

Editorial

The Diptera of Lesotho: a history of collecting in the Mountain Kingdom, summary of recent collecting sites and introduction to the topical collection in African Invertebrates

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Abstract

The Kingdom of Lesotho in southern Africa is entirely bordered by South Africa, with which it shares many geological and vegetation types, but the vast extent of alpine vegetation and high altitudes suggests that differences in insect diversity should be expected. Globally, the Diptera are one of the most diverse orders of insects, though biodiversity estimates for the order are lacking for many regions. Here, we present a summary of the limited historical Diptera collections from Lesotho, summarise our collecting expeditions in 2021, 2022 and 2023, and provide photographs and descriptions of the collecting sites. This paper is the first of a series of papers in a Topical Collection of the Diptera of Lesotho in African Invertebrates. We hope to stimulate more research on Afrotropical Diptera and to improve their conservation in Lesotho in particular.

Key words: Alpine entomology, biodiversity surveys, conservation, Insecta, southern Africa, species checklists, true flies

Introduction

The Kingdom of Lesotho is a small (30 355 km²), landlocked country surrounded by the Republic of South Africa. While Lesotho shares most vegetation and habitat types with South Africa, the exception being Western Lesotho Basalt Shrubland (Gd9) (Mucina and Rutherford 2006; SANBI 2006), the country has an average altitude ~900 m higher than South Africa, suggesting that differences in the fauna and flora may exist. As can be expected due to its smaller size, Lesotho has only 13 different vegetation types, all within the grassland biome, while South Africa has 466 vegetation types across nine biomes (Mucina and Rutherford 2006; SAN-BI 2006). Despite the smaller size, Lesotho's higher altitude means that alpine vegetation types are much more extensive (e.g., Drakensberg Afroalpine Heathland) and the country offers habitats for alpine adapted species that are less extensive in South Africa (Fig. 1). The eastern border of Lesotho is formed by the Drakensberg escarpment, which rapidly drops in altitude into the South African provinces of KwaZulu-Natal and, in the south west, the Eastern Cape. While small patches of alpine vegetation occur on the South African side of the border, these rapidly transition to mid-altitude vegetation. In the south, high altitude grasslands extend from Lesotho into the Eastern Cape, and in the west and north, highveld grassland and shrubland vegetation types occur on both sides of the border, in Lesotho and the Free State province (Mucina and Rutherford 2006; SANBI 2006).

Geologically, the country is similarly limited. The geology is solely comprised of Karoo Supergroup strata, predominantly Drakensberg formation basalts with some exposed sedimentary rocks of the Elliot formation in the river valleys and western lowlands. In the western lowlands, some exposed Tarkastad formation sedimentary rocks and Karoo Dolerite also occur. These four geological types are significantly fewer than the 119 lithographies found in South Africa. This pattern is also reflected in the geomorpholgy, with only the Lesotho Highlands and Eastern Escarpment Hinterland geomorphic provinces represented in the country, compared to 43 geomorphic provinces in South Africa (Partridge et al. 2010).

While there has been widespread collecting of insects, and Diptera in particular, in South Africa, collecting in Lesotho has been less common (Kirk-Spriggs 2017). The combination of regionally rare habitats and comparative under-sampling creates an opportunity for research in Lesotho. With this in mind, three field trips were undertaken: 3 to 14 December 2021, 21 November to 1 December 2022 and 21 to 30 January 2023 by the authors of this introductory article to enhance the Diptera collections from Lesotho.

To increase collection effort without identifying the material within the collections is short-sighted, and so this special collection of articles on the Diptera of Lesotho was conceived. This will turn these specimens into published knowledge of the Diptera of Lesotho and promote conservation in the country. We have chosen to initiate this as a collection of articles rather than a special issue, to allow family accounts to be published as they are completed and thus make the knowledge available more rapidly.

Historic collections

Specimens from Lesotho are in various South African and international collections, but large samples are less common. Expeditions to Lesotho were undertaken by the Lund Zoological Institute (Hanström 1955), Brian and Pamela Stuckenberg, KwaZulu-Natal Museum (NMSA, South Africa), A. Lionel Bevis, Durban Natural Science Museum (DMSA, South Africa), and Charles Jacot-Guillarmod, Albany Museum (AMGS, South Africa) (Kirk-Spriggs 2017).

One of the first major expeditions to include Lesotho was the "Lund University Swedish South African Expedition" of 1950–51 (Brink 1955; Brink and Rudebeck 1955; Hanström 1955; Kirk-Spriggs 2017). Historically, the term "South Africa" has been used to refer to both the Republic of South Africa and (less frequently) the entire Southern African region (e.g., Schultze 1908) and so while the majority of the expedition covered South Africa, collections were also made in Namibia (previously South West Africa) and Lesotho (previously Basutoland) and, to a lesser extent, Eswatini, Zimbabwe and Zambia (previously Swaziland, Southern Rhodesia or Rhodesia, and Northern Rhodesia) (Brink and Rudebeck 1955). The

expedition entered Lesotho twice, first collecting at Qacha's Nek before returning to South Africa and re-entering near Quthing, where they were based for ten days. From there, the expedition travelled by road to Nazareth. The expedition moved by air to Mokhotlong and collections were undertaken in the high mountains on horseback (Brink 1955; Brink and Rudebeck 1955). Twenty-five undescribed Diptera species were collected from Lesotho during this expedition, notably six Asilidae (Hull 1967), four Empididae (Smith 1967) and three Tipulidae (Alexander 1964), all published in the South African Animal Life series.

A.L. Bevis occupied various positions during his tenure at the Durban Museum and Art Gallery and travelled to Lesotho multiple times for collecting (see Clancey 1956; Stuckenberg 1956). These trips were multidisciplinary and not focussed on Diptera collecting, but still resulted in the discovery of undescribed species (e.g., Stuckenberg 1956). About 770 specimens were accumulated during these trips and are housed at the DMSA.

Brian and Pamela Stuckenberg collected at seven sites in Lesotho in 1963 and 1964. These collections generated 884 specimens. Most of the sites were in western Lesotho, though specimens were also collected on God Help Me Pass (Lekhalong La Molimo Nthuse) (on labels as Bushman's Pass) and Blue Mountain Pass (Lekhalong La Thaba Putsoa). These expeditions yielded undescribed species (e.g. Whittington 1992). Along with other specimens accumulated over time, these specimens form the bulk of the collection of approximately 1 100 specimens housed at the NMSA.

Charles Jacot-Guillarmod was Entomologist and later Director of the AMGS. His parents ran a trading post in Ha-Masupha (called Mamathes at the time, now Mamathe or Masupha are also used) and he collected many specimens while visiting them. The majority of his collections were of Hymenoptera, but approximately 1 500 Diptera specimens from this collection are housed at the AMGS.

Recent collecting expeditions

Three expeditions were undertaken to Lesotho (Fig. 1) at six sites in 2021, seventeen in 2022 and seven in 2023 (Figs 2–29). The primary focus of activity was in the eastern highland regions, though some lowland sites were also visited. Details of these sites are given in Table 1. We focused our collecting on the eastern highlands for two reasons. Firstly, the highlands in eastern Lesotho are more extensively covered in alpine vegetation elements (Fig. 1). Secondly, western Lesotho is more densely populated and agricultural pressure is more intense than in eastern Lesotho. This is not to say that environmental degradation is absent from eastern Lesotho. The greatest threats to the environment in all regions of Lesotho are overgrazing (Fig. 30) and agriculture in, or very close to, riparian zones (Figs 11, 12), which lead to soil erosion (Figs 12, 31). Significant threats from mining activities are also present. In general, these are much less extensive than agricultural activities, but pollution impacts may be carried further by streams and rivers. Conservation planning and management should be aware of these threats, though effective management advice is beyond the scope of this paper.

Most collecting was done using sweep netting and hand collecting (Figs 16, 24) but where conditions allowed, Malaise traps were also deployed. Depending on the sites, either Gressitt-and-Gressitt (Fig. 13) or Townes-style (Fig. 20) traps were used. In total, 7 144 specimens were collected in these three expeditions.

Table 1. Collecting sites and coordinates from 2021, 2022 and 2023 in Lesotho. Collecting methods are indicated by: 1– hand and sweep netting, 2– Malaise trapping, 3– light trapping, 4– pan traps. Vegetation types are according to Mucina and Rutherford (2006) and SANBI (2006).

District	Site Name	Expedition(s)	Coordinates	Vegetation type	Comments
Butha- Buthe	Afriski Lodge	2021 ^{1,2} , 2022 ^{1,2,4}	28°49.37'S, 28°43.68'E	Drakensberg Afroalpine Heathland (Gd10)	The area around Afriski lodge ranged from degraded to relatively pristine (Fig. 2). There was some grazing evident in places and localised building rubble and litter.
	Afriski, Malibamatšo tributary	20221	28°47.81'S, 28°41.26'E	Lesotho Highland Basalt Grassland (Gd8)	The valley in which this tributary lies was relatively pristine, though there was some evidence of grazing (Fig. 3).
	Moteng Pass	2022 ¹	28°44.76'S, 28°36.01'E	Lesotho Highland Basalt Grassland (Gd8)	Moteng Pass is similar to the Malibamatšo tributary, but was drier. Some evidence of grazing was present (Fig. 4).
	Khukhune Roadside drainage gully	20221	28°44.09'S, 28°25.8'E	Eastern Free State Sandy Grassland (Gm4)	The site was in the Khukhune village and badly degraded. Evidence of grazing, alien vegetation (<i>Acacia mearnsii, Eucalyptus</i> sp. and <i>Pyracantha koidzumii</i>) and other habitat modifications was observed (Fig. 5).
Leribe	Motebong Lodge	2021 ^{1,2,3}	29°6.06'S, 28°30.09'E	Lesotho Highland Basalt Grassland (Gd8)	The area around the Motebong lodge was mostly modified gardens with a large impoundment nearby. Some indigenous elements remained in the area, though there was evidence of grazing (Fig. 6).
Mafeteng	Maletsunyane Falls area	20231	29°52.63'S, 28°03.22'E	Lesotho Highland Basalt Grassland (Gd8)	The area around the view point was mostly agricultural land. Some indigenous elements remain on the periphery (Fig. 7). While the waterfall is in Maseru District, the collection site is in Mafeteng District.
Maseru	Between Roma and St Michaels	20221	29°26.19'S, 27°41.04'E	Eastern Free State Sandy Grassland (Gm4)	The area was moderately grazed. Alien vegetation (<i>Pyracantha koidzumii</i>) was present (Fig. 8).
	Blue Mountain Pass, along A3	20231	29°28.35'S, 28°01.21'E to 29°27.3'S, 27°58.88'E	Lesotho Highland Basalt Grassland (Gd8)	The area was moderately grazed. Alien vegetation was present (Fig. 9).
	God Help Me Pass, A3, nr Molimo Nthuse Lodge	20231	29°25.39'S, 27°54.33'E	Western Lesotho Basalt Shrubland (Gd9)	Small patch of indigenous forest. Modified garden with mostly alien vegetation, with some indigenous trees (Fig. 10).
	Koro-Koro	20221	29°29.58'S, 27°39.26'E	Basotho Montane Shrubland (Gm5)	Agriculture and grazing were evident. Alien vegetation was present in lower areas. On the steeper slopes the shrubland was more intact, but still grazed (Fig. 11).
	Matsaba Nkesi village	2022 ¹	29°40.14'S, 27°47.84'E	Western Lesotho Basalt Shrubland (Gd9)	Fallow agricultural fields in wetland areas. Some alien plants on the steeper slopes (Fig. 12).
	Roma Trading Post Lodge	2022 ^{1,2}	29°26.59'S, 27°42.22'E	Peri urban garden	A highly modified garden site (Fig. 13).
	Semonkong area, A5	20231	29°53.30'S, 28°06.5'E	Lesotho Highland Basalt Grassland (Gd8)	A highly modified garden site (Fig. 14).
	Semonkong Lodge, gardens and vegetation	20231	29°50.6'S, 28°2.6'E	Lesotho Highland Basalt Grassland (Gd8)	A highly modified garden site (Fig. 15).
	St Michaels village	20221	29°25.72'S, 27°40.47'E	Eastern Free State Sandy Grassland (Gm4)	Grazing and alien vegetation (<i>Acacia mearnsii</i> , <i>Pyracantha koidzumii</i>) was present, though fields with indigenous vegetation were extensive. Human settlement in close proximity to the wetland and stream (Fig. 16).
Mokhotlong	Roadside flowers at stream	20211	29°27.56'S, 29°8.77'E	Lesotho Highland Basalt Grassland (Gd8)	Modified habitat, a culvert under the road. Some grazing was evident (Fig. 17).
	Roadside flowers at swamp	2021 ¹	29°26.37'S, 29°7.94'E	Lesotho Highland Basalt Grassland (Gd8)	Modified habitat, a culvert under the road. Some grazing was evident.
	Roadside flowers in Khatleli village	20211	29°16.71'S, 28°56.55'E	Lesotho Highland Basalt Grassland (Gd8)	Roadside flowers next to large puddle. Modified village habitat (Fig. 18).

District	Site Name	Expedition(s)	Coordinates	Vegetation type	Comments
Qacha's Nek	Sehlabathebe National Park, new lodge	2023 ^{1,2}	29°52.71'S, 29°4.45'E	Lesotho Highland Basalt Grassland (Gd8)	Pristine grassland, minimal impact of grazing or alien species (Figs 19, 20).
	Sehlabathebe National Park, old lodge	2023 ¹	29°52.07'S, 29°7.13'E	Lesotho Highland Basalt Grassland (Gd8)	Pristine grassland, minimal impact of grazing or alien species (Fig. 21).
Quthing	Fallow lands near Letšeng- la-Letsie	2022 ¹	30°18.54'S, 28°7.98'E	Lesotho Highland Basalt Grassland (Gd8)	Fallow lands with various annual flowers (Fig. 22).
	Letšeng-la- Letsie	20221	30°18.77'S, 28°10.06'E	Lesotho Highland Basalt Grassland (Gd8)	Intensely grazed habitat. Very little impact from alien vegetation but degradation due to grazing evident (Fig. 23).
	Mphaki Cell towers	20221	30°11.55'S, 28°8.23'E	Lesotho Highland Basalt Grassland (Gd8)	Hill top in Mphaki town. Some peri urban development and grazing (Fig. 24).
	Mphaki Farmers Training Centre	2022 ^{1,2,4}	30°11.60'S, 28°07.83'E	Lesotho Highland Basalt Grassland (Gd8)	Modified garden with alien vegetation, vegetable gardens and fruit trees (Fig. 25).
	Mphaki Roadside	20221	30°13.21'S, 28°08.32'E	Lesotho Highland Basalt Grassland (Gd8)	Relatively pristine site, some evidence of grazing and agriculture (Fig. 26).
	Roadside seep/stream	2022 ¹	30°12.88'S, 28°08.31'E	Lesotho Highland Basalt Grassland (Gd8)	Relatively pristine site, some evidence of grazing and agriculture.
	Roadside swamp	20221	30°13.69'S, 28°08.44'E	Lesotho Highland Basalt Grassland (Gd8)	Relatively pristine site, some evidence of grazing and agriculture (Fig. 27).
	Wetland N of Letšeng-la- Letsie	2022 ¹	30°17.03'S, 28°08.14'E	Lesotho Highland Basalt Grassland (Gd8)	Relatively pristine site, some evidence of grazing and agriculture (Fig. 28).
Thaba- Tseka	Sani area	20211	29°35.05'S, 29°17.12'E	Lesotho Highland Basalt Grassland (Gd8)	Moderate to extensive evidence of grazing. Degraded habitat (Fig. 29).



Figure 1. Map of major collecting sites in Lesotho with vegetation types. White indicates historical collecting sites and red indicates sites from recent expeditions (2021, 2022 and 2023). Vegetation data taken from SANBI (SANBI 2006). Arrows 1–5 indicate vegetation types with extents too small to be clearly visible on the map, as indicated on the legend.



Figures 2–5. Collecting sites during recent expeditions **2** Afriski Mountain Lodge area, looking southwest down the valley. Large areas of grazed but otherwise undisturbed landscape and disturbed piles of building rubble are visible **3** valley land-scape around the tributary of the Malibamatšo River, looking southwest from the A1 road. While some grazing is evident, the landscape is otherwise undisturbed **4** view from Moteng Pass on the A1, looking southeast from near the top of the pass. The habitat is drier than surrounding sites **5** gulley in Khukhune village next to the A1. The area is disturbed, with evidence of grazing and multiple alien plant species (*Acacia mearnsii, Eucalyptus* sp. and *Pyracantha koidzumii* are visible in the photograph).



Figures 6–9. Collecting sites during recent expeditions **6** Motebong Lodge, looking east. Areas close to the lake are disturbed by fluctuating water levels and increased grazing pressure. Many non-native ornamentals were planted around the lodge **7** Maletsunyane Falls area, sampling area consisted of natural vegetation and is cordoned off with palisade fencing from the surrounding farmlands, protecting it somewhat from overgrazing **8** roadside *Pyracantha koidzumii* bushes on the A5 between Roma and St Michaels village, looking south. The bushes attract flies, disrupting indigenous pollination networks **9** Blue Mountain Pass, roadside rest stop on A3, moderately grazed, toilet paper and human faeces scattered near the road, less disturbance away from the road.



Figures 10–13. Collecting sites during recent expeditions **10** God Help Me Pass, Molimo Ntuse Lodge area on A3, indigenous and exotic trees, with grass elements **11** hillside and fields near Koro-Koro village, looking south. Flat lowland areas extensively cultivated and grazed, resulting in erosion as seen in the bottom left of the photograph. Steeper-sloped areas receive less grazing pressure, with small shrubs and other plants surviving **12** fallow and recently ploughed fields at Matsaba Nkesi, looking west from the A5 road. The dark area in the centre of the image is a seep that has been cultivated. The seep and surrounding areas included many *Ranunculus* sp. flowers, while the steeper sides have alien vegetation including *Pyracantha koidzumii* and *Rosa rubiginosa* **13** malaise trap on the grounds of Roma Trading Post Lodge. The site contained many exotic ornamental plants.



Figures 14–17. Collecting sites during recent expeditions 14 Semonkong roadside, brief sampling from shrubs and grasses on verge 15 Semonkong Lodge, mixed indigenous and exotic vegetation with some garden elements 16 seep and grassland at St Michaels village. Some *Ranunculus* sp. visible in foreground. Alien *Acacia mearnsii* visible in the background. Note the proximity of the latrine (top right) to the watercourse 17 stream next to the A14. Some grazing and disturbance due to road building.



Figures 18–21. Collecting sites during recent expeditions 18 puddle and flowers in Khatleli village on the A1. Environment is heavily degraded, with agriculture and domestic disturbances evident 19 Sehlabathebe National Park, grassland vegetation near the new lodge and camping area 20 Sehlabathebe National Park, Malaise trap over small stream near new lodge area 21 Sehlabathebe National Park, semi-wetland area near old lodge, sampling from grass and shrubs.



Figures 22–25. Collecting sites during recent expeditions 22 fallow field near Letšeng la Letsie (Letsie's Lake). Diverse annual flowers growing in a highly modified habitat 23 Letšeng la Letsie view looking northwest. The site is the largest water source in the area, providing a suitable environment for livestock and therefore heavily influenced by grazing 24 hill above Mphaki, looking westwards. The site is on the edge of town and has some domestic buildings and other disturbances 25 Mphaki Farmers Training Centre garden. Vegetation is mostly exotic: alien (*Cirsium* sp. visible), ruderal or agricultural (*Juglans* sp. and *Prunus* sp. visible).



Figures 26–29. Collecting sites during recent expeditions 26 steep roadside cutting with exposed rocks and flowering *Scenecio* sp. Alien species are evident, including *Salix* sp. growing in riparian zone and *Rosa rubiginosa* on the steeper slopes 27 seep with *Ranunculus* sp. flowers. Grazing and other agriculture evident in the image 28 large high-altitude wetland with *Ranunculus* sp. flowers. Evidence of agriculture is visible in the background 29 Sani Pass area, overgrazing and other human disturbance visible.



Figures 30, 31. Evidence of land degradation during recent expeditions **30** high grazing density at Letšeng la Letsie. Cattle, sheep, goats, horses and donkeys were observed **31** deep erosion gullies at Koro-Koro. Poor agricultural practices are the primary cause, for example ploughing of fields in the riparian zone (see fields in the background and in figs 11, 12). Scale bar: 1 m (**31**).

Table 2. Summary of families in major South African Diptera collections, both historic (AMGS, BMSA, DMSA, NMSA) and from recent collection trips (BMSA, NMSA). Higher classification follows Wiegmann et al. (2011), family sequence follows Kirk-Spriggs and Sinclair (2017a, b, 2021, in prep).

Higher Classification	Family	Historic Collections	Recent collection	Total
Tipulomorpha	Tipulidae	146	1	147
Psychodomorpha	Blephariceridae	19	1	20
Bibionomorpha	Psychodidae	0	8	8
	Bibionidae	2	35	37
	Keroplatidae	0	1	1
	Mycetophilidae	0	474	474
	Sciaridae	0	14	14
	Cecidomyiidae	0	7	7
	Scatopsidae	0	2	2
Culicomorpha	Culicidae	17	35	52
	Simuliidae	5	143	148
	Ceratopogonidae	0	13	13
	Chironomidae	7	16	23
Tabanomorpha	Vermileonidae	7	0	7
	Rhagionidae	9	122	131
	Athericidae	3	0	3
	Tabanidae	89	56	145
Stratiomyomorpha	Stratiomyidae	75	146	221
Unplaced Brachycera	Acroceridae	3	3	6
Xylophagomorpha	Nemestrinidae	29	3	32
Asiloidea	Bombyliidae	165	59	224
	Mythicomyiidae	0	3	3
	Asilidae	528	46	574
	Therevidae	3	3	6
	Scenopinidae	2	0	2
Empidoidea	Empididae	110	488	598
	Hybotidae	0	98	98
	Dolichopodidae	69	345	414
	Platypezidae	1	2	3
	Lonchopteridae	1	24	25
Phoroidea	Phoridae	1	6	7
Unplaced Cyclorrhapha	Syrphidae	318	490	808
	Pipunculidae	7	12	19
	Agromyzidae	19	88	107
	Periscelididae	0	1	1
	Sphaeroceridae	10	329	339
Acalypterata	Diopsidae	2	0	2
	Sepsidae	36	105	141
	Clusiidae	0	1	1
	Conopidae	15	4	19
	Sciomyzidae	6	2	8
	Lonchaeidae	13	46	59
	Platystomatidae	9	4	13

Higher Classification	Family	Historic Collections	Recent collection	Total
Acalypterata	Tephritidae	264	150	414
	Pyrgotidae	1	1	2
	Lauxaniidae	131	499	630
	Chamaemyiidae	61	106	167
	Milichiidae	32	1	33
	Chloropidae	72	284	356
	Chyromyidae	0	2	2
	Heleomyzidae	3	47	50
	Ephydridae	82	285	367
	Curtonotidae	3	11	14
	Diastatidae	0	2	2
	Drosophilidae	10	66	76
	Cryptochaetidae	1	1	2
Calypterata	Scathophagidae	65	37	102
	Anthomyiidae	30	150	180
	Fanniidae	1	33	34
	Muscidae	394	1770	2164
	Calliphoridae sensu strictu	45	23	68
	Rhiniinae	17	62	79
	Sarcophagidae	266	36	302
	Rhinophoridae	1	14	15
	Tachinidae	228	328	556
	Oestridae	3	0	3
Totals		3436	7144	10580

Contributions towards this special collection

In all, historic South African collections and the recent expeditions have generated a collection of approximately 10 580 Diptera specimens from Lesotho (Table 2), excluding the material from the Lund Expedition. Despite this, there is little published information on the Diptera of Lesotho. That which is published is mostly in the South African Animal Life series, based on the Lund expedition (e.g., Alexander 1964; Hull 1964, 1967; Smith 1967). Other publications are fragmented and sporadic. The aim of initiating this Topical Collection in African Invertebrates is to bring this information together in one series, creating a resource for a diverse set of users. While we endeavoured to collect a diverse group of specimens, it is inevitable that some groups were sampled more thoroughly than others. This collection should be seen as a starting point for future research in Lesotho. Despite this, it is still of value for conservation practitioners in the region as it is the first attempt at a consolidated Diptera checklist for the country. The details of the collecting sites provided in Table 1 and the site photographs (Figs 2-29) are also intended to pre-empt repetition in future contributions to this Special collection but also allows future collectors to plan their trips with existing material in mind.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

BSM confirms ethical clearance, number NMB ECC 2022/02, forming part of project 542 of the National Museum, Bloemfontein, South Africa.

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Author contributions

Bellingan, Jordaens, Midgley and Muller conceptualized the project. Phoofolo, Jordaens, Midgley, Muller and Theron joined the fieldwork. Midgley and Muller wrote the first draft of the manuscript. Bellingan, Phoofolo, Jordaens and Theron commented on the draft.

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Data availability

All of the data that support the findings of this study are available in the main text.

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