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Nest food provisioning in the Red-capped Lark *Calandrella cinerea* does not vary with parental sex differences and time of day

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Summary

The Red-capped Lark *Calandrella cinerea* inhabits some of the most highly threatened grassland ecosystems in Kenya. Although previous studies have been undertaken on feeding ecology of this species, a knowledge gap still exists in relation to its nest food provisioning behaviour. We studied the food provisioning behaviour of Red-capped Larks in open grassland habitat at Kedong Ranch in Naivasha, Kenya. Observations were completed on 18 active nests for a total of 163 observation hours between 07:00 and 18:00. Results confirmed that nestling diet comprised insect larvae (including caterpillars), grasshoppers, butterflies/moths, ants and beetles. Food provisioning rates for males and females combined, as well as independently, did not vary with the nestling age. In relation to specific prey items, provisioning rates of insect larvae and butterflies/moths during different hours of the day did not vary. However, there was a significant difference in provisioning rates of grasshoppers for the time periods. The findings provide an understanding of food requirements and feeding behaviour of the Red-capped Lark, and therefore are important for predicting how future changes in the availability of food resources could influence feeding, reproductive success, and possibly survival of the species.

Keywords Kedong Ranch, lark, grassland, nestling diet, insects

Introduction

Bi-parental care, where both female and male parents participate in taking care of the nestlings, occurs in more than 90% of avian species (Gwiazda & Ledwon 2015). The availability of food for nestlings may therefore influence parental behaviour as they strive to maximize their breeding success (Robb *et al*. 2008, Pedro *et al*. 2013, Stouffer *et al*. 2013). Different roles for female and male parents are predicted by the 'division-of-labour' hypothesis (Lormee *et al*. 2005), where parent birds may show variation in the provisioning behaviour at the nest (Mainwaring *et al*. 2011). Furthermore, the amount of time allocated to feeding maybe influenced by the need to increase reproductive success as well as to ensure survival (Lu & Zheng 2009).

In Kenya, the Red-capped Lark inhabits wet cool montane grasslands (2600 m) and dry/warm tropical grasslands (1200 m) (Ndithia *et al*. 2017). Although both male and female Red-capped Lark adults have streaked grey to brown upper parts, a rufous cap, red shoulders and white under-parts, males have redder plumage and a longer crest than females (Wamiti 2014, pers. obs.). Adults often begin breeding at the onset of the rains (Grizard *et al*. 2015), with the female laying two eggs in a ground-level open-cup nest, which she incubates while the male feeds her. Eggs hatch synchronously 12 d after incubation begins, and both parents feed the nestlings until they

fledge at 9–10 d. Insects are a major source of food, especially during breeding when parents are required to feed the nestlings.

Given that parental sex differences in food provisioning at the nest may exist in some avian species, this study aimed at assessing whether parental sex differences and time-of-day influenced food provisioning behaviour at the nest of Red-capped Larks.

Materials and Methods

Study area

Kedong ranch (0° 53′ 37″ S, 36°23′ 54″ E, 2077 m) is a privately-owned ranch in Naivasha that is sandwiched between two key conservation areas (Hell's Gate and Longonot National Parks) (Fig. 1). It is also adjacent to Lake Naivasha, an Important Bird Area and a Ramsar site (Bennun & Njoroge 2001). With a tropical savanna climate, the area has bimodal annual rainfall patterns with a short rainy season (October–November) and a long rainy season (March–May). Rainfall ranges from 600 to 1100 mm. The annual minimum temperature is 9.4° C and the average maximum temperature is 25.0° C.

Figure 1. A composite map showing location of the study area (source: Google Maps).

The savanna grassland ecosystem is exposed to intensive grazing by herds of wildlife and livestock. Some of threatened bird species found in the area include the endangered Grey-crested Helmeted-shrike *Prionops poliolophus*, Little Grebe *Tachybaptus ruficollis*, Lesser Flamingo *Phoeniconaias minor*, Red-knobbed Coot *Fulica cristata*, and African Spoonbill *Platalea alba.* Other resident terrestrial bird species found in the area include Rufous-naped Lark *Mirafra africana*, Grassland pipit *Anthus cinnamomeus*, Cattle Egret *Bubulcus ibis*, Pectoral-patch Cisticola *Cisticola brunnescens*, Northern Anteater Chat *Myrmecocichla aethiops*, Kori Bustard *Ardeotis kori*, African Goshawk *Accipiter tachiro*, and African Fish Eagle *Haliaeetus vocifer*. The open grassland ecosystem was chosen for study because of the large population of resident Red-capped Larks and their exposure to anthropogenic activities.

Methods

This study was part of a larger ongoing project examining the breeding strategy of Red-capped Larks led by the University of Groningen, The Netherlands. The project has trapped adult larks using mist nets, identified the sex of the birds using physical

differences (males have redder plumage and a longer crest than females), then banded larks with colour rings on both legs for individual identification.

Fieldwork for this study was conducted during the breeding season, occurring over a period of 150 d between March and August 2016. Individual adult larks were identified during nest observations using a telescope from inside a movable hide (a metal frame covered with a green cloth material and tree twigs on sides for camouflage) that was placed *c.* 15 to 20 m from nests. Colour rings were used to identify the sex of the parent birds as they delivered prey to the nestlings. Accurate identification of the sex of the parents was further confirmed through observations of nestling brooding, a behaviour only observed in female parents, especially on cold or hot days. The close distance to the nest allowed for identification of different prey items delivered to the nest, including small prey items (Geng *et al*. 2009). Although this was not always easy when identifying small prey items; for example, ants were correctly identified in most cases because parents delivered many of them while lumped together in the mouth. The open nature of the grassland habitat also facilitated the correct identification of prey items. Observations were completed for nests with nestlings aged 1–8 and 10 days old after hatching. However, there was no nest with nestlings aged 9 days old available for observation. Observations were made from dawn to dusk (07:00–18:00) except in instances of unfavorable weather (drizzling, windy or raining) (Schulze *et al*. 2000). The following information was recorded: age of nestlings, time of feeding, duration of each feeding session, type of food, and sex of the parent bird.

Data analysis

Data were tested for normality using the R-QQ plot for normality and Shapiro-Wilk Test, then analysed using R-program version 3.2.1 and PAST software. Analysis was done to examine differences in provisioning behaviour in relation to nestling age, sex of the parent bird, and hour of the day (07:00–18:00) during which food was provided. An analysis of variance (ANOVA) was used to examine between-nest variation in prey composition and prey delivery rates. A Student's t-test was conducted to examine differences in insect prey type and food provisioning rates by male and female parents. Mean values were reported as mean ±SE. For all statistical tests, the level of significance was set at $\alpha < 0.05$.

Results

Nestling diet composition

A total of 772 nest food provisioning observations at 18 nests (163 h of observation) was completed. All nests had two nestlings. Both parent birds provided a variety of food items that were placed into five classes: insect larvae (caterpillars and other larvae), grasshoppers, butterflies/moths, ants and small beetles. Parent birds primarily provided nestlings with more insect larvae (52% of total observations) than with grasshoppers (29% of total), butterflies/moths (16% of total), ants (2% of total) and beetles (1% of total). Although most of the time parent birds delivered a single prey item, there were instances when parents delivered two prey items at the same time. Of the total observations when the parents brought two food items (n = 21), 13 deliveries were by males and 8 by females. The mean delivery rate for insect larvae per nest/d was 22.7 ± 4.4, for grasshoppers 16.0 ± 2.3, for butterflies/moths 7.2 ± 2.0, for ants 1.9 ± 0.4 and 0.4 ± 0.2 for beetles.

Insect prey delivery by males and females

Mean delivery rates for food items based on sex of the parent are shown in Fig. 2. Results confirmed that mean delivery rates of insect larvae by males and females did

not vary ($t_{2, 17} = 0.09$, $p > 0.05$), nor did the provisioning rates by males and females of most individual prey items vary (Fig. 2). However, there was a significant difference in mean delivery rates of grasshoppers ($F_{10, 152} = 2.03$, $p < 0.05$) by the males (Fig. 2).

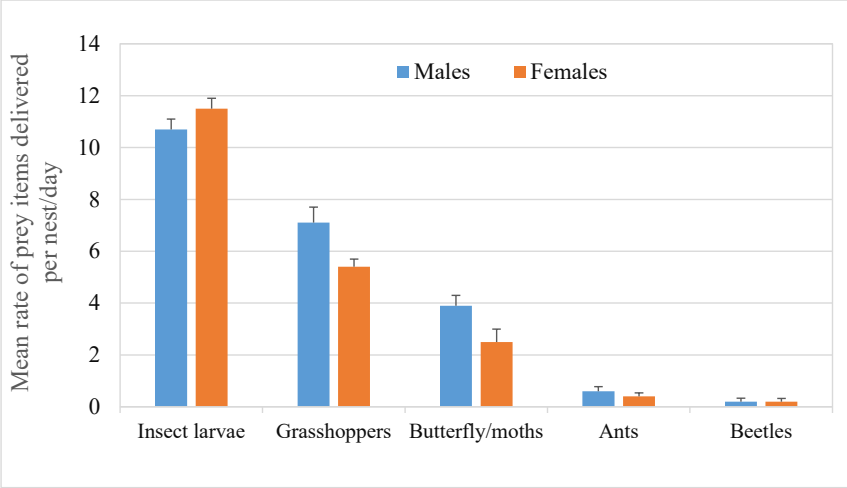


Figure 2. Mean delivery rates of food items to nestlings by males and females per nest/d (n = 18 nests).

Nestling diet composition and variation in prey numbers between nests

Parent birds were observed to feed nestlings until they reached 10 days old, after which they fledged. Nests observed all had 2 nestlings of different ages. Diet composition and mean delivery rates of different prey items per day varied considerably between nests. The mean delivery rates of insect larvae ($F_{10, 110} = 11.08$, $p < 0.05$), grasshoppers ($F_{10, 110} = 5.13$, $p < 0.05$) and butterflies/moths ($F_{10, 110} = 6.52$, $p < 0.05$) varied with nestling age (Fig. 3). On the other hand, for males and females combined, provisioning rates for all prey items did not vary ($F_{17, 72} = 1.13$, $p > 0.05$). While provisioning rates of insect larvae, grasshoppers and butterflies/moths increased for nestlings aged 3–7 days old, they decreased for those aged 8 and 10 days old (Fig. 3).

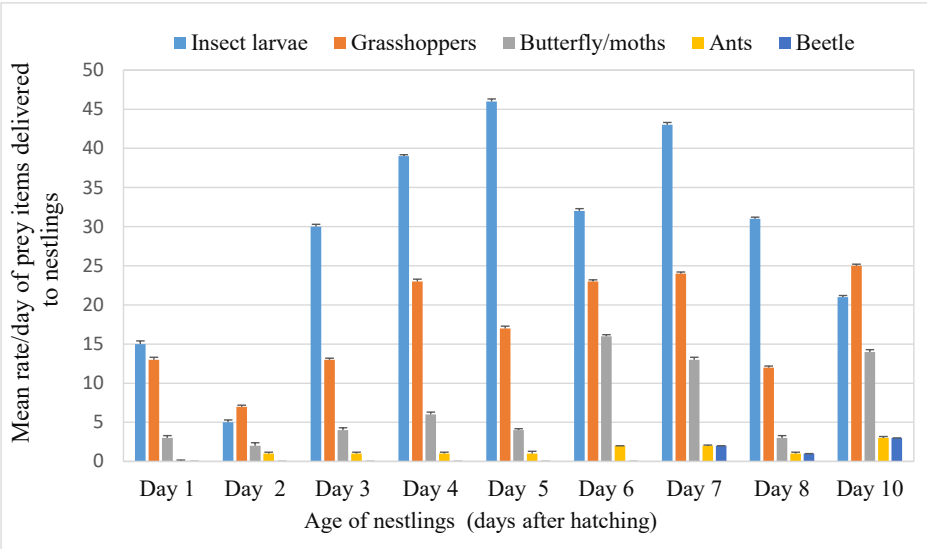
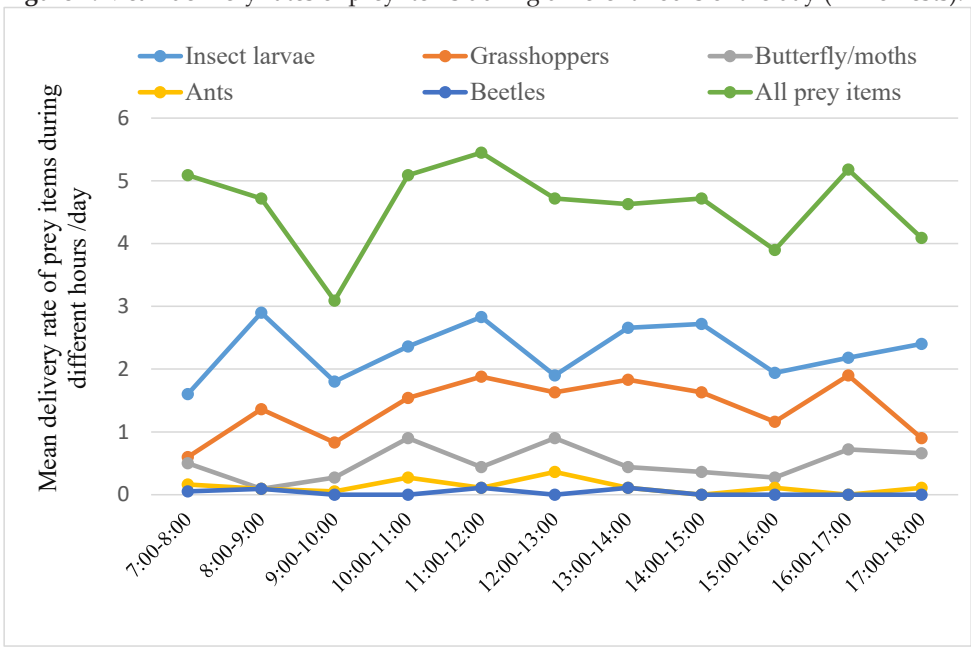


Figure 3. Mean delivery rates of prey items to nestlings of different ages per day (n = 18 nests).

Nest food provisioning and time-of-day effects

The provisioning rates of all prey items during 11 different hours of the day (07:00–18:00) did not vary ($F_{10, 110}=0.78$, $p>0.05$). However, there were two early morning peaks of delivery (07:00–08:00 and 10:00–11:00) averaging 5.09 ± 0.6 food items/h, a mid-morning (11:00–12:00) peak of 5.45 ± 1.3 items/h and one afternoon (14:00–15:00) peak of 5.18 ± 0.7 items/h (Fig. 4). The mean delivery rates of insect larvae ($F_{10, 152}=0.68$, $p>0.05$) and butterflies/moths ($F_{10, 152}=1.53$, $p>0.05$) during different hours of the day did not vary. However, mean delivery rates of grasshoppers for the time periods varied significantly ($F_{10, 152}=2.203$, $p<0.05$). The provisioning rates by female ($F_{10, 110}=1.09$, $p>0.05$) and male parents during the time periods did not vary ($F_{10, 110}=1.68$, $p>0.05$).

Figure 4. Mean delivery rates of prey items during different hours of the day (n = 18 nests).



Discussion

In tropical habitats that have less pronounced wet and dry seasons, factors that may influence breeding in birds include food availability, climate, and risk of nest predation (Gokula & Vijayan 2000). In insectivorous birds in particular, the type of prey and its abundance has been shown to be an important factor for the timing of reproduction (Garcia-Navas & Sanz 2011). In our study, insect larvae comprised the largest (51.9%) proportion of nestling diet. This was consistent with the findings of a study by Winterbottom & Wilson (1959) on the breeding behaviour of a Red-capped Lark population in Cape Town, and confirmed that caterpillars formed the highest proportion of nestling diet (45.7%) compared to other prey types (grasshoppers, moths, beetles). The importance of insect larvae has also been shown in another study on Red-capped Larks (Borrett & Wilson 1971) and numerous other studies of passerine species including, Blue Tits *Cyanistes caeruleus* (50% of diet, Banbura *et al.* 1994), Black-throated Blue Warblers *Dendroica caerulescens* (60–87% of diet (Goodbred & Holmes 1996), Great Tit *Parus major* (44% of diet; Pagani-Nuñez *et al*. 2011), and Cerulean Warbler *Setophaga cerulea* (53% of diet; Auer *et al*. 2016). The provision of larvae (including caterpillars) can be attributed to a preference by parent birds to

provide soft-bodied prey to young nestlings because of their limited ability to digest hard-bodied prey that contains high amounts of chitin (Or ł owski *et al*. 2015).

The quantity of food delivered to nestlings is influenced by the need to increase nestling survival (Oers *et al*. 2015), as well as to reduce predation, since nestlings that are not well fed are likely to beg more and attract predators in the process (Barati & McDonald 2017). This study revealed that the type and quantity of prey provided varied with nestling age, with provisioning rates increasing for nestlings aged 3–7 days old and decreasing for those 8–10 days old. Given that decreased food delivery reduces nestlings' survival (Mullers & Tinbergen 2009), increased provision of prey by parents may be attributed to the need by parents to increase chick survival during the crucial early days of their lives. Furthermore, the decline in provisioning rates towards the end of the nestling period may have been due to the need by parents to reduce the risk of being predated on while in or around the nest as well as to induce fledging (Adler & Ritchison 2011).

In our study time of day had an influence on food provisioning behaviour in Red-capped Larks. Provisioning rates were high in the morning and at mid-day, decreased in the afternoon, but increased again in the evening. This was likely because Red-capped Larks inhabit more open habitats where temperatures after mid-day may increase physiological stress on foraging adults because of heat load (Alonso *et al*. 2016) or depress insect activity to avoid unnecessary exposure to heat (Cao & Edery 2017).

Numerous avian reproduction studies have raised the question of whether parental care provided by male and female parent birds varies (Lormee *et al*. 2005, Ancona & Drummond 2013). In some species, the 'division of labour' hypothesis applies when each sex plays a different role in providing care (Morvai *et al*. 2016). In addition, investment by parents in socially monogamous birds may vary. There may be cases where great inequity in provisioning rates by the two sexes is evident (Palmerio & Massoni 2008), with male and female parents showing differences in provisioning behaviour (Mand *et al*. 2013) However, in some species, the investment may be more equitable. In our study, this was the case for the Red-capped Lark in relation to food provisioning with both parents actively providing this kind of care.

Study limitations and recommendations

Given that the study relied on direct field observations to identify prey items delivered by parents to nestlings, accurate identification of very small prey items, especially ants, was in some cases a challenge. Furthermore, the results of this study relied on data from one study area (Kedong area) over a period of only six months. Deeper insights into the diet and nest provisioning behavior of the Red-capped Lark in future studies may require more advanced and long-term studies such as the use of neck collars, faecal samples analysis, and video recordings.

Conservation implications

The findings of this study confirmed that insects, especially larvae and caterpillars, are very critical for the survival and reproductive success of the Red-capped Lark. Open grassland not only offers a habitat for the bird, but also harbours its insect prey species. The grassland habitat of birds at Kedong Ranch and elsewhere in Kenya is under pressure from intensified anthropogenic activities and should be protected from further degradation. With habitats of many tropical birds becoming threatened and increasingly fragmented, resulting in a huge loss of biodiversity, there is great need to integrate the findings of this study in a comprehensive biodiversity conservation management plan for Kedong Ranch and in similar plans for grassland species

elsewhere. This will safeguard insect food resources for the Red-capped Lark and other grassland birds to ensure their long-term conservation.

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