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Published in:
Journal of Avian Biology

DOI:
[10.1111/jav.01645](https://doi.org/10.1111/jav.01645)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2018

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Mwangi, J., Ndithia, H. K., Kentie, R., Muchai, M., & Tieleman, B. I. (2018). Nest survival in year-round breeding tropical red-capped larks *Calandrella cinerea* increases with higher nest abundance but decreases with higher invertebrate availability and rainfall. *Journal of Avian Biology*, 49(8), [01645]. <https://doi.org/10.1111/jav.01645>

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JOURNAL OF AVIAN BIOLOGY

Article

Nest survival in year-round breeding tropical red-capped larks *Calandrella cinerea* increases with higher nest abundance but decreases with higher invertebrate availability and rainfall

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Journal of Avian Biology

2018: e01645

doi: 10.1111/jav.01645

Subject Editor: Javier Perez-Tris
Editor-in-Chief: Jan-Åke Nilsson
Accepted 14 June 2018



Nest survival is critical to breeding in birds and plays an important role in life-history evolution and population dynamics. Studies evaluating the proximate factors involved in explaining nest survival and the resulting temporal patterns are biased in favor of temperate regions. Yet, such studies are especially pertinent to the tropics, where nest predation rates are typically high and environmental conditions often allow for year-round breeding. To tease apart the effects of calendar month and year, population-level breeding activity and environmental conditions, we studied nest survival over a 64-month period in equatorial, year-round breeding red-capped larks *Calandrella cinerea* in Kenya. We show that daily nest survival rates varied with time, but not in a predictable seasonal fashion among months or consistently among years. We found negative influences of flying invertebrate biomass and rain on nest survival and higher survival of nests when nests were more abundant, which suggests that nest predation resulted from incidental predation. Although an increase in nest predation is often attributed to an increase in nest predators, we suggest that in our study, it may be caused by altered predator activity resulting from increased activity of the primary prey, invertebrates, rather than activity of the red-capped larks. Our results emphasize the need to conduct more studies in Afro-tropical regions because proximate mechanisms explaining nest predation can be different in the unpredictable and highly variable environments of the tropics compared with the relatively predictable seasonal changes found in temperate regions. Such studies will aid in better understanding of the environmental influences on life-history variation and population dynamics in birds.

Keywords: nest predation, tropical, nest success

Introduction

Nest survival is an important component of natality for birds (Shaffer and Burger 2004), and thus plays critical roles in avian life-history evolution (Grant et al. 2005) and population dynamics (Cowardin and Johnson 1979, Arnold et al. 1993). Among



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the factors affecting nest survival, nest predation has been shown to be the major cause of nest failure in most bird species (Ricklefs 1969, França et al. 2016). For many species, nest survival varies over time (Grant et al. 2005, Koczur et al. 2014, Berkunsky et al. 2016, França et al. 2016, Polak 2016). Yet, studies evaluating the proximate factors involved in explaining nest survival, such as food, weather, and breeding activities of conspecifics, have mostly been carried out in temperate areas and rarely in the tropics (Thomson 1950, Martin 1987, Stutchbury and Morton 2008). Understanding the patterns and causes of temporal variation in daily nest survival rates is especially pertinent to the tropics, where nest predation rates are typically high (Skutch 1966, Ricklefs 1969, Robinson et al. 2000, Stutchbury and Morton 2008), and environmental conditions are favorable for breeding during much of the year (Moreau 1950, Stutchbury and Morton 2008, Ndithia et al. 2017b).

Birds are thought to time their breeding to optimize fitness, by balancing favorable environmental conditions, such as the well-studied factors of day length, temperature, and food availability for growing nestlings, with the risk of nest predation (Morton 1971, Dawson et al. 2001, Preston and Rotenberry 2006). In temperate zones, where calendar time predicts the environmental conditions that are important for successful nesting, breeding is synchronized and generally takes place during spring (Lack 1950). In these temperate regions, seasonal variation in nest survival is well-studied, and differences in nest predation between early and late nests is well-documented for many bird species with some species reportedly showing an increase, others a decrease and some show no variation with season (Götmark 2002, Grant et al. 2005, Wilson et al. 2007, Borgmann et al. 2013, Kentie et al. 2015). However, although some birds are known to forego breeding when perceived nest predation is too high (Spaans et al. 1998), birds faced with strong seasonal environments will not generally delay breeding to avoid higher nest predation (Preston and Rotenberry 2006).

Many tropical bird species have extended breeding seasons or even breed year round. In the tropics environmental factors, such as temperature, food availability and breeding activities of conspecifics, do not predictably covary with calendar month. Here, factors that determine their breeding are often less clear (Moreau 1950, Ndithia et al. 2017b). In addition, the predictive value of calendar month for nest predation risk is poorly studied in tropical regions (but see Spanhove et al. 2014). However, if nest survival rates do vary predictably over time, it could be hypothesized that tropical birds, especially, should time their breeding to coincide with comparatively low nest predation rates.

Factors that affect success rates of nests are manifold, varying from nest abundance (Sofaer et al. 2014, França et al. 2016), the behavior of parents or offspring in and around the nest (Martin et al. 2000, Haff and Magrath 2011), predator numbers and foraging behavior (Vickery et al. 1992) to environmental factors such as rainfall, temperature and food availability (Simons and Martin 1990, Shiao et al. 2015). These factors often interact with each other. For example,

rainfall and low temperatures can lead to reduced parental visitation rates, increased brooding time for eggs/chicks in the nest (Siikamäki 1995, Öberg et al. 2015), increased begging behavior by young as a result of decreased provisioning rates, and reduced foraging efficiency of parents due to reduced availability of prey (Siikamäki 1996). Food available to parents and nestlings has been shown to alter nest survival (Yom-Tov 1974, Simons and Martin 1990, Haley and Rosenberg 2013). In addition, the total food available to nest predators may affect nest predation by affecting nest predator numbers (Holmes 2011), or nest predators opportunistically encountering nests when in search of other food (Vickery et al. 1992). Opposite effects may also be possible, for example when breeding in synchrony reduces nest predation by diluting the effects of nest predators or by fostering group defense against nest predation (Westneat 1992).

To better understand the factors determining nest survival in the tropics, we exploited the opportunity to tease apart the effects of population-level breeding activity and environmental conditions on a year-round breeding bird, the red-capped lark *Calandrella cinerea*, in the understudied region of equatorial Africa (Xiao et al. 2017). Red-capped larks are ground-breeding open-cup nesters that experience high rates of nest predation, like many lark species (Tieleman et al. 2008, Praus et al. 2014, Ndithia et al. 2017a). At our study site in Kedong, Kenya, they breed year round and the timing of their breeding activities is not affected by rainfall, temperature or invertebrate availability (Ndithia et al. 2017b), although nestling growth rates increase with higher rainfall (Ndithia et al. 2017a). Insights into nest predation in this system may help understand the causes and consequences of breeding at different times, by shifting the focus from the number of breeding birds to the success of their nests.

During a period of 64 months, we investigated variation in daily nest survival rates of equatorial, year-round breeding red-capped larks over time and in relation to social and environmental factors. We continuously observed breeding activities, monitored nest survival, and recorded rainfall and temperature, in addition to sampling the availability of flying and ground-dwelling invertebrates. We made the following predictions: 1) daily nest survival rates will not show a predictable seasonal pattern, or consistent differences among years, in line with the lack of seasonal/annual patterns found in the timing of breeding (Ndithia et al. 2017a); nest survival rate will be 2) negatively correlated with nest index due to a higher probability of predators encountering nests, 3) positively correlated with rainfall and temperature as factors that increase food available for nestlings, and 4) positively correlated with invertebrate biomass as a proxy for food availability.

Material and methods

Study species and study site

We studied a population of red-capped larks in Kedong Ranch, Naivasha, Kenya (00°53.04'S, 036°24.51'E, 1890 m a.s.l.).

The red-capped lark is a small gregarious bird found in short-grass and bare-ground habitats (Zimmerman et al. 1996). Males and females form pairs during breeding but interact in mixed-sex flocks when not breeding (unpubl.). Clutch size is usually 2 eggs but 1–3 egg clutches occur occasionally (Ndithia et al. 2017a). The female incubates eggs for 12–14 d (mean 12.3 ± 0.21 SE, $n=38$). Nestlings leave the nest at around the age of 10 d (mean 10.1 ± 0.10 SE, $n=56$). Kedong Ranch is a 30 000 ha privately-owned ranch that lies at an altitude of between 1500 and 2200 m a.s.l. sandwiched between Mt Longonot and Hell's Gate National Parks on the floor of the Rift Valley escarpment in Naivasha, Kenya. For the entire study period, we monitored nests in a 5 km² field of continuous natural grassland within the ranch. The ranch is located 90 km from Nairobi and its land is used for extensive ranching with livestock and horticultural farming. Wildlife roams freely throughout the ranch and the adjacent national parks. Our study grassland was occasionally under mild grazing of livestock (< 100 heads of cattle on average 4 d a month) and continuously used by free ranging wildlife. Wildlife species found within the grassland consisted of mostly impala *Aepyceros melampus*, giraffe *Giraffa camelopardalis*, zebra *Equus quagga*, Thomson's *Eudorcas thomsonii* and Grant's gazelle *Nanger granti*, Coke's hartebeest *Alcelaphus buselaphus cokii* and bat-eared fox *Otocyon megalotis*. The area consists of grasslands dominated by the grasses *Cynodon digitaria*, *Digitaria* spp. and *Themeda triandra* interspersed with scattered woodlands dominated by short shrubs (*Acacia drepanolobium* and *Tarchonanthus camphoratus*).

Weather

We set up a weather station (2011–2014, Alecto WS-3500, Den Bosch, the Netherlands; 2014–2016, Vantage Vue, Davis, the Netherlands) in Kedong that recorded daily rainfall (mm), minimum (T_{\min} , °C) and maximum (T_{\max} , °C) temperature. Based on these measurements, we calculated monthly totals of rainfall and monthly averages of T_{\min} and T_{\max} .

Nests

We searched for nests, on average, for 20 ± 1.0 (SE) days per month (range 7–31 d month⁻¹) and 245 ± 31.2 (SE) hours per month (range 17–825 h month⁻¹) from January 2011 until June 2016, by observing breeding behavior or flushing birds from nests (for details, see Ndithia et al. 2017b). To quantify breeding intensity at the population level for each month, we calculated a monthly nest index, defined as the total number of nests found in a month per 10 person hours of search effort (Ndithia et al. 2017b). We did this because our search effort varied over time, but we assume that nest index was correlated to nest abundance. We quantified the person hours of search effort as number of hours searching for nests multiplied by the number of persons searching. The area searched for nests was constant during the entire study period. We recorded GPS coordinates for nests and

monitored them every 3 d to determine nest fate until nestlings fledged or the nest failed. Nest failure was further classified into nest predation (when the entire contents of the nest, with eggs or nestlings that were too young to fledge, disappeared) or abandonment (if the nest contents were still (partially) present but not attended to by the parents). Nests were considered successful if they reached the expected fledging date.

Invertebrate biomass

To estimate invertebrate biomass as a proxy for food availability, we used pitfalls and sweep-nets to collect ground-dwelling and flying invertebrates each month except in October 2011, September 2012, April and October 2014 due to tampering of the pitfall traps by local herders (Ausden and Drake 2006). For details, see Ndithia et al. (2017a, b). Briefly, we used four transects with five plastic cups each, inserted in the ground so that the top of the trap was level with the soil surface. Traps were half filled with formaldehyde to preserve invertebrates, harvested after five days in the field, and the contents sorted to taxonomic group. We also walked along the transects with a sweep net on the day we collected the contents of pitfalls. Invertebrates were identified using the National Museums of Kenya database collection as reference (Ndithia et al. 2017a) and Picker et al. (2003). To estimate monthly insect biomass, we used invertebrate calibration curves specific for 10 taxa categories to calculate dry mass from body length and width (Ndithia et al. 2017a). We used mean monthly biomass estimates to explore relationships among invertebrate biomass and daily nest survival rates.

Statistical analysis

As not all nests were found immediately after they were initiated, estimating the percentage of nests fledged would lead to an overestimate of nest survival because nests that failed before they were found would not be included. Therefore, we estimated daily nest survival rates (Mayfield 1975, Dinsmore et al. 2002), and evaluated how year and month, monthly nest index, rainfall, T_{\min} , T_{\max} , and invertebrate biomass affected daily nest survival rates. We pooled the egg and chick phases because we were able to estimate the age of only 31% of the nests (i.e. those found during laying, or those that hatched or fledged during our monitoring), due to the high nest predation rates.

Prior to model selection, we assessed the collinearity of the covariates with the variance inflation factor (VIF), using the function `vifcor` of R package `usdm` (Naimi 2015). The highest VIF was 1.4, and we thus did not consider collinearity (Zuur et al. 2010). We modelled daily nest survival with the package `RMark` ver. 2.2.0 (Laake 2013), which uses the R interface to run nest survival models in the program `MARK` (White and Burnham 1999). We did model selection of nest survival models using an information theoretical approach based on second-order Akaike information criterion for

small sample sizes (AICc) (Burnham and Anderson 2002). We used month as the temporal grouping variable to test for effects of the various covariates on daily nest survival. We followed a hierarchical modelling approach. Due to lack of seasonal or predictable temporal patterns of weather (rainfall, maximum and minimum daily temperature), food availability (invertebrate biomass) or breeding in our study (Ndithia et al. 2017b), we first tested for yearly and monthly effects on daily nest survival rates to choose a temporal variable that might best explain variation (Table 1A). Because some months during some years had no breeding larks, we included a variable yearmonth which described each year and month combination with nests. Hence, we did not test for the interaction of year and month. We then proceeded to model the variation in daily nest survival by substituting monthly effects by monthly nest index, weather covariates and invertebrate biomasses (Table 1B). To model effects of the covariates on daily nest survival, we excluded the four months lacking invertebrate data. With no single best model and to account for model selection uncertainty, we computed with the package MuMIn (Grueber et al. 2011, Barton 2018) a weighted average of the parameter estimates and 95% confidence limits for all the variables contained in the models which have a summed weight < 0.90 % (Table 2). We performed all statistical analyses in R 3.3.0 (R Core Team).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.gd6555j>> (Mwangi et al. 2018).

Results

Nest number and fate

We found and monitored a total of 848 nests during 41 of the 65 months of field work (Fig. 1A). We found nests at different stages: 260 (30.6%) during nest-construction, 44 (5.2%) during egg laying, 447 (52.7%) during incubation and 97 (11.4%) with chicks. From all the nests found, a total of 99 nests reached the fledgling stage. The remainder, 88.3% of all nests found, failed at various stages. Nest predation at 90% was the most likely cause of nest failure, while abandonment accounted for 10%. We could only determine the cause of nest abandonment of 13 of the 75 abandoned nests: three of the nests had been abandoned due to nest flooding after heavy downpour, three nests after an attack on chicks and brooding parents on nests by ants, four nests were demolished, and three nests were abandoned after trampling by a herbivore. Based on the pooled data over the entire study period, the overall daily nest survival rate was

Table 1. Model selection results of daily nest survival rates of red-capped larks for (A) a set of models including year and month and (B) a set of models with a summed weight ≤ 0.9 including monthly nest index (a measure of breeding intensity, equaling the total number of nests found in a month per 10 person-hours of effort), monthly rainfall (mm), monthly minimum (T_{min}) and maximum (T_{max}) temperature ($^{\circ}C$), biomasses of ground-dwelling and flying invertebrates (g), and year. Results for all models are presented in Supplementary material Appendix 1. Table 1B results exclude October 2011, September 2012, April and October 2014, months in which data on invertebrate biomass were lacking. Model averaged estimates with a summed weight ≤ 0.9 are presented in Table 2.

(A) Model	npar	AICc	DeltaAICc	Weight	Deviance
YearMonth	39	4190.464	0.000	0.998	4111.955
Year + Month	17	4203.096	12.632	0.002	4168.996
Year	6	4205.519	15.055	0.001	4193.505
Month	12	4219.209	28.745	0.000	4195.158
Constant	1	4221.254	30.791	0.000	4219.254
(B) Model	npar	AICc	DeltaAICc	Weight	Deviance
Rain + flying invertebrates + monthly nest index + year	9	3378.021	0.000	0.185	3359.985
Rain + T_{min} + flying invertebrates + monthly nest index + year	10	3378.649	0.628	0.135	3358.605
Rain + T_{max} + flying invertebrates + monthly nest index + year	10	3379.970	1.949	0.070	3359.925
Rain + ground invertebrates + flying invertebrates + monthly nest index + year	10	3379.998	1.977	0.069	3359.953
Rain + flying invertebrates + year	8	3380.047	2.026	0.067	3364.018
Rain + T_{min} + flying invertebrates + year	9	3380.157	2.136	0.064	3362.121
Rain + T_{min} + ground invertebrates + flying invertebrates + monthly nest index + year	11	3380.652	2.630	0.050	3358.598
Rain + T_{min} + T_{max} + flying invertebrates + monthly nest index + year	11	3380.658	2.637	0.050	3358.605
Rain + monthly nest index + year	8	3381.597	3.575	0.031	3365.568
Rain + T_{max} + ground invertebrates + flying invertebrates + monthly nest index + year	11	3381.852	3.830	0.027	3359.798
Rain + T_{min} + T_{max} + flying invertebrates + year	10	3381.989	3.967	0.026	3361.944
Rain + T_{max} + flying invertebrates + year	9	3382.018	3.996	0.025	3363.981
Rain + ground invertebrates + flying invertebrates + year	9	3382.047	4.026	0.025	3364.011
Rain + T_{min} + ground invertebrates + flying invertebrates + year	10	3382.129	4.108	0.024	3362.085
Rain + T_{min} + T_{max} + ground invertebrates + flying invertebrates + monthly nest index + year	12	3382.658	4.637	0.018	3358.595
Rain + ground invertebrates + monthly nest index + year	9	3382.886	4.864	0.016	3364.849
Rain + T_{min} + monthly nest index + year	9	3383.349	5.328	0.013	3365.313

Table 2. Model averaged estimates (\pm SE) on the effects of monthly nest index (a measure of breeding intensity, equaling the total number of nests found in a month per 10 person-hours of effort), rainfall (mm), minimum (T_{\min}) and maximum (T_{\max}) temperature ($^{\circ}\text{C}$), biomasses of ground-dwelling and flying invertebrates on daily nest survival rates (DSR) of red-capped larks in Kedong Ranch. Model averaged estimates were derived using all models within weight $\leq 0.90\%$ (Table 1B).

	Estimate \pm SE	95% Confidence limits
Intercept	3.220 \pm 0.786	1.679 \pm 4.761
Rain	-0.004 \pm 0.001	-0.006 \pm -0.001
Tmin	-0.029 \pm 0.051	-0.185 \pm 0.050
Tmax	-0.000 \pm 0.011	-0.045 \pm 0.042
Ground invertebrate	0.000 \pm 0.004	-0.015 \pm 0.017
Flying invertebrate	-0.012 \pm 0.006	-0.024 \pm -0.002
Monthly nest index	0.072 \pm 0.060	-0.002 \pm 0.194
2012	-0.648 \pm 0.383	-1.399 \pm 0.102
2013	-1.069 \pm 0.364	-1.782 \pm -0.357
2014	-1.039 \pm 0.327	-1.679 \pm -0.398
2015	-0.575 \pm 0.318	-1.198 \pm 0.049
2016	-0.262 \pm 0.323	-0.894 \pm 0.371

0.88 (± 0.004 SE), leading to a 5% chance that a nest would produce fledglings (nest survival rate) when considering 24 d of nesting activity.

Variation of daily nest survival rates with month and year

Daily nest survival rates varied between months and years (Fig. 1B). The highest daily nest survival rate was 0.95 (± 0.01 SE) in October 2011, which would correspond to a nest survival rate of 30%. The lowest daily nest survival rate was 0.50 (± 0.35 SE) in December 2015, corresponding to a nest survival rate of $< 1\%$.

Exploring the explanatory power of month and year for daily nest survival rate, we found that the best model included yearmonth (AIC weight 0.99, Table 1A) followed by year + month (AIC weight = 0.002), whereas month by itself explained almost no variation (AIC weight = 0.000, Table 1A) and year by itself explained slightly more but still very little variation (AIC weight = 0.001, Table 1A). This suggests that daily nest survival rates varied substantially with time but that there was no consistent annually recurring seasonal pattern or systematic differences among years.

Social and environmental factors influencing daily nest survival rates

To further explore the variation in daily nest survival rate, we replaced month with monthly nest index, weather parameters and invertebrate biomasses, which varied considerably over time (Fig. 1A, C, D, and E). Monthly nest index varied between 0.02 (November 2014) and 5.3 (March 2014) with a mean of 1.2 ± 0.21 SE during the 41 months in which breeding occurred (Fig. 1A). Rainfall varied annually between 224 mm (2013) and 531 mm (2014), and monthly between 0 mm (6 months, mainly in 2013) and 153 mm

(February 2014), with no consistent intra-annual pattern (see also Ndithia et al. 2017b) (Fig. 1C). Mean monthly T_{\max} was $26.3 \pm 0.46^{\circ}\text{C}$ (SE, $n=66$), and T_{\min} was $11.2 \pm 0.22^{\circ}\text{C}$ (SE, $n=66$). Between months, the monthly mean T_{\max} ranged from 16.4°C to 34.9°C while T_{\min} ranged from 6.2°C to 15.6°C (Fig. 1D). The mean monthly ground-dwelling invertebrate biomass was $15.7 \text{ mg} \pm 1.26$ SE ($n=60$) with the highest values recorded in January 2013 (69.3 mg), which was 14 times higher than the lowest values in August 2014 (5.0 mg, Fig. 1E). The mean monthly flying invertebrate biomass was $21.0 \text{ mg} \pm 1.31$ SE ($n=58$) with the highest value in February 2012 (55.5 mg), which was 13.7 times higher than the lowest values in May 2011 (4.1 mg, Fig. 1E).

Including this social and environmental variation in our model selection analysis, as well as year, we found that the highest ranked model, with the lowest AICc and a weight of 0.19, included monthly nest index, rain, flying invertebrate biomass, and year as the best predictors of daily nest survival rate (Table 1B). The next-best three models appeared to be within $\Delta \text{AICc} < 2$, but we note that this was within the penalty of 2 units with an addition of one parameter (from 9 to 10), which shows little support for adding the extra parameters (Arnold 2010). Table 2 shows model averaging results of all models with a summed weight of < 0.90 . Monthly nest index and ground invertebrate biomass were positively correlated with daily nest survival rate, whereas rainfall, flying invertebrate biomass, minimum and maximum daily temperature were negatively correlated with daily nest survival rate (Table 2, Fig. 2). However, confidence intervals for monthly nest index, ground invertebrate biomass, minimum and maximum daily temperature confidence intervals include zero, showing little evidence that they affect daily nest survival.

Discussion

In this study, we showed that daily nest survival rates of red-capped larks in Kedong varied with time, but not in a predictable seasonal fashion among months or consistently among years. Including socio-ecological and environmental factors in our model selection approach showed that monthly nest index, rainfall and flying invertebrate biomass had the highest relative importance in influencing daily nest survival. Daily nest survival was positively correlated with nesting activities of conspecifics and negatively correlated with rainfall and the availability of flying invertebrates. These findings support our first prediction that daily nest survival rates would not show an annually predictable seasonal pattern or consistent differences among years, in line with the lack of such patterns in the timing of breeding (Ndithia et al. 2017b). However, we did not find the expected negative relationship between daily nest survival rate and nest abundance, but instead found a weak positive relationship. Finally, in contrast with our third and fourth predictions, increased rainfall and flying invertebrate abundance was correlated with lower daily nest survival rates, while ground-dwelling

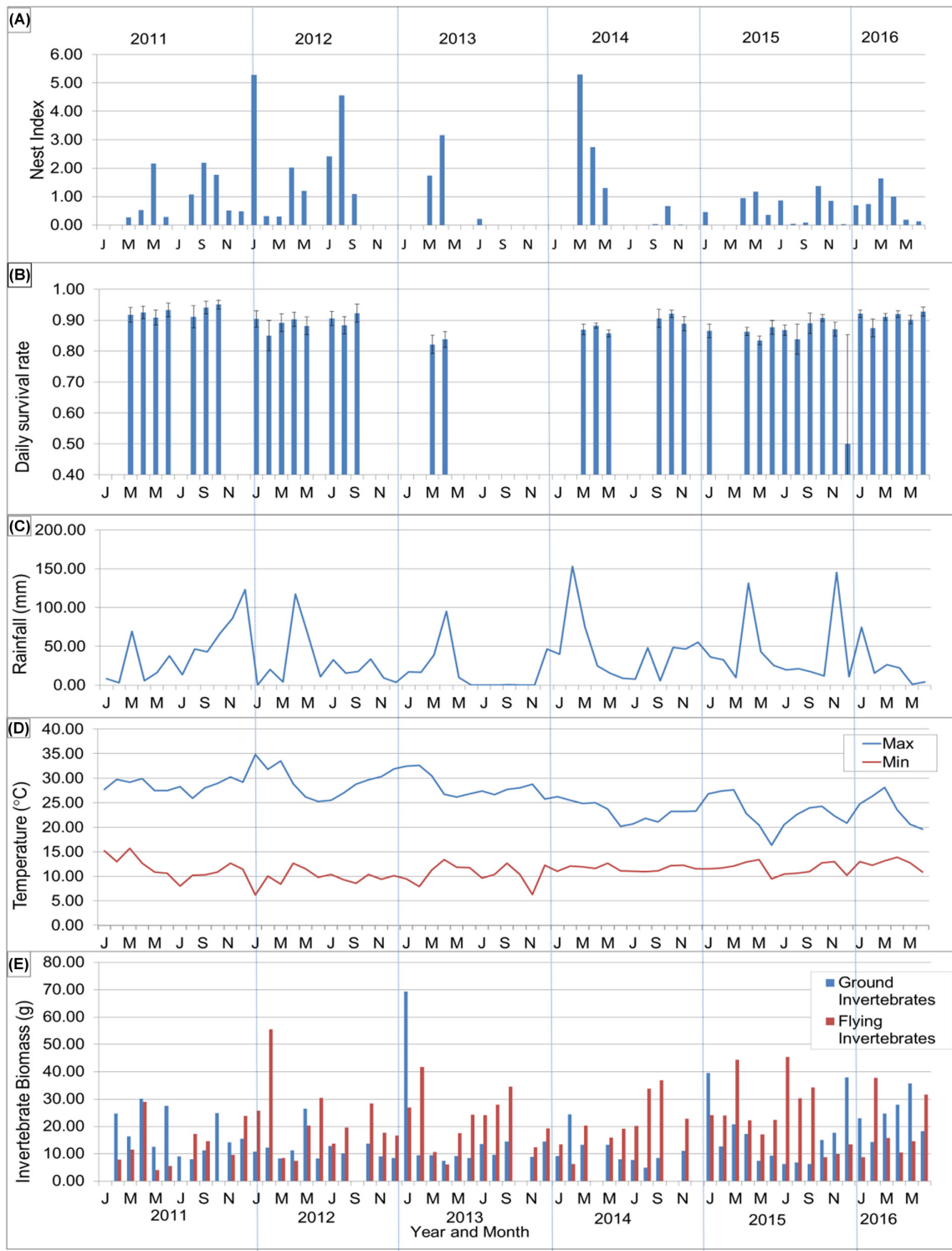


Figure 1. Temporal variation during January 2011–May 2016 in (A) monthly nest index (number of nests/10 search hours), (B) daily nest survival rates (\pm SE) of red-capped larks, (C) rainfall (mm), (D) average monthly minimum (T_{\min}) and maximum (T_{\max}) temperature ($^{\circ}$ C), and (E) biomasses (g dry weight) of ground-dwelling and flying invertebrates in Kedong Ranch, Kenya. Data for weather variables, invertebrates and monthly nest index for the period 2011–2013 were taken from Ndithia et al. (2017a).

invertebrates showed no correlation. Our study provides the first intensive long-term monitoring of nest fates in a tropical ground-breeding bird and, to the best of our knowledge, is

the first to model the effects of various covariates on long-term nest survival and daily survival rates in Afrotropical grasslands.

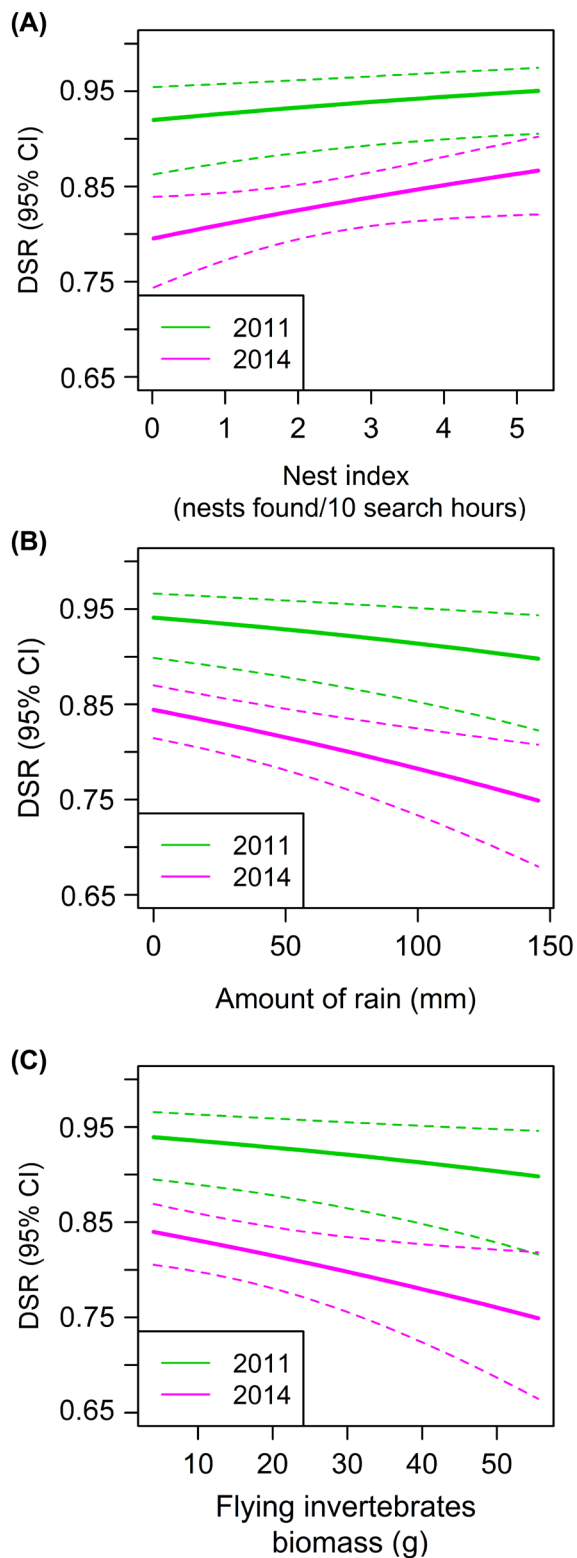


Figure 2. Marginal response curves (solid line) and 95% confidence intervals (dashed lines) of the two extreme years 2011 (year with highest nest survival) and 2014 (year with lowest nest survival) showing variation of daily nest survival probability (DSR) of red-capped larks with the three parameters in the best model: (A) monthly nest index, (B) rainfall and (C) flying invertebrates. The

High nest predation in the tropics

Nest predation accounted for most of the nest losses in red-capped larks, which is consistent with patterns reported from other tropical (Skutch 1949, Newmark and Stanley 2011), subtropical (Robinson et al. 2000), and temperate (Ricklefs 1969, Maphisa et al. 2009) regions. Although 75 nests were classified as abandoned 86% were suspected to be linked to depredation, the other 14% (18 nests) occurrences were few and far apart and so we did not distinguish between the specific causes of nest failure in calculating daily survival probabilities. Nest survival of red-capped larks is comparable to those reported for Afrotropical birds (Newmark and Stanley 2011) and sub-tropical birds in Panama (Robinson et al. 2000). Within the lark family, of which all members are ground-nesting grassland breeders, daily nest survival rates of red-capped larks were lower compared with species in more temperate regions (thekla lark *Galerda theklae* and lesser short-toed lark *Calandrella rufescens* (DSR=0.91), (Yanes and Suarez 1996), Rudd's lark *Heteromirafra ruddi* (DSR=0.96), (Maphisa et al. 2009), skylarks *Alauda arvensis* and woodlarks *Lullula arborea* (DSR=0.95, DSR=0.94), (Praus et al. 2014)), but similar to those of hoopoe larks *Alaemon alaudipes* in the Arabian Desert (DSR= range 0.81–0.87, (Tieleman et al. 2008)). Our study, therefore, supports the postulation that tropical ground-nesting birds experience higher predation rates than their temperate counterparts (Skutch 1949, Ricklefs 1969, Soderstrom 1999, but see Oniki 1979). Similar results have also been reported in forest species showing tropical nesting success to be approximately 23% lower than in temperate regions (Robinson et al. 2000). Higher nest predation in the tropics is attributed to a higher diversity of predators (Skutch 1949, Ricklefs 1969). We indeed observed a diverse range of predators preying upon red-capped lark nests, such as lesser kestrels *Falco naumanni*, black chested-snake eagles *Circaetus pectoralis*, domestic dogs *Canis lupus familiaris*, bat-eared foxes *Otocyon megalotis*, cattle egrets *Bubulcus ibis* and an unidentified snake. Although we were not able to quantify the relative contributions of the various predators to daily nest survival rate, most of the nest predation was carried out by bat-eared foxes and common kestrels (unpubl.).

Temporal variation in nest survival

In well-defined breeding seasons, both in tropical and temperate areas, temporal variation in nest predation is widely documented but the nature of the pattern varies among species, with some studies showing an increase as breeding season progresses (Grant et al. 2005), while others show a decrease (Davis 2005, Shustack and Rodewald 2011).

Figure 2. Continued

response curve for each variable was constructed while keeping the other two variables at their average value. We show the effects of only two years because the trend was the same for all years so we could reduce overcrowding of lines in the figure.

Our study of a year-round breeding bird without a well-defined breeding season showed high and unpredictable temporal variation in nest predation rates, a result that is consistent with two other Afrotropical studies, namely on the white-starred robin *Pogonocichla stellata* (Spanhove et al. 2009) and Cabanis's greenbul *Phyllastrephus cabanisi* (Spanhove et al. 2014) in Taita Hills (south-east Kenya). In our study, nest abandonment was not large enough to explain the variation in nest success. Temporal variation in the strength and direction of nest predation rates suggest that nest predators change and vary over time heterogeneously, e.g. with predator density and abundance (Yanes and Suarez 1996, Borgmann et al. 2013), predator activity patterns (Schmidt et al. 2001), primary prey availability and distribution (Vickery et al. 1992) or availability of alternative prey (Borgmann et al. 2013). We propose that the unpredictability of the temporal variation makes it difficult for red-capped larks to use nest predation risk as a cue to time their breeding.

Influence of monthly nest index on nest survival

Daily nest survival increased, albeit weakly supported, when more larks in the population were nesting. This, together with the inverse relationship between daily nest survival and flying invertebrate food, suggests that nest predation was incidental, i.e. lark nest contents were a secondary prey encountered by predators searching for a different primary prey (Vickery et al. 1992, Schmidt et al. 2001). When nest predation is caused by a primary nest predator, the relationship between nest abundance and survival is typically inverse, as reported in most studies (Schmidt and Whelan 1999, Gunnarsson and Elmberg 2008, Elmberg et al. 2009, Sofaer et al. 2014, França et al. 2016). A pattern similar to ours was reported for ground-nesting birds whose main predator were striped skunks *Mephitis mephitis* that primarily target invertebrates (Vickery et al. 1992). Indeed, the primary food of bat-eared foxes and lesser kestrels, the main nest predators that we observed, are invertebrates, although their diet also includes other opportunistic prey, such as birds and eggs (Nel 1978, Anderson et al. 1999, Stuart et al. 2003, Klare et al. 2011). Nest predation by incidental predators can be the major cause of nest failure and significantly decrease daily nest survival rates (Vickery et al. 1992, Yanes and Suarez 1996, Martínez-Padilla and Fargallo 2008). An alternative explanation for the positive relationship between daily nest survival rates and monthly nest index is that most birds start breeding when nest survival is high. We find this an unlikely explanation for year-round, opportunistically breeding birds such as our red-capped larks (Grant and Boag 1980, Ndithia et al. 2017b) because it requires that birds can accurately predict temporal variation of conditions influencing nest survival (Emmering and Schmidt 2011, Ibáñez-Álamo et al. 2015). Our interpretation that incidental nest predation may be the major cause of reduced nest survival in red-capped larks is also congruent with the negative relationship between daily survival rate and flying invertebrate biomass, the primary prey for the incidental nest predators.

Influence of rain and invertebrate biomass on nest survival

In contrast with our expectation that higher rainfall would increase invertebrate availability and thereby lead to higher nest survival (Illera and Díaz 2006), we found that increased rainfall decreased nest survival in red-capped larks. Moreover, we found that increased rain had a significantly negative effect on flying invertebrate biomass ($F_{1,56}=8.62$, $p=0.005$, Fig. 3), suggesting that the negative effects of both rainfall and flying (but not ground-inhabiting) invertebrate availability on nest survival are independent effects of these factors. Our findings of decreased nest success with rain are similar to those on green-backed tits *Parus monticolus* and rufous-faced warblers *Abroscopus albogularis* in subtropical Taiwan (Shiao et al. 2015). This suggests that food availability does not limit breeding in larks. This would be in line with the general notion that tropical birds lack the high within-brood losses during the nestling stage, which characterize starvation (Ricklefs 1969), and with the earlier finding that timing of breeding in red-capped larks was not related to flying or ground-inhabiting invertebrate biomass (Ndithia et al. 2017b). Increased rainfall may lead to decreased nest survival rates through decreased foraging efficiency or nest attendance

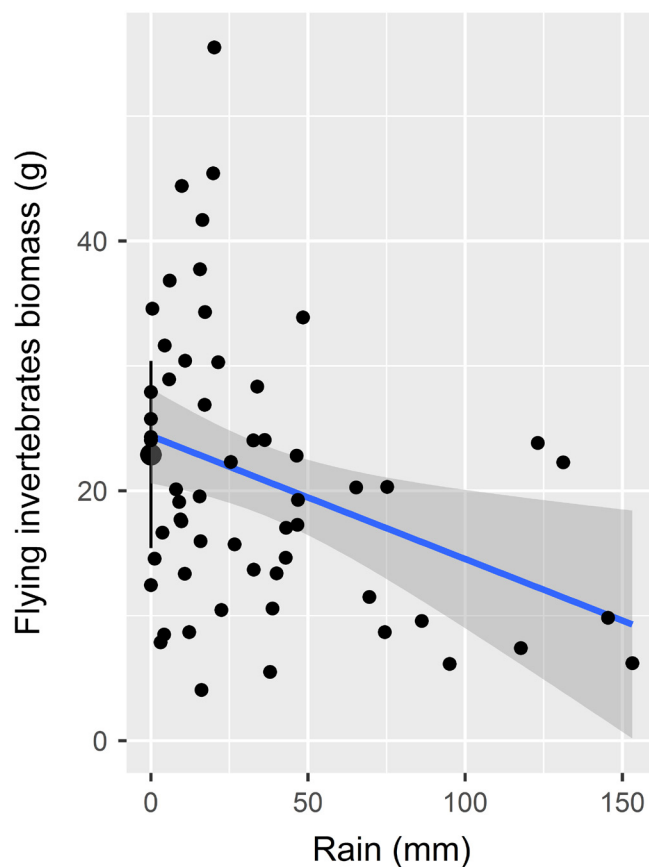


Figure 3. Regression analysis for the relationship between monthly averages for rainfall (mm) and flying invertebrate biomass (g dry weight). The shaded area represents the 95% confidence interval.

by parents (Radford et al. 2001, Arlettaz et al. 2010, Öberg et al. 2015, Rishworth and Pistorius 2015), leaving nests more vulnerable to both harsh weather conditions and exposure to nest predators (Rishworth and Pistorius 2015).

Our finding of reduced daily nest survival rates of red-capped larks with higher flying invertebrate biomass, again in contrast with our expectations, may be due to the activity and detectability of these invertebrates, the primary food of red-capped lark nest predators, as earlier discussed. A similar interaction is reported in Yanes and Suarez (1996), where daily nest survival of thekla larks and lesser short-toed larks was negatively correlated with the primary prey (rabbits) of their predators (canids). When nest predation is incidental, the magnitude of nest predation is determined by the predator's response to the abundance and distribution of the primary prey (or to the cumulative prey abundance) rather than the secondary prey (in our case lark nests) (Schmidt et al. 2001). However, verifying whether the negative effect of flying invertebrate biomass on daily nest survival rate is due to higher nest predation by incidental predators would require a detailed study on the identity and behavior of nest predators.

Acknowledgements – We would like to thank the management of Kedong for permission to conduct this research in the ranch. We are indebted to Peter Kinyanjui, Samuel Bakari, Paul Kimani, Abraham Mwangi, Mary Mwangi, Naomi Wanjiku, Ken Njuguna, Johana Kamau and Maaik Versteegh for the invaluable help in data collection. Sarah Higgins of Lake Naivasha Riparian Association provided accommodation and a base for logistics for the research team during the years of fieldwork. We also thank Esther Chang for comments on the manuscript. The National Museums of Kenya organized permission letters for access to the study area.

Funding – Funding for the study was provided by The Netherlands Fellowship Programme of Nuffic (grants no. CF9159/2013 to BIT and JMM, CF6833/2010 to BIT and HKN), the Netherlands Organization for Scientific Research (NWO-VIDI 864.10.012 to BIT), Lucie Burgers foundation (to JMM) and two grants from the Ecology fund of the Royal Netherlands Academy of Arts and Sciences (to JMM).

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Supplementary material (Appendix JAV-01645 at <www.avianbiology.org/appendix/jav-01645>). Appendix 1.