

Population status of the range-restricted Red Lark *Calendulauda burra* in a conservation area stronghold

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Many desert birds are vulnerable to anthropogenic global warming and landscape transformation, particularly in the case of range-restricted species. We quantified suitable habitat and the current population of Red Larks *Calendulauda burra* (family Alaudidae), a range-restricted southern African species, in a conservation area thought to be one of the species' strongholds — the Black Mountain Mine Conservation Area (BMMCA) in the Northern Cape, South Africa. We modelled habitat suitability and estimated home range sizes using telemetry data and kernel density estimates. Home range sizes did not differ between males (42.4 ± 28.3 ha; $n = 5$) and females (41.9 ± 31.3 ha; $n = 5$). Transect data and home range density models indicated densities of 0.086–0.127 individuals·ha⁻¹ for adults in suitable habitat. An estimated 33.2% (30.2 km²) of the BMMCA is suitable habitat for Red Larks, suggesting a population of 232–382 individuals. This population estimate is equivalent to <50% of the population estimated for the BMMCA in 1989. Our findings here, combined with a recent analysis showing that much of the species' range will become thermally unsuitable for its persistence by the end of the 21st century, suggest that urgent conservation action is needed to ensure the Red Lark's future in coming decades.

État de la population de l'Alouette ferrugineuse *Calendulauda burra*, espèce à aire de répartition restreinte, dans un bastion pour sa conservation

De nombreux oiseaux du désert sont vulnérables au réchauffement climatique anthropogénique et à la transformation du paysage, en particulier dans le cas des espèces à aire de répartition restreinte. Nous avons quantifié l'habitat approprié et la population actuelle d'Alouettes ferrugineuses *Calendulauda burra*, une espèce d'Afrique australe dont l'aire de répartition est limitée, dans une zone de conservation considérée comme l'un des bastions de l'espèce, la Black Mountain Mine Conservation Area (BMMCA). Nous avons modélisé l'adéquation de l'habitat et estimé la taille des domaines vitaux à l'aide de données télémétriques et d'estimations de la densité du noyau. La taille des domaines vitaux ne différait pas entre les mâles (42.4 ± 28.3 ha; $n = 5$) et les femelles (41.9 ± 31.3 ha; $n = 5$). Les données des transects et les modèles de densité du domaine vital ont indiqué des densités de 0.086–0.127 individus·ha⁻¹ pour les adultes dans l'habitat approprié. On estime que 33.2% du BMMCA (30.2 km²) est un habitat propice à l'Alouette ferrugineuse, ce qui indique une population de 232 à 382 individus. Cette estimation de la population équivaut à moins de 50% de la population estimée pour la BMMCA en 1989. Nos résultats, combinés à une analyse récente montrant qu'une grande partie de l'aire de répartition de l'espèce deviendra thermiquement inadéquate à sa persistance d'ici la fin du 21^{ème} siècle, indiquent une nécessité urgente d'implémenter une stratégie de conservation pour assurer l'avenir de l'Alouette ferrugineuse dans les décennies à venir.

Keywords: Alaudidae, Black Mountain Mine Conservation Area, desert birds, density transects, habitat suitability, home range, microclimate

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Introduction

Despite their extreme air temperatures (T_{air}), intense solar heat loads and scarce and unpredictable precipitation, deserts often support ecologically diverse but disturbance-sensitive animal and plant communities (Thuiller et al. 2005; Lovich et al. 2014; Vale and Brito 2015; Moore et al. 2018).

The sensitivity of arid-zone communities makes them highly vulnerable to accelerating global warming (Guo et al. 2016; Young et al. 2016; Iknayan and Beissinger 2018) and the consequent alteration of thermal landscapes (Midgley and Thuiller 2007; Sears et al. 2016). Birds, on account

of their small size, endothermic thermoregulation and predominantly diurnal habits, have emerged as a particularly vulnerable taxon. The recently documented collapse of avian communities in North America's Mojave Desert over the last century (Ikanyan and Beissinger 2018; Riddell et al. 2019) is emblematic of the effects of global heating on arid-zone avifauna, and several authors have predicted severe declines in arid-zone bird populations in coming decades because of increased exposure to thermal conditions beyond physiological tolerance limits or sublethal fitness costs of chronic heat exposure (Albright et al. 2017; Conradie et al. 2019; Conradie et al. 2020; Kemp et al. 2020). The threat posed by climate change to desert birds globally is exacerbated by only 20% of projected thermal refugia currently falling in protected areas (Ma et al. 2023).

The *Calendulauda* larks of the southern African arid zone may be highly vulnerable to climate change, particularly in light of the rapid warming that has occurred in this region (Kruger and Sekele 2013; van Wilgen et al. 2016). Three southern African members of this genus, namely the Karoo Lark *Calendulauda albescens*, Red Lark *C. burra* and Dune Lark *C. erythrochlamys*, diverged ~4 MYA and currently show a high degree of specialisation to habitats and climatic conditions prevailing in the region (Alström et al. 2013). Two of these species, the Red Lark and Dune Lark, occupy restricted ranges with limited overlap with congeners (Dean and Ryan 2005). The limited distribution of the Red Lark makes it a flagship species for understanding threats faced by range-restricted arid-zone species. Confined almost entirely to South Africa's Northern Cape Province and Red Listed as Vulnerable (Peacock 2015; IUCN 2020), the species is thought to have an area of occupancy of ~6 000 km², is restricted to red sands, and is highly sensitive to environmental disturbances such as structural vegetation changes (Peacock 2015). Dean et al. (1991) observed that Red Larks were absent within dune habitats where vegetation cover was reduced by overgrazing. In addition to sensitivity to habitat transformation, the species experiences fitness costs associated with sustained periods of hot weather, with Kemp et al. (2020) finding that male Red Larks experience a net 24-h loss of body mass on days when maximum T_{air} exceeds 33.5 °C.

The Black Mountain Mine Conservation Area (BMMCA), a protected area in the Koa River valley dune system, has long been recognised as a stronghold for the Red Lark (Dean et al. 1991). Previous authors estimated the BMMCA supported ~700 individuals, representing ~7.5% of the species' total population of ~9 400 individuals (Dean et al. 1991). In consideration of this species' sensitivity to habitat alteration, the growing threat posed by climate change and the importance of this site for the species, we quantified the recent (2017–2019) Red Lark population at BMMCA to provide an updated and robust baseline estimate against which future population changes can be detected. To do so, we combined telemetric tracking, a suitable method for quantifying and visualising a species' landscape use and home range or core range (Bastian et al. 2020), with habitat suitability modelling, an increasingly popular approach for assessing the impact of climate change and/or land transformation (Austin and Knott 1996; Peterson 2003; Thuiller 2003).

Materials and methods

Study site and species

We monitored and surveyed Red Lark populations in the Koa River valley dune system within the 9 024 ha BMMCA (29°18' S, 18°49' E; ~800 m a.s.l.), south of the town of Aggeney in the Northern Cape Province, South Africa, from October 2017 to January 2019. The Koa River valley dune system is sparsely vegetated with shrubs such as *Rhigozum trichotomum*, *Hermannia affinis*, *Lycium eonii* and *Calabota spinescens* and with perennial tussock grasses such as *Stipagrostis amabilis*, *S. ciliata*, *S. brevifolia*, *S. anomala* and *S. namaquensis* in drainage lines. Vegetation growth is mostly restricted to the red sand substrate, forming relatively small dunes (~14 m height) separated by gravel plains (Figure 1). The Red Lark is a monogamous, territorial, solitary nester that uses *S. amabilis* tufts to create south-facing cup nests. Breeding mainly occurs between August and May, but is highly erratic and rainfall-dependent (Dean and Ryan 2005). We checked for breeding activity from one week prior to the start of study to the end, and found no evidence that individuals in our study population were breeding.

For the telemetry component of the study, ten Red Larks (five males, five females) were captured using spring traps baited with a superworm *Zophobas morio* during early mornings (05:00–08:00). The person who removed the bird from the trap was covered in a large piece of fabric, as the larks were semi-habituated for a concurrent study of foraging and heat-dissipation behaviour, and we wanted to minimise the risk of compromising their habituation. Each individual bird was fitted with a SAFRING metal ring and a colour combination as well as with a VHF transmitter weighing <1.0 g (Model BD-2 [frequency range: 138–235 MHz; pulse rate: 40 pulses per minute]; Holohil Systems, Carp ON, Canada) attached to the dorsal skin immediately above the synsacrum using Osto-Bond latex adhesive (Osto-Bond, Montreal, Canada), after which the bird was released at the site of capture. The body mass (M_b , mean \pm SD) of males and females was 41.6 \pm 3.1 g ($n = 5$) and 33.4 \pm 2.8 g ($n = 5$), respectively, determined using an electronic scale (Scout Pro SPU602 [Ohaus Corporation, Pine Brook, New Jersey] or EJ-610 [A&D Company, Toshima-Ku, Tokyo Japan]). Movement data were collected from 21 October to 15 December 2017. Transmitters typically remained on birds for 1–2 weeks before falling off, after which they were recovered and attached to a new individual.

Telemetric tracking protocol

Location data were obtained by one of four observers during three sampling periods: morning (sunrise–10:00), midday (11:00–15:00) and afternoon (16:00–sunset). Observers were randomly assigned to individual birds during each sampling period. During the midday period, birds were primarily monitored at $T_{\text{air}} < 30$ °C on account of their greatly reduced activity levels at $T_{\text{air}} > 30$ °C (Kemp et al. 2020). During the midday period, when birds retreated to a shaded microsite to escape intense solar radiation and remained stationary for >20 min, observations were abandoned. Using a handheld receiver (Comm-Spec R1000 Telemetry Receiver) and a 3-element Yagi antenna, the location of a

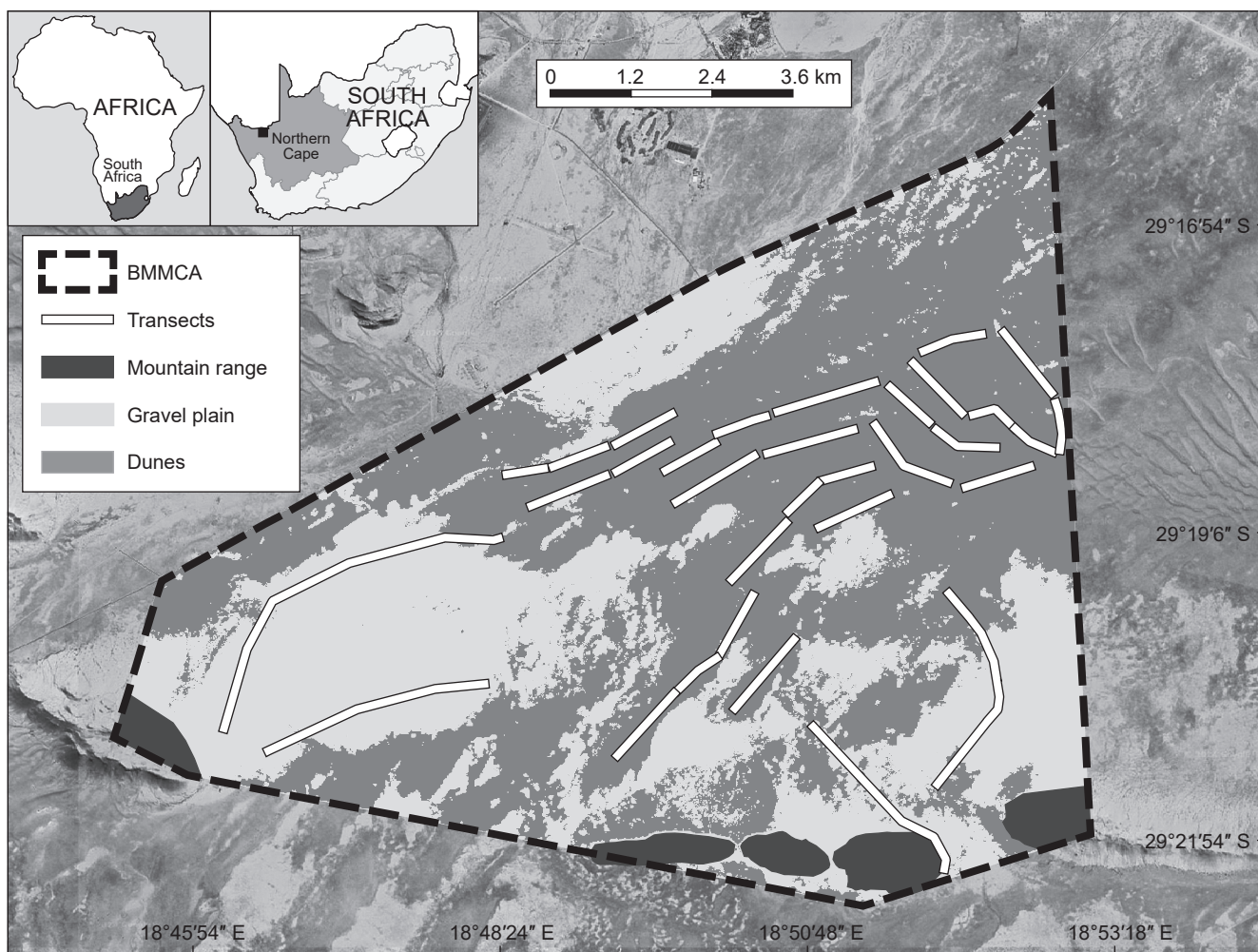


Figure 1: Habitat types at Black Mountain Mine Conservation Area (BMMCA), South Africa (black outline); the area (~9 023 ha) is comprised of dunes, gravel plains and mountains. Dashed lines show the 32 transect lines used to survey Red Larks *Calendulauda burra*. (Satellite imagery courtesy of the European Space Agency – Sentinel-2)

focal bird was established and recorded every 10 min. We used laser range finders (Nikon LRS-500) to determine the distance of a bird from the observer, allowing for exact locations to be recorded. Each bird was tracked during only one of the three sampling periods (i.e. morning, midday or afternoon) per day, increasing the likelihood of observing a bird across its entire home range. Location data were obtained for at least three days per week per individual (~60 locations per bird). The transmitters' short battery life (3–4 weeks) and tendency to fall off limited us to a short data-collection period per individual (typically 1–2 weeks).

Habitat and density surveys

To census birds for the population estimate, Red Larks were surveyed along 32 line transects (Figure 1) in the BMMCA, during January 2018, April 2018 and January 2019. Transects were positioned to include all major landscape features at the BMMCA (Figure 1): dune troughs, dune slopes, rocky slopes/outcrops and gravel flats. Vegetation was categorised as bare ground, dwarf shrub, tall shrub, grass or ephemeral herbaceous vegetation. Transects

were walked in a single direction at a constant pace, with the sparse, low vegetation reducing the likelihood of double contacts biasing the data. Transect data included behaviour (foraging, resting, perching, displaying or vocalising), location (latitude/longitude), number of individuals observed, distance from observer, bearing from observer, and habitat feature occupied by the bird. Transects averaged 980 m in length (range = 500–3 000 m) and were separated by ~500 m. Transect lengths were limited to the specific landscape elements (e.g. dune top, dune troughs or gravel plains) within which they were located. The southwestern section of the BMMCA consists primarily of sandy/gravel plains, which allowed for longer transects of ~3 km.

Data analysis

Home range and core area estimates

The *rhr* package (reproducible home ranges: Signer and Balkenhol 2015) was used to calculate an asymptote for sampling density (range size as a function of the number of location data). We then modelled the home range (95%)

and core area (50%) using the fixed kernel density estimate (KDE; Worton 1989) with a reference bandwidth (*href*: Worton 1989). Previous approaches for estimating home range and core area used various methods and lacked standardisation (Macdonald et al. 1980; Worton 1987; Powell 2000; Boyle et al. 2009). Various home range metrics are used, such as the grid-cell method (Haugen 1942) or the low convex hull (Getz et al. 2007). However, the most frequently used metrics include the minimum convex polygon (MCP) (Mohr 1947; Hayne 1949; Odum and Kuenzler 1955; Jennrich and Turner 1969) and KDE (Worton 1989). Minimum convex polygon metrics assume animals use the entire area within their home range equally (Mohr 1947; Hayne 1949; Odum and Kuenzler 1955; Jennrich and Turner 1969). Conversely, KDE metrics (Powell 2000; Börger et al. 2006) involve complex, nonparametric analysis of home range data (Worton 1989) and are often regarded as the more accurate method. We, therefore, opted to use the KDE rather than the MCP metrics, along with density models to estimate the upper and lower population estimates during the population analysis, but calculated the MCP to facilitate interspecific comparisons.

The home range analysis was extrapolated over the entire study site using the capture locations of 78 Red Larks from previous behavioural and physiological studies (i.e. Kemp and McKechnie 2019; Kemp et al. 2020). We assumed each capture location was within proximity to the core area of that particular individual. Because we had KDE home range estimates for only 10 individuals with little overlap, we made the simplifying assumption that home ranges are approximately circular, and overlaid a standardised circular area of 9.6 ± 6.0 ha at each of the capture locations, using the buffer geoprocessing tool in ArcGIS (ESRI 2015) (Supplementary Figure S1). These 78 home ranges provided a means to calculate the degree of home range overlap and the average nearest neighbour estimate to the core point (e.g. capture location). The ‘average nearest neighbour’ function (a geostatistical tool used to calculate the average distances between the bird of interest and its nearest neighbour, repeating it for the entire dataset) in ArcGIS (ESRI 2015) was used to calculate the average distance between Red Lark core points within the home ranges. The ‘intersect geoprocessing’ function was used to determine the percentage of overlap observed across all 78 home ranges. We then calculated the area (ha) of each core range that does not overlap with those of neighbouring males (hereafter, the ‘no overlap area’). To obtain the density estimate of Red Larks in the BMMCA, we calculated the ratio between the total suitable area with the no overlap area and the KDE core range.

Habitat and density modelling

To assess the suitability of habitats in the study area, we used the Biomod2 ensemble modelling platform (Thuiller et al. 2016) implemented in the R programming environment (R Development Core Team). The *biomod2* package uses a predictive modelling framework to model interactions between response and predictor variables. As an ensemble modelling platform, it allows the use of more than one classification algorithm (Thuiller et al. 2016). Transect data were summarised in a binary matrix as presence (1)

or absence (0), and were used as the response dataset in the modelling framework. European Space Agency (ESA) Sentinel-2 satellite data products were used to generate classification variables for the ensemble model. Classification variables included individual spectral bands, as well as normalised difference indices (NDIs). The NDIs used included the Carotenoid Reflectance Index (CRI), Plant Senescence Reflectance Index (PSRI), Normalised Difference Infrared Index (NDII), and Soil Adjusted Vegetation Index (SAVI). Variable importance was assessed using Jackknife training and test gain to assess which variables contributed the most to predict performance. Model performance and predictive efficiency were assessed using the receiver operating characteristic (ROC) and associated area under the curve (AUC) calculated using the package *PresenceAbsence* (Freeman and Moisen 2008).

Response curves and statistics were assessed to evaluate the noted interactions between response and predictor variables, both within individual model runs, as well as across all model runs ($n = 20$). ROC plots with the associated AUC were generated and compared, along with graphs of error measures (Freeman and Moisen 2008). Training and test model omission rates were also evaluated to infer predictive performance. The best-derived model based on test statistics was then applied to a rasterized area of interest (i.e. the BMMCA) consisting of the same predictor variables used in the model train/test to yield a probabilistic layer representing predicted habitat suitability. This raster layer with predicted probabilities of habitat suitability ranged between 0 and 1. Threshold error plots and associated statistics were generated using the R package *PresenceAbsence* to assess threshold selection. The most appropriate threshold identified was applied to the raster to convert it from a continuous probability-based raster to a binary output representing suitable (1) and unsuitable (0) habitats. Under the Spatial Analyst Tools in ArcGIS (ESRI 2015), we used the ‘extract values to points’ function to obtain the habitat suitability for each location datum used to construct the KDE home ranges for each individual.

To obtain abundance and density estimates from line-transect data collected across the BMMCA, we used a distance sampling framework in the package *Distance* (Miller 2019). Several detection function models were fitted to line-transect data and included: half normal and hazard-rate key detection functions; cosine and polynomial adjustment terms; and, models with and without truncation (Miller et al. 2019). Model goodness of fit was then assessed using the Cramer von Mises test, together with a quantile–quantile plot displaying any deviations from good fit (Buckland 2006; Miller 2019). The shape of the fitted detection function was also assessed and considered when assessing the model fit (Miller et al. 2019). Lastly, models were compared using the Akaike information criterion (AIC) and p -values as derived from the model comparison table generated by the *Distance* package.

Population estimates

We used two approaches to estimate the BMMCA Red Lark population size: (i) integrated telemetric measures of home range size across suitable habitats, and (ii) habitat suitability modelling (i.e. remote sensing data)

Table 1: Kernel density estimator (KDE) and minimum convex polygon (MCP) home ranges and core ranges for male and female Red Larks *Calendulauda burra* at Black Mountain Mine Conservation Area, Northern Cape province, South Africa. For each variable, a Welch two-sample *t*-test was conducted to evaluate differences between sexes

	Home range (ha)		Core area (ha)	
	KDE	MCP	KDE	MCP
Male mean \pm SD	42.4 \pm 28.3	27.7 \pm 17.6	9.6 \pm 6.0	6.7 \pm 4.3
Male range	25.4–91.6	12.9–57.3	4.2–19.5	2.2–12.9
Female mean \pm SD	41.9 \pm 31.3	31.2 \pm 16.9	9.5 \pm 7.8	9.7 \pm 7.6
Female range	18.6–87.9	17.8–56.4	4.4–22.7	3.4–22.8
<i>t</i>	-0.046	-0.005	0.322	0.790
df	7.792	7.530	7.987	6.366
<i>p</i> -value	0.964	0.997	0.756	0.458

in conjunction with habitat-specific density estimates from transect counts. We also extrapolated our results for the BMMCA to provide an estimate of the entire Red Lark population using the estimate of suitable habitat ratio from Dean et al (1991) (whereby the BMMCA comprises 5% of suitable habitat for Red Larks) and the estimated proportion of the entire population (i.e. ~7.5% of the Red Lark population occurs with the boundaries of the BMMCA).

Results

Home range

Sampling saturation for male and female Red Larks was reached after 83 ± 19 and 79 ± 18 sample points, respectively (Supplementary Table S1). For males, the home range (95% KDE) was 42.4 ± 28.3 ha and the core area (50% KDE) was 9.6 ± 6.0 ha, with neither significantly different (Table 1; Figure 2) from those of females (Table 1). Estimates based on MCPs similarly did not differ between sexes. The average nearest-neighbour distance between core points with home ranges, based on the 78 individuals involved in previous studies, was 341 m (NNRatio: 0.94, NNZScore: -1.05; $p = 0.30$), with a total overlapping area of 62.9% for the KDE home range and a no-overlap area of 15.7 ha, approximately double the KDE core home range.

Our dataset included the movements of both individuals of a single pair (Figure 3). For this male and female, the KDE home ranges for the male and female were 27.8 ha and 19.3 ha, respectively, whereas MCP home ranges were 22.1 ha and 18.9 ha, respectively. The male's KDE core area was 8.3 ha, and the female's 5.1 ha; the MCP core areas were 6.4 ha and 6.9 ha, respectively (Figure 3).

Habitat suitability

Habitat suitability models produced a final training and test (AUC = 0.95) and an independent validation (AUC = 0.99). When converting the model to binary output, the MaxKappa threshold produced the highest accuracy measure from error plots and the lowest omission rates of occupied sites. Jackknife training and test gain suggested variables contributing the most to predictive performance were the Carotenoid Reflectance Index (CRI) (1.67 and 1.67), Normalised Difference Infrared Index (NDII; 0.95 and 1.1), and Plant Senescence Reflectance Index (PSR) (0.90 and 0.93), followed by Soil-adjusted Vegetation Index

(SAVI) (0.24 and 0.37) (Supplementary Figure S2). Habitat suitability was positively influenced by the increased cover of senescent vegetation, with greater concentrations of carotenoid pigments relative to chlorophyll (i.e. increased CRI and Photochemical Reflectance Index [PRI]). Furthermore, suitability decreased with increased NDII and SAVI. The habitat-suitability model produced an output score of 0 for unsuitable and 1 for suitable. Only 33.2% (~3 003 ha) of the BMMCA was considered suitable habitat for Red Lark occupancy (Figure 4).

Population estimate

Presence/absence assessments (Figure 4) suggested areas identified as suitable habitat, with 1 139 ha supporting densities of 0.084 Red Larks ha⁻¹ and 1 864 ha supporting 0.087 Red Larks ha⁻¹ (Figure 4), whereas 6 021 ha of 9 024 ha (i.e. 67% of the BMMCA area) support only 0.001 Red Larks ha⁻¹; the habitats largely comprise gravel plains, rocky outcrops and completely unvegetated dunes. Habitat suitability and associated density estimates suggest the BMMCA currently supports ~263 mature Red Larks. From the habitat suitability and home range assessments (assuming male and female presence in each territory), we estimated the ~3 003 ha of suitable habitat at the BMMCA could potentially support ~382 mature Red Lark individuals at a density of ~0.127 individuals ha⁻¹. Assuming the BMMCA still supports 7.5% of the total population, we estimate that the current Red Lark population across the species' entire range is 3 500–5 093 mature individuals.

Discussion

Our results suggest the recent (2017–2019) Red Lark population at the BMMCA consists of 262–382 individuals, compared to the 700 individuals estimated for this site in the late 1980s by Dean et al. (1991). There were several methodological differences between our study and that of Dean et al. (1991). For instance, Dean et al. (1991) primarily surveyed areas in which the larks were known to occur, with these authors' estimated density of 0.147 individuals ha⁻¹ based on a single transect covering 34 ha within the BMMCA. The present study involved density estimates based on 32 transects covering ~600 ha and we integrated empirical estimates of home range size and habitat-suitability modelling based on remote sensing data.

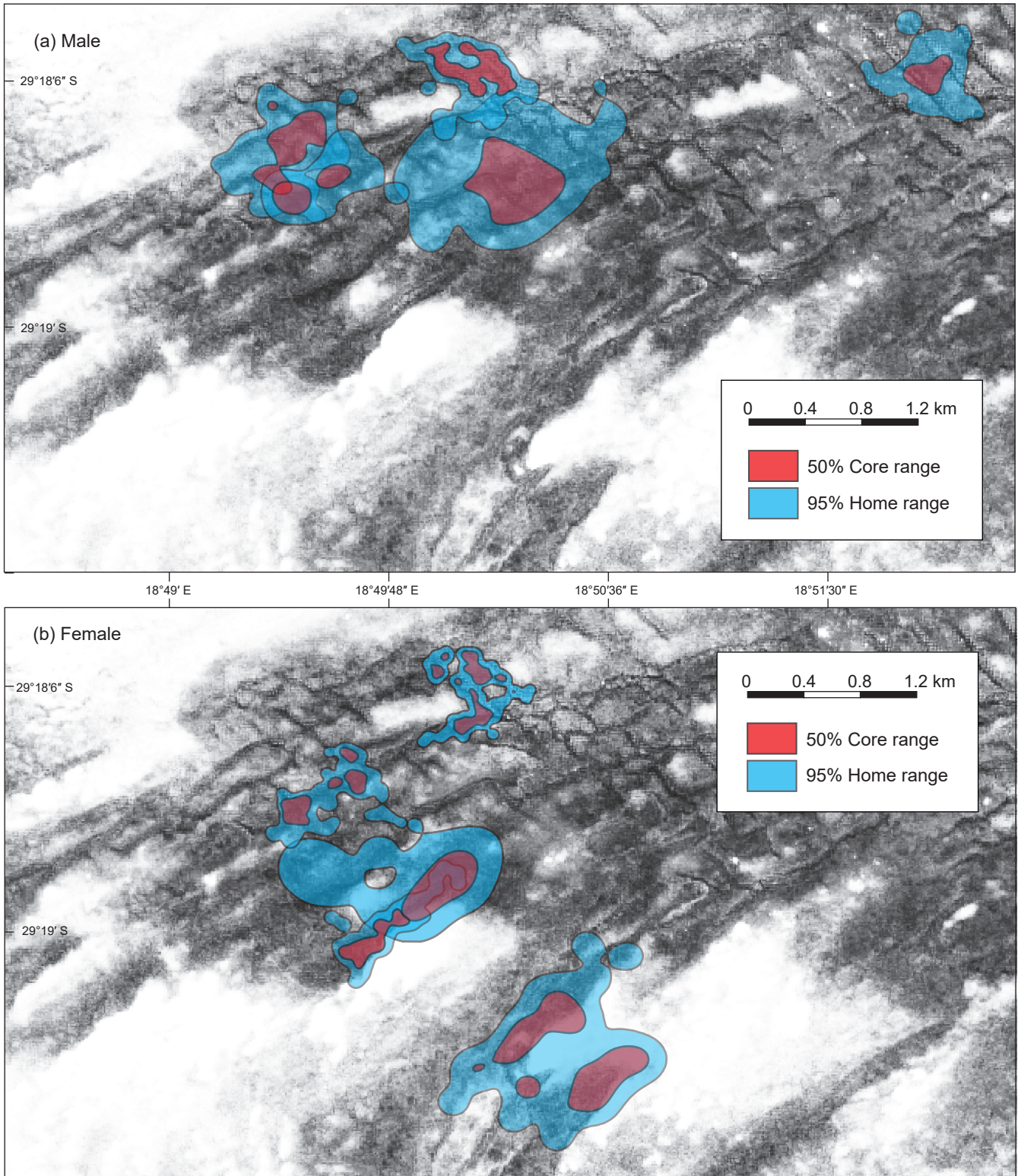


Figure 2: Kernel density estimated home ranges and core areas for 5 male and 5 female Red Larks *Calendulauda burra* at Black Mountain Mine Conservation Area, South Africa, superimposed on the habitat suitability model. (Satellite imagery courtesy of the European Space Agency – Sentinel-2)

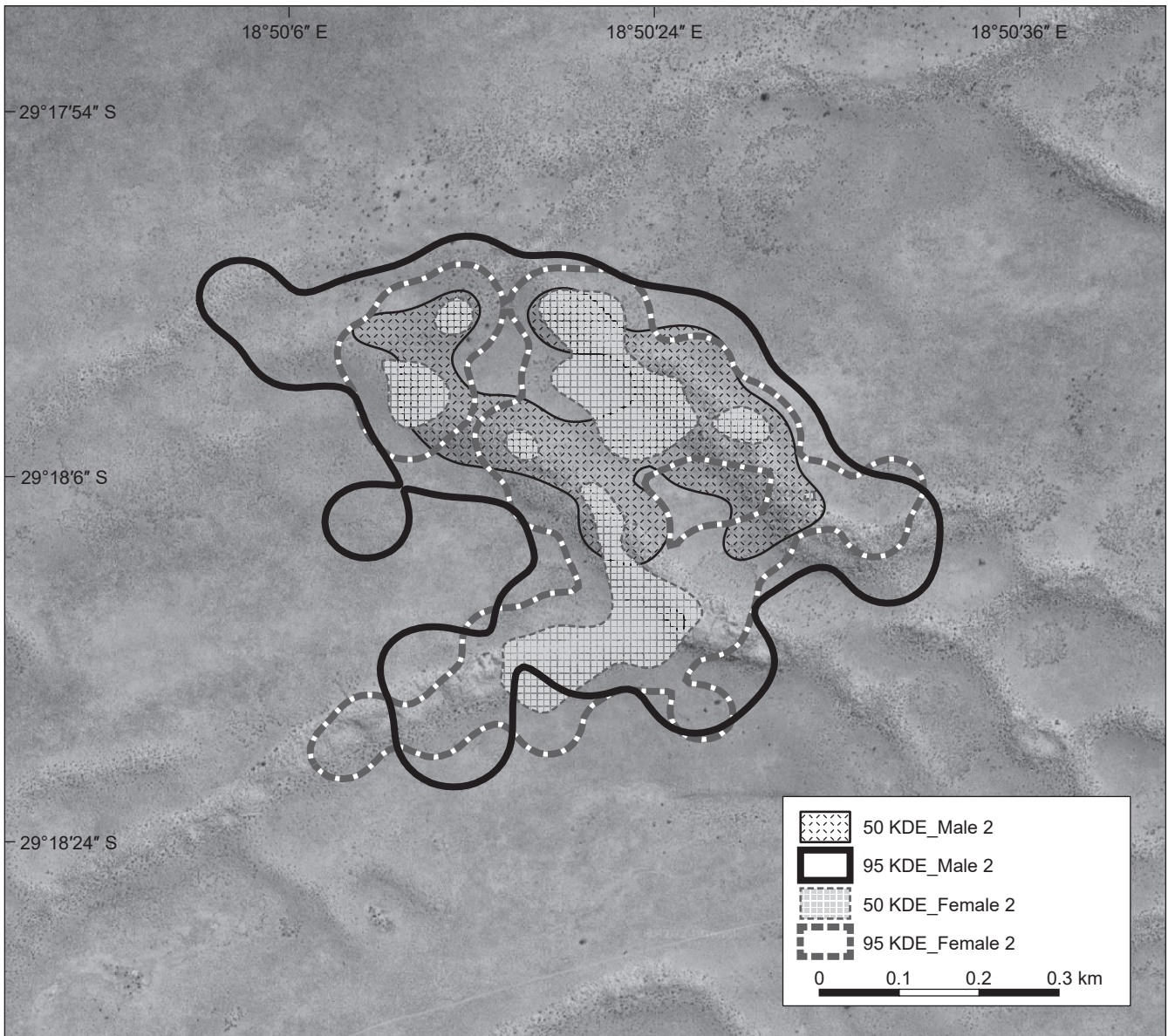


Figure 3: Home ranges (95% kernel density estimate [KDE]) and core ranges (50% KDE) for one male and one female Red Lark *Calendulada burra* at Black Mountain Mine Conservation Area, South Africa. (Satellite imagery courtesy of the European Space Agency – Sentinel-2)

However, we doubt that methodological differences alone account for our much lower population estimate. Climate differences during the periods preceding the two studies might have also played a role. Most of the surveys by Dean et al. (1991) at Aggeneys (including the BMMCA) took place following or during *La Niña* conditions during the second half of 1988 and the first half of 1989, whereas more neutral Southern Oscillation Index conditions prevailed during the period 2017–2019 when the present study took place (<https://www.ncei.noaa.gov/access/monitoring/enso/soi>). Red Larks breed opportunistically between August and May following rain (Tarboton 2001), and the higher densities encountered by Dean et al. (1991) may reflect generally wetter conditions.

Our lower population estimate compared with three decades earlier may also reflect climate change during this period (IPCC 2021), both in terms of direct effects on Red Larks and indirect effects on habitat suitability. For example, our habitat-suitability analysis indicated that only one-third (~30 km²) of the BMMCA is currently suitable for Red Lark occupation, less than half the ~70 km² of suitable habitat estimated three decades ago by Dean et al. (1991). In terms of direct impacts of increasing air temperatures, data from the South African Weather Service weather station at Pofadder (29°07'33.6" S, 19°23'45.6" E), ~55 km east of BMMCA, reveal the average frequency of days per year with a maximum T_{air} of >35°C have increased by ~43%, from ~35 d yr⁻¹ in the late 1980s to ~50 d yr⁻¹ in

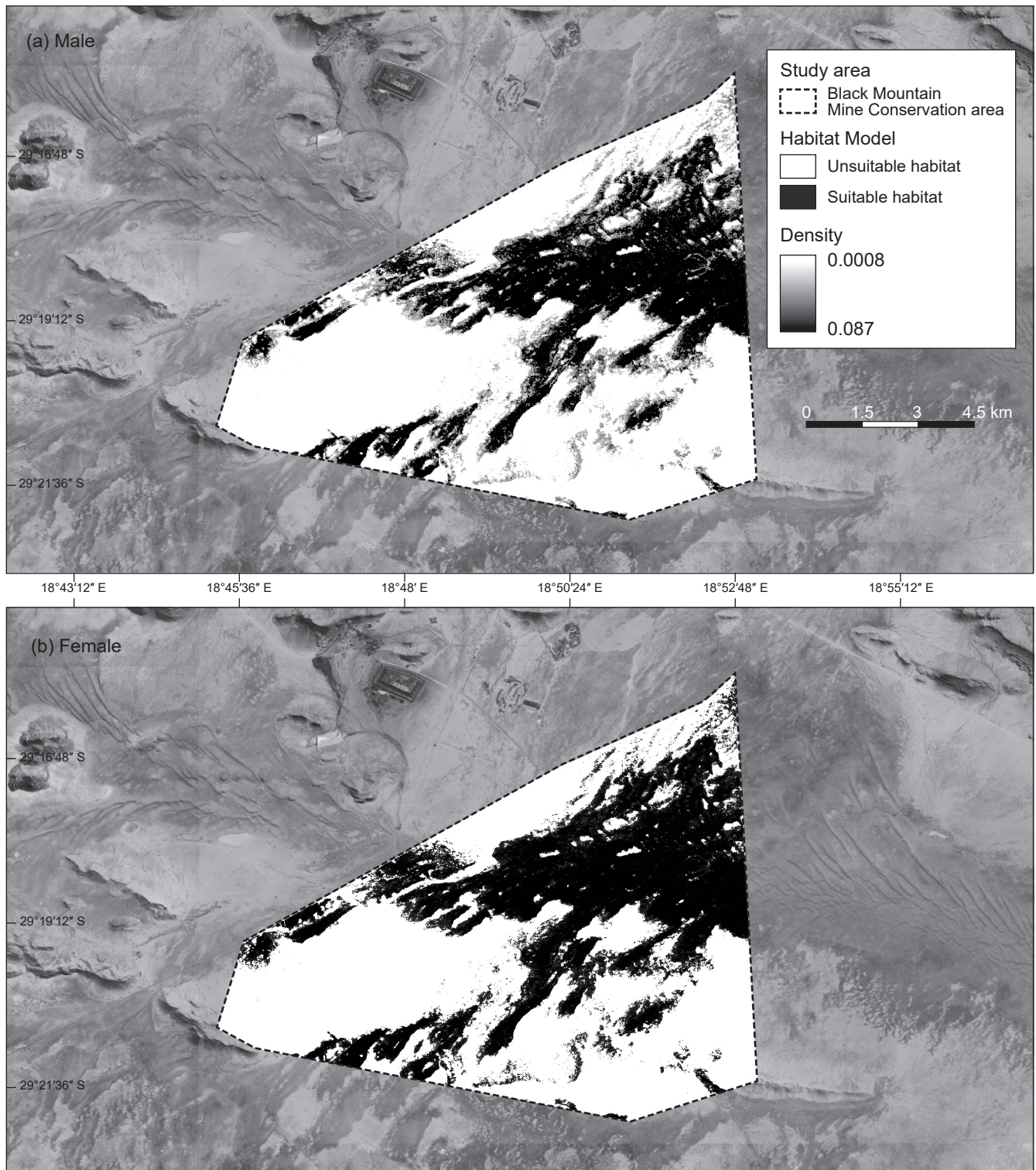


Figure 4: Density and habitat suitability models for Red Larks *Calendulauda burra* at Black Mountain Mine Conservation Area, South Africa. The density model ranges from 0.0008 (white) to 0.087 (black) individuals ha^{-1} . The habitat suitability model represented unsuitable (white) and suitable (black) habitat. (Satellite imagery courtesy of the European Space Agency – Sentinel-2)

recent years (Figure 5). Taken together with the net loss of body mass experienced by male Red Larks on days with maximum $T_{\text{air}} > 33.5 \text{ }^{\circ}\text{C}$ (Kemp et al. 2020), the warming

trend for this region may well have resulted in declines on account of the fitness costs associated with chronic exposure to hotter recent conditions. Warming anticipated

for the end of the century is likely to result in substantial declines, with much of the Red Lark's current range becoming too hot for its persistence (Kemp et al. 2020), a scenario similar to that predicted for other arid-zone species (Conradie et al. 2019).

Lee and Wright (2024) recently estimated a total range-wide population size of 32 000–72 000 Red Larks, calculated using an extent of occupancy (EOO) of ~33 000 km² estimated from field surveys. Dean et al. (1991); however, estimated EOO for Red Larks as ~112 500 km², but noted that just 5 625 km² were suitable habitat, similar to the 6 000 km² estimated by Peacock (2015). However, once land use was taken into account, just 1 406 km² of suitable Red Lark habitat was estimated to exist by Dean et al. (1991). If Lee and Wright's (2024) estimate of suitable habitat is accurate, the ~30 km² at the BMMCA represents <0.1% of the total for the species, instead of the 5% estimated by Dean et al. (1991).

Our study provides new insights into the home ranges of Red Larks, revealing that non-breeding individuals spend most of their time in a relatively small core area (~9.6 ha) embedded within a much larger home range (~42.0 ha), overlapping to some extent with neighbouring individuals. Unfortunately, we did not have sufficient range data between paired individuals to perform detailed analysis and comparison between a pair. However, if an individual was tracked, the other individual of the assumed pair was always near the tracked individual (R Kemp and MT Freeman, pers. obs.). Our assumption that both members of a pair have similar core areas and home ranges is supported by the one pair for which we did obtain detailed movement data (Figure 3). This pattern is similar to those documented in other taxa, including species representing Strigiformes (Olsen et al. 2011) and Piciformes (Wiktander et al. 2001). The home ranges of Red Larks (KDE analysis: 41.9 ± 28.1 ha; MCP analysis: 29.4 ± 16.4 ha) are the largest yet reported for a member of the Alaudidae, potentially reflecting the mesic habitats occupied by species for which home estimates exist, namely the Horned Lark *Eremophila alpestris strigata* (2.1 ± 0.9 ha: Slater and Treadwell 2016), Dupont's Lark *Chersophilus duponti* (8.1 ha: Garza et al. 2005) and Red-capped Lark *Calandrella cinerea* (19.9 ± 17.1 ha: Mwangi et al. 2020). These studies have emphasised the role of factors such as breeding intensity (Mwangi et al. 2020), resource availability (Schoener 1968), and, importantly, vegetative structure and suitability (Wells et al. 2008) on spatial distribution, landscape use, and home range dynamics.

Assessing factors shaping home ranges was peripheral to our main goal of quantifying overall home range size and shape, but our habitat-suitability analysis nevertheless offers some insight in this regard. We found strong correlations between higher values of the CRI, PSRI and habitat suitability, suggesting that Red Larks favour areas with more senescent vegetation cover, with more carotenoid pigments relative to chlorophyll. The larks' association with senescent vegetation may, in part, arise from the availability of shaded microsites to which they retreat during the heat of the day. The distribution of this vegetation profile was largely confined to dune habitat features (i.e. dune crests, slopes, and marginally within

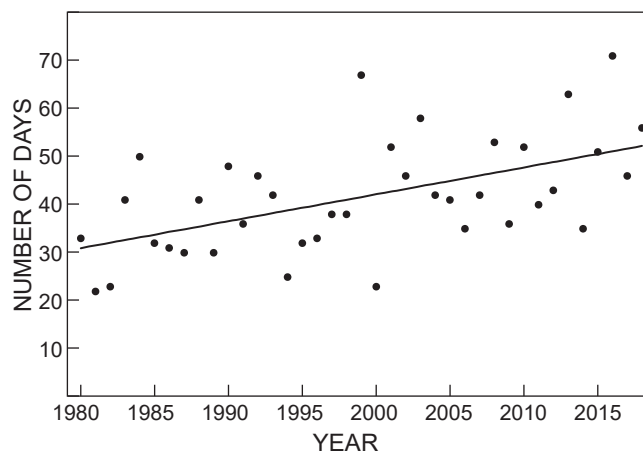


Figure 5: Number of days per year when the daily maximum air temperature (T_{air}) exceeded 35 °C, from 1980 to December 2018 (data from the weather station at Pofadder, South Africa, ~55 km from the Red Lark *Calendulauda burra* study site), fitted with a linear regression, showing an increase from ~35 d yr⁻¹ in the late 1980s to ~50 d yr⁻¹ in recent years

troughs). The absence of typical vegetation characteristics had consequences for Red Lark occupancy. Specifically, population stability and persistence may decrease in the future if characteristic vegetation complexes on dune structures are lost, degraded, reduced in extent or become more isolated within a matrix of unsuitable or lower-quality habitats (Driscoll et al. 2013; Mendenhall et al. 2014; Fahrig 2017; Freeman et al. 2018). Vegetation is vital in providing suitable microrefugia in arid and semi-arid regions (Facelli and Temby 2002), wherein birds may avoid extreme environmental temperatures during hot weather. Vegetation cover on dunes may influence resource availability via shifts in seed availability and arthropod distribution and/or density (Siemann et al. 1998; Asteraki et al. 2004). The arrangement and extent of available suitable habitat in fragmented landscapes directly affect occupancy and persistence (Ricketts 2001; Haddad et al. 2015). Our density and habitat-suitability assessment models support the notion that increases in Red Lark densities were largely driven by the presence/absence of dune vegetation, with birds almost always absent from adjacent gravel plains, rocky mountain slopes and unvegetated dunes.

In addition to direct thermoregulatory costs, increases in environmental temperatures have negative consequences on vegetation persistence through reductions in specialised and/or an overabundance of a subset of species (Svenning and Sandel 2013). For many bird species, including Red Larks, vegetation structure plays an important role in occupancy and provides thermally buffered refugia, nesting sites, and resources, and is therefore essential for ecological stability (Cunningham et al. 2015; Lembrechts et al. 2019; Yang et al. 2019; Zellweger et al. 2019; Zhu et al. 2019; Kemp et al. 2020). The persistence of many desert species may hinge on the maintenance of vegetation within their distribution, without which they would likely succumb to environmental temperatures beyond their thermoregulatory capabilities (Cunningham et al. 2013). For example, Kemp

et al. (2020) showed the importance of shaded microsites within a homogeneous arid-zone thermal landscape where Red Larks spent 50% of their time seeking shade under shrubs when the air temperatures were ≥ 25.4 °C, escaping direct solar radiation and avoiding conditions that may result in lethal dehydration and/or hyperthermia (Albright et al. 2017). Combined with climate change (Engelbrecht et al. 2015; IPCC 2021), increased drought prevalence and overgrazing caused by the mismanagement of arid landscapes (Leistner 1967) could therefore have severe consequences for desert species. Such changes to habitat structure would inevitably decrease the distributions of habitat-specialist species, such that they become smaller and more isolated, thereby increasing the risk of local extirpation and even potential extinction of range-restricted arid-zone species to future disturbances (e.g. heat waves; McKechnie and Wolf 2010; McKechnie et al. 2021). Such concerns are particularly relevant for species such as the Red Lark and possibly other range-restricted Afrotropical larks, including Liben's Lark *Heteromirafra archeri*, Rudd's Lark *H. ruddi*, Botha's Lark *Spizocorys fringillaris* and the Dune Lark.

In conclusion, the Red Lark population of the BMMCA, thought to represent a conservation stronghold of the species, is ~50% of that estimated three decades ago. Whereas the causes of this difference remain unclear, we strongly suspect that the 43% increase in the frequency of days hotter than 35 °C since the survey of Dean et al. (1991) has been a contributing factor. The habitat sensitivity of the Red Lark and its vulnerability to warming highlights the need for active management of landscapes, both in terms of preserving suitable vegetation and developing ways to ensure access to thermally buffered microsites. The provision of artificial shade can influence avian behaviours like drinking in arid landscapes (Abdu et al. 2018; Morar 2022) and breeding success (Corregidor-Castro et al. 2023). Providing high-quality shade in dune areas with high densities of Red Larks may give individuals access to cooler microsites than they encounter in typical midday resting locations in the dappled shade of vegetation.

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