Quaternary Science Advances 13 (2024) 100170

Contents lists available at ScienceDirect

Quaternary Science Advances

journal homepage: www.sciencedirect.com/journal/quaternary-science-advances

A zooarchaeological perspective on late pleistocene/early holocene human behaviour in the Maloti-Drakensberg region, southern Africa: The view from Ha Makotoko and Ntloana Tšoana rock-shelters, Lesotho

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ARTICLE INFO

Keywords:
Robberg technocomplex
Faunal analysis
Later stone age
Late pleistocene
Early holocene
Maloti-Drakensberg region
Southern Africa

ABSTRACT

Re-excavation of Ha Makotoko and Ntloana Tšoana rock-shelters in western Lesotho, produced abundant faunal remains (both macro and micro) from people using the Robberg technocomplex during the late Pleistocene (Ha Makotoko and Ntloana Tšoana (15.4–13.4 kcal. BP) and early Holocene (Ntloana Tšoana 11.1–10.2 kcal. BP). This faunal material allows us to identify the subsistence strategies they employed, using the unbiased Simpson's evenness index (1-D′), and Shannon's evenness index to track diet breadth. Detailed analyses of the sites' microfauna indicates that eagle owls and/or small carnivores — not humans — were responsible for introducing them into the deposits. A chi-squared test comparing diet breadth across the sites identifies hunting strategy, focused on size 2 and 3 migratory ungulates (equids, suids, and bovids), supplemented with size 1 and 4 bovids. Comparing the evenness values from Ha Makotoko and Ntloana Tšoana to published data from other Robberg-associated sites in the wider Maloti-Drakensberg region (Sehonghong, Rose Cottage Cave and Tloutle) allows variability in subsistence strategies to be addressed. A chi-squared test comparing ungulate size classes, small mammals and fish with the evenness index reveals two important statistical differences: the warm period occupation (16.5–14.3 kcal. BP) at Rose Cottage Cave presents a narrow diet heavily focused on size 3 ungulates (with a lack of fish). At the other end of the climate spectrum, cold conditions at Sehonghong immediately before the Last Glacial Maximum were associated with a narrow diet focused on intensive fishing, with lower-than-expected numbers of size 3 ungulates. The deposits at Ntloana Tšoana, Ha Makotoko, and Tloutle, along with the Younger Dryas-associated assemblage from Sehonghong, on the other hand, present broad diets. Fish and small mammals make more of a contribution to the expanding diet in the highlands. Our approach demonstrates the flexibility that makers of Robberg tools displayed in adapting to the changing climatic and ecological conditions of this high-elevation region in the interior of southern Africa during Marine Isotope Stage 2 and across the Pleistocene/Holocene transition.

1. Introduction

Over the past decade there has been renewed interest in the human behavioural implications of the transition from Middle Stone Age (MSA) to Later Stone Age (LSA) industries in southern Africa and their associated subsistence and mobility systems (Loftus et al., 2019; Low and Mackay, 2018; Pargeter et al., 2017a,b; Pazan et al., 2023; Porraz et al., 2016; Stewart and Mitchell, 2018a, 2018b.). In particular, the Robberg technocomplex, identified across southern Africa associated with bladelets, small flakes, freehand and bipolar core reduction, and a low frequency of formal tools (Pargeter, 2016), seems to have developed with the onset of the Last Glacial Maximum (LGM: 24.0–17.5 kcal. BP; Chevalier and Chase, 2016; Fitchett et al., 2016a) with early sites known from the rock-shelters of Melikane and Sehonghong in the Maloti-Drakensberg Mountains of Lesotho ~24 kcal. BP (Pargeter et al., 2017a,b; Pazan et al., 2023; Stewart and Mitchell, 2018a, 2018b). Both the Maloti-Drakensberg Mountains and the Caledon Valley to their west along the border between Lesotho and South Africa are rich in Robberg

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https://doi.org/10.1016/j.qsa.2024.100170
Received 21 November 2023; Received in revised form 5 February 2024; Accepted 7 February 2024
Available online 8 February 2024

sites (Fig. 1), with bladelets first appearing in earlier MSA assemblages, suggesting *in situ* development of miniaturised technologies (Loftus et al., 2019; Pazan et al., 2023; Wadley, 1997). Bladelet technologies are a remarkably flexible and economically efficient set of tool production strategies that can be made on small cores and produce more cutting edge by mass (Pargeter, 2016). Microliths are often found in archaeological sites from cold climates, habitats with low and/or highly variable rainfall, and with subsistence strategies focused on large migratory mammals (e.g. Elston and Brantingham, 2002; Goebel, 2002). The importance of reliably securing sufficient food and other resources under such time-stressed conditions may help explain why microlithic technologies, which express both the reliable and maintainable design strategies identified by Bleed (1986), were favoured in such environments, including those of late Pleistocene southern Africa (McCall and Thomas, 2009; Mitchell, 1988; Pargeter and Dusseldorp, 2022; Pazan et al., 2023).

The large-scale shifts in temperature and rainfall over the LGM likely drove substantial palaeoenvironmental changes, requiring hunter-gatherers to reshape their subsistence and settlement systems. The Maloti-Drakensberg Mountains and the Caledon Valley are connected by a steep gradient that affects temperature and precipitation, producing distinct biogeographic zones and affecting resource availability in ways that likely required flexible adaptive strategies, particularity under varying climatic states. Stewart and colleagues (2012, 2016) have developed a 'push-pull' model of landscape use for the region, supported by the distribution of radiocarbon dates (Stewart and Mitchell, 2018b), which proposes that during periods that were unstable, cold or dry, river valleys in Lesotho's well-watered highlands were most suitable for occupation. The model predicts that as the region became colder/drier, people moved into these highland river valleys as they continued to receive orographic rainfall. During warming periods and an increase in effective moisture, the western lowlands of Lesotho and adjacent parts of South Africa's Free State province within the Caledon Valley would have been less severe enabling people to live in both regions. However, under conditions of extreme cold, like those prevailing at the peak of the LGM, even the highlands were abandoned (Mitchell, 1995; Pargeter et al., 2017a,b; Stewart and Mitchell, 2018a, 2018b; Stewart et al., 2012, 2016). Stewart and Mitchell (2018a) also note that the frequency of fish to mammal bone during the late Pleistocene is highest in the highlands during cold periods (Layers BAS and RF at Sehonghong, ~25–23 and ~15.0–13.6 kcal. BP respectively). Invoking principles of hunter-gatherer subsistence variation in relation to climate developed by Binford (2001), they proposed that colder conditions in the highlands, initiated by the LGM, likely dropped effective temperatures below the 12.75 °C threshold where foragers can rely primarily on plant foods. In these situations, groups sometimes fallback onto aquatic resources such as fish (Binford, 2001). Under such cold conditions, the Drakensberg Afroalpine heathland belt (Mucina and Rutherford, 2006), dominated by nutrient poor C_3 grasses would have shifted down lowering ungulate carry capacity, decreasing encounter rates and increasing search costs for large game (Stewart and Mitchell, 2018a). Ungulate richness is tightly correlated with rainfall irrespective of habitat type (Faith, 2013), and search costs would indeed increase as the region dropped from intermediate to low rainfall. Stewart and Mitchell (2018a) propose that during particularly cold and dry periods, people packed into highland river valleys, expanding their diet to include fish as a substitute resource and source of fat. As the highlands would have maintained orographic rainfall, even dry periods would have supported riverine ecosystems allowing for regional intensification of fish.

Evidence for resource intensification can be modelled using diet breadth or 'taxa-free' evenness indices (Faith and Du, 2018; Faith and Lyman, 2019). The assumption is that as encounter rates with preferred (typically large) game decreases, people will add species they encounter, broadening the diet, reflected as a more even diet (Kelly, 2013; Stiner et al., 2000; Munro, 2004). If people encounter species that can be mass captured (ie. spawning fish or gregarious herd animals), the evenness index will lower as it is dominated by that resource category, reflecting a less even or narrow diet (Dewar et al., 2006). It should also be acknowledged that a narrow diet can reflect a poor-quality or resource-poor environment with a lower carrying capacity, causing people to focus on what few species are available (Zeder, 2012). At the other end of the spectrum, a broad diet can reflect a high-quality environment with abundant resources and higher carrying capacity (Zeder, 2012). This is why local palaeoenvironmental indicators are critical to understanding how people are using the landscape.

In 2022 Pargeter and Dusseldorp tested the fish intensification model at Sehonghong by comparing Stewart and Mitchell's (2018a) fish: mammal ratio to an unbiased Simpson's evenness index (1-D′) based on the mammal remains: ungulates, small mammals, and micromammals (and not fish). By not including the fish, they found a statistically insignificant weak positive Pearson correlation ($r = 0.38$, $p = 0.40$).

To test and further contribute to this model, we use both the macro and microfaunal remains from Ha Makotoko and Ntloana Tšoana Rockshelters. These two archaeological sites ~2 km apart along the Phuthiatsana River (Caledon Valley) are in the lowlands of western Lesotho with well-dated sequences, allowing us to investigate evidence for subsistence strategies and their palaeoenvironmental signals. These data increase the sample size from the lowlands and contribute an

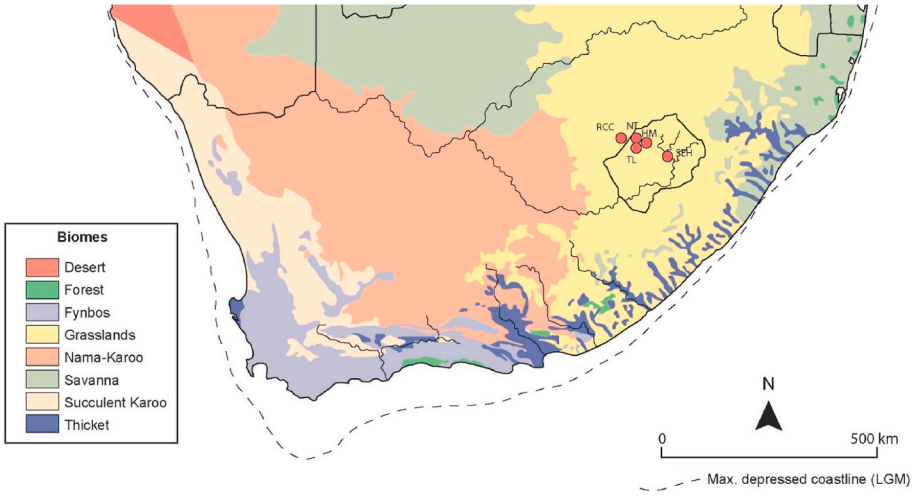

Fig. 1. Map of southern Africa and the study region showing the location of the sites mentioned in the text: HM (Ha Makotoko), NT (Ntloana Tsoana), RCC (Rose Cottage Cave), SEH (Sehonghong), and TL (Tloutle).

extensive micromammal study. We calculate evenness indices for these new sequences and compare our results to published faunal assemblages from the Caledon Valley and Sehonghong (Mitchell, 1993a, 1993b; Plug, 1993, 1997; Plug and Engela, 1992; Plug and Mitchell, 2008a, 2008b). As we argue below that the micromammals at Ha Makotoko and Ntloana Tšoana (and likely Sehonghong) are not anthropogenic in origin, we re-evaluate the correlation between the unbiased Simpson's evenness index (1-D′) at Sehonghong, replacing the micromammal category with fish, the animals that are being intensively captured.

1.1. Current environment and palaeoenvironmental signals

Our study region lies within the summer rainfall zone of southern Africa and experiences a continental climate with warm summers and cold winters. Rainfall is variable and depends on distance from the mountains. The uKhahlamba-Drakensberg Escarpment receives >1500 mm a year while the Caledon and Senqu Valley sites, lying in rain shadows, only receive between 580 and 700 mm a year (Bawden and Carroll, 1968; Stewart and Mitchell, 2018b). Temperature is moderated by altitude, with higher elevations (~3000 m a.s.l) reflecting much colder conditions with mean annual values of <6 °C on the highest mountains and ~15 °C in the Caledon Valley (~1600 m a.s.l.) (Grab, 1997). Snow can fall at any time of year, but especially the winter months, between May and September, persisting on south-facing slopes for up to six months, while frost is also widespread (Bawden and Carroll, 1968).

Aspect also affects temperature with north-facing slopes warmer than south-facing ones, impacting the distribution of vegetation. Today the Caledon Valley vegetation is characterized by a *Cymbopogon-Themeda-Eragrostis* C_4 grassland with numerous trees and evergreen shrubs that also intrudes along the lower reaches of the Senqu valley and its tributaries, including the Sehonghong River (Acocks, 1975). C_4 grasslands dominate below *c.* 2100 m a.s.l. while less palatable C_3 grasses (Afroalpine shrubland) dominate above *c.* 2700 m a.s.l. with mixed vegetation in between. However, the temperature differences based on aspect means that south-facing slopes see the transition to C_3-dominated Alpine vegetation already occurring at *c.* 2100 m a.s.l. (Parker et al., 2011; Roberts et al., 2013). Temperature changes in the past would have resulted in altitudinal movement of these vegetation zones (Roberts et al., 2013; Stewart and Mitchell, 2018b), even sustaining small glaciers at the highest elevations during the LGM (Grab and Knight, 2016).

By the early nineteenth century the range of medium to large faunal species in the Maloti-Drakensberg had been reduced from 61 in the Pleistocene/Holocene archaeological record down to 22 (Grab and Nash, 2020). By the 1820s there were already differences in species diversity between the highlands and the lowlands, likely due to continuously expanding human settlements blocking access for both migratory and non-migratory species to the highlands (Grab and Nash, 2020). Grazers were common with red hartebeest (*Alcelaphus buselaphus*) and mountain reedbuck (*Redunca fulvorufula*) known from both regions, while black wildebeest (*Connochaetes gnou*), plains zebra (*Equus quagga*), blesbok (*Damaliscus pygargus phillipsi*) and the now extinct blue antelope (*Hippotragus leucophaeus*) were present in the lowlands. In both regions eland (*Taurotragus oryx*), a mixed feeder, was common, along with two small species oribi (*Ourebia ourebi*) and klipspringer (*Oreotragus oreotragus*) (Plug, 1997; Plug and Mitchell, 2008a). Browsers including grey rhebok (*Pelea capreolus*), steenbok (*Raphicerus campestris*), and grey duiker (*Sylvicapra grimmia*) were also present in deep river valleys (Grab and Nash, 2020). By the 1860s, most of these species were either locally extinct or restricted to the highlands, where the last eland, red hartebeest, steenbok, as well as grey duikers were reported. Today, pockets of reedbuck, grey rhebok, oribi and klipspringer are all that remain, confined to the highlands (Grab and Nash, 2020).

Additional species identified from Robberg period sites in the region include the now-extinct giant hartebeest (*Megalotragus priscus*), blue wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*), roan (*Hippotragus equinus*), bontebok (*Damaliscus pygargus)*, and warthog (*Phacochoerus africanus*), with large grazers found primarily in the Caledon Valley (Plug, 1997; Plug and Mitchell, 2008b). Note that the archaeological evidence indicates that people also consumed geophytes like *Watsonia* spp. and *Moraea* spp., and a wide variety of fruits and seeds, likely including those of some grass species (Carter et al., 1988; Nic Eoin, 2015a,b, 2016). Along the Senqu — and perhaps other rivers — fish formed another important resource (Mitchell et al., 2011; Stewart and Mitchell, 2018a).

Previous palaeoenvironmental studies from Ha Makotoko and Ntloana Tšoana used stable isotopes of bulk soil organic matter, ungulate enamel, and plant wax biomarkers (Patalano et al., 2023; Roberts et al., 2013; Smith et al., 2002), to track shifting vegetation zones. The most recent synthesis of palaeoenvironmental proxy data from Ha Makotoko, ranging from ~60,000 to 1000 years ago, indicates the presence of a C_3-dominated ecosystem during the Pleistocene, while Holocene warming that promoted the expansion of C_4 grasslands only started around 5000 years ago (Patalano et al., 2023). The bulk $\partial^{13}C$ values suggest a shift towards a mixed C_3/C_4 ecosystem and a potential period of acute aridity between ~10 and 6.8 kcal. BP, while the phytoliths from the early Holocene deposits at Ntloana Tšoana are dominated by C_3 pooid forms but with a notable presence of panicoids and some C_4 chloridoids (Patalano et al., 2023; Parker et al. in prep). The hydrogen isotopes suggest a wet later Holocene compared to a dry but stable Pleistocene and early Holocene (Patalano et al., 2023). Overall, the stability of the climate in the region is predicted to have provided consistent and reliable resources during the Pleistocene, leading to persistent, though not continuous, occupation of the Caledon Valley (Patalano et al., 2023). It is important to note that there is no signal for the LGM (Chevalier and Chase, 2016) at Ha Makotoko.

The highland sites of Melikane and Sehonghong register occupation in the early LGM at 25–24 kcal. BP with reduced rainfall and increased cold, although remarkably, the presence of browsing antelope that require cover suggests that trees and shrubs were present in deep river valleys (Plug and Mitchell 2008; Stewart and Mitchell, 2018b; Stewart et al., 2012). In the Caledon Valley, lowered primary biomass likely led to reduced occupation (Loftus et al., 2019). Meanwhile people packed in along deeply incised river corridors in the highlands (Stewart and Mitchell, 2018a; Stewart et al., 2012, 2016), linked to intensifying the resource base to include more fish (Plug and Mitchell, 2008a; Stewart and Mitchell, 2018a). As cold conditions deepened, however, during the height of the LGM, the entire region seems to have been abandoned until ~16 kcal. BP when Sehonghong (Layers RBL/CLBRF) and Rose Cottage Cave (Layer DB) were re-occupied. This is also when peat formed at the Braamhoek wetland site, implying a revival of moister conditions (Chevalier and Chase, 2016). There may however have been very brief forays into the area registered by radiocarbon dates from Rose Cottage Cave and Sehonghong at 17,800 BP (22.2–20.8 kcal. BP) and 15,700 BP (19.0–18.6 kcal. BP; Loftus et al., 2019; Pargeter et al., 2017a,b).

As the climate warmed and became wetter, the Caledon Valley and the highlands both see more evidence for occupation, likely as primary biomass improved. Mean $\delta^{13}C$ and $\delta^{18}O$ values of 2.5‰ and 0.6‰ from grazer teeth at Rose Cottage Cave (Layer DB) signal cool temperatures (grazer diets with ~70% C_4 plants) and high moisture availability ~16 kcal. BP, becoming warmer and drier (diets of 90–100% C_4 plants) roughly a millennium later (Smith et al., 2002). Supporting this, Layer DB's charcoals contain frost-tolerant taxa typical of high altitude or fynbos vegetation regimes today. However, their diversity, and factor analysis results confirming high moisture availability, caution against overstating the ecological impoverishment of the pre-Holocene landscape (Esterhuysen, 1996). Sehonghong's taxonomically diverse terminal Pleistocene assemblage again includes smaller, browsing and canopy-loving antelope (Plug and Mitchell, 2008a), with a $\delta^{13}C$ sediment value of 19.8‰ from Layer RBL/CLBRF (~15.7–15.2 kcal. BP; Pargeter et al., 2017a,b) suggesting an enhanced presence of C_4 plants, and thus markedly warmer conditions, relative to the LGM (Loftus et al.,

2015).

This pattern did not last long, with the onset of the Antarctic Cold Reversal (ACR; 14.6–13 kcal. BP), precipitating widespread and sustained cooling of the Southern Hemisphere (Pedro et al., 2016). At Ntloana Tšoana, a low $\delta^{13}C$ value of 10.4‰ from a zebra tooth from the base of Layer BLOS (equivalent to Phase 5b) indicates a diet almost entirely composed of C_3 plants and, by extension, annual temperatures 6 °C lower than present ~14.0 kcal. BP (Smith et al., 2002), matching the sediment isotopes from the same layer (Roberts et al., 2013). Similar conditions seem likely at Sehonghong where Layer RF returned a $\delta^{13}C$ sediment value of 21.8‰ (Loftus et al., 2015) dated, at two-sigma, by several radiocarbon determinations to ~14.9–13.7 kcal. BP (Pargeter et al., 2017a,b). Pollen, phytoliths, diatoms, and charcoals at Braamhoek signal wetter conditions from ~14 kcal. BP, while fynbos pollen taxa indicate persistent cold (Finné et al., 2010; Norström et al., 2014).

In contrast, the succeeding two millennia are poorly understood, though evidence of dryness and variable cold is widespread in the summer rainfall zone, perhaps in response to the Younger Dryas stadial (~13.0–11.5 kcal. BP). Thereafter, between ~11.5 and ~8.5 kcal. BP the region went from a cool, heavily grass-dominated open landscape to a warmer, more fragmented environment with more woody vegetation (Stewart and Mitchell, 2018b). At the very start of the Holocene (~11.5–11.1 kcal. BP), the Caledon Valley experienced mild to considerable warming relative to earlier phases of the Last Glacial-Interglacial transition. $\delta^{13}C$ sediment values at Ha Makotoko imply greater input of C_4 plants relative to those dating to the Antarctic Cold Reversal at nearby Ntloana Tšoana (Roberts et al., 2013); a mean $\delta^{13}C$ value of 2.3‰ from grazer teeth at the same site implies a ~60% C_4 grassland with temperatures only slightly cooler than present (Smith et al., 2002). The same proxies then show a sudden cold reversal just after 11 kcal. BP, followed by high-magnitude oscillations between warmer and cooler temperatures that cannot be resolved closely in absolute time because of rapid sedimentation (at Ntloana Tšoana) combined with the effects of the early Holocene radiocarbon plateau (Roberts et al., 2013). A sharply cold episode is, however, clearly indicated ~10.5 kcal. BP when faunal $\delta^{13}C$ signals at Ha Makotoko imply an almost wholly C_3 grassland (Smith et al., 2002).

Thus, when it was cold and dry people were living in the Sehonghong and Melikane valleys in the highlands. The warming and higher moisture content from 16 to 15 kcal. BP saw occupation at Sehonghong (Layers RBL/CLBRF) and in the Caledon Valley at Rose Cottage Cave (Layer DB) and Ha Makotoko. The return to cooler conditions during the Antarctic Cold Reversal saw occupation at Sehonghong (Layer RF) and Ntloana Tšoana (Layer BLOS, broadly equivalent to Phase 5b as discussed here). During the onset of the Younger Dryas there was an ephemeral Robberg occupation at Sehonghong (Layer BARF) in the highlands, and finally a post-Younger Dryas early Holocene occupation at ~11–10.5 kcal. BP at Ntloana Tšoana (Phase 5a and BLOS a).

2. Stratigraphic background

Ha Makotoko (29°20′S, 27°48′E) and Ntloana Tsoana (29°19′19″S, 27°49′05″E) rock-shelters were located ~2 km apart on the southern bank of the Phuthiatsana River, the largest tributary of the Caledon River in western Lesotho. Situated within Clarens Formation Sandstone at an elevation of ~1640 m above sea level, both sites were drowned by the impoundment of the Metolong Dam in 2014. With a total area of 820 m^2, a dripline some 60 m in length and a maximal depth of 22 m, Ha Makotoko was by far the largest rock-shelter along the Phuthiatsana (Esterhuysen and Mitchell, 1997; Mitchell, 1993a, 1994; Plug, 1997; Mitchell and Arthur, 2014). Ntloana Tsoana was smaller, but still substantial, with a total area of ~280 m^2, a 20 m-long dripline and a maximum depth of ~16 m.

Both rock-shelters were originally excavated by one of us (PM) in 1989 (Mitchell, 1993a). However, at that time the LSA sequences at both sites were understood to begin with the non-microlithic Oakhurst technocomplex and no trace of a Robberg technology was identified at either of them. The sites were re-excavated in 2009 and 2010 (Fig. 1) by a team led by Charles Arthur ahead of their flooding by the Metolong Dam. The new, much larger excavations produced abundant archaeological material, including faunal remains ranging from the late Pleistocene to the late Holocene (Arthur et al., 2018; Mitchell and Arthur, 2014). They also significantly expanded our knowledge of the sequence at both sites, identifying a series of MSA assemblages at Ha Makotoko and producing occupational debris attributable to the Robberg at both sites. In the case of Ha Makotoko this material comes from Trench 52 near the rear of the rock-shelter and from the Phase 8 deposits in the main excavation area (Trench 54). The Robberg assemblage from Trench 52 is described by Mitchell and Arthur (2014), while that from the Phase 8 component of Trench 54 has recently been analyzed as an undergraduate dissertation at the University of Oxford (Seneši, 2023). At Ntloana Tšoana Robberg material is now recognized from both Phase 5a and Phase 5b of the site's deposits and is under study as part of a doctoral dissertation at the University of Oxford (Arlt in prep.). Excavation methods along with brief descriptions of the relevant sedimentary contexts are covered by Mitchell and Arthur (2014) for Ha Makotoko and Arthur (2018, 2022: Table 1) for Ntloana Tšoana.

Two radiocarbon dates are available for the Robberg assemblage from Ha Makotoko, one from Trench 52 (12,580 ± 35 BP, 15,106–14,535 cal. BP), the other from Trench 54 (12,781 ± 51 BP, 15,374–15,006 cal. BP). They overlap at two-sigma, suggesting a relatively short post-LGM occupation pulse when the region was warming, and the relevant faunal data are combined in our analysis. The situation at Ntloana Tšoana is more complex. The much higher-level resolution excavations of 2009–10 place the first of the site's two Robberg occupations in Phase 5b. Three AMS radiocarbon dates place Phase 5b between 12,330 ± 30 and 11,830 ± 90 BP (14,806–14,079 and 13,991–13,461 cal. BP respectively). A fourth, conventional radiocarbon date from the 1989 excavation of the site that most likely equates to contexts immediately overlying this series overlaps with these other dates (Pta-5236: 12,110 ± 120 BP, 14,764–13,606 cal. BP). A significant hiatus then appears to have intervened in Ntoana Tšoana's occupation, broadly coincidental with the Younger Dryas stadial and the earliest centuries of the Holocene. Phase 5a has two radiocarbon dates. Both come from the older part of this phase and are broadly consistent when calibrated at two-sigma with a further date (Pta-5237) from the site's original excavation. In conjunction with the radiocarbon dates available from the overlying deposits of Phase 4 of the Ntloana Tšoana sequence, they suggest that Phase 5a dates to *c.* 11,100–10,800 cal. BP. An earlier conventional date from the 1989 excavation of 10,200 ± 100 BP (Pta-5208) has an unhelpfully broad range when calibrated (12,434–11,281 cal. BP), cannot be linked to the more recently excavated deposits, and should probably be discarded. Two OSL dates obtained by Zenobia Jacobs from the same context in Phase 5a (12.2 ± 0.6 and 11.7 ± 0.8 kya) are not incompatible with the radiocarbon dates but may — like those from Phase 4 above them — have been affected by vertical movement of sediments through bioturbation (cf. Arthur, 2022).

3. Materials and methods

The faunal collections discussed here from Ha Makotoko and Ntloana Tšoana come from the 2009–2010 excavations. The Robberg period faunas recovered from the 1989 excavations were analyzed by Ina Plug (of the then Transvaal Museum, Pretoria, South Africa) and published in Mitchell (1993a) as Ntloana Tšoana Layer BLOS. Recognizing that Layer BLOS contains material which broadly equates with both Phases 5a and 5b, we present the data here as BLOS a (~Phase 5a) and BLOS b (~Phase 5b) in Supplementary Data Table 1.

3.1. Macrofauna

Morphological identification of the macrofaunal (>1 kg live weight)

Table 1
Calibrated and uncalibrated radiocarbon dates for archaeological faunal assemblages considered in this analysis (Mitchell and Arthur, 2014; Pargeter et al., 2017a,b; Loftus et al., 2019; Arthur, 2022; Seneši, 2023). As explained in the text, Tloutle Layer BC has no radiocarbon date and a date of 10,200 ± 100 BP (Pta-5208) from Ntloana Tšoana cannot be related to the Phase 5a/5b sequence. Two dates on bulk bones sample from Sehonghong have also been excluded as they cannot be tightly provenanced within the site's stratigraphy (Carter et al., 1988). All dates have been recalibrated using OxCAl 4.4 and SHCal 20).

Site	Layer	Laboratory number	Date BP	Dates 2-sigma cal. BP (OxCal 4.4 and SHCal 20)	Climatic observation
Ntloana Tšoana	Phase 5a	UGAMS-8979	9570 ± 30	11,081–10,692	Early Holocene, slightly cooler than present but wetter and significantly warmer than the Younger Dryas
		OxA-23231	9505 ± 55	11,074–10,523	
		Pta-5237	9420 ± 110	11,074–10,257	
Rose Cottage Cave	LB and DCM	Pta-7228	9340 ± 80	10,694–10,254	
		OxA-35528	9560 ± 40	11,083–10,604	
		Pta-7275	9560 ± 70	11,141–10,585	
Sehonghong	BARF	Pta-6065	11,090 ± 230	13,432–12,622	Younger Dryas stadial (13.0–11.5 kya), cold and dry
Sehonghong	RF	OxA-32926	12,010 ± 50	14,041–13,618	Antarctic Cold Reversal (14.6–13.0 kya), cool and wet
		Pta-6282	12,180 ± 110	14,804–13,771	
		OxA-32925	12,355 ± 50	14,822–14,084	
		Pta-6062	12,410 ± 45	14,847–14,166	
		OxA-32924	12,420 ± 50	14,856–14,177	
		Pta-6058	12,470 ± 100	15,030–14,148	
Ntloana Tšoana	BLOS	Pta-5236	12,110 ± 120	14,764–13,606	
Ntloana Tšoana	Phase 5b	OxA-X-2460-49	11,830 ± 90	13,991–13,461	
		UGAMS-8981	12,280 ± 30	14,316–14,060	
		UGAMS-8982	12,330 ± 30	14,806–14,079	
Ha Makotoko	Trench 52	UGAMS-11599	12,580 ± 35	15,106–14,535	Post-Last Glacial Maximum (17.5–14.6 kya), cool and humid, but becoming warmer and drier; significantly warmer overall than at the Last Glacial Maximum
	Trench 54	OxA-42907	12,781 ± 51	15,374–15,006	
Rose Cottage Cave	DB	Pta-5593	12,690 ± 120	15,480–14,359	
		Pta-5601	13,360 ± 150	16,494–15,601	
Sehonghong	RBL/ CLBRF	Q-3173	12,800 ± 250	15,934–14,200	
		OxA-32923	12,870 ± 55	15,556–15,145	
		OxA-32921	12,960 ± 55	15,647–15,258	
		Pta-884	13,000 ± 140	15,934–15,121	
		Q-3172	13,200 ± 150	16,241–15,333	
Sehonghong	BAS	Pta-6060	15,700 ± 150	19,341–18,691	Last Glacial Maximum (24.0–17.5 kya), cold and dry
		Q-1452	17,820 ± 270	22,253–20,890	
		Pta-6281	19,400 ± 200	23,782–22,973	
		Pta-918	19,860 ± 220	24,442–23,212	
		OxA-32920	20,270 ± 100	24,619–23,971	
		Pta-6077	20,200 ± 200	24,802–23,802	

assemblages followed standard zooarchaeological analysis and recording (Lyman, 2008). All elements were identified to the lowest possible taxon by comparison with the African mammal collection at the Royal Ontario Museum and the Savage Zooarchaeology Laboratory at the University of Toronto, Canada. The bone is highly fragmentary and primarily consists of unidentifiable pieces of trabecular bone and shaft fragments lacking evidence for a medullary cavity or diagnostic muscle markings. Due to the high number of ungulate and in particular bovid species in southern Africa, identifying fragmented bone to species and even genus can be difficult. All identified mammal specimens were minimally assigned to Brain's (1981) size classes: Size 1 = 5–23 kg, Size 2 = 23–84 kg, Size 3 = 84–296 kg, Size 4 > 296 kg; while Small mammals are <4.5 kg. In some cases, long bone fragments were attributed to size class based on cortical thickness (Reynard et al., 2014). To be recorded, long bone fragments had to present both an intact medullary cavity and periosteal cortical bone. The total number of specimens (bone and dentition) is presented as NSP. The element, side, end, and proportion were recorded following Klein and Cruz-Uribe (1984) to calculate the Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI). All evidence for taphonomic modifications was recorded. Heat alteration was identified on the basis of colour changes such as yellow-red to purple-red for scorched bone that has been exposed to fires ranging from 300 to 550 °C; blue-black for charred bone exposed to 600–900 °C; and white for calcined bone exposed to temperatures >1000 °C (Johnson, 1989; Shipman et al., 1984). To identify the primary accumulator of the large mammals, the identified bone was assessed for evidence of carnivore and/or rodent gnawing. Human modification to bone was also recorded including cut marks and percussion marks (Blumenschine et al., 1996), while weathering was recorded following Behrensmeyer (1978). Evidence for root and acid etching as well as rounding of the edges due to water rolling and surface flaking were recorded when present. Long bone fragmentation angle and shape were recorded after Villa and Mahieu (1991) to identify fresh versus post depositional or dry breaks. Experimental studies show that without post depositional breakage, ~4.5% of long bones show right angle or dry bone fractures (Marean et al., 2000a).

MNI values were calculated from the highest frequency of an element accounting for side and age based on the state of long bone fusion. Species richness is presented as NTAXA and Fisher's α ((NTAXA = α x ln (1+N/α), where N equals assemblage sample size), as NTAXA is known to be sensitive to assemblage sample size while Fisher's α is not (Faith, 2013; Lyman, 2008). Diet breadth or evenness was recorded using the unbiased Simpson's Index (1-D′) where $D' = \Sigma((ni(ni-1)/(N(N-1))$ and n_i is the abundance of taxon i and N the total number of individuals (species, NTAXA) (Faith and Du, 2018). The unbiased Simpson's index is a measure of dominance and represents the probability that two random samples will belong to the same taxon. D′ values range from 1/NTAXA when all taxa are equally abundant to 1 when an assemblage is dominated by a single taxon. It is presented as 1-D′ so that as evenness increases the value increases to 1. It is invariant to changing sample size, which means it presents an unbiased estimate of evenness, even when few taxa are recovered (Faith and Du, 2018; Faith and Lyman, 2019; Lyman, 2008). Shannon's evenness/equitability index was also calculated to confirm our results, with values ranging from 0 to 1, with 1 reflecting maximum evenness. It should be acknowledged that Shannon's evenness is more susceptible to rare taxa and small sample sizes, than the unbiased Simpson's evenness index and is only used to confirm the Simpson's index. To compare the results relevant to understanding diet to previously published data and to increase sample size, the evenness of the taxa is presented by ungulate (equids, bovids and suids) size class (1–4), small mammals, and fish based on MNI. For example, a MNI of three zebra and two wildebeest would contribute five individuals to the MNI category ungulate size 3. Additionally, two adult steenbok, a warthog, and a juvenile size 2 bovid would contribute four individuals to the MNI category for ungulate size 2. As NISP and MNI are both measures of taxonomic abundance that scale to each other in a predictable manner, either measure will reflect the data, while an overabundance of fish remains, and microfauna would make the use of NISP difficult to compare (Faith, 2008, 2013; Grayson, 1984; Lyman, 2008). Following Faith (2008), the comparative samples must have a total MNI of at least four individuals. We also present the fish:mammal ratio based on MNI to test the (Pearson's) correlation with the unbiased Simpson's evenness index. The chi-squared (χ^2) statistic was then used to compare the diet breadth across sites using the size categories (ungulate sizes 1–4, small mammals, fish). Statistical differences were identified using standardized residuals (−2<X > 2). All statistics were run in the software program PAST 4.0.

While, as noted above, Layer BLOS at Ntloana Tšoana dates to roughly the same periods as Phases 5a and 5b (Table 1), their data are presented here separately as they were identified by different analysts and come from different excavation blocks. We compare our results to the same variables for faunal assemblages belonging to the Robberg technocomplex from other sites in the Maloti-Drakensberg region: Sehonghong (Layers BAS, RBL/CLBRF, RF, and BARF), Rose Cottage Cave (Layers DB, LB, and DCM), and Tloutle (Layer BC) (Table 2) (Plug, 1993, 1997; Plug and Mitchell, 2008a, 2008b). Of note, the Robberg layers at Rose Cottage Cave were identified in three lenses, and, while the published faunal assemblage consists primarily of material from Layer DB (Late Pleistocene), bone from Layers LB and DCM dating to the early Holocene was also included in the analysis (Plug and Engela, 1992). The dates from the Rose Cottage Cave Robberg layers (LB, DCM, and LB) reflect the same occupation periods as Ha Makotoko, NT BLOSa and Phase 5a (Table 1), yet the faunal signature at Rose Cottage Cave is distinct. The dominance of size 3 ungulates and lack of size 1 bovids, small mammals, and/or fish at Rose Cottage Cave reflects a Late Pleistocene signal and suggests that much of the bone does indeed originate from layer DB. Unfortunately, unlike Ntloana Tšoana's Layer BLOS, we cannot separate out the data from LB, DCM, and DB and so treat the Rose Cottage Cave assemblage as a single Late Pleistocene deposit.

3.2. Microfauna

Ha Makotoko produced an unusually high frequency of micromammal remains throughout the deposit. These small bones and teeth are so abundant that they were identified separately producing two Masters theses, Zastrow et al. in prep identifies the elements to species, that were further analyzed using carbon and oxygen stable isotopes (Sparrow et al. in prep). The taxonomic study on the Robberg material focused on dental remains (molars, mandibles, and maxillae with and without dentition) of rodents and insectivores that were analyzed and recorded to the lowest taxonomic classification possible using a 10x–100× magnification Euromax microscope. We focused on dentition because the postcranial elements of most rodents cannot be identified to species. Several identification guides were used (e.g. Avery, 2007; De Graaff, 1981; Happold, 2013; Hillson, 2005; Monadjem et al., 2015; Skinner and Chimimba, 2005) as well as the microfaunal comparative collection from the Durban Natural Science Museum, South Africa. NISP and MNI were calculated to identify the most abundant species in the assemblage. Whereas NISP includes all skeletal elements, MNI is based on the most frequent skeletal element within a taxon (Lyman, 2008). Richness (NTAXA) and evenness (1-D') indices were also calculated for the microfauna (Faith and Du, 2018; Faith and Lyman, 2019; Lyman, 2008).

The taphonomic study used both cranial and postcranial remains and is based on the methods initiated by Andrews (1990) and Fernandéz-Jalvo et al. (2016) to identify the accumulating agent(s) responsible for the microfaunal assemblages. Different predators cause different kinds of modifications on teeth and bones. Thus, predator identification is based on the documentation of digestive corrosion, and etching intensity on teeth and bones and the skeletal element representation and bone breakage of the material following Fernandéz-Jalvo et al. (2016).

Table 2
Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) of the macrofauna at Ha Makotoko and Ntloana Tšoana.

Taxon		Ha Makotoko NISP/MNI	Ntloana Tšoana Phase 5b NISP/MNI	Ntloana Tšoana Phase 5a NISP/MNI
Serval	*Leptailurus serval*			1/1
Size 1 carnivore		1/1		
Size 2 carnivore				
Rock hyrax	*Procavia capensis*	14/2		
Hare	*Lepus capensis*	4/1		
Warthog	*Phacochoerus aethiopicus*	3/1		
Plains zebra	*Equus quagga*	3/1	1/1	1/1
Equid				2/[a]
Hartebeest	*Alcelaphus buselaphus*	2/1		
Blesbok	*Damaliscus dorcas*	1/1		
Alcelaphine		1/[a]		
Oribi	*Ourebia ourebia*	1/1		
Southern mountain reedbuck	*Redunca fulvorufula*	1/1		1/1
Grey duiker	*Sylvicapra grimmia*			3/1
Springbok	*Antidorcas marsupialis*	4/2		
Klipspringer	*Oreotragus oreotragus*			3/1
Blue antelope	*Hippotragus leucophaeus*		1/1	
Eland	*Taurotragus oryx*	1/1		
Bovid 1		3/[a]	2/1	10/[a]
Bovid 2		49/[a]	7/2	19/[a]
Bovid 3		20/1	2/1	11/1
Bovid 4		1/1		1/1
Mammal size class 1		209/[a]	52/1	99/1
Mammal size class 2		464/[a]	166/[a]	163/[a]
Mammal size class 3		121/[a]	20/[a]	40/1
Mammal size class 4		12/[a]	3/1	6/[a]
Small fish		5/1		
Medium fish		6/1	1/1	
Small bird	Song bird	4/1		1/1
Med bird	Goose size	38/3	1/1	
Large bird	Eagle size	1/1		
Small snake			2/1	
Medium snake		6/1		
Large snake				1/1
Tortoise		1/1	1/1	2/1
Frog		47/9		1/1
Lizard		4/1		
Black mussel	*Choromytilus meridionalis*	1/1		
Land snail	*Trigonephrus* sp.	1/1		
Total NISP		1677	260	365
Total MNI		36	12	13
MNI ungulates$_{1\text{-}4}$ +fish + small mammals		16	9	9
NTAXA		23	9	12
NTAXA ungulates$_{1\text{-}4}$ +fish + small mammals		11	7	7
Fisher's alpha		3.49	7.87	5.71
1-D′ ungulates$_{1\text{-}4}$ +fish + small mammals		0.86	0.89	0.86
Shannon's evenness index ungulates$_{1\text{-}4}$ +fish + small mammals		1.0	1.0	1.0

[a] No additional individuals were added to the calculation of MNI.

Predators were then categorized into three groups: nocturnal raptors (e.g. owls); diurnal birds of prey (e.g. kestrels) and mammalian carnivores, including humans (Dewar and Jerardino, 2007). Digestive corrosion was documented on molars and incisors as well as on bones, with a focus on the proximal femora and the distal humeri. The level of digestion follows the categories distinguished by Andrews (1990): light, moderate, heavy, and extreme but intermediate categories as "light/moderate" and "moderate/heavy" were also considered (cf. Rhodes, 2019).

Digestion on dental elements was counted on teeth that were more than three-quarters complete to prevent overestimation. Breakage was recorded for long bones and jawbones (mandible and maxilla) following Andrews' (1990) portion and breakage categories. Burning was identified on teeth and bones following the visual criteria and categories developed by Stiner et al. (1995).

3.3. Palaeoenvironmental proxies

To assess palaeoenvironmental conditions at Ha Makotoko and Ntloana Tšoana, we use modern analogue indicator species, such as the presence of browsers and suids, which prefer dense bushes and cover. We also comment on the prevelence of carnivores as a proxy for environmental health. The presence of southern African vlei rats (*Otomys irroratus*) and shrews reflects the local availability of moist dense vegetation, while Sloggett's vlei rats, also called ice rats (*Otomys sloggetti*), are adapted to cold, high-altitude environments (Skinner and Chimimba, 2005).

4. Results

4.1. Ha Makotoko

4.1.1. Macrofauna

Most of the bone from Ha Makotoko and Ntloana Tšoana was reduced to small unidentifiable pieces of trabecular bone or long bone shafts <1 cm in length and therefore lacking sufficient morphological features or medullary bone to identify it even to size class.

The NSP of the Ha Makotoko macrofaunal bone assemblage consists of 35,372 bones weighing 5.62 kg, of which 1677 were identified to size class or lower taxon (Table 2). This produced a high fragmentation index of 6.3 bones/g with an identification rate of 4.7%, which is typical of the region. Table 2 lists the NISP, MNI, NTAXA, Fisher's α, 1-D′, and Shannon's evenness index values for the identified specimens. Mammals dominate the assemblage, but various fish, birds, reptiles, frogs, and invertebrates were also documented. As many of the birds, reptiles, and invertebrates were likely deposited in the rock-shelter by carnivores or birds, they are not included in the analysis of the anthropogenically deposited prey species. All prey species were locally present in the precolonial past, but the presence of a black mussel shell (*Choromytilus meridionalis*) indicates a connection (via trade or long-distance mobility) with South Africa's Indian Ocean coast.

There is a low frequency of fish (MNI = 2) and small mammals (a

hare and two rock hyrax) while the ungulates consist primarily of size 2 and 3 migratory grazing species (Table 2). Size 1 (oribi) and 4 (eland) bovids are present though less common and reflect mixed feeders. The evenness index (1-D') = 0.86, which is relatively high and suggests an even or broad diet confirmed by the evenness index at 1.0. The seasonality of occupation is most likely to have focused on spring and summer as 27%MNI of the mammals (4/15) are juvenile.

4.2. Taphonomy

The high frequency of micromammals throughout the deposit at Ha Makotoko (Table 4) suggests that carnivores or raptors may have contributed to the macrofaunal assemblage, but low carnivore gnaw marks (0.5%) and a total lack of gastric acid etching suggests that they were not the primary accumulators (Table 3). The gnaw marks were found primarily on the small and medium size bird bones, but two size 2 and one size 3 mammal also presented puncture marks. There was only one small carnivore in the deposit and no juveniles that might indicate a den. The low frequency of surface flaking (1.1%) and abundant micromammal bone (Table 4) indicates that the pH of the sediments did not remove fragile carnivore juveniles through density mediated attrition. There was no evidence for rodent gnawing indicating they were not contributing to the assemblage either. The lack of size sorting and edge smoothing (<1 %), indicates that bone was not water rolled. The very low evidence for root etching suggests a rapid depositional rate while low weathering rates (0.9–2.6%), suggesting that bone was not exposed to the elements for extended periods. This indicates that geogenic factors are unlikely to have drastically affected the assemblage.

Evidence for human activities at the site is more compelling with 179 identified elements (10.7%) exhibiting cut-marks and 48 (2.8%) long bones exhibiting clear percussion marks. A high frequency of scorched and charred bone (34%) supports the identification of humans as the primary accumulator of the large mammals. While the proportion of calcined bone is low (1.7 %), it does reflect the presence of intentional, high temperature fires made and fed by humans. This level of burning would have weakened the bone, leaving it susceptible to breakage. This is reflected by an unusually high frequency of dry bone (post-depositional) breaks with 64 % of long bones exhibiting at least one dry break (Table 3) and a low mean long bone length at 2.93 cm ranging from 0.5 to 8.0 cm (Fig. 2). The high fragmentation and evidence for burning are likely obscuring evidence for carnivore gnawing and cut marks alike. The most compelling evidence is that humans were the primary accumulator of the large mammal remains.

Table 3
Number of Identified Specimens (NISP) and %NISP of macrofauna with taphonomic modifications at Ha Makotoko and Ntloana Tšoana.

Category	Ha Makotoko NISP/%NISP	Ntloana Tšoana Phase 5b NISP/% NISP	Ntloana Tšoana Phase 5a NISP/% NISP
Cut marks	179/10.7%	5/1.9%	6/1.6%
Percussion marks	48/2.8%	10/3.9%	14/3.8%
Scorched[a]	1544/4.4%	4/0.07%	31/0.4%
Charred[a]	10,411/29.4%	377/6.4%	917/10.8%
Calcined[a]	583/1.7%	993/16.9%	1019/12.0%
Carnivore gnawing/ punctures	8/0.5%	5/1.9%	0/0%
Rodent gnawing	0/0%	0/0%	0/0%
Gastric acid etching	0/0%	0/0%	0/0%
Surface flaking	18/1.1%	10/3.9%	23/6.3%
Root etching	4/0.2%	0/0%	0/0%
Water rolled	4/0.2%	0/0%	0/0%
Weathering 1	44/2.6%	27/10.4%	17/4.7%
Weathering 2	15/0.9%	23/8.9%	6/1.6%
Weathering 3	2/0.12%	13/5%	0/0%
Weathering 4	2/0.12%	0/0%	0/0%
Green breaks	124/36.3%	106/45%	156/45%
Dry breaks	218/63.7%	132/55%	188/55%
No. of long bone ends assessed	342	238	344
Mean length of long bones	2.93 cm	2.20 cm	2.65 cm
Range	0.5–8.0 cm	0.5–8.5 cm	0.5 to 9.4

[a] Scorched is yellow-red to purple-red; charred is blue-black; calcined is white. All %NISP values were calculated from total NISP with the exception of heat alteration values, they are evaluated against total NSP as the entire assemblage could be assessed. The green and dry break values are based on long bone breaks and are thus a smaller subset of the assemblage.

Table 4
Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) of microfaunal species at Ha Makotoko and Ntloana Tšoana.

Microfaunal species		Ha Makotoko NISP/MNI	Ntloana Tšoana Phase 5b NISP/MNI	Ntloana Tšoana Phase 5a NISP/MNI
Common mole rat	*Cryptomys hottentotus*	5/1		
	Cryptomys sp.	1/1		
Bats	Chiroptera sp.	9/3		
Golden moles	Chrysochloridae	2/1		
Namaqua rock rat	*Aethomys* sp.	1/1		
Vlei rat	*Otomys irroratus*	355/104		1/1
Ice rat	*Otomys sloggetti*	22/4		
	Otomys sp.	1006/105	2/1	3/*
Four-striped grass mouse	*Rhabdomys pumilio*	7/2		
	Rhabdomys sp.	1/1		
	Muridae sp.	5/2		
	Insectivora sp.	23/8		
Greater red musk shrew	*Crocidura flavescens*	22/3		
Forest shrew	*Myosorex varius*	63/7		
	Myosorex sp.	5/1		
Total		1527/244	2/1	4/1
NTAXA		9	1	1
Unbiased Simpson's Evenness Index (1-D')		0.47	1.0	1.0

4.2.1. Microfauna

A total NSP of 1,826 cranial and dental elements were present in the Robberg assemblage from Ha Makotoko, while the postcrania consist of 983 elements that can only be identified to order or class. The NISP of the microfaunal assemblage consists of 1,527 crania and dental elements (84 % identification rate) representing an MNI of 244 individuals with a NTAXA of nine species (Table 4). The species list is dominated by two species of vlei rat, *O. irroratus* (southern African vlei rat) and *O. slogetti* (Sloggett's vlei rat, also known as the ice rat), followed by the shrews *Myosorex varius* (forest shrew) and *Crocidura flavescens* (greater red musk shrew). The 1-D' value of 0.47 indicates a very narrow diet focused on *O. irroratus* (Table 4).

At least three kinds of taphonomic modifications are evident: digestion, breakage, and burning. Evidence of digestion was recognized on dental and postcranial elements, however, less than a quarter of all the examined teeth present traces of digestion: 19.0 % of molars and 15.3 % of incisors (Table 6). Most teeth with digestive etching are within the light to light/moderate range although ~2.2 % are moderate/heavy to heavy (Table 6).

Postcranial digestion was present on robust elements (Table 5): distal humeri (NISP = 78) and proximal femora (NISP = 7). The pattern of digestion on postcrania shows a higher frequency of destruction on the upper hindlimbs in comparison to the upper forelimbs, although there are fewer femora to assess. The postcrania with acid etching are again

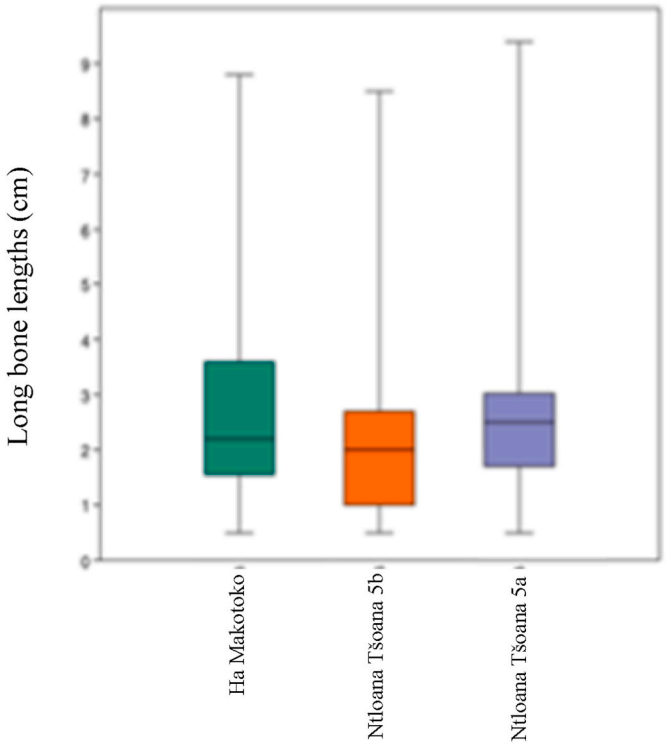

Fig. 2. Box plots of long bone lengths from Ha Makotoko, Ntloana Tšoana 5b, and Ntloana Tšoana 5a.

Table 5
Number of Identified Specimens (NISP) and %NSIP of microfaunal crania and postcrania at Ha Makotoko with evidence for digestive etching by digestion phase.

Digestion phase	Crania		Postcrania	
	Molars	Incisors	Proximal femora	Distal humeri
Light	80/7.3%	5410.6%	6/4.2%	39/16.9%
Light/moderate	51/4.6%	15/2.9%	1/0.7%	19/8.2%
Moderate	50/4.5%	7/1.4%		18/7.8%
Moderate/heavy	25/2.3%	1/0.2%		
Heavy	8/0.7%	1/0.2%		2/0.9%
Heavy/extreme				
Extreme				
Total NISP	1103	510	144	231
Total NISP digested	214	78	7	78
% digested	19.0%	15.3%	4.9%	33.8%

Table 6
Number of Identified Specimens (NISP) and %NISP of microfaunal long bone breakage patterns at Ha Makotoko.

	Humerus	Ulna	Femur	Tibia
Complete	3/0.7%	1/0.4%	2/0.7%	0/0%
Near complete	13/3.0%	8/3.4%	3/1.1%	0/0%
Proximal	138/32.0%	**132/55.5%**	**144/53.3%**	47/18.7%
Shaft	36/8.4%	67/28.2%	9/3.3%	79/31.5%
Distal	**231/53.6%**	30/12.6%	112/41.5%	**125/49.8%**
Total	431	238	270	**251**

within the light to light/moderate range although one specimen displayed heavy etching (Table 6). Comparing the data to Andrews's (1990) list of predator categories and the evidence for their impact on dental and postcranial elements, the most likely accumulator of the Ha Makotoko material is therefore a category 2 or 3 predator, such as an eagle owl (*Bubo* sp.) or small carnivore. Humans were not responsible for the deposition of the microfauna as they are a stage 5 predator (Dewar and Jerardino, 2007). Both small carnivores and an eagle owl-sized bird are present in the macrofaunal assemblage (Table 2).

Dental elements were isolated with only a few mandibles and maxillae with teeth in the assemblage. Overall, more molars were found *in situ* within alveolar sockets compared to incisors. The small amount of *in situ* teeth found indicates high cranial breakages, which demonstrates either consumption by a highly destructive predator such as diurnal raptors or small carnivores or destruction by trampling or sediment compaction. The low number of complete or nearly complete bones (2.5%) across the sample also indicates a destructive predator (cf. Andrews, 1990). The breakage distribution was calculated for the skeletal elements humerus, femur, ulna, and tibia for both rodents and insectivores.

The postcranial breakage pattern reflects a dominance of distal humeri, distal tibia, proximal ulnae, and proximal femora (Table 6). The sample reflects the resistance of long bone epiphyses that fuse first in the body and are therefore more resistant to destruction (Andrews, 1990; Fernandéz-Jalvo et al., 2016). The results of the relative completeness, as well as the proportional comparison of proximal against distal ends for postcranial elements, confirm the action of a moderately (category 2–3) destructive predator.

Burning was identified on both dental and postcranial remains with the highest percentage of burned bones and teeth identified as burning category 3, i.e. fully carbonized (Table 7). A total of 60 (6.1%) postcranial elements were burned, higher than the dental remains at 1.1 % (N = 15).

Summing up, it was therefore not humans but either eagle owls or small carnivores or both that introduced the abundant micromammals into the Ha Makotoko deposit.

4.3. Palaeoenvironment

The ungulates present in the Robberg fauna at Ha Makotoko are all grazers or mixed feeders, indicating the presence of grasses in the local environment. Oribi, mountain reedbuck, and blesbok are local territorial water-obligate grazing species. Migratory species include both large grazers (zebra and hartebeest) and large (eland) and medium (springbok) mixed feeders. The lack of small-bodied browsers may reflect a dry signal where forage was not high quality enough to support them (Olff et al., 2002), while the very low frequency of carnivores may also signal a dry or poor quality environment. The migratory species were likely present during the summer rains when fresh grass is available. The presence of warthog indicates dense vegetation, likely within the Phuthiatsana Valley. There are only a few fish, but nine frogs and the water-obligate species attest to the presence of standing water.

The abundance of *O. irroratus* signals a consistent presence of wet dense vegetation. Today, its sister species *O. slogetti,* the ice rat, typically lives above 2000 m a.s.l. in the C_3 Alpine heathlands of the Maloti-Drakensberg Mountains (Skinner and Chimimba, 2005) and signals a

Table 7
Number of Identified Specimens (NISP) of microfauna at Ha Makotoko by category of burnt dentition and postcrania.

Burning category	Molars	Incisors	Postcrania
1	1		
1/2			
2	1		5
2/3		1	10
3	6	4	29
3/4	1		4
4			3
4/5			5
5	1		3
5/6			
6			1

cool period. Together, the two taxa suggest that the region was wet and that C_3 alpine grasses had migrated down altitudinally as HM is ~1640 m a.s.l. The shrew species identified are also indicative of dense vegetation, while the presence of the Namaqua rock rat (*Aethomys* sp.) could signal arid periods as it prefers dry environments, including temperate grasslands.

Finally, we note the presence of a single black mussel shell. Today, black mussels grow from Namibia to Gqeberha (previously Port Elizabeth, Eastern Cape). As they prefer cold water the shell must either have come from ≥500 km away or the sea surface temperature (SST) of the Indian Ocean ~300 km away was colder than present.

4.4. Ntloana Tšoana phase 5b

4.4.1. Macrofauna and microfauna

A total NSP of 5,882 bones weighing 0.92 kg were excavated from the Phase 5b deposits at Ntloana Tšoana, but only 260 were identified to size class or lower taxon. This produced a high fragmentation rate of 6.4 bones/g and an identification rate of 4.4%. Table 2 lists NISP, MNI, NTAXA, Fisher's alpha, the unbiased Simpson's Evenness Index (1-D′), and Shannon's evenness index based on the identified specimens. Mammals dominate the assemblage and include a blue antelope (*Hippotragus leucophaeus*), a species that became extinct in the region during the nineteenth century, which has been identified in previous analyses of sites in the Caledon Valley in more recent Oakhurst contexts of early Holocene age (Plug, 1997). A small mammal, a fish, a bird, a tortoise, and a small snake were also documented. There is only one micromammal, an *Otomys.* sp. specimen, marking the Phase 5b assemblage as very different from that at Ha Makotoko.

In addition to blue antelope, the prey species consist of zebra and bovids of size classes 1, 2, and 4. As there is only one size 4 bovid in the region, the eland, and they are known to migrate with zebra this animal is likely an eland. Evaluating the evidence for diet, people were primarily encountering size 2 and 3 ungulates, producing an unbiased Simpson's index to 0.89 and the evenness index to 1.0 (Table 2), in other words a very even or broad diet. The relatively high proportion of juveniles at the site (2/8 or 25 % MNI of mammals) suggests that the occupation is likely to have been during spring and summer although other seasons are not discounted.

4.5. Taphonomy

The low frequency of rodents (MNI = 1) and other small animals suggests that neither small carnivores nor birds of prey contributed much to this assemblage. This is supported by the lack of any evidence for carnivores or carnivore gnawing in the assemblage (Tables 2 and 3). There is also no rodent gnawing on the bone. There is also very low evidence for geogenic processes affecting the assemblage: pH has not affected preservation since only ten elements (3.9%) exhibiting surface flaking, and fish and micromammal bone were preserved, even if in small numbers. There is no evidence for water transport nor root etching, while a slightly higher proportion of bone is weathered (0–10.4%) in the Phase 5b assemblage at Ntloana Tšoana than from Ha Makotoko, but still in relatively small numbers (Table 3).

Evidence for anthropogenic modifications includes five bones exhibiting cut-marks (1.9%), 10 (3.9%) presenting percussion marks, and 40% were exposed to fire. More importantly, 17% are calcined, reflecting exposure to a human-fed fire. This level of burning would have weakened the bone, leaving it susceptible to breakage. This is shown by a high frequency of post-depositional breaks; 55 % of long bones exhibit at least one dry break (Table 3) and the mean long bone length is 2.2 cm, ranging from 0.5 to 8.5 cm (Table 3, Fig. 2).

4.6. Palaeoenvironment

The identification of zebra and blue antelope (both large migratory grazers) suggests that grass was readily available, likely during the summer rains. The lack of any small-bodied browsers could suggest a dry environment as bushes and trees require higher precipitation than grasses, although the water obligate zebra indicates that some standing water was nearby. The lack of carnivores also suggests a potentially dry or poor-quality environment.

4.7. Ntloana Tsoana phase 5a

4.7.1. Macrofauna and microfauna

A total NSP of 8,465 bones weighing 2.55 kg were excavated from the Phase 5a deposits at Ntloana Tšoana, but only 365 were identified to size class or a lower taxon. This produced a relatively high fragmentation rate of 3.3 bones/g and an identification rate of 4.3%. Table 2 lists NISP, MNI, NTAXA, Fisher's α,1-D′, and Shannon's evenness index based on the identified specimens. Mammals (including a small mammal) dominate the assemblage, but, a serval, a bird, a tortoise, a frog, and a large snake were also documented. There are no fish and only one species of micromammal was identified, *O. irroratus.*

Evaluating the evidence for hunting strategy the prey species consist of large grazers (zebra and mountain reedbuck) and small-bodied browsers (grey duiker and klipspringer), plus a size 3 bovid and size 4 bovid (likely eland; see above). Evaluating diet breadth, the unbiased Simpson's index is 0.86 and the evenness index is 1.0. Once more these values reflect an even or broad diet (Table 2). The seasonality of occupation is likely to have been spring and summer as 22 % MNI of the mammals (2/9) are juvenile, although other seasons are not ruled out.

4.8. Taphonomy

Once more we see a very low frequency of micromammals, but the serval in the assemblage is known to hunt both day and night, preying on rodents (particularly vlei rats), small birds, frogs, lizards, and insects. However, there are no identified carnivore or rodent gnaw marks nor evidence of gastric etching (0%) on the large mammal assemblage, although a high level of fragmentation may be masking evidence for carnivory. Very few indications of geogenic factors are present. In fact, only 23 (6.3%) elements exhibit evidence for surface flaking and low numbers (0–4.3%) of bone exhibited weathering. With no evidence for root etching this suggests a rapid deposition rate.

Human modifications to the bone assemblage are slightly more convincing: six elements exhibit cut-marks (1.6%) while 14 (3.8%) have percussion marks (Table 3). Heat alteration was present on 35% of the assemblage and 12% of it is calcined, indicating exposure to human-fed fires (Table 3). Burning likely left the bone susceptible to post depositional breakage as 55% of the long bones exhibit at least one dry break and the mean size of the long bones is 2.7 cm, ranging from 0.5 to 9.4 cm (Table 3, Fig. 2). The lack of evidence for carnivore action on the bone suggests that humans were the primary accumulators of the large mammal assemblage.

4.9. Palaeoenvironment

The identification of zebra and mountain reedbuck, both water dependant grazers, suggests that the river is in flow while the migrating zebra suggests people were present at Ntloana Tšoana during Phase 5a when grass was palatable, i.e. during the summer rains. The identification of grey duiker and klipspringer, both browsers, suggests an increase in the amount of dense vegetation, signalling an increase in precipitation and/or warming or both. The low visibility of carnivores suggests that while the environment was improving, the range of carnivores had not yet returned to the region.

4.10. Statistical analysis

There is no statistical difference in the diet breadth of ungulates, fish,

and small mammals ($\chi^2 = 2.9$, df = 10, P = 0.98) between the three assemblages. This indicates that the people living at the two sites were primarily encountering size 2 and 3 grazing ungulates, although size 1 and size 4 bovids were also present. While there is very limited evidence for catching fish (Table 2), small mammals, and even birds, they are not abundant and do not seem to be an important part of the diet.

5. Comparing breadth of diet across the landscape

The MNI, NTAXA, Fisher's α, 1-D′, and Shannon's evenness index values for the Robberg deposits from the Caledon Valley are presented in Table 8. Assessing these data, we see that fish and small mammals make very little contribution to the overall diet, while size 2 and 3 ungulates are encountered most often. Size 1 and 4 bovids are present in high enough numbers to increase the evenness or the diet breadth in Layers BLOS a and BLOS b from the 1989 excavations at Ntloana Tšoana and Tloutle. However at Rose Cottage, the assemblage is dominated by size 3 grazers, causing the unbiased Simson's evenness index to drop to 0.56 (Shannon's evenness index is 0.70), indicating a narrow or specialised diet. While size 3 grazers are not prone to intensification, based on biogeographic principles, this pattern likely reflects people returning to the region, re-familiarizing themselves with the landscape and/or during a period with improving but not yet stable environmental conditions (Zeder, 2012). The lack of browsers from all but the early Holocene deposits at NT (Table 8) suggests that precipitation was not high enough to support the small-bodied bovids and people were potentially following migrating ungulates into the region during the late Pleistocene.

Comparing the unbiased Simpson's evenness index across the Caledon Valley produces a statistically insignificant difference ($\chi^2 = 30.4$, df = 30, p = 0.44) reflecting a consistent use of the landscape through the late Pleistocene and early Holocene.

The results for the Robberg assemblages at Sehonghong in the Lesotho highlands are quite different (Table 9). In these deposits fish do make a more substantial contribution to the diet ranging from 14 to 59% of total MNI. The evenness indices reflect a relatively broad diet in all layers except for Layer BAS. The LGM deposit (Layer BAS) presents a narrow or specialised diet with an unbiased Simpson's index of 0.61 and a Shannon's evenness index of 0.74 with fish driving the trend in the data. As fish can be intensified, we are likely seeing a low ranked species being elevated to a high ranked species through mass harvesting. The consistent presence of browsers (14–31% of ungulates) throughout the deposit suggests more C_3 bushes and shrubs were available (higher rainfall) than we see in the lowlands, likely in the deep river valleys.

Comparing the unbiased Simpson's evenness index across the deposits at Sehonghong produces a statistically significant difference ($\chi^2 = 40.7$, DF = 15, $p < 0.0003$) driven by a higher-than-expected number of fish in Layer BAS (standardized residual = 3.15) and lower than expected number of fish during the warm period Layer RBL/CLBRF (standardized residual = −3.3) reflecting a different use of the landscape through the late Pleistocene.

Comparing the faunal signals from the lowland and highland deposits, there is a very significant difference ($\chi^2 = 129.2$, DF = 50, $p < 0.000001$). The warm Post Last Glacial assemblages at Rose Cottage and Layer RBL/CLBRF at Sehonghong, have fewer fish than expected (standardized residuals = −2.95 and −2.43 respectively), while unsurprisingly Rose Cottage has more size 3 ungulates than expected (standardized residual = 4.1). Layer RBL/CLBRF does have some fish, but at this time people relied more heavily on small mammals to diversify the diet. Layer BAS has higher than expected fish (standardized residual = 5.4) while lacking size 3 bovids (standardized residual = −2.1) compared to the other deposits. This suggests that at the onset of the LGM people were not encountering the same number of size 3 ungulates, likely due to a reduction in good quality graze, or an increase in search costs if the ground was covered in snow (cf. Stewart and Mitchell, 2018a), with the result that people were intensifying fish.

While we do not know exactly when Tloutle's Robberg Layer BC dates to, it also has lower than expected fish (standardized residual = −2.0) but more than expected small mammals (standardized residual = 2.19), which is quite like the RBL/CLBRF assemblage. This suggests that it could have been occupied during a warm period or that its occupants simply did not access fish at the site and instead relied on small mammals; in contrast to Sehonghong, Ha Makotoko, and Ntloana Tšoana, but, just like Rose Cottage Cave, Tloutle does not have immediate access to a river.

Comparing the unbiased Simpson's evenness index with the fish: mammal ratio calculated using MNI, there is a statistically significant negative correlation for the Sehonghong Robberg assemblages (r = −0.97, p = 0.03), indicating diet breadth narrows when fish are increasing relative to mammals. This supports the Stewart and Mitchell (2018a) model that fish are intensively harvested during the cold occupations. The lowland sites, however, produce a moderately positive

Table 8
Minimum Number of Individuals (MNI) and %MNI of prey size categories, fish:mammal ratio, NTAXA, Fisher's alpha, the Unbiased Simpson's Evenness index (1-D′), and Shannons's Evenness index and in chronological order from the Caledon Valley.

Site	Fish	Small Mammal	Ungulate 1	Ungulate 2	Ungulate 3	Ungulate 4	Fish: mammals	NTAXA	Fisher's alpha	1-D′ Ungulate $_{1\text{-}4}$ + fish + small mammal	Evenness Ungulate $_{1\text{-}4}$+fish + small mammal
Ntloana Tšoana (Phase 5a)	0/0%	1/12.5%	2/25%	1/12.5%	3/37.5%	1/12.5%	0	7	5.71	0.86	1.0
Ntloana Tšoana (BLOSa contexts 24–29)	1/ 6.3%	3/18.8%	3/18.8%	3/18.8%	5/31.3%	1/6.3%	0.66	10	3.49	0.84	1.0
Ntloana Tšoana (BLOSb contexts 30–32)	0/0%	0/0%	1/20%	0/0%	3/60%	1/20%	0	4	3.17	0.70	1.0
Ntloana Tšoana (Phase 5b)	1/ 11.1%	1/11.1%	1/11.1%	2/22.2%	3/33.3%	1/11.1%	0.12	7	7.87	0.89	1.0
Ha Makotoko	2/ 12.5%	3/21%	2/12.5%	4/25%	4/25%	1/6.3%	0.14	11	3.49	0.86	1.0
Rose Cottage Cave (DB, LB and DCM)	0/0%	1/3.5%	0/0%	8/28.6%	17/61%	2/7.1%	0	23	1.28	**0.56**	**0.7**
Tloutle (BC)[a]	0/0%	5/38.4%	1/7.7%	3/23.1%	4/30.8%	0/0%	0%	7	1.97	0.76	1.0

[a] Tloutle has no date and is thus listed at the end of the table.

Table 9
Minimum Number of Individuals (MNI) and %MNI of prey size categories, fish:mammal ratio, NTAXA, Fisher's alpha, the Unbiased Simpson's Evenness index (1-D′), and Shannons's Evenness index and in chronological order from Sehonghong.

Site	Fish	Small Mammal	Ungulate 1	Ungulate 2	Ungulate 3	Ungulate 4	Fish: mammal	NTAXA	Fisher's alpha	1-D′ Ungulate $_{1\text{-}4}$ + fish + small mammal	Evenness Ungulate $_{1\text{-}4}$+fish + small mammal
Sehonghong (BARF)	5/ 26.3%	5/26.3%	2/10.4%	3/15.6%	3/15.6%	1/5.2%	0.36	10	3.02	0.84	1.0
Sehonghong (RF)	29/ 38.2%	12/15.8%	6/7.9%	13/17.1%	12/15.8%	4/5.2%	0.69	18	1.53	0.78	0.92
Sehonghong (RBL/CLBRF)	9/ 14.1%	14/21.9%	10/15.6%	12/18.8%	15/23.4%	4/6.3%	0.16	21	1.62	0.83	0.98
Sehonghong (BAS)	67/ 59.3%	10/8.8%	9/7.9%	9/7.9%	16/14.2%	2/1.8%	1.46	22	1.35	**0.61**	**0.74**

but insignificant correlation with the fish:mammal MNI ratio ($r = 0.60$, $p = 0.40$).

6. Discussion

The re-excavations of Ha Makotoko and Ntloana Tšoana identified a previously unknown Robberg period occupation at Ha Makotoko and increased the faunal sample from Ntloana Tšoana. Despite being only a few kilometers apart, the two shelters reflect different occupation pulses. The very high frequency of microfauna at Ha Makotoko suggests it was occupied by humans less extensively than Ntloana Tšoana, although the robust sample size during the Robberg period suggests that when Ha Makotoko was occupied it was for a longer period or included more people than Ntloana Tšoana. While occupied during different phases (Ha Makotoko during the Post Last Glacial warming period and Ntloana Tšoana at the beginning of the ACR and later during the early Holocene), the large mammal faunal assemblages appear to reflect a similar and consistently broad diet. The presence of large migratory species and the presence of juvenile individuals suggests that people continually used this landscape during spring and summer, although we cannot exclude their presence at other times of the year. The lack of browsers suggests that the carrying capacity and likely rainfall was too low to support these small bodied species during the late Pleistocene.

The only species identified that were not present in local historical records are the ice rat and the black mussel. The former likely reflects the descent of the alpine heath belt and therefore cooler conditions than present. The black mussel suggests social connections or long-distance movement to the coast, most parsimoniously that of the Eastern Cape, where the species now occurs as far east as Gqeberha, although it may have lived further north given colder late Pleistocene seas. Long-distance connections between inland sites and the coast are known from other Robberg assemblages, notably at Sehonghong, where a *Nerita* sp. pendant and a fragment of *Trachycardium* sp. shell in slightly later contexts dating to ~14.9–13.7 kcal. BP attest to links extending over a minimal straight-line distance of 200 km, allowing for exposure of the continental shelf (Plug and Mitchell, 2008a). Strontium isotope analysis of ostrich eggshell beads from the same layer (RF) indicates that they likely derive from areas where Ecca/Dwyka Group and Lower Stormberg Group rocks form the bedrock, i.e. from ≥110 to 160 km away (Stewart et al. 2020). Lower Stormberg rocks, we note, are exposed in the Caledon Valley where Ha Makotoko and Ntloana Tšoana are located and the Robberg assemblage at the former includes both beads and evidence of on-site bead production (Mitchell and Arthur, 2014). Although other connections are feasible, it is possible that the communities using Sehonghong and Caledon Valley sites during the late Pleistocene were connected via alliance networks that included movements of ostrich eggshell beads and seashell ornaments.

As far as diet is concerned, high evenness indices identify a subsistence strategy at both sites that focused on size 2 and size 3 ungulates, diversifying the diet to include size 1 and 4 bovids, adding small mammals and fish when encountered. However, neither fish nor small mammals were used as intensively in the Caledon Valley as they were at Sehonghong.

Acid digestion, breakage, and burning patterns showed that the mammalian microfaunas present, especially at Ha Makotoko, entered the deposit through the efforts of a category 1 and/or 2 predator, most likely birds of prey and/or small mammals. Likely candidates are the eagle owl-sized bird and small carnivores identified in the macrofaunal remains. In support of this determination, no elements exhibited evidence for a category 5 predator, a class that includes humans. This is important as it means that the microfauna should not be included in the evenness indices evaluating human hunting practices, unless there is other supporting evidence to include them as Holocene communities are known to have consumed rodents (Dewar and Jerardino, 2007; Jerardino et al., 1992).

6.1. Palaeoenvironmental conditions

In this study, the black mussel and the ice rats are the only new species to be identified for the study region. While the mussel is likely a trade item, the ice rats do contribute to the palaeoenvironmental story. The Ha Makotoko Robberg assemblage, like the Rose Cottage Cave and Sehonghong RBL/CLBRF layers date to the Post-Last Glacial warming period and all three sites produced abundant grazers and some mixed feeders indicating the presence of grasses in the local environment. At Ha Makotoko and Rose Cottage Cave territorial water-obligate grazers are present (oribi, mountain reedbuck, and blesbok), while large migratory grazers include zebra and hartebeest, plus large (eland) and small (springbok) mixed feeders. Additionally at Rose Cottage Cave four more grazers were identified including the territorial water-obligate roan and three migratory species: black wildebeest, giant hartebeest, and the now-extinct Bond's springbok (a specialised grazer). In the highlands at Sehonghong, additional species include the grazing blue antelope and bontebok, plus the browsing grey duiker and mixed feeding klipspringer, while giant hartebeest, Bond's springbok, and roan are not present. Abundant *O. irroratus*, *O. slogetti* and shrews at Ha Makotoko signal a consistent presence of wet dense vegetation, while the presence of the ice rat suggests that during some periods, C_3 alpine grasses migrated down altitudinally (likely reducing available fodder to short grasses). Finally, Namaqua rock rats signal arid periods, supporting the enamel isotopes from Rose Cottage Cave (Stewart and Mitchell, 2018b). Together the evidence suggests the Post-Last Glacial warming period saw fluctuating environmental change, but the dominance of grazers suggests consistent grasslands in the region, able to support a diversity of grazers, while at times the highlands also had more canopy available to support smaller browsers, likely in the deep river valleys.

Ntloana Tšoana Phase 5b and BLOS b date to the early part of the Antarctic Cold Reversal and their fauna consists primarily of large migratory grazing (zebra, blue antelope, and wildebeest/hartebeest), and mixed feeding species (eland). The lack of local/territorial species

suggests either environmental change reduced local ungulate populations and/or a shift in hunting strategies that targeted large migratory species. The high evenness indices for these layers suggests a subsistence strategy focussed on the local availability of nutrient-rich grasses improved, likely during the summer rains. The available stable isotope evidence indicates a predominantly cool and wet C_3 grassland environment during the Antarctic Cold Reversal (Patalano et al., 2023; Roberts et al., 2013; Stewart and Mitchell, 2018b), which may have brought poor quality short Alpine grasses down into the lowlands.

In the early Holocene faunal assemblage from Phase 5a and BLOSa at Ntloana Tšoana, on the other hand, the presence of small browsers in addition to the large migratory grazers suggests an increased availability of bushes and trees in the lowlands. Of interest is the lack of small browsers at Rose Cottage Cave from the early Holocene Robberg layers (DCM and LB). The emphasis on higher ranked species and lack of fish in all these layers could further support the argument for a warming-related increase in primary biomass that increased the availability of fodder for ungulates.

While the date of the Robberg-associated material at Tloutle is unclear, it also produced primarily large grazing species, including the migratory zebra and territorial water-obligate species (blesbok and mountain reedbuck), consistent with the warm signal late Pleistocene occupations at Ha Makotoko, Rose Cottage Cave, and even Sehonghong RBL/CLBRF.

6.2. *Regional diet breadth*

Comparing these results across the region, important patterns emerge. First, the focus on ungulates remains the same for all sites: size 2 and 3 ungulates were encountered more often than size 1 and 4 species. This suggests that even as primary biomass fluctuated people were recurrently present in the region during the summer when rainfall, temperature, and ecological productivity would have been at their highest.

Second, regional differences are apparent in the species selected for intensification. People in the Lesotho highlands at Sehonghong seem to have relied more heavily on small mammals and fish than those in the Caledon Valley (Tables 8 and 9). The highly negative correlation between the fish:mammal ratio and 1-D' reflects intensification of fish procurement in the highlands when the diet narrowed during the two coldest period occupations at Sehonghong (Layers BAS and RF), confirming the relationship between temperature and fish previously identified by Stewart and Mitchell (2018a).

7. Conclusion

The Robberg technocomplex remained relatively consistent through time from the LGM through to the early Holocene (Mitchell, 2002), indicating that the environment did not drive cultural innovations. The rock-shelters in the Maloti-Drakensberg region were occupied in pulses and at different times with lowland occupation associated primarily with warming conditions during the Pleistocene and early Holocene and the highlands during both cold and warm phases. The faunal data from these shelter deposits reveal flexibility in subsistence strategies as environmental conditions fluctuated: evidence for a narrow diet focusing on size 3 ungulates at Rose Cottage Cave, likely reflects people tracking migratory herds into the lowlands when summer rains rejuvenated C_4 grasses. As conditions improved, people moved further into the foothills using Ha Makotoko, Ntloana Tsoana, and Tloutle, where size 1 and 4 bovids, small mammals and fish were added to a broadening diet. By the early Holocene, small-bodied browsers were also available as shown in the deposit at Ntloana Tšoana. In the highlands, people encountered migratory grazers and small bodied browsers throughout the Pleistocene, likely possible due to orographic rainfall, also adding small mammals and fish to the diet. When the region became too cold and search costs for large grazers were too high (Layer BAS), people packed into highland river valleys, intensifying fishing, and otherwise narrowing the diet. We also record regional differences, with more extensive use of small mammals and fish at Sehonghong in the Lesotho highlands. This is likely due to altitudinally linked temperature shifts with poor quality grasses in the higher elevation Alpine heathlands descending through the highlands under colder conditions, effectively reducing the availability of fodder capable of supporting browsing and grazing ungulates alike. Ultimately, as the LGM reached its peak, this resulted in people effectively abandoning the region until the return of warmer conditions several millennia later (Stewart and Mitchell, 2018b).

CRediT authorship contribution statement

Genevieve Dewar: Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Julia Zastrow:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Charles Arthur:** Project administration, Investigation. **Peter Mitchell:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Data curation.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests.

Peter Mitchell reports financial support was provided by The World Bank Group. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We want to first thank two reviewers for their constructive criticism that improved the quality of the paper. We also thank the Metolong Authority for its support of our fieldwork at Ha Makotoko and the World Bank, the British Academy (Grant SG102337M), and the University of Oxford (through the Boise and James Fell Funds) for their financial assistance. We are grateful to Lesotho's Department of Culture and the people and chiefs of Aupolasi, Ha Masakale, Ha Matjeke, and Ha Seeiso for permission to excavate at Ha Makotoko and Ntloana Tšoana. A particular debt is owed to everyone who participated in the excavations, especially Will Archer, Kyla Bluff, Wesley Flear, Kate Leonard, Alex Mackay, the late Rethabile Mokhachane, Teboho Mokotjo, Puseletso Moremi, Chris Naisbitt, Pulane Nthunya, Ros O'Maolduin, Hugo Pinto, Joseph Ralimpe, and Aara Welz. Radiocarbon dates from the Oxford Accelerator were funded by a NERC grant (2011/2/4) and we thank Dr Tom Higham for his help in securing and interpreting them. Information on OSL dates was generously supplied by Dr Zenobia Jacobs (University of Wollongong).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.qsa.2024.100170.

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