($F_{10,44} = 1.21$, $p > 0.05$) parents to nestlings of varying ages. There was no

significant differences in the mean delivery rates of insect larvae ($F_{0.05, 10, 153} = 1.5, p > 0.05$) and grasshoppers ($F_{0.05, 10, 153} = 1.47, p > 0.05$) delivered by females for the different nests. In addition, there was no significant differences in the mean number of insect larvae ($F_{0.05, 10, 152} = 1.1, p > 0.05$) delivered by males. However, there was significant difference in mean delivery rates of grasshoppers ($F_{0.05, 10, 152} = 2.03, p > 0.05$) delivered by the males.

For all nests combined, the difference in mean rates of delivery of food by females and males was compared using a paired t-test. There were no significant differences in the mean delivery rates of insect larvae provided by male and female parents (paired t-test ($t_{0.05, 2, 17} = 0.09, p > 0.05$)) (Figure 15). In addition, there were no significant differences in the mean numbers of grasshoppers ($t_{0.05, 2, 18} = -1.38, p > 0.05$), butterflies/moths ($t_{0.05, 2, 16} = -0.89, p > 0.05$) and ants ($t_{0.05, 2, 19.18} = -0.84, p > 0.05$) delivered by males and females. There was no significant difference in the mean number of beetles delivered by the males (0.2 ± 0.13) and by females (0.2 ± 0.12), which was very minimal.



Different types of food items delivered by males and female parents

Figure 15: The mean delivery rates of different food items delivered by male and female parents to nestlings/nest/day (n= 18 nests)

3.4.3 Nestling diet composition and variation in prey numbers between nests

Parent birds of the Red-capped Lark were observed to feed nestlings until they reached 10 days after which they fledged. There was variation in diet composition and number of food items provided to the nestlings of these different ages per day. Although there was no significant nest variation in the mean delivery rates of all prey items that were delivered by adults to nestlings ($F_{0.05, 17, 72} = 1.13, p > 0.05$) during the different hours of the day, the mean rates of different prey items provided varied considerably between nests (Figure 16).

The mean delivery rates of insect larvae, grasshoppers and butterflies/moths delivered increased for nestlings aged 3-8 days old. There were significant differences in the mean delivery rates of insect larvae ($F_{0.05, 10, 110} = 11.08, p < 0.05$), grasshoppers ($F_{0.05, 10, 110} = 5.13, p < 0.05$) and butterflies/moths ($F_{0.05, 10, 110} = 6.52, p < 0.05$) that were fed to nestlings of different ages during the various hours of the day.

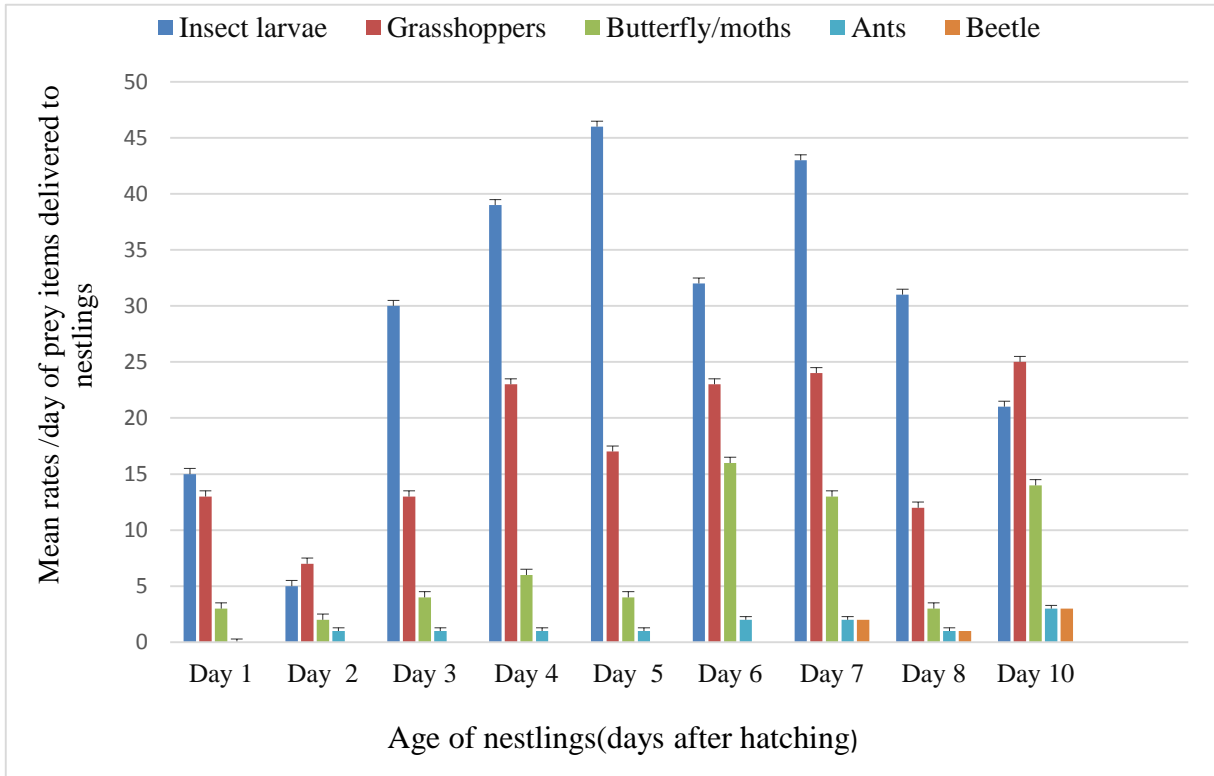


Figure 16: Mean rates of delivery of different prey items delivered to nestlings of different ages per day (n = number of nests observed; n = 18 nests)

3.4.4 Adult nest provisioning and time of the day effects

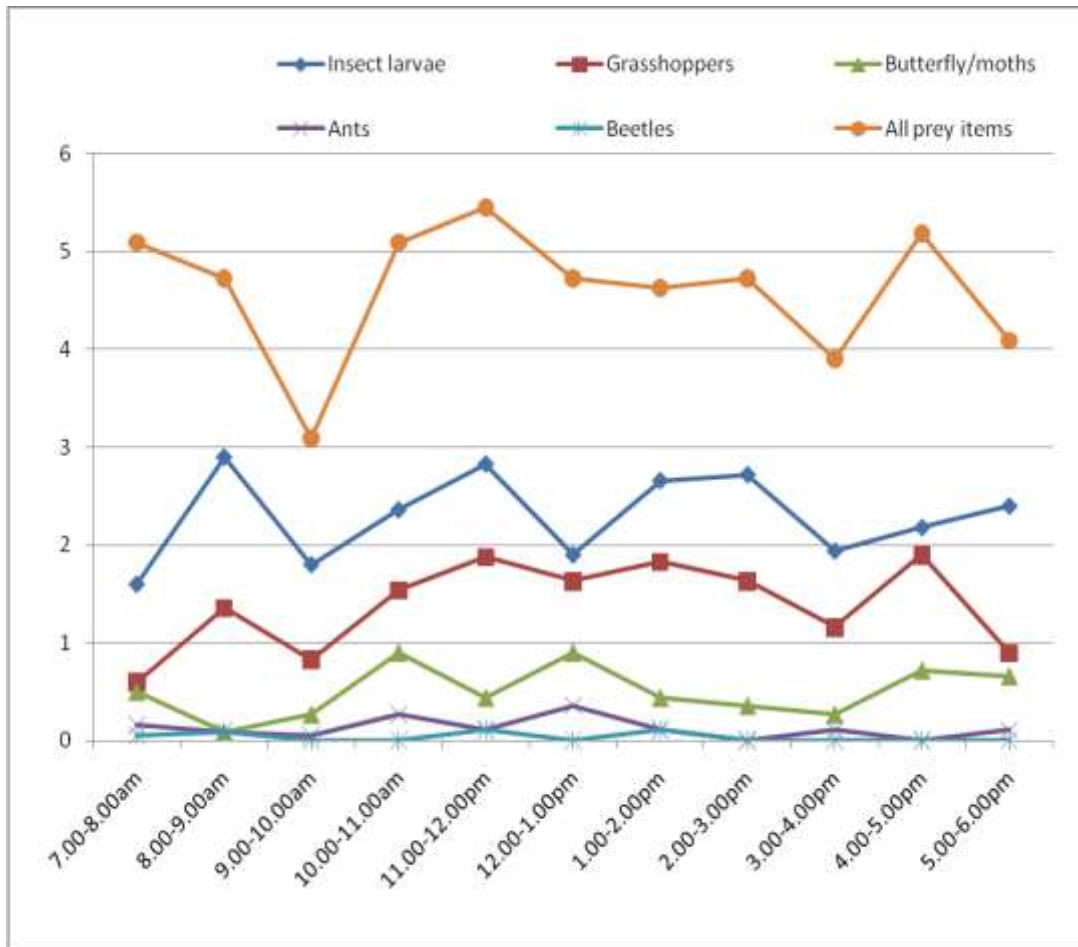
The total number and type of prey items provided to the nestlings by adult parents was also found to vary with the time of the day. Data collected on food provisioning behaviour of parent birds at the nests revealed that there was no significant difference in the mean delivery rates of all prey items provided to nestlings during 11 different hours of the day ($F_{0.05, 10, 110} = 0.78, p > 0.05$).

However, there was a morning peak of prey delivery averaging 5.09 ± 0.63 food items/hour (7.00-8.00 am 10.01-11.00am), a mid-morning peak averaging 5.45 ± 1.27 items/hour (11.01am-12.00pm) and an evening peak of 5.18 ± 0.75 items/hour (4.01pm-5.00pm) (Figure 17). The highest number of food items delivered to nestlings was recorded between 11.01am-12.00pm (5.45 ± 1.27 /hour) while the lowest was between 9.01-10.00am (3.09 ± 0.98 /hour).

A one way ANOVA test for differences in the mean delivery rates of different prey items fed to nestlings during various hours of the day showed that there were no significant differences in the mean delivery rates of insect larvae ($F_{0.05, 10, 152} = 0.68, p > 0.05$) and butterflies/moths ($F_{0.05, 10, 152} = 1.53, p > 0.05$) provided during the 11 different hours of the day. However, there was a significant difference in the mean delivery rates of grasshoppers delivered for the periods ($F_{0.05, 10, 152} = 2.203, p < 0.05$).

There were no significant differences in the mean delivery rates of prey items delivered by female parent birds ($F_{0.05, 10, 110} = 1.09, p > 0.05$) and male parent birds ($F_{0.05, 10, 110} = 1.68, p > 0.05$) during the 11 different hours of the day.

Mean rates of all prey items delivered during different hours of the day



Different hours of the day when food was delivered to the nestlings

Figure 17: Mean rates of delivery of all and different prey items delivered during different hours of the day (n= number of nests sampled; n = 18)

CHAPTER FOUR: DISCUSSION, RECOMMENDATIONS AND CONCLUSIONS

4.1 Diet of the Red-capped lark, availability and utilization of insect prey

The study confirmed that the Red-capped Lark is omnivorous and relies on animal food (insect prey) and plant diet (grass seeds). Birds have been considered to feed primarily on insects in orders Orthoptera, Coleoptera, Hymenoptera (Okolie *et al.*, 2015; Mwansat and Tushak, 2011). Previous studies on diet of the Red-capped Lark have revealed that its animal diet consists of ants (Hymenoptera), Lepidoptera (moths, butterflies and their larvae), Coleoptera (beetles) and Orthoptera (grasshoppers) (Hockey *et al.*, 2005). Majority of birds rely on insect diet whose nutritional value is considered adequate due to its rich and easily digestible fat and protein (Okolie *et al.*, 2015). In addition, insect food provides birds with essential elements of growth such as phosphorous, protein, non-chitin carbohydrates, lipids, vitamins and minerals (Klasing, 2000). These factors are likely to play a role in preference of insect diet by the Red-capped Lark. The findings of this study also suggested that the Red-capped Lark provides the ecosystem service of pest-reduction by feeding on insect pests such as the black maize beetle (*Heteronychus arator*), one of the most important coleopteran pests that feeds on cultivated crops. Such services have also been confirmed to be played by 11 sympatric bird species in Australia (Crisol-Martinez *et al.*, 2016).

The results of this study revealed that when compared to plant diet, the largest proportion of the Red-capped Lark's diet comprised of insect diet (63.2 % of diet during breeding period and 81.5 % during non-breeding period). This was also reported for a small passerine tropical bird (Fork tailed drongo, *Dicrurus adsimilis*) in South West Nigeria (86 % insect diet and 14% plant food) (Okosodo *et al.*, 2016), White-naped Jay (*Cyanocorax cyanopogon*) in central Brazil (59 % insect diet, 28 % vegetable food, 13 % food waste) (Barros *et al.*, 2014), Curl crested jays (*Cyanocorax cristatellu*) in central Brazil (48 % insect diet, 40 % plant diet, 12 % nectar)(Amaral & Macedo, 2003) and Plush-crested jays (*Cyanocorax chrysops*) in Brazilian Atlantic forests(88.9 % insect diet, 3.7 % plant food, 7.4 external sources such as food waste) (Uejima *et al.*, 2012). A study on insect diet of some afro-tropical insectivorous passerines at the Jos wildlife park in Nigeria showed that insects in the family Formicidae (order Hymenoptera) were insect key food source for birds (Mwansat and Tushak, 2011).

The Red-capped lark complemented insect diet with seeds from the *Eragrostis tenuifolia* and *Harpachne schimperi* grass species. Stomach contents of the Red-capped Lark have confirmed that the bird feeds on grass seeds (Brachiaria and Setaria seeds) (Wilson & Borrett, 1971) found in herb and ground layers (Nkwabi *et al.*, 2010). Grass seeds of annual grasses such as *Schizachyrium spp.* are a key food source for tropical granivorous birds in Australia that inhabit grasslands (Garnet & Crowley, 1999). The importance of grass seeds as food has also been revealed in the West African Thrush (*Turdus pelios*) (Akinpelu and Oyedipe, 2004). Grass seeds have high energy content (Ndithia and Perrin, 2006), hence the grass substrate acts not only as a habitat for insect prey of the Red-capped Lark but also as a source of plant diet. Furthermore, the grassland habitat provides the Red-capped Lark with leaves, fibers and grasses needed for nest-construction during breeding.

4.2 Feeding, foraging substrates and food prey abundance/diversity

The foraging behaviour of birds is influenced by habitat structure given that prey visibility defines the quality of a habitat for birds (Gokula and Vijayan, 2007; Asokan and Ali, 2010). The diversity and abundance of insect prey for birds may hence be influenced by vegetation type. The open grassland was the habitat of the Red-capped Lark while the woodlands (Acacia-woodland and *Tarconathus*-Acacia woodland) were adjacent to the grassland habitat. Sampling insects in the three vegetation types was expected to shed light on the influence of insect prey diversity and abundance in the selection of the grassland habitat by the bird as a habitat over the woodlands.

Since the Red-capped Lark only inhabits the open grassland in the study area, the positive correlation between insect prey types that were available and utilized is likely to have been due to abundance of the prey and grass seeds in the grassland. Furthermore, birds had more accessibility to insect food in the grassland when compared to the woodlands adjacent to the habitat. Preference for the grassland has also been reported for the Red-capped Lark population inhabiting the grasslands of Serengeti in Tanzania (Nkwabi *et al.*, 2010). Birds prefer specific habitats, hence the open grassland in the study area is an important habitat for the Red-capped Lark. Apart from open grasslands, the Red-capped Larks have been observed to prefer heavily grazed pastures (Wilson and Borrett, 1971). In birds, prey availability (abundance of potential prey items in a micro-habitat) is a key factor that influences successful foraging (Thivyanathan,

2016), and suitability of a habitat by birds is hence influenced by the key factors of availability, abundance and distribution of food resource. Habitats vary in the relative availability of food resource for avian species, and the link between insect prey availability and feeding behaviour of birds can be related to the vegetation type in the habitat. An important factor that hence most likely influenced preference of the grassland habitat by the Red-capped Lark was availability of grass seeds and insect food.

Breeding in the Red-capped Lark population at the Serengeti grasslands (Tanzania) was affected by the vegetation structure (Gottschalk *et al.*, 2007). The vegetation type/cover in a given area influences insect abundance and diversity (Wardle and Baker, 1997). In addition, the type of food substrate where birds obtain food from influences food intake rate, type of feeding method and ability to increase vigilance to probably reduce predation risk. During both breeding and non-breeding periods, the open grassland that Red-capped Lark preferred as a habitat over adjacent woodlands had a high abundance of prey types as compared to the woodlands adjacent to it. Since evidence has suggested that vegetation structure strongly influences the success and foraging behaviour of birds (Robinson and Holmes, 1984), food availability due to the vegetation structure of the open grassland was likely to have influenced its preference by the Red-capped Lark. Since some habitats may have higher prey abundance than others, Red-capped Larks are likely to prefer the open grassland habitat with high abundance of food prey types compared to adjacent woodlands which had low abundance. Higher abundance ensured increased food intake for the bird in the grassland as compared to the woodlands.

The findings of this study confirmed that insect prey diversity was a key influencing factor for diet and feeding behaviour of the Red-capped Lark. For instance, during the breeding period, preference of the open grassland by the Red-capped Lark over the woodlands could be attributed to higher diversity of insect prey species in the grassland as compared to the Acacia woodlands and *Tarconathus*- Acacia woodland. Although during the non-breeding period insect species diversity was higher for Acacia woodland as compared to that in open grassland and *Tarconathus*- Acacia woodland, preference of the grassland by the Red-capped Lark was likely due to the higher abundance of the insect prey species in the grassland (Orthoptera, Lepidoptera, Coleoptera, Hymenoptera) rather than their diversity. This is consistent to findings of a study on

insectivorous passerine bird species in Nigeria that suggested that utilization of insects by birds in the Jos Wildlife Park was probably a reflection of insect abundance (Mwansat and Tushak, 2011). There was minimal similarity between insect species that were sampled in the three vegetation types (the values were less than 0.5), an indication that abundance and diversity of insect prey in the habitat of the Red-capped Lark is likely influence choice of a habitat.

The selection of prey in birds may be influenced by the type of foraging substrates (Gokula & Vijayan, 2000; Ndithia and Perrin, 2006). As a result, the Red-capped Lark's preference of the open grassland can also be attributed to presence of dung (due to grazing of large herbivores in the grassland (cattle and wildlife)) and fresh soil moulds dug overnight by mammals. The dung beetle communities that inhabit the dung of large herbivores require grassland ecosystems and for the Red-capped Lark, the animal waste (dung) is likely to increase availability of beetles as food source and more importantly during the breeding season when parents greatly rely on dung beetle larvae to feed nestlings. Birds also obtained ants/termites from fresh soil moulds hence they are important foraging substrates of the bird. The significant disproportionate use of foraging substrates as observed in the Red-capped Lark was also seen in insectivorous *Polylepis* bird community in Southern Peru, and was considered to be an indication of substrate specialization (Lloyd, 2008). The observed selection of foraging substrates for food capture by the Red-capped Lark can be linked to availability such that the most selected substrate had the highest density and vice versa. The grass substrate was the most selected, followed by dung and soil moulds. The estimated densities of the substrates revealed that the grass density during breeding season was higher than that of non-breeding, most likely due to seasonal rainfall that resulted to increased vegetation growth (Borghesio and Laiolo, 2004) during the breeding season.

The availability of food items for birds is influenced by micro-habitat conditions and seasonal variations in temperature and rainfall (Girma *et al.*, 2017). Similar to findings of a study on 49 tropical avian species in relation to exploitation and abundance of insect food source in Venezuela (Poulin *et al.*, 1992), the study did not reveal clearly defined seasonal variation in insect species that were sampled. During the breeding and non-breeding periods, insect prey types found to be abundant in the open grassland habitat were those most frequently consumed by the Red-capped Lark. For instance, insects in the orders Orthoptera (family *Acrididae*),

Coleoptera, Hymenoptera (ants) and Lepidoptera (butterflies/moths) which were the most frequently consumed animal food items were found to be the most abundant amongst all insects collected during breeding and non-breeding seasons. The findings that there was higher abundance of insects in the open grassland habitat of the Red-capped Lark as compared to the woodlands suggests that grassland habitats of birds may have higher abundance of grains, invertebrates, insects and small mammals when compared to forested habitats (Shochat *et al.*, 2010).

Tropical environments provide a broader an array of resources (Ricklefs, 2000), hence the presence of the Red-capped Lark and other avian species in the same habitat suggest their ability to exploit different resources or availability of abundant food for species that reduces competition. Although feeding in flocks as observed in the Red-capped Lark may increase intra-specific competition for food, foraging in flocks for one species or multi-species in tropical birds is considered advantageous when foraging efficiency is increased by flushing of insects by flock members coupled with the employment of specialized feeding techniques (Balakrishnan, 2014). Inter-specific and intra-specific interactions among birds are likely to be influenced by food availability especially during the non-breeding season (Robb *et al.*, 2008). The Red-capped Lark showed intra-specific interactions with other birds while feeding in flocks or individually. In addition, birds were observed many times feeding in close vicinity of another grassland species (the Grassland pipit, *Anthus cinnamomeus*). Agonistic behaviour of the Red-capped Lark towards two other grassland species (the Grassland pipit (*Anthus cinnamomeus*) and Ant-eater Chat (*Mymecocichla aethiops*) that was observed was likely due to competition for food resources. On the other hand, there were instances when it was observed that there was no aggression between Red-capped Larks and the Grassland pipit. In most cases, it is competition for resources that result to inter-specific and intra-specific aggression among species that inhabit a given habitat especially when there is food limitation (Hui, 2016). Studies in Southern Africa indicated that Red-capped Larks tend to flock while foraging with individuals of same species or other species. Since predation is considered to be a significant factor in how flocking in birds evolved (Beauchamp, 2004), foraging of the Red-capped Lark in flocks may have been a strategy to reduce the risk of predation due to increased vigilance by birds while in the flock (“many eyes effect”) (Sridhar *et al.*, 2009).

For both breeding and non-breeding periods, picking and gulping were the most preferred food capture and handling techniques respectively. When searching for food, the Red-capped Lark employed active foraging with most of feeding occurring on the ground. The employment of picking as the preferred food capture technique by the Red-capped Lark population was likely due to its open grassland habitat where grass seeds and insect prey were easily available on the ground. In addition, birds were observed gulping (swallowing small prey items quickly without any additional manipulation) food as compared to tearing & gulping. Similar to findings of a study on another tropical bird in Brazil, the Large-headed Flatbill (*Ramphotrigon megacephalum*) (De Melo and Guilherme, 2016), this may have been an advantage to the Red-capped Lark because less energy was required compared to greater energy that birds would require to tear and consume insect prey of huge sizes.

4.3 Feeding and time activity budget

The need to balance between risk of predation and starvation influences daily patterns in avian foraging behaviour (Bonter *et al.*, 2013). Apart from feeding, the diurnal time-activity budget of the Red-capped Lark was characterized by time allocation to other activities such as searching for food, scanning for predators, walking, resting, preening and courtship displays. Searching for food was a key activity for birds in relation to feeding, with search rates for the Red-capped Lark during non-breeding period being higher than those during breeding season. The variation in rates may be attributed to low insect abundance during the dry non-breeding season when there was a dramatic decline in rainfall and availability of insects (Jahn *et al.*, 2010). The search times for insect prey by birds are hence predicted to be longer during the non-breeding season. This could possibly explain why search rates of the Red-capped Lark were higher for the non-breeding season than the breeding season. Feeding was the dominant activity of the Red-capped Lark in the morning and evening during breeding and non-breeding periods. This was also observed in another tropical passerine bird (West African Thrush (*Turdus pelios*)) (Akinpelu and Oyedipe, 2004) and the Somali ostrich (*Struthio molybdophanes*) in Samburu (Kenya) (Mutiga *et al.*, 2016).

The findings of the study on the Red-capped Lark support optimal foraging behaviour models that incorporate aspects of starvation and risks of predation, with a bimodal pattern of feeding

predicted throughout the day (Bonter *et al.*, 2013). A study on the tropical Rock fire finch (*Lagonosticta sanguinodorsalis*) revealed that the bird had a bimodal foraging pattern, with the dominance of the feeding activity being attributed to the fact that insects were most active at the time (Brandt and Cresswell, 2009). It is during the peak in feeding activity at the morning when birds aim at replenishing energy reserves lost during the previous night of fasting. On the other hand, during the mid-morning period, birds tend to be inactive, maintain low-energy reserves and avoid exposure to predators. The second peak in foraging activity that occur in the evening aims at obtaining energy reserves required for the coming night. In tropical environments, this is considered to be likely when high temperatures lead to desiccation of the substratum surface (Morrier and Mcneil, 1991). In this case, the birds are likely to limit intensive feeding activity to periods when the risk of starvation may outweigh the risk of predation (after dawn and before dusk). This bimodal pattern of feeding is considered to be adaptive in environments where accumulation of energy can be quick and resources predictable.

4.4 Adult provisioning behaviour at the nest, nestling diet and factors influencing the behaviour

The findings of this study confirmed that there is a link between insect prey availability and feeding behaviour of the bird. The ability of passerine species such as the Red-capped Lark to exploit seasonally abundant resources and high post-natal growth rates are considered to be promoted by their altricial habits and high basal rates (McNab, 1988; McNab, 2016). In tropical habitats such as the study area that have less pronounced wet and dry seasons, factors that are considered to influence breeding include availability of food, climate and risks of nest predation (Gokula and Vijayan, 2000). As a result, avian breeding phenology may therefore not be adequately explained by differences in seasonal food supply (Steward *et al.*, 2013). Many avian species that rely on insects as a key food source depend on a short period of food abundance in order to feed their young. Birds therefore need to time their reproduction to match availability of Lepidoptera larvae which is their main prey (García-Navas and Sanz, 2010). Although tropical birds are considered not to share the same narrow breeding periods like temperate birds, conventional thinking often consider tropical breeding seasons to be discrete periods that are influenced by rainfall seasonality (Lloyd 2008; Stouffer *et al.*, 2013).

The seasonal peak abundance of insect species in tropical environments is expected to occur during the wet season (Anu *et al.*, 2009), with the importance of rainfall in timing of the breeding season in South African and zone birds being well established (Lloyd, 2008). A study by Young (1994) on tropical House Wrens (*Troglodytes aedon*) reported that birds timed breeding to match a period when food was plenty. The findings of this study showed that rainfall seasonality is a key factor during the breeding of Red-capped Larks. The amount of rainfall measured prior and during the breeding season increased while the amount of rainfall during the non-breeding season was decreased. However, some Red-capped Larks continued to breed during the dry period when rainfall amounts decreased. This was also observed in tropical rainforest birds in Central Amazonian forest (Stouffer *et al.*, 2013) and African insectivorous birds in the equatorial area of Serengeti, East Africa (Sinclair, 1978). The lag period before birds start breeding after the wet season begins has been attributed to the time that birds require for the development of gonads, recovery of body condition and building up of reserves for eggs. This period is also necessary to allow growth of vegetation and development of insect larvae that birds need to feed the nestlings. It may hence be advantageous for the birds to respond to seasonality to ensure they have adequate food for the nestlings. This differed with results of another study on conditions affecting nestling growth in the Red-capped Larks at Kedong that have suggested that timing of breeding is affected by other factors (social factors, protein reserves of individual females and nest predation) other than food (Ndithia *et al.*, 2017b).

Seasonality had an influence on the feeding behaviour of the Red-capped Lark with respect to the proportion of animal and plant items in the diet. One of the factors that may influence food delivery by parents to the nestlings is food availability (Martin *et al.*, 2011). The functional link between seasonality and insect food abundance for the Red-capped lark was confirmed by a strong correlation for insects in the order Lepidoptera (butterflies/moths) (0.756) given that the value was greater than 0.5. An increased abundance of Lepidoptera during the breeding period is likely to have increased the availability of the Lepidopteran larvae which is a key food source for the nestlings. In most cases, abundance and diversity of insect species that contribute to caterpillar peak are important in breeding. Data obtained from filming nests of Great Tit (*Parus major*) nestlings in a Mediterranean Iberian forest reported that caterpillars were the main prey (44 % of the total prey) that parent birds provided to nestlings (Pagani-Nunez *et al.*, 2011). In

addition, previous studies on avian adult provisioning behaviour at the nest confirmed that as compared to other insects, insect larvae constituted by far the greatest proportion of food items provided to nestlings by parent birds (Goodbred and Holmes, 1996), with the larval Lepidoptera comprising 60-87% of the estimated prey biomass (Garcia-Navas and Sanz, 2011). The findings of this study on the Red-capped Lark to some extent supported the breeding currency hypothesis that asserts that bird species that rely on insect food source tend to exploit large/soft-bodied prey during breeding season as compared to non-breeding season when they shift to small/ hard-bodied prey (Felicity *et al.*, 2014). The data obtained on parent provisioning behaviour of the Red-capped Lark at the nest also confirmed that as compared to the grasshoppers, butterflies/moths, beetles and ants, insect larvae comprised the largest proportion (51.9 %) of the nestling diet.

A study on breeding biology of the Coal-crested Finch (*Charitospiza eucosma*) (an omnivorous species endemic to central Brazil and Bolivia that feeds mainly on grass seeds and insects) pointed out that the breeding peaks may have been paralleled to the distribution of these two types of food resources (Diniz *et al.*, 2013). In savannas and grasslands of central Brazil, the peak of arthropod abundance that occurred between September and December was found to coincide with a period of first breeding peak of finches and the breeding season of most other insectivorous bird species. Since food can limit the reproductive performance of birds with this being largely manifested through lower survival of nestlings and poor growth, Lepidoptera larvae is an important food source for nestling diet. This was found to be the case for the Red-capped Lark where breeding was preceded by increased rainfall leading to increased numbers of Lepidoptera and insect larvae.

The data collected on food provisioning by parents in the Red-capped Lark revealed that although there was no significant difference in the mean numbers of food items provided to the nestlings of varying ages, the mean number of prey items delivered increased for nestlings aged between 3-8 days old compared to those aged 1,2 and 10 days old. This was in contrary to findings on food provisioning behaviour of the Great Tit (*Parus major*) at the Mediterranean Iberian forest where the quantity of prey items delivered did not vary with the age of the nestlings (Pagani-Nunez *et al.*, 2011). The quantities of food delivered to nestlings by parent

birds may be influenced by both the need to increase nestling survival as well as to reduce predation when nestlings that are not well fed beg more and in the process attract predators (Goodbred and Holmes, 1996). Since decreased delivery of food to nestlings reduces their survival (Mullers and Tinbergen, 2009), increased delivery of caterpillars and grasshoppers by parent birds of the Red-capped Lark especially those aged 3 days and above may be attributed to the need to increase chick survival. This was also the case in Double-toothed Kites (*Harpagus bidentatus*) where throughout the nestling period, insects delivered to nestlings increased (Schulze *et al.*, 2000).

Although food provisioning rates in temperate birds that nest and forage in understory forest such as the Black-throated Blue warblers (*Dendroica caendescens*) have been reported not to vary with time-of-day for birds (Goodbred & Holmes, 1996), time-of-day effects influenced parent provisioning behaviour of the Red-capped Lark. This may be attributed to the fact that the Red-capped Lark inhabits the more open habitats where mid-day temperatures may increase physiological stress on foraging adults or depress insect activity. Prey delivery for the Red-capped Lark was high in the morning hours, decreased from mid-day to afternoon period but increased again from 4.00-5.00 pm. For the Red-capped Lark, there was a morning peak of delivery for periods 7.00-8.00 am, 10.01-11.00am, 11.01am-12.00pm and 4.01pm-5.00pm. Such diurnal patterns similar to the one of the Red-capped Lark differ with findings of a study on Double-toothed Kites (*Harpagus bidentatus*) in a Guatemalan tropical lowland forest that confirmed that delivery rates followed a bimodal pattern of feeding where delivery rates peaked in the morning and evening (Schulze *et al.*, 2000).

Bi-parental care which is very common in avian species (Marques, 2004), was observed in the Red-capped Lark. Food provisioning is considered to be one of the most important forms of parental care provided by birds. In the Red-capped Lark, both parent birds provided prey items to the nestlings. The findings were similar to those of a study on parental behaviour in the Long-tailed finch (*Poephila acuticauda*) in Australia where the male and female parents showed coordination in their parental behaviour (Rooij & Griffith, 2013). Parent birds of the Red-capped Lark also showed coordination where the female bird while brooding was observed moving out of the nest when the male made a signal call after arriving with food, stood at the edge of the nest while the male fed nestlings and immediately returned back to the nest when the male left.

This behaviour was also observed in the Male Northern Mockingbirds (*Mimus polyglottos*) where the male made a signal call during food delivery whenever the female was brooding the nestlings (Breitwisch *et al.*, 1989). This was also considered to be an indication that in vicinity of the nest, the male played a predominant role in vigilance against predation. Apart from feeding, parental care was characterized by scanning for predators and brooding especially during very hot or cold/wet periods (only by the female). Among tropical passerines such as the Red-capped Lark, long-term pair bonds tend to be common (Gorrell *et al.*, 2005).

In altricial species, nestlings tend to entirely rely on parents to provide food until they fledge. As a result, the ability of parent birds to provide food to the nestlings is important for reproductive success (Rooij and Griffith, 2013). The delivery of two prey items at a time by Red-capped parent birds was probably efforts by parents to increase survival of nestlings by ensuring nestlings did not starve. Parental care in bird species is both potentially risky to the survival of the parents, influences lifetime reproductive success and is energy-demanding (Goodbred and Holmes, 1996). Predation reduces chick survival hence scanning was another key behaviour observed in parent birds. The Red-capped Lark parent birds, both male and female, allocated a substantial portion of the time to deliver food and scan for predators to increase chick survival. For example, the two parent birds always scanned around for predators when approaching the nest, during feeding and just before leaving the nest. There was even one instance where a Red-capped Lark parent bird that was observed approaching the nest with food first chased away an ant-eater chat (*Mymecocichla aethiops*) before coming back to the nest to deliver the food. This allows parents not only to assess but also to respond to predation risk for nestlings and themselves (Lima, 2009; Ghalambor *et al.*, 2013).

The presence of the female parent of the Red-capped Lark in the nest while the male was away could have therefore been a strategy to reduce predation by increasing vigilance while the other was away. Ground foraging in birds may result to high predation risk for adults, making mates and breeding partners important for predator vigilance. Vigilance in the Red-capped Lark parent birds increased during the breeding season compared to non-breeding season. This could be attributed to the fact that parent birds are often sensitive to the risk of predation when they are near the nest (Ghalambor *et al.*, 2013). Bi-parental care is expected to evolve when the benefits

of enhanced offspring survival tend to exceed the costs of both parents providing care to the nestlings. Some differences in parental investment between the two sexes have been related to the differences in costs that are incurred by each sex. For instance, costs of fledging the chicks are likely to be higher for females since they begin investing in the chick earlier than the males, or their need to recover from depletion of reserves used up during egg production (Weimerskirch *et al.*, 1997).

Numerous avian reproduction studies have raised the question of whether the parental care provided by male and female parent birds is equal (Lormee *et al.*, 2005). The parental care provided by both parents of the Red-capped Lark in relation to food provision did not vary significantly. Consistent with the findings of a study on White-rumped Tanagers (*Cypsnagra hirundinacea*) in Brazil (Santos and Marini, 2010), the mean rate of food delivery rate to nests by both male and female parents of the Red-capped Lark did not differ significantly. In some avian species, the “division of labour” hypothesis applies where each sex plays different roles in parental care (Lormee *et al.*, 2005). In addition, investment for parents in socially monogamous avian species may vary, with cases of great inequity in nestling provisioning rates by the two sexes being observed (Palmerio and Massoni, 2008). However, in some species, the investment may be more equitable (Goodbred and Holmes, 1996; Palmerio and Massoni, 2008). This was the case for the Red-capped Lark in relation to food provisioning and scanning for predators, with both parents becoming actively involved in providing this kind of care. This differed from findings of a study on Pied Flycatcher (*Ficedula hypoleuca*) where the male and female parent birds showed variation in the provisioning behaviour at the nest (Mänd *et al.*, 2013).

4.5 Conclusion and Recommendations

4.5.1 Conclusions

The study provided key knowledge on diet and feeding behavior of the Red-capped Lark, and how it was influenced by factors of seasonality and insect prey abundance/diversity. Seasonality, vegetation type in the habitat, food availability and time-of-day were identified as key factors that influence the diet and feeding behavior of the Red-capped Lark.

The Red-capped Lark predominantly consumes animal diet consisting of insects of the orders Coleoptera, Orthoptera, Lepidoptera, and Hymenoptera. The animal diet is supplemented by grass seeds from two grass species; *Eragrostis tenuifolia* and *Harpachne schimperi*. Insect prey abundance and diversity significantly influences the diet and feeding behaviour of the Red-capped Lark with findings highlighting the importance of insects as food source for the bird.

Food abundance and availability is an important factor that influences the foraging behaviour of the Red-capped Lark, hence the open grassland habitat is a suitable habitat that provides a habitat for insect prey species and provides supplementary seed diet for the bird. As a result, the Red-capped Lark may have adapted to feeding largely on abundant insect species present in the open grassland area as compared to woodlands adjacent to its grassland habitat. This is likely to have made picking and gulping the most preferred food capture and food handling techniques respectively. There were non-significant differences in feeding and searching rates for food between seasons.

For the two observation periods of the day (morning and evening), feeding and walking/movement were the two dominant activities of the time budget. This supports the bimodal pattern of avian feeding where there is an early morning feeding peak, a mid-morning period of relative inactivity and a second peak late in the day.

There was positive correlation between availability and utilization of the prey items, an indication that the open grassland habitat of the Red-capped Lark is suitable for harbouring insects that are food source and providing grass seeds required for survival and reproduction.

Observations on adult provisioning behaviour at the nest confirmed that there were no significant differences in the mean number of all prey items that were delivered by adults to nestlings of different ages. In addition, there were no significant differences in the mean number of all prey items delivered by females and males to nestlings of varying ages as well as those delivered during the different hours of the day. However, there were significant differences in the mean number of insect larvae, grasshoppers and butterflies/moths that were fed to nestlings of different ages. The number of prey items delivered increased for nestlings aged 3-8 days old.

4.5.2 Recommendations

1. Deeper insights into the diet and feeding behavior of the Red-capped Lark will require more advanced and long-term studies on the species. This may include the use of video recordings, stomach content analyses, faecal samples analysis, use of stable isotopes/mercury concentrations and next-generation sequencing (NGS)). This will provide better understanding of dietary habits and guide development of effective conservation strategies for the species and other grassland species.
2. Since the results of this study relied on data collected from one study area (Kedong area) over a period a period of six months, replication of such a study in other habitats with Red-capped Lark populations for a longer time period will be important in acquiring much larger data sets for different populations. Furthermore, future studies for longer periods will be important in exploring clearly the link between rainfall, seasonality, insect abundance/diversity and breeding in the Red-capped Lark.
3. The study provided a comprehensive list of insect prey species of the Red-capped Lark with identification of many to the genus level. Further research study on the insect biodiversity and taxonomy in the Kedong area will be critical in providing better and comprehensive information on the various insect prey species. This will be important in preservation of food resources aimed at ensuring successful conservation of the avian grassland species.
4. Tropical grasslands are becoming increasingly fragmented at a rapid rate hence resulting to huge loss of biodiversity and loss of habitats for avian species. The study confirmed that the

grasslands are very critical for the conservation of grassland avian species such as the study species, hence need to be protected from alteration through anthropogenic activities. There is need for the findings of this study to be integrated in a comprehensive grassland bird management plan of the Kedong ranch to ensure human activities that are undertaken do not result to loss of critical grassland habitats for birds.

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Appendix 1: Insect species abundance in the open grassland area during the breeding period

Order	Family	Species	Abundance	Percentage
Coleoptera	Carabidae	<i>Scarites sp.</i>	3	4.1
Coleoptera	Carabidae	<i>Tefflus sp.</i>	10	1.3
Coleoptera	Carabidae	<i>Cypholoba sp.</i>	1	0.13
Coleoptera	Scarabaeidae	<i>Heteronychus sp.</i>	42	5.57
Coleoptera	Lagridae	<i>Lagria sp.</i>	5	0.6
Coleoptera	Carabidae	<i>Chlaenius sp.</i>	1	0.13
Coleoptera	Tenebrionidae	<i>Sepidium muscosum</i>	51	6.76
Coleoptera	Tenebrionidae	<i>Zophosis sp.</i>	12	1.6
Coleoptera	Coccinellidae	<i>Coccinellidae sp.</i>	1	0.13
Orthoptera	Acrididae	grasshopper	274	36.3
Lepidoptera	Lycaenidae	<i>Actizera stellata</i>	68	9.01
Lepidoptera	Nymphalidae	<i>Junonia orithya</i>	29	3.84
Lepidoptera	Lycaenidae	<i>Actizera lucida</i>	12	1.6
Lepidoptera	Pieridae	<i>Appias epaphia</i>	4	0.53
Lepidoptera	Pieridae	<i>Colias electo</i>	8	1.06
Lepidoptera		caterpillar	8	1.06
Hymenoptera	Formicidae	<i>Dorymyrmex sp.</i>	112	14.8
Hymenoptera	Halictidae	<i>Lasioglossum sp.</i>	15	2
Hymenoptera	Sphecidae	<i>Philanthus sp.</i>	1	0.13
Hymenoptera	Sphecidae	<i>Bembecinus sp.</i>	8	1.06
Hymenoptera	Scoliidae	<i>Campsomeris sp.</i>	2	0.26
Squamata	Lacertidae	<i>Nucrus boulengeri</i>	8	1.06
Diptera	Asilidae	fly	10	1.3
Diptera	Calliphoridae	<i>calliphoridae sp.</i>	5	0.6
Araneae		spider	26	3.4
Hemiptera	Cicandellidae	bug	9	1.2
Coleoptera	Coccinellidae	ladybird beetle	1	0.13
			N=754	100%

Appendix 2: Insect species abundance in the Acacia woodland during the breeding period

Order	Family	Species	Abundance	Percentage
Coleoptera	Carabidae	<i>Scarites sp.</i>	4	7.27
Coleoptera	Carabidae	<i>Tefflus sp.</i>	11	20
Coleoptera	Tenebrionidae	<i>Zophosis sp.</i>	1	1.9
Orthoptera	Acrididae	grasshopper	9	16.4
Orthoptera	Gryllidae	cricket	2	3.63
Hymenoptera	Formicidae	<i>Dorymyrmex sp.</i>	15	27.3
Hymenoptera	Sphecidae	<i>Philanthus sp.</i>	4	7.3
Hymenoptera	Sphecidae	<i>Bembecinus sp.</i>	1	1.8
Araneae		spider	2	3.6
Diptera	Asilidae	fly	2	3.6
Lepidoptera	Lycaenidae	<i>Actizera stellata</i>	2	3.6
Lepidoptera	Nymphalidae	<i>Junonia orithya</i>	2	3.6
			N=55	100%

Appendix 3: Insect abundance in *Tarconathus*- Acacia woodland during breeding period

Order	Family	Species	Abundance	Percentage
Coleoptera	Carabidae	<i>Scarites sp.</i>	2	3.6
Coleoptera	Carabidae	<i>Tefflus sp.</i>	3	5
Coleoptera	Tenebrionidae	<i>Sepidium.muscosum</i>	2	3.3
Coleoptera	Tenebrionidae	<i>Zophosis sp.</i>	1	1.6
Orthoptera	Acrididae	grasshopper	10	16.5
Hymenoptera	Formicidae	<i>Dorymyrmex sp.</i>	22	36.6
Hymenoptera	Scoliidae	<i>Cathimeris sp.</i>	1	1.6
Hymenoptera	Sphecidae	<i>Philanthus sp.</i>	4	6.7
Araneae		spider	8	13.4
Diptera	Asilidae	fly	3	5
Lepidoptera	Nymphalidae	<i>Junonia orithya</i>	4	6.7
			N=60	100%

Appendix 4: Insect species abundance in open grassland area during non-breeding

Order	Family	Species	Abundance	Percentage
Coleoptera	Carabidae	<i>Scarites sp.</i>	2	0.47
Coleoptera	Tenerionidae	<i>Sepidium muscosum</i>	7	1.67
Coleoptera		ladybird beetle	1	0.23
Orthoptera	Acrididae	grasshopper	176	42.2
Orthoptera	Gryllidae	cricket	2	0.47
Hymenoptera	Formicidae	<i>Dorymyrmex sp.</i>	40	9.56
Hymenoptera	Sphecidae	<i>Philanthus sp.</i>	11	2.63
Araneae		spider	4	0.95
Diptera	Asilidae	fly	6	1.43
Hemiptera	Cicandellidae	bug	4	0.95
Lepidoptera	Pieridae	<i>Colias electo</i>	8	1.91
Lepidoptera	Lycaenidae	<i>Actizera stellata</i>	144	34.4
Lepidoptera	Nymphalidae	<i>Junonia orithya</i>	10	2.5
Lepidoptera		<i>Appias epaphia</i>	1	0.2
Hymenoptera	Halictidae	<i>Lasioglossum sp.</i>	1	0.2
Diptera	Sarcophagidae	fly	1	0.2
			N=418	100

Appendix 5: Insect species abundance in the Acacia woodland during the non-breeding period

Order	Family	Species	Abundance	Percentage
Coleoptera	Carabidae	<i>Scarites sp.</i>	2	3.12
Coleoptera	Carabidae	<i>Tefflus sp.</i>	1	1.56
Coleoptera	Tenebrionidae	<i>Zophosis sp.</i>	5	7.81
Coleoptera	Tenebrionidae	<i>Sepidium muscosum</i>	4	6.25
Orthoptera	Acrididae	grasshopper	10	15.62
Orthoptera	Gryllidae	cricket	6	9.37
Hymenoptera	Formicidae	<i>Dorymyrmex sp.</i>	12	18.75
Hymenoptera	Sphecidae	<i>Philanthus sp.</i>	2	3.12
Hymenoptera	Sphecidae	<i>Bembecinus sp.</i>	2	3.12
Araneae		spider	7	10.9
Diptera	Asilidae	fly	10	15.62
Lepidoptera	Lycaenidae	<i>Actizera stellata</i>	2	3.12
Lepidoptera	Nymphalidae	<i>Junonia orithya</i>	1	1.56
			N=64	100%

Appendix 6: Insect species abundance in the *Tarconathus*-Acacia woodland during non-breeding season

Order	Family	Species	Abundance	Percentage
Coleoptera	Carabidae	<i>Scarites sp.</i>	2	2.53
Coleoptera	Tenebrionidae	<i>Sepidium muscosum</i>	7	8.86
Orthoptera	Acrididae	grasshopper	12	15.1
Orthoptera	Gryllidae	cricket	2	2.53
Hymenoptera	Formicidae	<i>Dorymyrmex sp.</i>	40	50.6
Hymenoptera	Sphecidae	<i>Philanthus sp.</i>	7	8.8
Araneae		spider	3	3.78
Diptera	Asilidae	fly	6	7.8
			N=79	100%