Biodiversity Observations (2026) 16: 41-47

Primary moult of four species of larks: preliminary results for Large-billed Lark, Spike-heeled Lark, Grey-backed Sparrow-lark and Red-capped Lark

HD Oschadleus, LG Underhill & T Scott

Oschadleus HD, Underhill LG, Scott T 2026. Primary moult of four species of larks: preliminary results for Large-billed Lark, Spike-heeled Lark, Grey-backed Sparrow-lark and Red-capped Lark. Biodiversity Observations 16: 41–47.

7 April 2026

DOI: [10.15641/bo.2033](10.15641/bo.2033)

Biodiversity Observations (2026) 16: 41-47

ORNITHOLOGY

Primary moult of four species of larks: preliminary results for Large-billed Lark, Spike-heeled Lark, Grey-backed Sparrow-lark and Red-capped Lark

HD Oschadleus, LG Underhill & T Scott

Biodiversity and Development Institute, 25 Old Farm Road, Rondebosch 7700, South Africa

email: doschadleus@gmail.com

Abstract

Knowledge about the parameters of primary moult of larks (Aladidae) is minimal. This paper presents preliminary results for four species: Large-billed Lark *Galerida magnirostris*, Spike-heeled Lark *Chersomanes albofasciata*, Grey-backed Sparrow-lark *Eremopterix verticalis* and Red-capped Lark *Calandrella cinerea*. The results are based on small samples and should not be treated as definitive. The purpose of the paper is to encourage collaboration so that gaps in knowledge can be filled.

Introduction

There are large knowledge gaps relating to the moult of larks (Alaudidae). Larks are not represented in a database of 143 bird species to which the moult model of Underhill & Zucchini (1988) had been applied to estimate the parameters of primary moult (Scott & Underhill 2024). Hockey et al. (2005) wrote 31 species texts for the larks occurring in southern Africa; for 15 of these species the section on moult was reduced to “no data”, and for the remainder the available knowledge can be summarized as severely incomplete. We therefore report the primary moult data we have observed on four lark species: Large-billed Lark *Galerida magnirostris*, Spike-heeled Lark *Chersomanes albofasciata*, Grey-backed Sparrow-lark *Eremopterix verticalis* and Red-capped Lark *Calandrella cinerea*.

Methods

Primary moult was recorded from birds in the hand during ringing. Moult was recorded using the standard protocol (Ashmole 1962, de Beer et al. 2000). The main site at which larks were the target species, both for mist nets and for spring traps was near Vanrhynsdorp on the lower slopes of the Maskam Mountain (31°38’S, 18°47’E) (Figure 1).

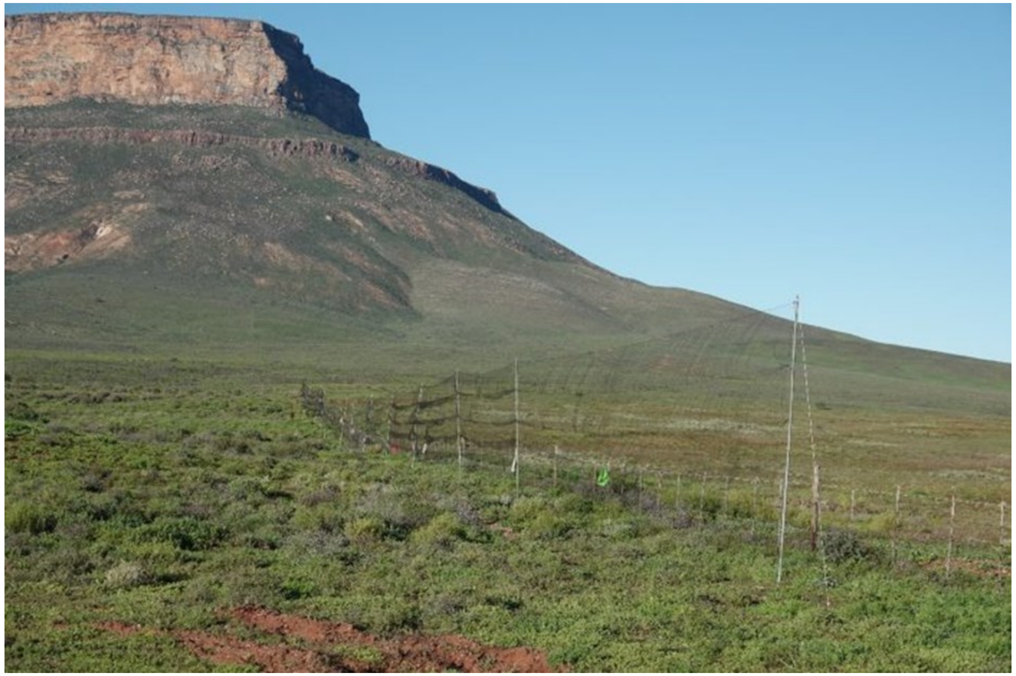

Figure 1: A line of mist nets at the base of slopes of the Maskam Mountain near Vanrhynsdorp, Western Cape, South Africa. This was the site at which the main target species were larks.

We observed primary moult in four species of larks: Large-billed Lark *Galerida magnirostris*, Spike-heeled Lark *Chersomanes albofasciata*, Grey-backed Sparrow-lark *Eremopterix verticalis* and Red-capped Lark *Calandrella cinerea*. We report on these results. Larks have nine large primaries, and a tiny 10th primary. Our focus here is on the nine large primaries.

To calculate proportion feather mass grown (PFMG) we used a database of feather mass data (complied by Peter G Ryan and LGU); this contained primary masses for six lark species, and these were used to estimate relative feather masses (Table 1). Relative primary feather masses were available for the Red-capped Lark (Table 1) and these were used for the calculation of proportion feather mass grown (PFMG) for this species. An average value for larks was used for Large-billed Lark (Table 1). Both sets of relative primary feather masses are similar to that developed by Bonnevie (2010) as suitable for passerines with nine primaries (Table 1).

Table 1: Relative primary feather masses (expressed as percentages), for Red-capped Lark (n=2 birds), for larks in general (average for 14 birds of six species) and for passerines with nine primaries (n=10 species, Bonnevie 2010).

Primary	Species		
	Red-capped Lark	Larks	Passerines with nine primaries
P1	7.46	8.34	8.0
P2	8.53	8.74	8.6
P3	9.24	9.15	9.2
P4	9.32	9.83	10.0
P5	10.5	11.18	11.4
P6	13.5	13.04	12.4
P7	13.7	13.08	13.0
P8	13.42	13.35	13.5
P9	14.33	13.31	14.0

Results and discussion

For the four species we produced scatterplots of observation date and proportion feather mass grown (PFMG) (Figures 2–5). The sample sizes were small: 12 for Large-billed Lark, four for Spike-heeled Lark, 10 for Grey-backed Sparrow-lark and 22 for Red-capped Lark. The interpretations are tentative and cautious.

Hockey et al. (2005) reported that no information was available on the moult of the Large-billed Lark. In the winter rainfall area, the 11 available records for the Winter Rainfall Area suggest that primary moult here is in summer to autumn (Figure 2).

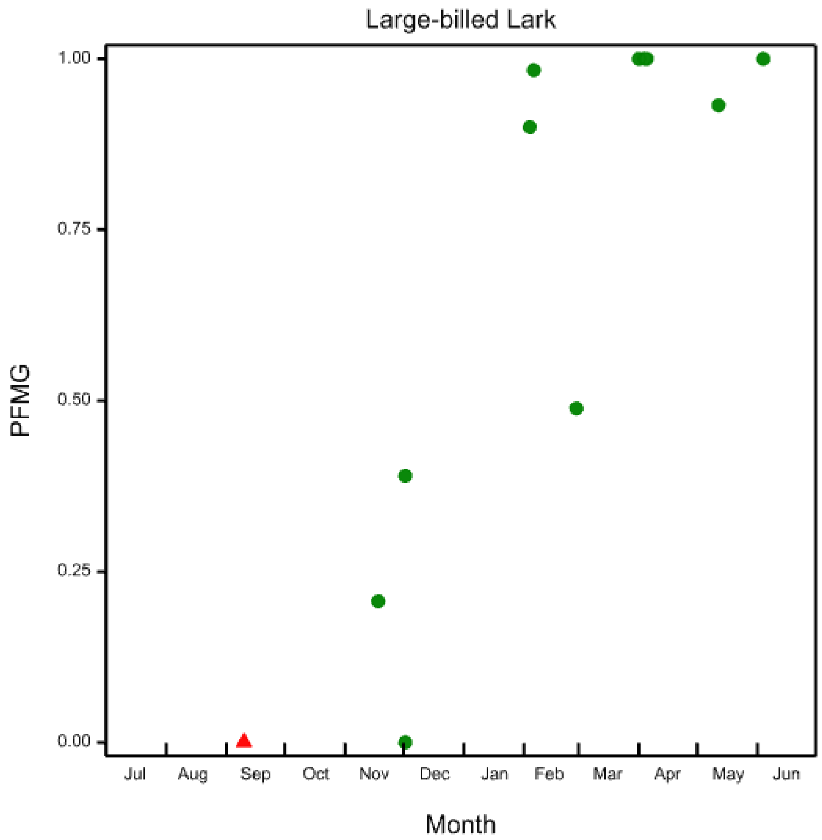

Figure 2: Proportion feather mass grown for 12 Large-billed Larks, 11 in the Winter Rainfall Area of the Western Cape (green circles) and one in the Karoo (red triangle).

Hockey et al. (2005) reported that no information was available on the moult of the Spike-heeled Lark. Two birds, with advanced PFMG of 0.77 and 0.98 were mist netted near Vanrhynsdorp on 7 February 2023; two birds had primaries classified as new in the Karoo in September (Figure 3).

Hockey et al. (2005) reported that no information was available on the moult of the Red-capped Lark. Of the 11 winter rainfall area records (green circles in Figure 4), six had not yet started moult; four were in moult: PFMG scores of 0.03 on 30 December, of 0.77 on 5 February, and of 0.33 and 0.49 on 27 February. One bird had completed moult on 31 March. There was no primary moult in four birds at New Holme birds in mid-September (Figure 4).

Five out of 127 Grey-backed Sparrow-larks examined for moult between 3 and 9 September 2023 at New Holme Farm in the Karoo were in the initial stages of primary moult, involving either only P1 or P1 and P2, with PFMG scores between 0.01 and 0.08 (Hatley et al. 2023). Eight were ringed here one year later, between 11 and 14 September 2024, and none were in moult. There were six records from Gifberg on 1 December 2023; five in moult (PFMG = 0.36, 0.39, 0.43 and two at 0.64, and one completed moult). These observations, and those of Willoughby (1971) support the preliminary hypothesis made by Hatley et al. (2023) that Grey-backed Sparrow-larks undertake a pre-breeding primary moult, through spring and mid-summer (Figure 5).

The Grey-backed Sparrow-lark is gregarious and mobile, with breeding depending on sufficient rainfall. To reduce the chances of breeding opportunities arising while moulting, this species appears to undertake a pre-breeding moult during spring and mid-summer.

We considered applying the moult model of Underhill & Zucchini (1988), which is a three-parameter model to the records. However, Walter Zucchini (pers. comm.) developed a guideline that, in any statistical model, a minimum of seven well-spaced data points is needed per parameter estimated to have a chance of reliable estimates of parameters. Thus, according to this guideline, the minimum sample size before an analyst should consider before fitting even the simplest possible model (a straight line, a two-parameter model) to a set of data is 14 points.

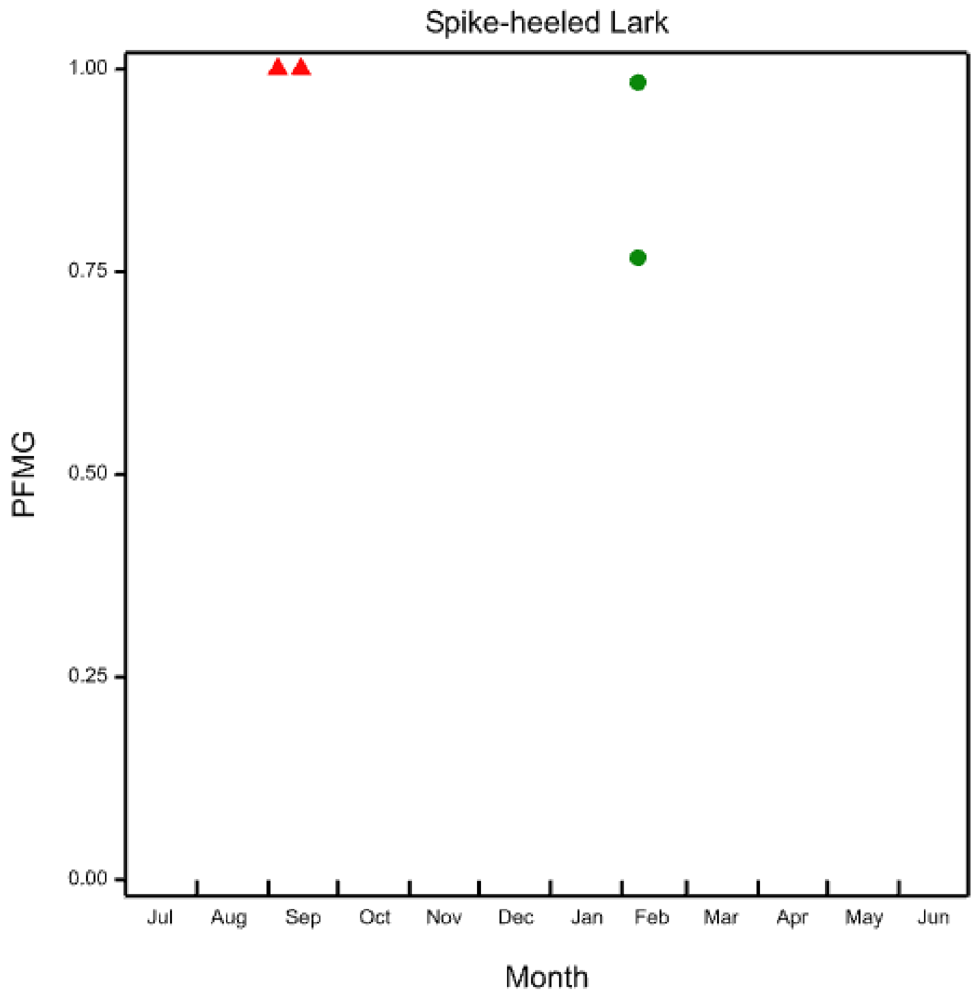

Figure 3: Proportion feather mass grown for four Spike-heeled Larks. Two were in the Winter Rainfall Area of the Western Cape (green circles) and two in the Karoo (red triangles).

In our case we had less than the minimum sample size of 21 points to fit the three-parameter UZ model for the four species. The available sample sizes for Large-billed Lark in the winter rainfall region was 11 and for the Red-capped Lark was 21, 11 in the Winter Rainfall Area and 10 in the Karoo. Fitting models for the other species would have

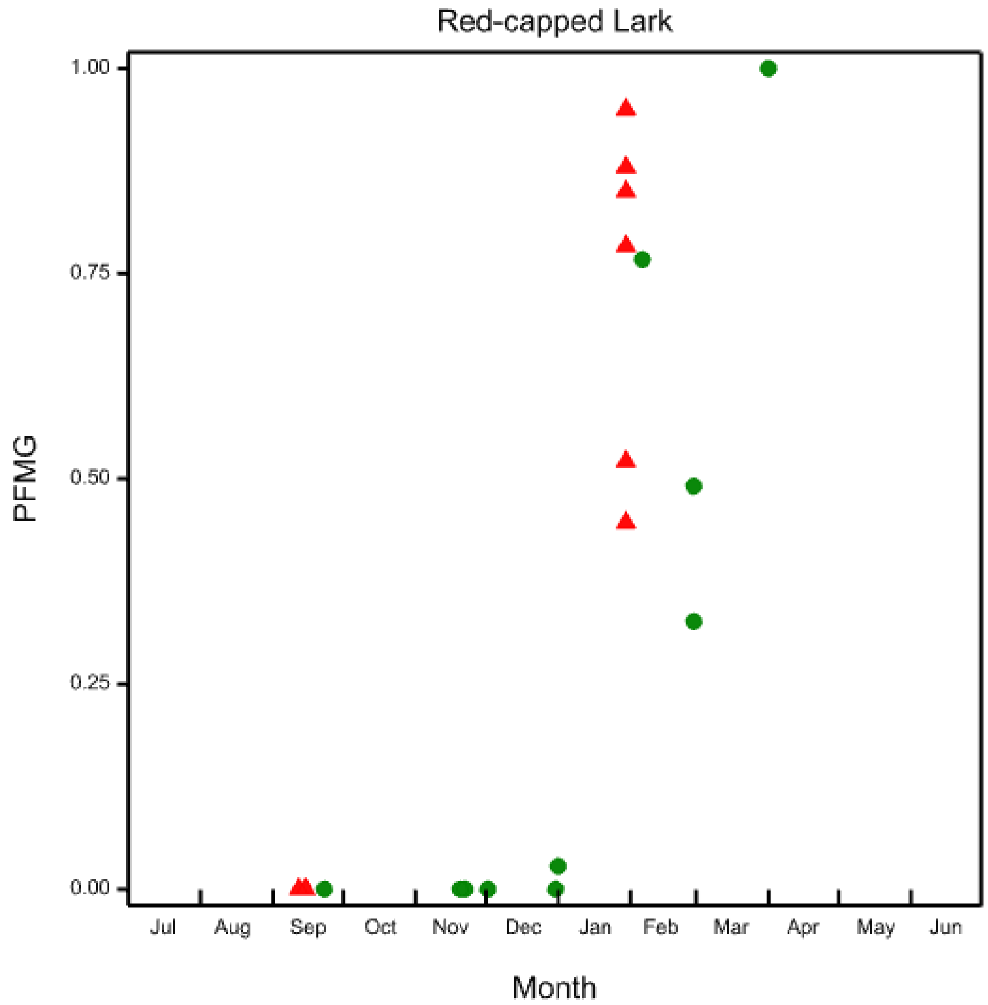

Figure 4: Proportion feather mass grown for 21 Red-capped Larks, 11 in the Winter Rainfall Area of the Western Cape (green circles) and 10 in the Karoo (red triangles).

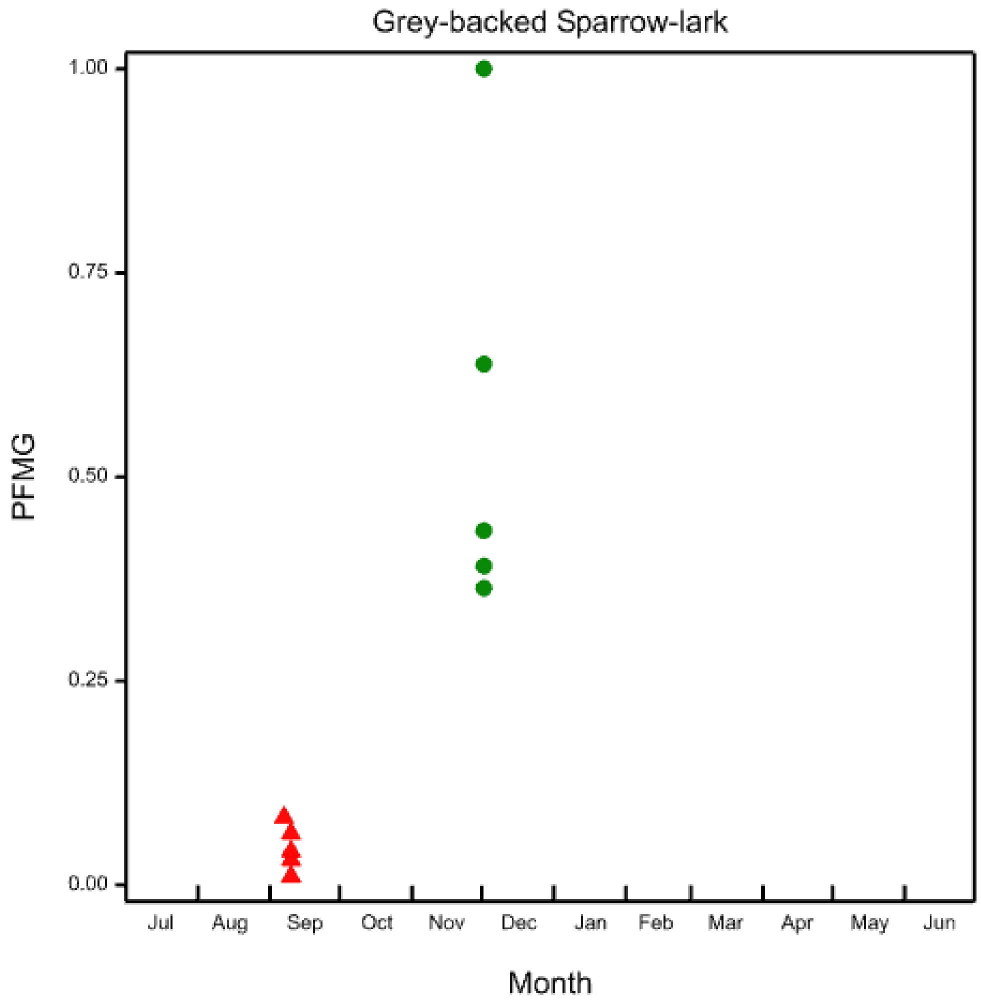

Figure 5: Proportion feather mass grown for 10 Grey-backed Sparrow-larks. Six were in the Winter Rainfall Area of the Western Cape (green circles). Only the five records in primary moult of birds in the Karoo (red triangles) are shown .

 Biodiversity Observations (2026) 16: 41-47

Table 2: Provisional parameter estimates for the primary moult of Large-billed Lark and Red-capped Lark using the Underhill-Zucchini moult model fitted using the software developed by Erni et al. 2013. WRA=Winter Rainfall Area; SE=standard error; N=sample size. See text for caveats.

Species	Duration (SE)	Start date (SE)	Standard deviation of start date (SE)	N
Large-billed Lark	146.8 (37.6)	24 October (37.5)	42.3 (13.6)	11
Red-capped Lark	69.7	25 December (11.2)	22.2 (5.9)	21
Red-capped Lark	80.8 (19.7)	WRA 05 January (10.9)[1]	17.6 (4.8)	21
		Karoo 30 November (12.5)[1]		
Joint analysis	116.7 (22.5)	Large-billed Lark WRA 15 November (17.4)[2]	35.0 (8.0)	32
		Red-capped Lark WRA 26 December (13.1)[2]		
		Red-capped Lark Karoo 05 November (17.7)[2]		

[1] As estimated by the algorithm, moult in the Karoo was 36 days earlier than in the Winter Rainfall Area, and it is this difference that had a standard error of 12.5 days.

[2] As estimated, moult of Large-billed Lark was 41 days earlier than that of Red-capped Lark in the WRA, SE 17.4 days, and moult of Red-capped Lark in the Karoo was 51 days earlier than that of Red-capped Lark in the WRA.

been irresponsible. As anticipated, when we fitted the moult model to the small samples of available data for the two species, the standard errors were so large that the models have no value; this was also the case when we allowed different starting dates for the Red-capped Larks in the two regions (Table 2).

However, we did a joint analysis for the Large-billed and Red-capped Larks. We made two assumptions, and thereby reduced the number of parameters down to five. We make the assumptions that the durations of primary moult of the two species are the same and that their standard deviation parameters are the same. Based on experience with other taxa (Scott & Underhill 2024), these assumptions ought to be approximately correct. We estimated three starting dates: Large-billed Lark in the Winter Rainfall Area, Red-capped Lark in both the Winter Rainfall Area and the Karoo. We thus had five parameters, and a total of 32 data points. The assumptions placed the focus of the analysis on differences in starting date between the species and location. The sample size of 32 was three short of Zucchini's guideline of needing a minimum of 35 points to estimate five parameters. The results still need to be treated as tentative, both because of sample size considerations and the assumptions. The analysis suggested a common duration of 117 days, and that Large-billed Lark in the Winter Rainfall Area started primary moult on 15 November (Table 2). Also, in the Winter Rainfall Area, the Red-capped Lark started primary moult 41 days later than the Large-billed Lark, on 26 December (Table 2). The Red-capped Lark in the Karoo was estimated to start moult 51 days earlier than in the Winter Rainfall Area, on 05 November (Table 2).

For many species, primary moult is the next component of the annual cycle after breeding (Jenni & Winkler 2020). This is particularly true of solitary and resident species, of which Large-billed Lark and Red-capped Lark are examples, and thus follow the traditional pattern of a seasonal breeding period followed by primary moult.

This provided a potential explanation for apparently earlier moult in the Large-billed Lark compared with that of the Red-capped Lark in the Winter Rainfall Area and suggested that we examine the timing of breeding. Unfortunately, this timing is poorly quantified for these two species in this region. However, there are suggestions that the Large-billed Lark breeds during the winter-rainfall period from August onwards, whereas the Red-capped Lark tends to breed towards the end of the winter rains (Winterbottom 1968, Hockey et al. 1989, Dean 1997a, 1997b). Estimated from the data summarized by Winterbottom (1968), the median date of egg-laying for Red-capped Lark is in the first week of October, based on 133 records, whereas that for the Large-billed Lark is second week of September (49 records). The difference is about three weeks. The difference in mean moult start dates was about six weeks (41 days). Both differences point in the same direction, but these results should be regarded as a weak quantification, both because of the small sample sizes and because the breeding data calculations assumed that the records for each month were spread evenly through the month.

Similarly, the seven-week (51-day) difference between the mean start date of primary moult of Red-capped Lark in the Karoo and the Winter Rainfall Area (Table 2) was not unexpected. In the latter area it breeds after the winter rains, but it breeds prior to the summer rains in the eastern half of South Africa (peaking July to September), as done by many insectivorous passerines (Skinner 1995, Allan et al. 1997, Hockey et al. 2005, Tarboton 2011). The seven-week difference is in the anticipated range. Thus, although these results are tentative, they are biologically plausible.

The results of this paper are too uncertain to be added to the database of estimates of moult parameters assembled by Scott & Underhill (2024). The objective of this paper is to encourage other ringers in Africa with substantial datasets related to the primary moult of these and other lark species to collaborate so that we can jointly fill these gaps in knowledge.

Acknowledgements

We are grateful to Per Alström for pointing out the paucity of information and for being the catalyst for this note. The information, however sketchy, helps fill gaps in a monograph on the larks (family Alaudidae) which he is co-authoring.

References

Allan DG, Harrison JA, Herremans M, Navarro R, Underhill LG 1997. Southern African geography: its implications for birds. In Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ (eds) The atlas of southern African birds. Vol. 1: Non-passerines. Johannesburg: BirdLife South Africa: lxv–ci.

Ashmole NP 1962. The Black Noddy *Anous tenuirostris* on Ascension Island, part 1, general biology. Ibis 103b: 235–273.

Bonnevie BT 2010. Relative feather mass indices: are feather masses needed to estimate the percentage of new feather mass grown for moult regression models? Ostrich 81: 59–62.

Dean WRJ 1997a. Redcapped Lark *Calendrella* cinerea. In Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ (eds) The atlas of southern African birds. Vol. 2: Passerines. Johannesburg: BirdLife South Africa: 30–32.

Dean WRJ 1997b. Thickbilled Lark *Galerida magnirostris*. In Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ (eds) The atlas of southern African birds. Vol. 2: Passerines. Johannesburg: BirdLife South Africa: 40–41.

de Beer SJ, Lockwood GM, Raijmakers JHFA, Raijmakers JMH, Scott WA, Oschadleus HD, Underhill LG 2000. SAFRING bird ringing manual. ADU Guide 5: 1–102.

Erni B, Oschadleus HD, Bonnevie BT, Altwegg R, Underhill LG 2013. moult: An R package to analyse moult in birds. Journal of Statistical Software 52: 1−23.

Hatley G, Oschadleus HD, Underhill LG, Ramsay J 2023. Biometrics and moult of Grey-backed Sparrow-lark *Eremopterix verticalis* in the Karoo, September 2023. Biodiversity Observations 13: 239–246.

Hockey PAR, Dean WRJ, Ryan PG (eds) 2005. Roberts birds of southern Africa, 7th edition. Cape Town: John Voelcker Bird Book Fund.

Hockey PAR, Underhill LG, Neatherway M, Ryan PG 1989. Atlas of the birds of the southwestern Cape. Cape Town: Cape Bird Club.

Jenni L, Winkler R 2020. The biology of moult in birds. London: Helm.

Scott T, Underhill LG 2024. Global review of quantitative studies of primary moult of birds using the Underhill-Zucchini moult model. Frontiers in Bird Science 3: 1370918.

Skinner N 1995. The breeding seasons of birds in Botswana – I. Passerine families. Babbler 29: 9–23.

Tarboton W 2011. Roberts nests and eggs of southern African birds. Cape Town: John Voelcker Bird Book Fund.

Underhill LG, Zucchini W 1988. A model for avian primary moult. Ibis 130: 358–372.

Willoughby EJ 1971. Biology of larks (Aves: Alaudidae) in the central Namib Desert. Zoologica Aficana 6: 133–176. Available online at https://www.ajol.info/index.php/az/article/download/150907/140485

Winterbottom JM 1968. A check list of the land and fresh water birds of the western Cape Province. Annals of the South African Museum 53: 1–276.

Biodiversity Observations

The scope of Biodiversity Observations includes papers describing observations about biodiversity in general, including animals, plants, algae and fungi. This includes observations of behaviour, breeding and flowering patterns, distributions and range extensions, foraging, food, movement, measurements, habitat and colouration/plumage variations. Biotic interactions such as pollination, fruit dispersal, herbivory and predation fall within the scope, as well as the use of indigenous and exotic species by humans. Observations of naturalized plants and animals will also be considered. Biodiversity Observations will also publish a variety of other interesting or relevant biodiversity material: reports of projects and conferences, annotated checklists for a site or region, specialist bibliographies, book reviews and any other appropriate material. Further details and guidelines to authors are on the journal website (https://journals.uct.ac.za/index.php/BO/).

ISSN 2219-0341

Editor: LG Underhill