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RESEARCH ARTICLE

TIME-OF-DAY BUT NOT SEASONALITY INFLUENCES FEEDING AND DIURNAL TIME ACTIVITY BUDGET OF ADULT RED-CAPPED LARK (*Calandrella cinerea*).

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Abstract

Passerines are unusually rich and successful avian species. As a result, the diverse life history traits of tropical passerines that have not been intensively studied offer researchers unique opportunities to fill in existing knowledge gaps on their ecology as well as test the evolutionary and ecological theory. This study assessed the feeding behaviour of the all year round breeding tropical Red-capped Lark in relation to its diurnal time activity. Observations on adult birds were undertaken between March-August 2016 at their natural open grassland habitat (Naivasha, Kenya) during breeding and non-breeding seasons. We found no significant difference in mean feeding rates and search rate between seasons. However, time-of-day influenced feeding activities.When breeding, mean feeding rates were significantly higher for morning than mid-morning. The mean search rates were significantly higher for evening than for morning and mid-morning. During non-breeding season, mean feeding rates were significantly higher for morning than mid-morning but no significance difference in mean search rates for the time periods. This study provides key knowledge on Red-capped Lark's feeding behaviour that in combination with future studies on other aspects of the behaviour can contribute to improving the management of threatened habitats of grassland birds.

Introduction:-

Knowledge on foraging ecology of many tropical birds still remains incomplete (Mansor & MohdSah, 2012). The Red-capped Lark is one of the tropical birds inhabiting highly threatened grasslands whose feeding ecology has not been intensively studied. In Kenya, the bird primarily 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). Red-capped Larks mainly breed all the year round (Ndithia *et al*., 2017a), with breeding pairs building ground-level open-cup nests often placed next to a grass tuft or scrub.

In avian feeding behaviour, aspects such as amount of time allocated to feeding activities are important in understanding time activity budgets and factors influencing time allocation to activities (Barros *et al*., 2014), as well as the ecological needs of species (Saidi *et al*., 2016). Furthermore, the proportion of time allocated to feeding

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activities by birds provides some insight into their feeding behaviour, physiological condition and costs of foraging (Lu & Zheng, 2009). Given that food can limit the survival and level of reproductive success in a species, time allocated to various activities while birds are feeding is very important in understanding their foraging behaviour (Wishart & Seal, 1980; Sullivan, 1990; Osterblom & Olsson, 2002). Currently, there is limited knowledge on the feeding behaviour of the Red-capped Lark in relation to its time activity budget, and factors influencing the behaviour. Due to these knowledge gaps, there is poor understanding of how this grassland bird is adapted to its habitat and how factors such as food availability, time-of-day and seasonality affect its feeding behaviour. The study therefore aimed at assessing the feeding behaviour of the Red-capped Lark in relation to the diurnal time-activity budget and how factors of seasonality and time-of-day influence it.

Materials and Methods:-

Study area:-

The feeding behavior of adult Red-capped Larks was studied at Kedong ($0^0 53' 37''$S, $36^0 23' 54''$E, 2077 m above sea level), a private ranch in Naivasha (Kenya) with an estimated area of 60,000- hectares. The site is of high conservation priority and is sandwiched between two conservation areas (Hell's Gate and Longonot National Parks). It's also adjacent to Lake Naivasha {(an Important Bird Area (IBA) and a Ramsar site} (Bennun and Njoroge, 2001). The area has a tropical savannah climate characterized by bimodal annual rainfall ranging from 600-1100 mm (long rainy season in March-May and short rainy season in October-November). The annual average maximum temperature is 25.0° C and average minimum temperature 9.4° C. The savannah grassland ecosystem is inhabited by various species of wildlife hence exposed to intensive grazing by herds of wildlife and livestock. The acacia-woodland and *Tarconanthus camphoratus*-acacia woodland are the two main vegetation types found along the edges of the grassland habitat of the Red-capped Lark. 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. The open grassland area in Kedong private ranch offers habitat to a high population of resident Red Capped Larks, making it a suitable study site.

Focal animal sampling to assess feeding behaviour of adult birds:-

Field work was conducted between March and August 2016. Data on feeding behavior of adult birds was obtained through the focal animal observation technique (Martin & Bateson, 1988; Nhlane, 1992; Akinpelu & Oyedipe, 2004), with birds being observed from a distance of about 50 m using a Swarovski Optik telescope. Behavior observations were conducted during three time periods (morning- 7.00-0900 hrs, mid-morning- 0901-1100 hrs and evening- 1600-1800 hrs) (Felicity *et al*., 2014). Observers walked across the open grassland study area while searching for birds. Every third bird located and identified as actively foraging was first observed for 10 seconds without recording any data. This time period minimized the likelihood of recording only the conspicuous behavior while at the same time ensured that the bird resumed normal activity patterns in the presence of the observer (Block, 1991). Observations of the bird while feeding were then made continuously for 15 minutes per individual (with 30 seconds intervals in between observations) and timed data collected using a stop-watch. Each focal bird was observed for 15 minutes (consisting of one minute observations with 30 seconds intervals in between the observations). The frequency of each behavior (feeding, searching for food, scanning, walking, resting, preening and courtship display) per minute was recorded. These activities were defined as provided by Remsen and Robinson (1990) and Fitzpatrick and Bouchez (1998). When the focal bird stopped foraging or was lost from sight, another adult bird was identified to complete the observation period (De Melo & Guiherme, 2016). Behavioral event data was used to determine time allocated to activities and the frequency of each behavior/ one minute. To avoid re-sampling the same bird, the observer moved 150 m from a location before sampling of the next bird began (Munoz & Colorado, 2012). A total of 1250 independent focal observations were completed for 176 birds (136 hours of observation) on non-consecutive days. Out of the 1250 observations, a total of 486 focal observations (on 82 birds) were completed during the breeding season and 764 focal observations (on 94 birds) during the non-breeding season.

Data analysis:-

Statistical tests were performed using R- program version 3.2.1 and PAST software. Data were tested for normality using the R-QQ plot for normality and Shapiro-Wilk Test. The mean values were reported as means ± SE. All records on observations were treated as independent in the analysis. Rates for activities were compared between seasons and three time periods of the day (morning, mid-morning, evening). A z-test was used to examine differences in adult behaviour patterns between seasons. A one way analysis of variance (ANOVA) test was used to

examine adult behaviour patterns for the three time periods during the breeding and non-breeding seasons. A multiple comparison test (Tukey HSD) was used to examine significant difference in rates for behavior recorded in the morning (7.00 - 9.00 am), mid-morning (9.01 - 11.00am) and evening (4.00 - 6.00pm). In all the statistical tests conducted, the level of significance was always set at $\alpha < 0.05$.

Results:-

The feeding behaviour and diurnal time activity budget of the adult Red-capped Lark was not influenced by seasonality. However, time-of-day was a key influencing factor. During both breeding and non-breeding seasons, the diurnal time- activity budget was dominated by the feeding activity. The birds also partitioned behaviour to searching for food, walking, vigilance (scanning), resting, reproductive (courtship) behaviour and self-maintenance behaviour (preening). For both seasons, mean rates for feeding were highest followed by rates for walking, scanning, searching for food, resting, preening and courtship behavior. A *z* test to compare mean rates between seasons revealed that mean rates for feeding ($z = 1.59$, $P = 0.16$, df = 484), searching for food ($z = 0.6$, $P = 0.56$, df = 484), walking ($z = 2.76$, $P = 0.06$, df = 484), scanning ($z = 0.77$, $P = 0.43$, df = 484) , resting ($z = 1.0$, $P = 0.31$, df = 484) and courtship behavior ($z = 0.76$, $P = 0.44$, df = 484) did not vary significantly (Fig 1). However, there was significant difference in mean rates for preening ($z = 2.81$, $P = 0.004$, df = 484) between seasons.

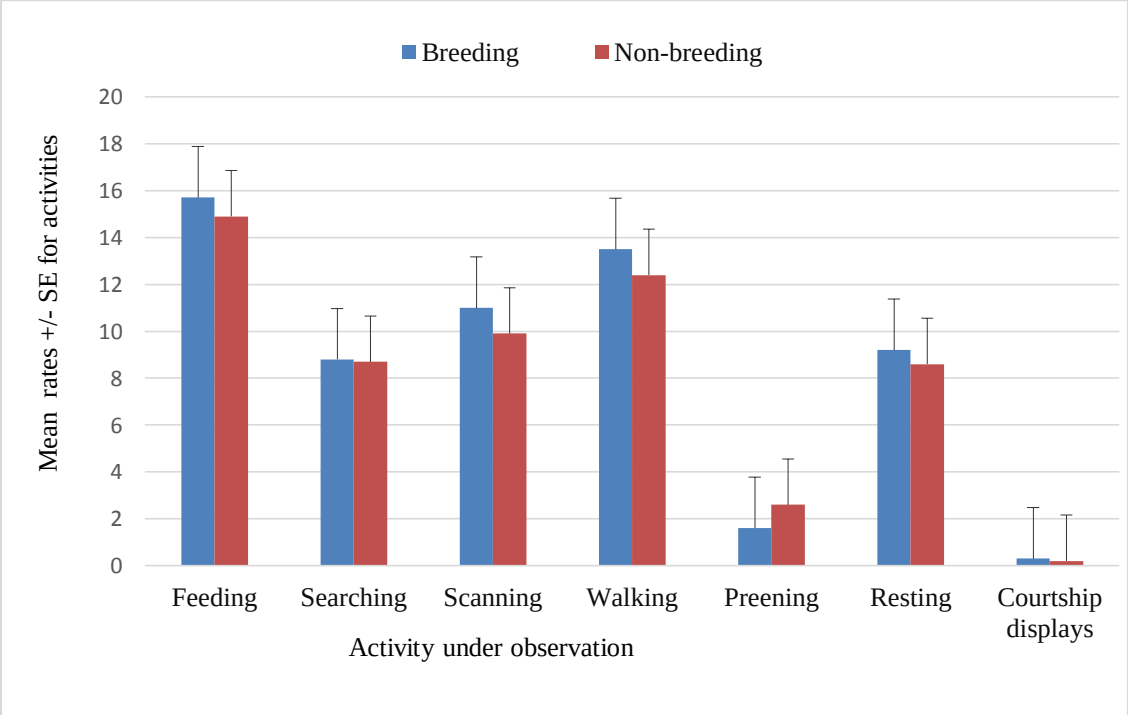

Fig 1:- Seasonal variation in mean rates ± SE /min for activities allocated time by the Red-capped Lark. Feeding was the most dominant behaviour for both seasons.
(The values represent rates per one minute focal observation that birds engaged in an activity).

To analyse the influence of time-of-day effect on adult behaviour patterns, observations were divided for three time periods - morning, mid-morning and evening. The mean proportion of time allocated to different activities varied with the time of the day {(morning (7.00 - 9.00am), mid-morning (9.00-11.00am) and evening (4.00 - 6.00 pm)}. As compared to the other activities, feeding and searching for food were the two key activities related to feeding behaviour. During the breeding season, feeding was the predominant activity in the morning and evening (Fig 2). The mean feeding rates for morning were 18.8 ± 0.83 pecks/min, 12.6 ± 0.8 pecks/min for mid-morning and 23.2 ± 0.61 pecks/ min for the evening. Time allocated to searching for food was highest in the evening and lowest in the morning (9.0 ± 0.47 for morning, 10.2 ± 0.48 for mid-morning and 22.2 ± 0.29 for evening).

To test for differences in mean rates for activities during the three time periods of the day, a one way ANOVA test on rates was conducted. Findings confirmed that during the breeding season, there was significant difference in

mean rates for feeding ($F_{0.05, 2,375} = 12.07$, $P = 0.004$) with rates being significantly higher for morning than mid-morning, significantly lower for morning than evening and significantly higher for evening than mid-morning (post hoc Tukey HSD, $P < 0.05$). There was significant difference in the mean search rates ($F_{0.05, 2, 375} = 6.77$, $P = 0.0003$) 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, $P > 0.05$).
For the three observation time periods, there was significance difference in mean rates for resting ($F_{0.05, 2,375} = 7.38$, $P = 0.0001$), preening ($F_{0.05, 2, 375} = 7.64$, $P = 0.04$) and walking ($F_{0.05, 2, 375} = 8.43$, $P = 0.03$). However, there was no significant difference in mean rates for scanning ($F_{0.05, 2, 375} = 1.22$, $P = 0.31$) and courtship ($F_{0.05, 2, 375} = 0.99$, $P = 0.4$) during the periods.

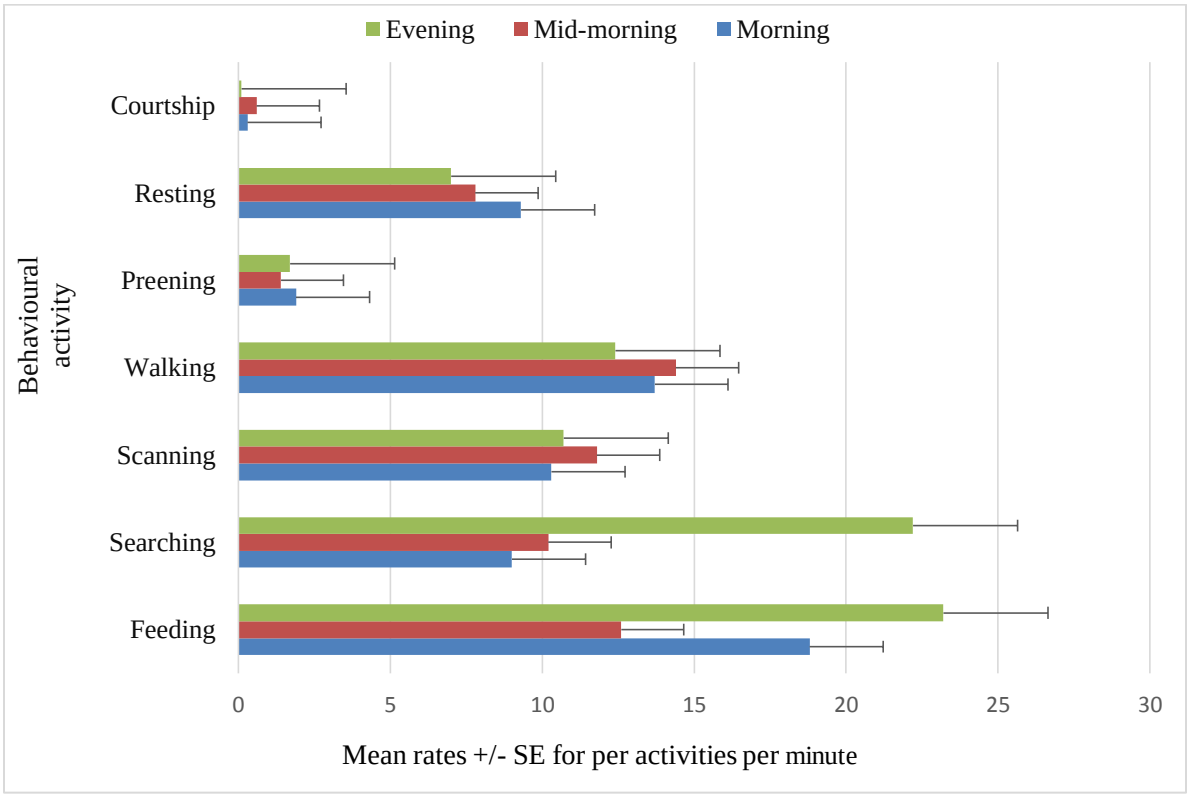

Fig 2:- Variation in diurnal time-activity budget for the Red-capped Lark in the morning, mid-morning and evening during the breeding season. The mean rates for feeding and searching for food significantly varied for the three time periods.

For the non-breeding season, the highest amount of time per minute in the morning and evening was allocated to feeding (Fig 3). A one-way ANOVA test confirmed that there was significant difference in mean rates for feeding ($F_{0.05\ 2, 582} = 16.24$, $P = 0.0002$) for the three time periods with rates being significantly higher for morning than mid-morning, and significantly higher for evening than mid-morning (post hoc Tukey HSD, $P < 0.05$). There was significant difference in mean rates for searching for food ($F_{0.05, 2, 582} = 4.36$, $P = 0.0053$) with mean rates not significantly higher for morning than evening or mid-morning (post hoc Tukey HSD, $P > 0.05$).

There was significant difference in rates for scanning ($F_{0.05, 2, 582} = 7.9$, $P = 0.0358$), walking ($F_{0.05, 2, 582} = 6.05$, $P = 0.0006$), preening ($F_{0.05, 2,582} = 6.37$, $P = 0.0004$) and resting ($F_{0.05, 2, 582} = 5.44$, $P = 0.0014$) during the three different periods. However, there was no significant difference in mean rates for courtship behaviour for the time periods ($F_{0.05, 2, 582 =} 0.13$, $P = 0.93$).

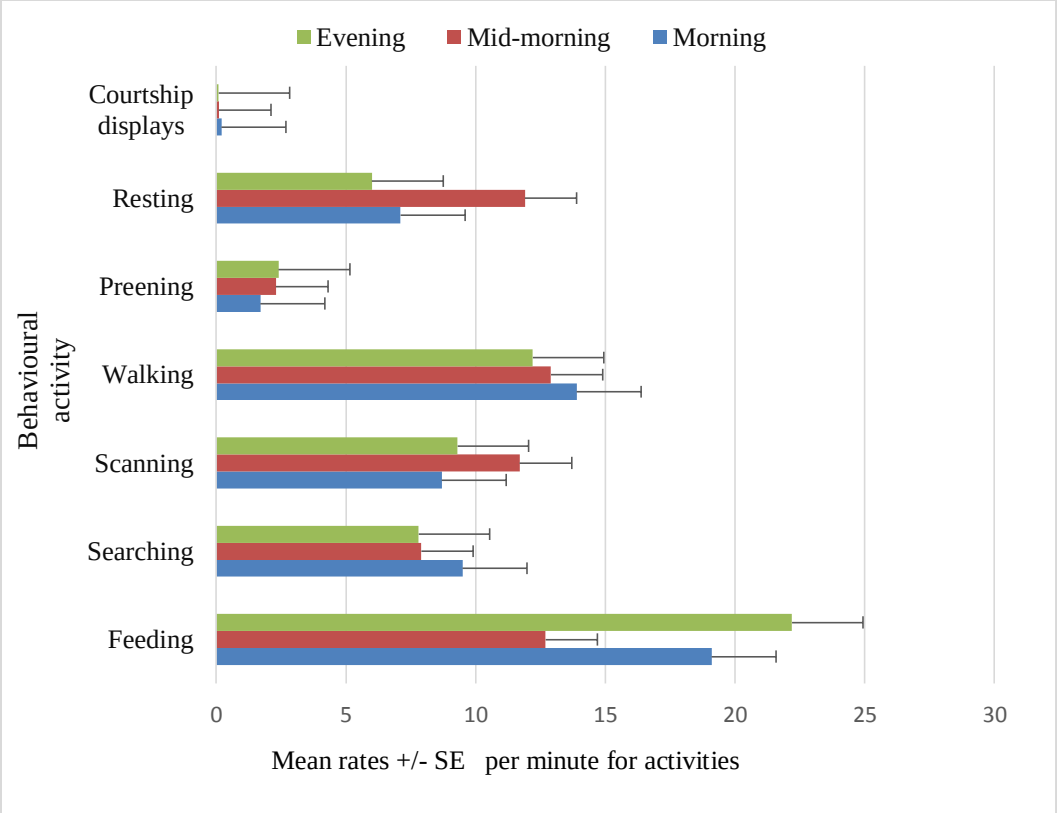

Fig 3:- Variation in diurnal time-activity budget for the Red-capped Lark in the morning, mid- morning and evening during the non-breeding season. The highest proportion of diurnal time budget was allocated to feeding with mean feeding rates for morning, mid-morning and evening varying significantly.

Discussion:-

Daily patterns of activities in avian species are influenced by various factors. For instance, the need to balance between the risk of predation and starvation influences avian foraging behaviour (Bonter *et al*., 2013). As a result, the diurnal time-activity budget of the Red-capped Lark was characterized by time allocation to feeding and other activities (scanning for predators, searching for food, walking, resting, preening and courtship displays). However, as compared to other activities, feeding was reported as the most common overall activity. This has also been confirmed in many other avian species. The findings on another tropical passerine bird, the West African Thrush (*Turdus pelios*) (Akinpelu & Oyedipe, 2004) were consistent with those of the Red-capped Lark where feeding was the dominant activity during both breeding and non-breeding seasons. A study on other tropical birds {Egyptian Geese (*Alopochen aegyptica*), Red-knobbed Coots (*Fulicata cristata*), Glossy ibises (*Plegadis falcinellus*) and Yellow-billed ducks (*Anas undulata*)} at Lake Ol'Bolossat in Kenya confirmed that feeding was significantly allocated more time than any other activity (Njeri & Kinyamario, 2012). In the Pacific lowlands of Costa Rica, a study on Chestnut-backed Antbirds (*Myrmeciza exsul*) reported that feeding accounted for over 90% of the birds' activity (Marcotullio & Gill, 1985). Feeding was also the dominant activity during the daylight period for the White-naped Crane *Grus vipio* in north-eastern Mongolia (Bradter *et al*., 2007) and Common Pochard *Aythya ferina* at Lac des Oiseaux in Algeria (Saidi *et al*., 2016). The allocation of a large proportion of time to feeding in the Red-capped Lark was probably due to feeding being a very critical activity that allows the bird to meet its energy requirements required for its survival. The birds are hence likely to allocate a significant proportion of their diurnal time budget to the activity (Markman, 2014).

Results of this study revealed that apart from feeding and searching for food, other common activities of the Red-capped Lark observed were walking and scanning. Allocation of time to these activities can probably be attributed to the need for an optimal forager to increase feeding efficiency while reducing the risk of predation. Findings of a study on Small Bee-eaters (*Merops orientalis*) in Southern India revealed that the largest proportion of time allocated for activities was accounted for by scanning (52.5 % of the time) and feeding (21.3 % of time) compared

to flying, resting, preening (Mohamed & Asokan, 2015). In the White-breasted Kingfisher *Halcyon smyrnensi*, studied at Cauvery Delta Region (India), the two activities allocated the highest proportion of activity budget was scanning (54% of time) and feeding (23% of time), with less time allocated to flying (13% of time), preening (6 %) and resting (4% of time). In the Hooded crane (*Grus monacha*) studied at Shengjin Lake National Nature Reserve in China, activities that were confirmed to be most common in the time-budget were feeding, scanning and movements, with feeding and scanning accounting for more than 70 % of the total time budget (Li *et al*., 2015). The dominance of these activities in the time activity budget of the Red-capped Lark like in other avian species is possibly an indication of their importance in complementing success in feeding activities and reducing the risk of predation.

Walking which is considered to account for a significant time-activity budget of many species (Schreiber & Burger, 2001) was the second most common activity for the Red-capped Lark after feeding. Although time allocated to movement (walking) would be expected to reduce during the wet /breeding season due to increased availability of insect food (Mutiga *et al*., 2016), the mean rates for walking in the Red-capped Lark did not vary significantly between the seasons. This was supported by findings of a study on the wild Somali ostrich (*struthio molybdophanes*) in Samburu, Kenya (Mutiga *et al*., 2016) where there was no significant difference in time allocated to movement between seasons. Lack of significant differences in mean rates for walking for the Red-capped Lark could likely result from lack of significant differences in insect prey abundance during the two seasons such that availability of insect food is similar.

In the Red-capped Lark, seasonality did not have significant influence on mean rates for all other activities (feeding, searching for food, walking, scanning, and courtship display) except preening. Results for the Red-capped Lark were similar to those reported for the White-breasted Kingfisher (*Halcyon smyrnensi)* where there was no significant difference in feeding rates between seasons (Asokan & Mohamed, 2010). The findings however differed with those on the African Spoonbill (*Platalea alba*) studied in Lake Ziway (Ethiopia) (Moges & Balakrishnan, 2014) and the Somali ostrich (*Struthio molybdophanes*) in Samburu, Kenya (Mutiga *et al.*, 2016) that showed that feeding significantly varied between seasons. This was also revealed in Greater Rheas in South eastern Brazil where time-budgets were influenced by seasonality (Azevedo *et al*., 2010). Another key activity related to feeding was searching for food, with search rates for the Red-capped Lark during the non-breeding season being higher than those during breeding season. Similar results were given for Tropical Kingbirds (*Tyrannus melancholicus*) in the Amazon Basin. This variation in search rates has been attributed to low insect abundance during the dry non-breeding season when there is 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 in the Red-capped Lark were higher for the non-breeding than breeding season.

Scanning ensures birds remain vigilant to avoid predation. Given that predator avoidance is one of the fundamental factors influencing survival in birds, scanning is seen to be one of the activities through which birds remain vigilant while feeding (Zimmer *et al*., 2011; Beauchamp, 2014). Scanning was also a key activity in the time-budget of the Red-capped Lark and was allocated a significant proportion of the diurnal time budget. For ground foragers such as the Red-capped Lark, there is often a high predation risk (Fedy & Stutchbury, 2005), hence the need to remain vigilant in the Red-capped Lark was likely to be a response to predation risk that made it necessary for birds to scan for predators while feeding (Mutiga *et al*., 2016). Li *et al* (2013) in a study on wintering Red-crowned cranes (*Grus japonensis*) in Yancheng Nature Reserve also confirmed the importance of scanning in birds found in the grasslands. The mean scan rates for the Red-capped Lark did not vary significantly between seasons, possibly due to ground foraging and nature of its open grassland habitat that may require birds to consistently remain vigilant to avoid predation. Furthermore, this may also be attributed to the possibility that insect food density did not vary significantly between seasons since levels of vigilance may vary with changes in food density (Li *et al*., 2015).
Given that the Red-capped Lark inhabits an open grassland area that may expose it to high temperatures especially when dry, resting activity observed (often under grass tufts and forbs) especially during mid-hours of the day most likely aimed at avoiding increased temperatures and allowed dissipation of heat load (Nilsson *et al*., 2016).

Courtships displays observed in the Red-capped Lark and are important in breeding when males compete to win mating partners are common in avian species. This may explain why rates for courtship displays in the Red-capped Lark during the breeding season were higher than non-breeding season. Another behavior, preening in birds, plays very critical roles of aligning feathers for insulation and waterproofing, strengthening feathers, removing dirt and providing defense against ecto-parasites/micro-organisms (Zolnierowicz *et al*., 2016). For the Red-capped Lark,

preening rates were significantly higher during the non-breeding than breeding season. Since temperatures tend to be higher during the non-breeding season when it becomes hot and dry, some of the factors that may explain differences in preening include ; the need to increase preening effectiveness when feathers are exposed more to the sunlight given that most ecto-parasites are negatively phototactic (Koop *et al*., 2012); and the need to improve maintenance/strengthen the feathers to reduce the damaging effects of UV radiation (Galvan & Solano, 2016) when birds are exposed to increased temperatures in the open grassland area.

Daily patterns in avian feeding behaviour are considered to be influenced by the need to balance counteracting risks of starvation and predation (Bonter *et al*., 2013). The findings of this study on the Red-capped Lark support optimal foraging behaviour models that incorporate aspects of starvation and risks of predation (starvation-predation risk trade-off) (Zimmer *et al*., 2011), with a bimodal pattern of feeding predicted throughout the day (Bonter *et al*., 2013). During the breeding and non-breeding seasons, feeding rates in the Red-capped Lark were higher for evening and morning than mid-morning. There was a significant difference in feeding rates for the periods. For many different animal taxa, a peak in feeding activity in the morning has been reported (Reyes-Arriagada *et al*., 2014). This pattern of feeding has hence bee reported in birds. This pattern was evident in the Red-capped Lark, with dominance of feeding behaviour in the Red-capped Lark during early morning and late evening possibly due to the findings on other avian species that these are time periods when birds are most active in feeding (Felicity *et al*., 2014). Some of the factors that may influence feeding patterns in birds include food resource variability (Lange & Leimar, 2004), energy requirements and risk of predation (Bonter *et al*., 2013). Availability of food can influence avian foraging behaviour given that resource variability is considered to result to feeding peaks in the morning and late afternoon. For example, in birds, early morning is considered to be one of the most active feeding time periods because insects become more active when the environment is warmed up by the sun. When insect activity increases (Siregar *et al*., 2016), it becomes easier for birds that rely on insect food to search and capture prey more successfully. Due to the warmth experienced in the study area in the morning when the sun rises, the dominance of feeding activities in the morning as compared to other activities for the Red-capped Lark may hence be attributed to the need to take advantage of high insect activity to feed. In addition, energy needs in birds may have played a role in determining the feeding patterns. 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 (Bonter *et al*., 2013). 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 & Mcneil, 1991). This may reduce insect prey availability when insect activity decline to allow insects avoid dessication.

For tropical birds such as the Red-capped Lark found in areas that experience high environmental temperatures, increased resting at mid-hours of the day is likely to be a strategy to reduce the heat load (Martinez, 2000; Asokan & Mohamed, 2010). This may also result from the need by birds to limit intensive feeding activity to periods when the risk of starvation may outweigh the risk of predation (after dawn and before dusk). Allocation of more time to feeding in the morning and evening as compared to mid-morning was also evident in the White-breasted Kingfisher (*Halcyon smyrnensis)* in Tamil Nadu, India with feeding accounting for 25.6 % of activity in the evening, 22.5 % in the morning and 15.1 % in mid-day (Asokan & Mohamed, 2010). Results on the Red-capped Lark were also consistent with those of the tropical Rock fire finch (*Lagonosticta sanguinodorsalis)* (Brandt & Cresswell, 2009) and White-naped Crane *Grus vipio* in north-eastern Mongolia (Bradter *et al*., 2007) that also revealed that the birds had a bimodal foraging pattern. This bimodal pattern of feeding was also confirmed for the Red-capped Lark. This pattern is considered to be adaptive in environments where accumulation of energy can be quick and resources predictable (Bonter *et al*., 2013).

Conclusion and recommendations:-

The study provided key knowledge on the feeding behavior of the Red-capped Lark and how it was influenced by time-of-day effects and seasonality. Given that the results of this study relied on data collected from one study area over a period of six months, replication of such a study in other locations focusing on other Red-capped Lark populations for a longer time period will be important in acquiring much larger data sets (for different populations over a longer time periods) for analysis. There is therefore need for more advanced and long-term studies in order to acquire more data and provide an in-depth understanding of the feeding behavior and time activity budgets. This will also complement findings of this study and allow conclusive isolation of effective conservation strategies for the protection of the species and other grassland species. With the rate of habitat loss of many avian species

intensifying especially in the tropics, the findings of such studies will be important in ensuring successful conservation of avian grassland birds based on findings of ecological studies.

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