

Rediscovery of a long-lost lark reveals the conspecificity of endangered *Heteromiraфра* populations in the Horn of Africa

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Abstract The African lark genus *Heteromiraфра* is thought to consist of three threatened species inhabiting mid-altitude grasslands, one in South Africa and two in the Horn of Africa. One of the latter, Archer's Lark *H. archeri* of Somaliland, has not been seen with certainty since 1922. We surveyed its type locality as well as a nearby area of grassland east of Jijiga in adjacent north-eastern Ethiopia, where sightings of *Heteromiraфра* larks have recently been made. First, we used a combination of morphological and molecular evidence to show that these recent sightings refer to the same taxon as Archer's Lark. Second, we used a combination of morphological, molecular and vocal evidence to show that these populations are conspecific

with the Liben (Sidamo) Lark *H. sidamoensis* of southern Ethiopia, but that the Horn of Africa populations are highly distinct from Rudd's Lark *H. ruddi* of South Africa. Third, we suggest that the extent and quality of their habitat in north-eastern Ethiopia is small and poor, and that the type locality of Archer's Lark in Somaliland has been completely transformed. Taken together, these results imply that there is a single species of *Heteromiraфра* in the Horn of Africa (for which the scientific name *H. archeri* has priority, and which we suggest retains the English name Liben Lark), consisting of two tiny populations separated by 590 km of apparently unsuitable habitats. Environmental niche models suggest that there are no environmentally similar locations elsewhere within the region. Despite the discovery of a second population, the Liben Lark remains a highly threatened species in urgent need of conservation intervention to avert the extinction of both of its populations.

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Zusammenfassung

Die Wiederentdeckung einer lange verschollenen Lerchenart belegt die Konspezifität der gefährdeten *Heteromiraфра*-Populationen am Horn von Afrika

Die afrikanische Lerchengattung *Heteromiraфра* besteht Annahmen zufolge aus drei bedrohten Arten, die Grasland in mittleren Höhenstufen besiedeln—eine davon in Südafrika, die zwei anderen am Horn von Afrika. Eine der beiden letzteren, die Somalispornlerche *H. archeri*, konnte in Somaliland seit 1922 nicht mehr mit Sicherheit nachgewiesen werden. Wir untersuchten sowohl die Typuslokalität als auch ein benachbartes Graslandgebiet östlich von Jijiga im angrenzenden Nordost-Äthiopien, wo kürzlich *Heteromiraфра*-Lerchen gesichtet wurden. Erstens konnten wir durch eine Kombination aus morphologischen und molekularen Anhaltspunkten zeigen, dass es sich bei diesen neuerlichen Beobachtungen um dasselbe Taxon wie die Somalispornlerche handelt. Zweitens gelang es, mittels einer Kombination aus morphologischen, molekularen und bioakustischen Hinweisen zu belegen, dass diese Populationen konspezifisch mit der Sidamospornlerche *H. sidamoensis* des südlichen Äthopiens sind, sich die Populationen am Horn von Afrika aber deutlich von der Transvaalspornlerche *H. ruddi* in Südafrika unterscheiden. Drittens vermuten wir, dass der Lebensraum in Nordost-Äthiopien von kleinem Ausmaß und schlechter Qualität ist und dass sich die Typuslokalität in Somaliland seither vollständig verändert hat. In der Summe legen diese Ergebnisse nahe, dass es am Horn von Afrika nur eine einzige *Heteromiraфра*-Art gibt (für die der wissenschaftliche Name *H. archeri* Priorität besitzt und für die wir den englischen Namen Liben Lark (deutsch: Libenlerche) vorschlagen), welche aus zwei winzigen, durch 590 km offenbar ungeeignete Habitats getrennte Populationen besteht. Ökologische Nischenmodellierungen legen nahe, dass es in dieser Region nirgends Orte mit vergleichbaren Lebensräumen gibt. Trotz der Entdeckung einer zweiten Population bleibt die Libenlerche eine äußerst bedrohte

Art, die dringend auf Schutzmaßnahmen angewiesen ist, damit es nicht zum Aussterben beider Populationen kommt.

Introduction

The highly distinctive lark genus *Heteromiraфра* has a disjunct distribution in south-western and north-eastern Africa, a pattern shared with several other unrelated bird genera (Cohen 2011) as well as other taxa (Lorenzen et al. 2013). All three currently recognised *Heteromiraфра* species occur in mid-altitude grasslands: Rudd's Lark *H. ruddi* in South Africa, Archer's Lark *H. archeri* in western Somaliland (north-western Somalia), and Liben (formerly Sidamo) Lark *H. sidamoensis* in southern Ethiopia (e.g., Ash and Miskell 1998; Ryan 2004; Collar and Stuart 1985). All three have tiny geographical ranges and are threatened with extinction: Rudd's Lark, known from several small areas of mesic grassland in eastern South Africa, is listed as Vulnerable on the IUCN Red List (BirdLife International 2012b); Archer's Lark, known with certainty only from a small area of arid grassland called the Wajale Plain in Somaliland, close to the Ethiopian border, is listed as Critically Endangered (BirdLife International 2012a); and Liben Lark, confined to the tiny (<35 km²) Liben Plain near Negele-Borana in southern Ethiopia (Fig. 1), is likewise Critically Endangered (BirdLife International 2012c).

Archer's Lark has not reliably been seen since June 1922, when Geoffrey Archer, governor of the then British Somaliland, found seven nests on the Wajale Plain, having earlier secured at least 18 specimens (not 17 as reported) at the site in 1918–1920 (Stephenson Clarke 1920, Archer and Godman 1961). The type locality has since remained largely inaccessible owing to political instability, although 15 visits to the site or to areas adjacent to it, between 1970 and 2008, failed to find any birds and discovered widespread habitat disturbance (BirdLife International 2012a). However, in the last decade three separate sightings of *Heteromiraфра* larks were made ca. 50 km to the south-west of the type locality, east of the town of Jijiga in neighbouring Ethiopia (by H. Shirihai, M. N. Gabremichael, and DH & NT); the most recent bird seen (found in January 2011 by DH & NT) was photographed and confirmed to be a *Heteromiraфра* lark very similar in appearance to Liben Lark. The same area was identified by environmental niche models of the Liben population as being the only other potentially suitable site in the region (Donald et al. 2010). Given the proximity of these sightings to the Wajale Plain, it appeared plausible that this population might be conspecific with Archer's Lark.

In addition to uncertainty about its persistence and geographical range, the taxonomic status of Archer's Lark

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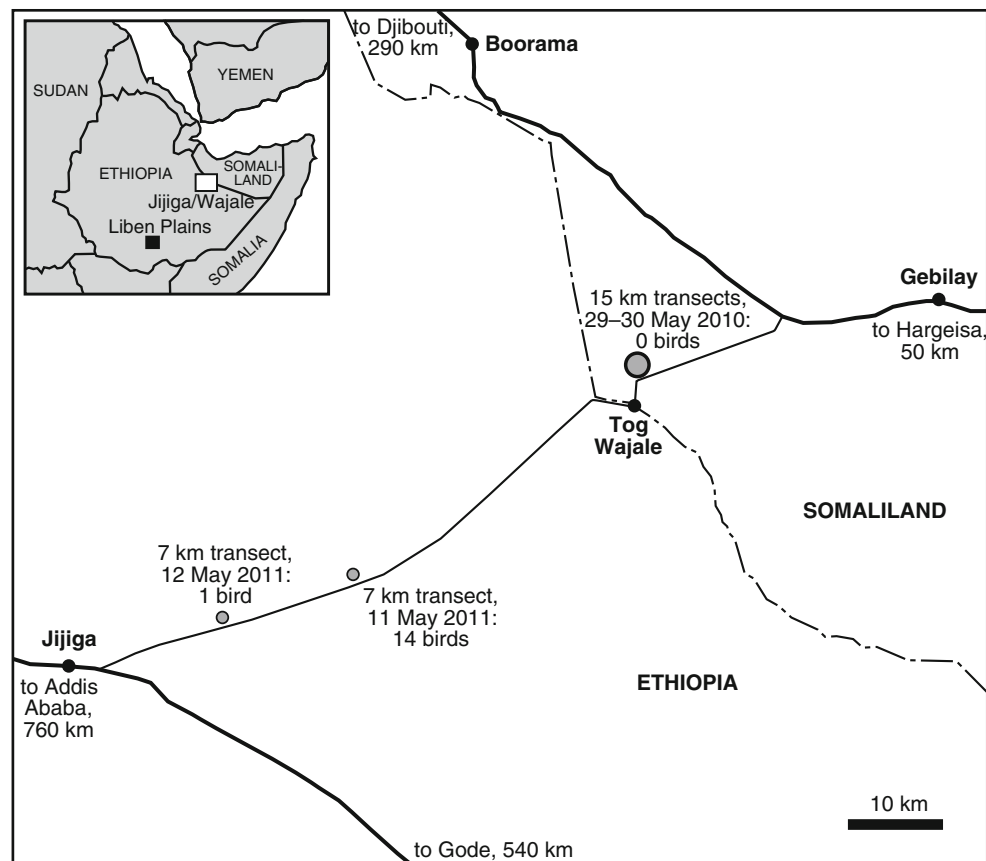


Fig. 1 Current and historical distribution of *Heteromiraфра* larks in north-eastern Ethiopia and Somaliland

has long deserved thorough inquiry, as it is morphologically very similar to both other *Heteromiraфра* species and its song was never recorded or described. In particular, the possibility that it is conspecific with Liben Lark needed to be assessed. The two species both occur (or occurred) in seasonal grassland, separated by 630 km of what is assumed to be unsuitable habitat (largely desert and high mountains). However, climatic conditions in the Horn of Africa were considerably wetter in the early Holocene, with two periods of aridification occurring between 8500 and 3800 years BP, when the present-day dry climate became established (Jung et al. 2004). Thus, it is reasonable to speculate that gene flow may have occurred at this time between present-day Archer's and Liben Lark populations, which may have experienced relatively little differentiation since. Clarifying this point is important in view of the precarious conservation status of both populations, the latter having recently been shown to be in considerable danger of extinction (Spotiswoode et al. 2009; Donald et al. 2010; Collar et al. 2008). Moreover, the discovery in 2011 of a *Heteromiraфра* population in north-eastern Ethiopia gives us the

opportunity to reassess both the taxonomic and conservation status of Liben and Archer's Larks in the light of new data.

In this paper we address three questions. First, does the recently discovered population of *Heteromiraфра* larks at Jijiga belong to the same taxon as Archer's Lark? We address this using analyses of mitochondrial DNA extracted from two live birds we captured at Jijiga, and toe-pad samples from historical specimens of Archer's Lark collected at the type locality. Second, do these two populations belong to the same taxon as Liben Lark? We address this using a combination of fresh and ancient DNA samples, field data and sound recordings, and re-examination of museum specimens. Third, what is the nature and extent of habitat of *Heteromiraфра* in north-eastern Ethiopia and Somaliland, and how does it compare to the Liben Plain? We address this with the results of brief transect surveys conducted at Jijiga in Ethiopia and the Wajale Plain in Somaliland and by the use of environmental niche models to assess the regional distribution of similar environments. Finally, we discuss the biogeographical and conservation implications of our findings.

Methods

Field surveys

All surveys took place at times of year in which breeding has been recorded. First, we visited the Wajale Plain, Somaliland, on 19 and 29–30 May 2010 to search for *Heteromira* larks at the type locality of Archer's Lark. We walked 10.2 km of transects including vegetation surveys every 250 m, and an additional ca. 5 km of transects searching for larks without pausing for vegetation surveys. All transects were carried out between sunrise and 1030 hours. After 1030 hours, further explorations were made to cover the area as comprehensively as possible, and informal interviews made with local farmers and villagers.

Second, we visited Jijiga, Ethiopia, on 9–12 May 2011 to find, sample and briefly survey the reported *Heteromira* population to the east of the town. We captured birds by manoeuvring them into a ca. 60 m line of mistnets in a small area where several pairs appeared to be present. Captured birds were measured and ringed, and blood samples taken before the birds were released. We made sound recordings of five different individuals in song-flight. We walked 14.6 km of transects, in two sections 16 km apart (Fig. 1). Additionally, we sought crudely to gauge the amount of appropriate-looking habitat by driving as far east as Tog Wajale (the Somaliland border) and south-east along the road towards Gode, although in the latter case security considerations curtailed travel distance.

At both sites we carried out vegetation surveys using methods previously applied at the Liben Plain (details in Spottiswoode et al. 2009). Briefly, we stopped every 250 m along transect lines and visually assessed number of trees, bushes and cowpats, proportion coverage of bare ground, and grass height in four categories (>5 cm, 5–15 cm, 15–40 cm and > 40 cm). Habitat variables at Jijiga and the Liben Plain were analysed using *t* tests for unequal variances on ranked data (Ruxton 2006), owing to persistent departures from normality.

Morphometrics, plumage and voice (and associated characters)

We measured *Heteromira* larks held in the American Museum of Natural History, New York (AMNH), Natural History Museum, Tring (BMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), Museum of Comparative Zoology, Harvard (MCZ), United States National Museum, Washington DC (USNM) and Zoologisches Museum Berlin (ZMB). Measurements were bill to skull, wing curved, tarsus, hind-claw, and tail tip to point of insertion, and all were made by NJC. To these were added

the measurements of the two birds captured alive and released at Jijiga (measured by CNS using the same technique). Differences in plumage were assessed through direct comparison of specimens, supplemented by digital photographs of wild birds and specimens.

Since Archer's Lark has not been seen with certainty since 1922, no sound recordings exist from the type locality, nor did the discoverer mention any vocalisation (Archer and Godman 1961). We used Raven Pro 1.4 (Bioacoustics Research Program 2011) to analyse our own field recordings of Liben Lark and the newly discovered lark population at Jijiga, and recordings of Rudd's Lark downloaded from www.xeno-canto.org. We also drew on our own experiences of, and reviewed the literature on, Rudd's Lark display-flights and breeding behaviour, and compared this information with evidence from our recent fieldwork in the Horn of Africa.

Molecular analyses

The DNA samples were obtained from the following sources: (1) fresh blood samples from one Liben Lark we captured on the Liben Plain in June 2007; (2) fragments of tissue attached to the flight feathers of a Liben Lark freshly predated on the Liben Plain in June 2008; (3) fresh blood samples from each of the two Jijiga larks captured and released in May 2012 (see Field surveys, below); and (4) toe-pad samples of two Rudd's Lark and two Archer's Lark individuals kindly provided by the BMNH. Additionally, we included a third Rudd's Lark sequence from a previous study (Barnes 2007; Alström et al. submitted). Clapper Lark *Mira* *apiata* was used as the outgroup based on results from Barnes (2007) and Alström et al. (submitted).

The DNA was extracted using QIA Quick DNEasy Kit (Qiagen, Inc), according to the manufacturer's instructions, but with 30 µl DTT added to the initial incubation step for the extraction from feathers and toepads. We sequenced the mitochondrial cytochrome *b* (*cytb*) gene for all samples. Amplification and sequencing of the fresh samples followed the protocols described in Olsson et al. (2005). The toepads were sequenced with specifically designed primers (Table S1).

Phylogenetic analyses

Sequences were aligned using MegAlign 4.03 in the DNASTAR package (DNASTAR Inc.). Phylogenies were estimated by Bayesian inference using MrBayes 3.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). Default priors in MrBayes were used. Two simultaneous analyses of four incrementally heated Metropolis-coupled MCMC chains with temperature 0.2 were run for 2 million generations and sampled every 1,000 generations.

Instead of selecting a substitution model a priori, we used the ‘mixed’ command to sample across the GTR model space in the Bayesian MCMC analysis (Huelsenbeck et al. 2004). In some analyses, this was combined with rate variation across sites according to a discrete gamma distribution with four rate categories (Γ ; Yang 1994) or an estimated proportion of invariant sites (I; Gu et al. 1995). Convergence to the stationary distribution of the single chains was inspected using a minimum threshold for the effective sample size. The joint likelihood and other parameter values reported large effective sample sizes ($>1,000$), and were inspected in Tracer 1.5.0 (Rambaut and Drummond 2009). Good mixing of the MCMC and reproducibility was established by multiple runs from independent starting points. Each analysis was run twice, and topological convergence was examined by eye and by the average standard deviation of split frequencies (<0.005). The first 25 % of the generations were discarded as ‘burn-in’, well after stationarity of chain likelihood values had been established, and the posterior probabilities were calculated from the remaining samples (pooled from the two simultaneous runs). The different models (‘mixed’, ‘mixed’ + Γ , ‘mixed’ + Γ + I) were compared using Bayes Factors (Newton and Raftery 1994; Kass and Raftery 1995), calculated in Tracer 1.5.0 (Rambaut and Drummond 2009).

Pairwise sequence divergences were calculated in PAUP* (Swofford 2002) following the recommendations by Fregin et al. (2012), i.e., only comparing homologous parts of the gene (same part, same length), deleting all positions with any uncertain base pairs from the matrix, and using the best-fit model (GTR; as calculated by MrModeltest 3.2; Nylander 2004). The shape parameter alpha and estimated proportion of invariable sites were obtained through Bayesian Inference, since PAUP* cannot estimate these parameters under the distance criterion. Uncorrected p distances were also calculated in PAUP*.

Environmental niche modelling

We used MaxEnt 3.3.3e (Phillips et al. 2006) to model the likelihood of occurrence of *Heteromiraфра* larks in the Jijiga area and more widely in the region, and to assess environmental similarities between Jijiga and the Liben Plain. Within a background region covering 3.5°–10.0°N and 36.0°–44.5°E, which includes the Liben Plain, Jijiga and all areas between (Fig. 2), we modelled the potential distribution of larks as a function of altitude (from 90 m).

We used Shuttle Radar Topography Mission SRTM (USGS 2004), unclassified NDVI (mid-monthly dekads for each month, averaged over 2006–2010, downloaded from the SPOT-Vegetation platform and clipped to the study region using VGTEExtract) and five bioclimatic

variables (mean annual temperature, temperature range, temperature seasonality, mean annual rainfall and rainfall seasonality) from the interpolated BioClim dataset (Hijmans et al. 2005). We used the distribution of spatially referenced lark sightings in the Jijiga area collected in 2011 ($n = 14$) and on the Liben Plain collected between 2007 and 2011 ($n = 183$) to identify other areas that might support *Heteromiraфра* larks in the region. Variables making a less than 1 % contribution to the model were removed and the model run again. The logistic threshold for equal training sensitivity and specificity was used to assess the threshold probability to determine likely presence or absence. The ability of each model to discriminate between occupied and unoccupied areas was estimated from the area under the curve (AUC) of the receiver operating characteristic (ROC) (Phillips et al. 2006).

Results

Range of *Heteromiraфра* in north-east Ethiopia and Somaliland

Our survey of the type locality of Archer’s Lark, the Wajale Plain (approx. 9°39’N 43°18’E) in Somaliland, failed to produce any evidence of *Heteromiraфра* larks. The habitat was heavily transformed by mechanised agriculture (millet, sorghum and maize) and grazing (cattle, goats, sheep and camels) and was extensively invaded by the American weed *Parthenium hysterophorus*. This weed was estimated to cover 17.6 % (s.d. = 14.5 %; range 0–90 %) of surface area in vegetation transects ($n = 39$ point estimates on five transects). Interviews with local people revealed that the Wajale Plain was the focus of a Soviet-supported agricultural programme in the 1980s during which vast areas were planted with wheat, sorghum and maize, and that to their knowledge no area remained of natural grassland that had never previously been cultivated.

Our survey of the grassland east of Jijiga town in north-eastern Ethiopia, from where *Heteromiraфра* sp. had recently been reported, immediately produced sightings in the vicinity of 9°26’00’’N 43°03’30’’E, where we captured two birds on 10 May 2011. We then carried out two 7-km transects on 11 and 12 May 2011 (Fig. 1): the first, starting at the coordinates above, produced 14 *Heteromiraфра* individuals (at 12 point locations), of which all but two were detected by their display-flights. The second transect revealed only a single bird, detected in display-flight, although the habitat appeared similar and the weather was no different.

Throughout these transects, and so far as we could see with binoculars along the Jijiga–Tug Wajale road, the grasslands east of Jijiga were heavily degraded. There were

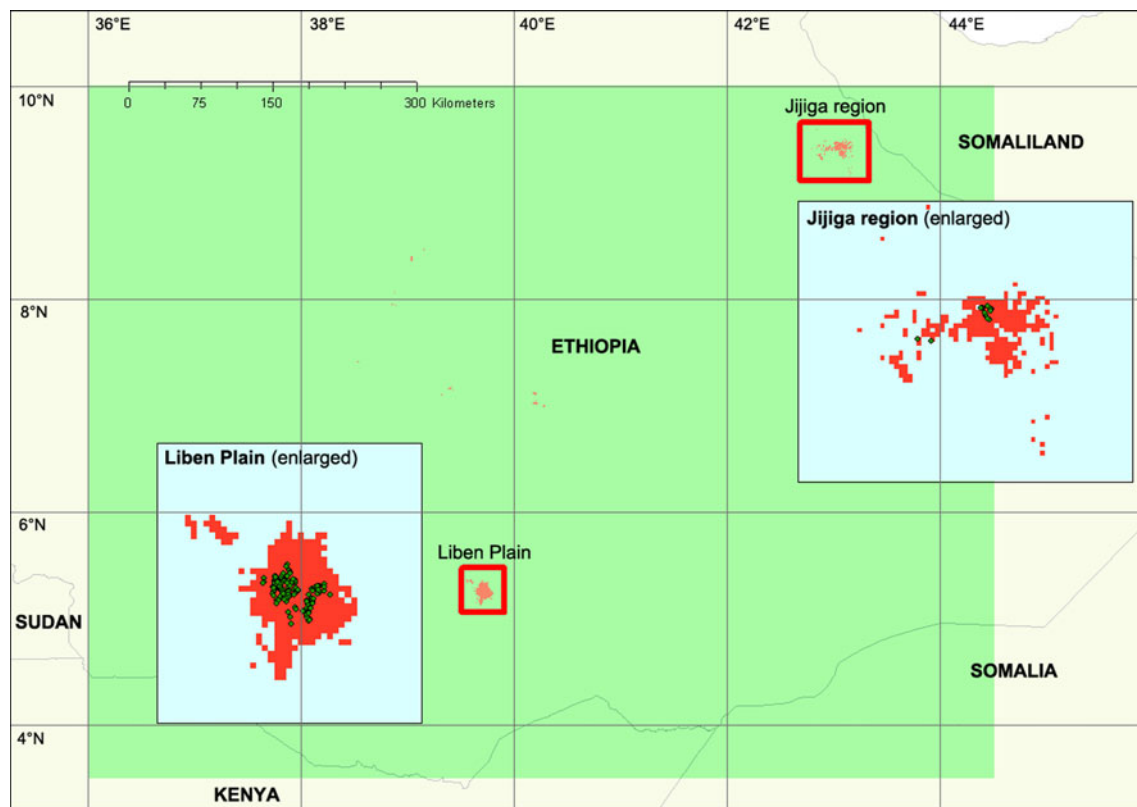


Fig. 2 Modelled distribution of *Heteromiraфра* larks in southern Ethiopia. The blue rectangle indicates the area over which the model was estimated. 1-km cells with an estimated occupancy value exceeding the logistic threshold of equal training sensitivity and

specificity are shown in red, with insets showing the Liben Plain (left) and Jijiga (right) areas in higher resolution and showing the location of lark sightings (green) used as training data

many recently cultivated long and narrow fields (ca. 100–500 m \times 70 m in extent) lying fallow, and much of the surface area showed signs of previous cultivation. Grass cover was low and sparse, and being heavily grazed by livestock (cattle, goats, sheep and camels).

Moreover, the grassland was very limited in extent. Driving east from the lark locations above to the Somaliland border revealed that natural grassland ceased within 3 km of transect 1 above, whereupon the habitat changed to rocky plains and scrub. We detected no apparently suitable habitat along the first 40 km of the road south-east of Jijiga towards Gode, which was also rocky and scrubby. This suggests that the probable extent of habitat is <20 km from west to east. It is unlikely to extend more than ca. 2 km south of the Jijiga–Tog Wajale road. Its extent north of the road is less clearly curtailed and deserves further investigation when security considerations allow. However, satellite imagery (Google Earth, image date 30/06/2011) suggests a maximum possible extent of ca. 10 km, before being curtailed by mountains.

This was supported by the results of the niche modelling. The AUC of the final model was 0.997, indicating good discrimination of occupied and random locations. The

model output suggested that apart from a few small scattered sites in central Ethiopia, the Liben Plain and Jijiga are the only occupied sites, and that both populations are confined to small areas (Fig. 2). The total number of 1-km cells with modelled values exceeding the logistic threshold of equal training sensitivity and specificity (0.277) was 580.

Habitat of *Heteromiraфра* in the Horn of Africa

We compared vegetation variables between Jijiga and the Liben Plain, surveyed within a week of one another in May 2011, although regional variation in rainfall could have influenced this comparison. There was a higher proportion cover of very short grass (<5 cm) at Jijiga than at the Liben Plain ($t'_{79.78} = 6.0$, $P < 0.001$), whereas there was a higher proportion cover of medium-length grass at the Liben Plain than at Jijiga (5–15 cm: $t'_{-24.14} = 233.5$, $P < 0.001$; 15–40 cm: $t'_{-3.77} = 185.8$, $P < 0.001$). Neither site had any grass taller than 40 cm except at a single sampling point on the Liben Plain. The proportion of bare ground was similar at both sites ($t'_{87.3} = 1.51$, $P = 0.13$) but a greater density of cowpats on the Liben Plain than Jijiga

was suggestive of higher cattle grazing pressure ($t'_{116,16} = -6.2$, $P < 0.001$). We did not quantitatively compare these data to those for the Wajale Plain because they were collected in 2010 when rainfall was much higher; however, in that year bush and grass cover was generally much denser and taller than at Jijiga or the Liben Plain.

For the Jijiga population, we compared vegetation characteristics of locations where larks were recorded to randomly sampled sites. Small sample sizes ($n = 60$ random locations and $n = 12$ locations with lark sightings) and departures from normality of residuals precluded a modelling approach as previously taken for similar data from the Liben Plain (Spottiswoode et al. 2009), so we instead carried out bivariate comparisons of lark versus random locations using unequal variances t tests on ranked data. This revealed that locations where larks were sighted tended to have a lower proportional coverage of very short grass (<5 cm) (mean for random locations: 83.3 % versus lark locations 85.8 %; $t'_{30,25} = 2.29$, $P = 0.033$) and a higher proportion coverage of medium-length grass (5–15 cm) (mean random 2.4 % vs. larks 4.6 %: $t'_{30,25} = 20.90$, $P < 0.001$) than random transects, mirroring results from the Liben Plain (Donald et al. 2010), although the means show that these effects were of small absolute magnitude. No other habitat variables differed between lark and random locations.

Morphometrics

Summary statistics for all taxa are given in Table S3. To examine this variation graphically, we used principal

components analysis on a covariance matrix of wing, tail, tarsus and bill measurements to generate two principal components (PCs) summarising 97 % of the variation: PC1 (loadings: bill 0.31, tarsus 0.74, wing 0.95, tail 0.93) explained 87 % of the variation, and PC2 (loadings: bill 0.01, tarsus 0.15, wing 0.30, tail 0.36) explained a further 10 %. We then plotted PC2 against PC1, with symbols corresponding to population and sex (Fig. 3). This shows that Rudd's Lark (triangles) forms a cluster distinct from the Horn of Africa taxa, whereas Archer's Lark, Liben Lark and the two Jijiga birds overlap entirely with one another. The three unsexed individuals (the two Jijiga birds and one Liben Lark) were also the only birds measured in the field, but these fall within the range of values from museum skins. In summary, Rudd's Lark was highly distinct from the three Horn of Africa populations, which were indistinguishable from one another.

Plumage

First, we compared the *Heteromiraфра* larks of the Horn of Africa to Rudd's Lark of South Africa. Unexpectedly, there were no clear, consistent plumage differences between them. Museum specimens and photographs suggest that Rudd's Lark may usually appear to possess a slightly more prominent cream supercilium owing to the slightly darker (black vs dark brown), less buff-edged crown feathers above it; and it may generally possess narrower and less prominent buffy fringes to the feathering of the upperparts which in Horn of Africa larks can appear as strong scalloping. Overall coloration above and below is, however, very similar, and the spotting on the breast is, in all taxa and populations, essentially the same in quantity, distribution and type (small tear-drops in shape, partially aligned).

Next, we compared the two populations of *Heteromiraфра* larks within the Horn of Africa. Each of the 11 plumage characters with which Liben Lark was originally distinguished from Archer's Lark (Erard 1975), again assessed through comparisons of skins and photographs, fails to hold with the single exception of the former's more strongly russet-beige wing-panel, flanks, underwing-coverts, belly and undertail-coverts (Fig. 4), although these could result from staining by the red soils of the Liben Plain, clearly apparent in other species there, including Somali Short-toed Lark *Calandrella somalica*. One character suggested to differ in the opposite direction to an overall more rufous cast in Liben Lark was the colour of the wing-coverts and tertial feather shafts (whiter in Liben Lark according to Erard 1975); however, we could not detect any pronounced or consistent difference in this character between populations.

Finally, we could not detect any differences between the larks we caught at Jijiga and museum skins of Archer's

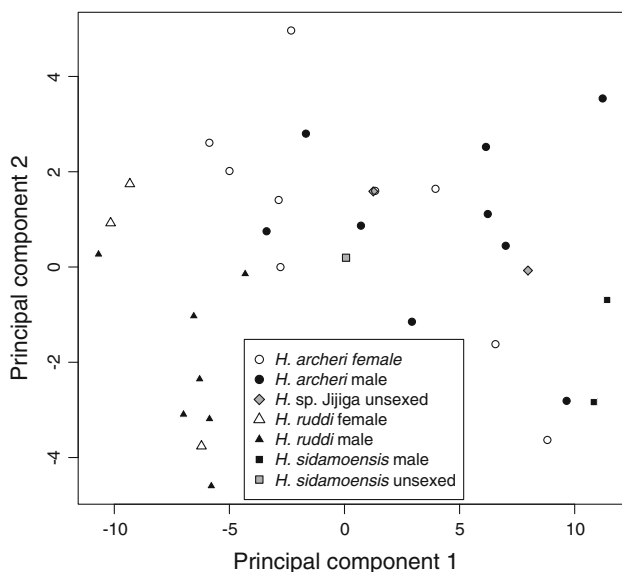


Fig. 3 Plot of two principal components summarising *Heteromiraфра* morphometrics (tarsus, wing, tail and bill length); see main text for details of loadings



Fig. 4 Photographs of *Heteromirafr* larks at Jijiga (left) and the Liben Plain (centre and right). (Photos: CNS, Greg Davies, and PFD)

Larks from the type locality in either coloration or pattern of markings.

Display, voice and breeding

Apart from occasional bursts from the ground, the Liben Lark delivers its song in a distinctive display-flight, flying up at a steep angle in a fluttering flight, beginning to sing within 1–2 s of commencing the ascent, and within ca. 5 s reaching a height of 5–15 m and hovering with legs dangling for some 20–35 s, before abruptly arching the wings into a parachute shape and gliding to the ground; these displays are repeated at short intervals usually over a period of five or 10 min (Collar et al. 2008 and further observations by authors). The larks at Jijiga performed and delivered extremely similar display-flights.

Liben Lark songs (Fig. 5) lasted 11–38 s (mean $22.6 \pm \text{sd } 14.1$ s; $n = 3$ individuals) and were composed of hurried strophes of short rasping notes, interspersed with a few short thin whistled notes. Notes were delivered in multi-note blocks given two or more times (identical or similar); within each block, the pitch generally either fell or rose. The repetition of the ‘blocks’ and the variation in pitch produce a cyclical, undulating rhythm, with a frequency range of 4.95 ± 0.33 kHz. The songs of the larks at Jijiga were very similar (Fig. 5), with a length of 18–29 s (mean 21.1 ± 6.1 s; $n = 4$ individuals) and a frequency range of 4.78 ± 0.34 kHz. We caution that small sample size and individual variation preclude a robust test of any consistent differences between the populations.

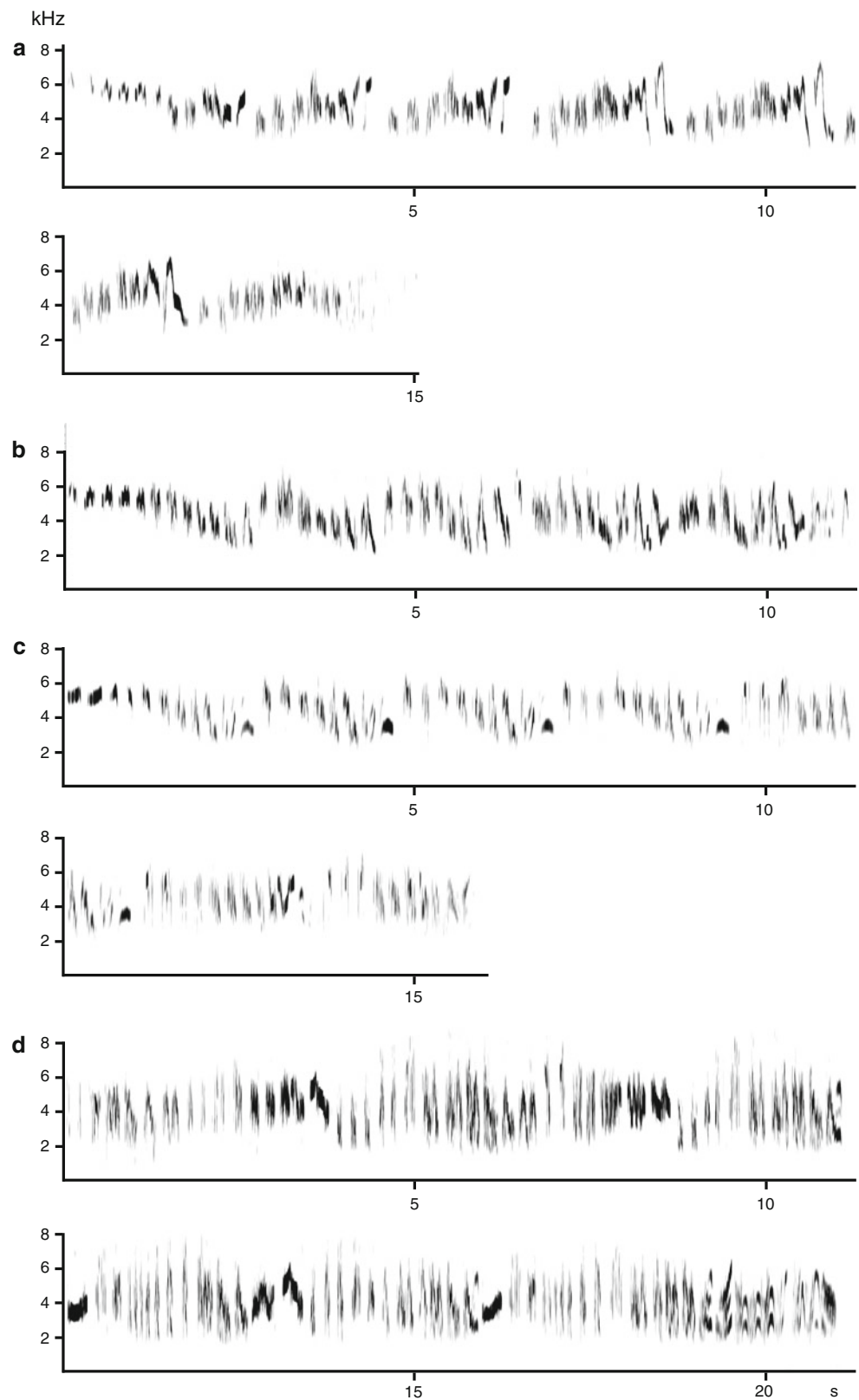
By contrast, the song and display of Rudd’s Lark is highly distinct from that of the Horn of Africa populations (e.g., Xeno-Canto accession number XC62296;

descriptions in Ginn et al. 1989; Hockey et al. 2005). It has a much more protracted display-flight than Liben Lark, ranging from a few minutes to half-an-hour, involving undulations (song at the apex) in windy conditions, and zigzags and circling in calm ones. The song itself is a long series of buzzy 3–8-note variable phrases, each lasting 1 s and separated by 5–6 s, hence entirely different from that of the Horn of Africa taxa.

Breeding ecology is little known in the Horn of Africa populations and only 2–3 nests are known from each. The eggs of the two taxa are similar: seven Archer’s Lark eggs measured a mean 21.8 (21 – 23) mm \times 14.4 (14 – 16) mm (Archer and Godman 1961), while three eggs from the only known nest with eggs of Liben Lark all fell within these ranges (Collar et al. 2008). The colour and pattern of the only egg attributed to Archer’s Lark in BMNH (register number 1969.8.103; unfortunately broken and with no accompanying data) closely resemble those of the only known clutch of Liben Lark (Fig. S1).

One point of possible divergence is that of nest architecture, since the nest of *archeri* was described as ‘funnel-shaped... extending deep into the roots of the clump of grass in which it is concealed’ (Archer and Godman 1961). This contrasts with Liben Lark, as none of the three nests found to date was conspicuously funnel-shaped, although two were recessed among the basal stems of a herb (Collar et al. 2008) while the third was a lightly woven cup in the base of short-sward grass (pers. obs.). However, Rudd’s Lark is known sometimes to construct an elongated funnel structure, but sometimes not (Hockey et al. 2005), suggesting that such an addition is facultative. Furthermore, Rudd’s Lark usually constructs a dome over the nest (Maphisa et al. 2009), a feature not yet recorded in the Horn of Africa populations.

Fig. 5 Sonograms of the songs of **a,b** *Heteromira* sp. at Jijiga, 9–11 May 2011 (Xeno-Canto accession numbers XC121598 and XC121599), and **c,d** Liben Larks at the Liben Plain (Xeno-Canto accession numbers XC42144 and XC 42145), 19 June 2007. One complete songstrophe per individual. Recordings by CNS



Molecular analyses

The aligned sequences of the two Liben Larks, two larks from Jijiga, two Archer's Larks and three Rudd's Larks comprised 1,076 base pairs (bp), of which 77 (7.2 %) were parsimony-informative. For the five sequences from fresh material the complete target stretch was obtained, while the four toepad sequences were incomplete, with 345, 694, 706 and 854 bp respectively. No unexpected stop codons, indels or distinct double peaks in the chromatograms that would indicate the presence of nuclear pseudogenes (e.g., Sorenson and Quinn 1998) were found in the coding *cytb* sequences.

The Bayes Factor analysis strongly supported the 'mixed' + Γ and 'mixed' + Γ + I over the 'mixed' model (ln Bayes Factors ≥ 13), but did not favour any of the two former ones. The trees based on these three models are identical in topology and more or less so in posterior probability values; the 'mixed' + Γ tree is shown in Fig. 6. There is a deep split between two well-supported ingroup clades, one containing Rudd's Lark and one containing Archer's Lark from Somaliland, Liben Lark from the Liben Plain, and the samples from Jijiga. There is no significant structure within any of these clades.

The genetic distances between Rudd's Lark and the Horn of Africa taxa/populations were ca. 16–17 %, whereas the distances between the three Horn of Africa taxa/populations were <1 % (Table 1).

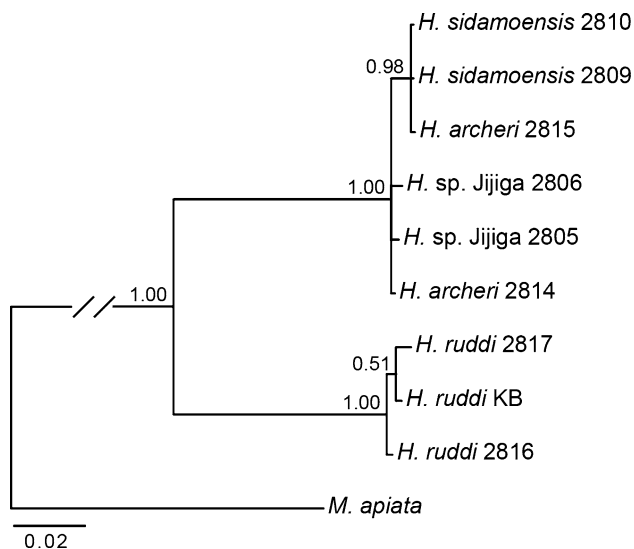


Fig. 6 Cytochrome *b* tree of Liben Lark *H. sidamoensis*, *Heteromira* sp. at Jijiga, Archer's Lark *H. archeri* and Rudd's Lark *H. ruddi*, with Clapper Lark *Mirafra apiata* as outgroup, estimated by Bayesian inference under the GTR + G model

Table 1 Cytochrome *b* distances between Liben Lark *H. sidamoensis* from the Liben Plain, *Heteromira* sp. from Jijiga, Archer's Lark *H. archeri* from its type locality in Somaliland, and Rudd's Lark *H. ruddi* from South Africa

		1	2	3	4	5	6	7
1	<i>H. sidamoensis</i> 2810	–	0	0.7	0.8	*	*	16.9
2	<i>H. sidamoensis</i> 2809	0	–	0.7	0.8	*	*	16.9
3	<i>H. sp. Jijiga</i> 2806	0.4	0.4	–	0.5	*	*	16.1
4	<i>H. sp. Jijiga</i> 2805	0.4	0.4	0	–	*	*	16.1
5	<i>H. archeri</i> 2815	0	0	0.4	0.4	–		
6	<i>H. archeri</i> 2814	0.4	0.4	0	0	0.4	–	
7	<i>H. ruddi</i> KB	*	*	*	*	*	*	–

Values above diagonal based on 1,000 base pairs corrected by HKY + I model, below diagonal based on 722 base pairs corrected by HKY model

* No calculation done

Discussion

Taxonomy and biogeography of *Heteromira*

Using a combination of morphological, vocal and molecular genetic evidence, we conclude that (1) the recently discovered *Heteromira* lark population near Jijiga in north-eastern Ethiopia is conspecific with the presumed extinct Archer's Lark of Somaliland, which our recent survey failed to detect at the type locality; (2) Archer's Lark is so poorly differentiated from the Liben Lark of southern Ethiopia that these two taxa should be treated as conspecific; (3) Rudd's Lark of South Africa is clearly distinct in voice, morphometrics and mtDNA (but not plumage) from all populations in the Horn of Africa; and finally (4) the recently discovered Archer's Lark population near Jijiga in north-eastern Ethiopia appears to be very small and seemingly under great threat.

All members of the genus *Heteromira* have long been recognised as extremely similar morphologically. They are so similar to one another that the first two to be described, Rudd's Lark of South Africa and Archer's Lark of Somalia, were, at least briefly, treated as conspecific (Mackworth-Praed and Grant 1955; Mayr and Greenway 1960). In his original description of Archer's Lark, Stephenson Clarke (1920) confessed that 'the two species are so alike that had it not been for the enormous gap in the distribution, I should have had little hesitation in calling them subspecies of the same bird'. Only after the third taxon, Liben Lark, was discovered in 1968 was the evidence cautiously set out for separating all three taxa at species level (Erard 1975).

This arrangement has been followed by all subsequent authors. However, in this paper we have shown that neither

morphological, genetic nor vocal evidence supports consistent differentiation between the two Horn of Africa taxa, Archer's Lark and Liben Lark. We consider each line of evidence in turn.

First, the only consistent morphological difference was a subtle shift in overall cast of plumage colour (warmer in Liben Lark). This corresponds to gross differences in soil colour between the two areas (greyish-brown in the Jijiga and Wajale Plains, and rich brownish-red on the Liben Plain). Such variation in substrate colour is a common factor driving apparent subspeciation in larks (de Juana et al. 2004), being associated for example with geographical (often clinal) variation within each of several species of southern Africa's arid zone (e.g., Ryan and Bloomer 1999) but also causing such notable mosaic patterns that even subspecific recognition is avoided (Mayr and McEvey 1960). However, we do not know the extent to which these differences reflect minor adaptive variation in camouflage or are the result of (potentially adaptive) staining from the environment. Their nests and eggs also seem similar, albeit based on a very small sample. Second, we found that Archer's Lark and Liben Lark were not only genetically very similar but did not even form separate monophyletic groups, whereas they were deeply divergent from Rudd's Lark in South Africa. This is suggestive of recent gene flow between the Horn of Africa populations, or very recent separation. Finally, the song of the newly discovered population near Jijiga is very similar to that of Liben Lark (Fig. 5), and accompanied by a very similar display-flight.

Climatic evidence is consistent with the hypothesis that recent aridification has separated the Horn of Africa *Heteromira* populations into their present disjunct distributions: the Horn of Africa has experienced marked fluctuations in aridity during the Holocene (Gillespie et al. 1983); most recently, two marked aridification phases began in 8,500 and 6,000 BP, before the current semi-arid climate was established about 3,800 BP (Jung et al. 2004). It is thus quite plausible that grassland habitat could have extended between the two isolated pockets that, so far as is known, make up the range of *Heteromira* in the Horn of Africa.

The conspecificity of Liben Lark with Archer's means that *H. sidamoensis* becomes either a synonym or a subspecies of *H. archeri*. Although we cannot be sure of the extent to which the former's plumage is stained rather than genuinely coloured more rufous-beige, we precautionarily assume the latter and suggest retaining it as a subspecies.

Conservation implications

The evidence presented here strongly supports the suggestion that Archer's and Liben Larks are conspecific. Both taxa are currently considered Critically Endangered. We

therefore need to consider whether this taxonomic rearrangement and the recently discovered new population of Archer's Lark might have any bearing on their conservation status.

Unfortunately, the species remains in a perilous situation. The conservation prospects on the Liben Plain are worsening with the rapid advance of commercial agriculture (Donald et al. 2010; Spottiswoode et al. 2009), and the data reported give little hope the recently discovered population near Jijiga is less imperilled. While local densities can apparently be relatively high (e.g., 12 singing birds heard within an area of ca. 500 ha on one transect), its likely geographical extent appears very limited (at most 20 km × 12 km) and from conditions in 2011 it seems to be highly threatened and in steep decline. The Jijiga grasslands are heavily grazed and many small, narrow strips are cultivated or have been in the past. Point locations where larks were recorded tended to have taller grass than random locations, yet overall grass height was low and on average lower than at the also heavily overgrazed Liben Plain. Our transects were located in what appeared to be among the least degraded existing grassland, and yet even here 83 % of grass cover was under 5 cm in height.

The conservation of both populations represents a major challenge. The population on the Liben Plain has been shown to be experiencing an ongoing steep decline (Spottiswoode et al. 2009; Donald et al. 2010), although it is now subject to a significant international conservation recovery effort implemented by the Ethiopian Wildlife and Natural History Society. Meanwhile, the Jijiga region remains unstable and security concerns mean much of the area is often inaccessible. It is subject to frequent droughts such as the recent one in mid- to late 2011 which may have had adverse impacts subsequent to our brief survey in May that year. The plain was very dry at the time and also in January 2012, when a day's searching at the site of our first transect revealed no birds (G. Nicholls pers. comm.). Another priority for future work will be to survey the region between the two sites for additional still undiscovered populations. Maximum entropy modelling based on remotely sensed data from the Liben Lark has already been used to attempt to identify additional pockets of potential *Heteromira* habitat on a wider geographical scale (Donald et al. 2010). The only substantial area revealed by the model was a pocket to the south-east of Jijiga (i.e., to the south of the new population reported here), towards the town of Gode, but security in this area will need to improve before it can be investigated. Repeating this modelling with the addition of new data from the Liben Plain and, for the first time, point data from the Jijiga area (Fig. 2), yielded no evidence of other likely sites, with the exception of a very small area to the east of Goba.

Our survey of the type locality of Archer's Lark in Somaliland also revealed an additional potential threat to the habitat of the species in the Horn of Africa: the area was densely overrun with the Neotropical weed *Parthenium hysterophorus*, a well-established and economically deleterious invasive species in north-eastern Africa (Nigatu et al. 2010; McConnachie et al. 2011) as it is elsewhere in Africa, Asia and Australia. In February 2012 we also noted *P. hysterophorus* in small numbers at the type locality of Liben Lark near Negele. Although we did not note dense invasions of *P. hysterophorus* at Jijiga, it is known from this region (McConnachie et al. 2011). Weed populations at both Jijiga and Negele should be closely monitored and if possible, controlled, as substantial spread could further reduce the quality and extent of the small remaining areas of grassland at both sites.

Finally, the English name of 'Liben Lark' was established only recently, at the express request of local people who take pride in its existence and support its conservation (Collar 2009). To change it now to 'Archer's Lark' would not be helpful and we suggest, for the time being at least, to retain the use of 'Liben Lark' for all populations of *H. archeri*.

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