ACKNOWLEDGEMENTS

We thank His Royal Highness Prince Sultan bin Salman, President of the Saudi Commission for Tourism and National Heritage (SCTH), and Prof. Ali Ghabban, Vice President, for permission to carry out this research. We also thank our Saudi colleagues from the SCTH, especially Jamal Omar, Abdulaziz al Omari, and Habeeb Turki for their support and assistance during fieldwork in Shuwaymis and Jubbah.
Financial support was provided by the SCTH, the European Research Council (grant number 295719, to MDP), and the Max Planck Society.
ABSTRACT

**Aim:** Our knowledge of the prehistoric distribution of animal species is so far largely dependent on the location of excavated archaeological and palaeontological sites. In the absence of excavated faunal remains, many species that were present in the Levant and North Africa have been assumed to have been absent on the Arabian Peninsula. Here we explore representations of four species that were identifiable in the rock art, but had not previously been reported in north-western Arabia.

**Location:** Jubbah and Shuwaymis UNESCO world heritage rock art sites in Ha’il province, north-western Saudi Arabia

**Methods:** In total, the rock art panels surveyed and recorded in Jubbah and Shuwaymis contain 6618 individual animal depictions. Species were identified based on diagnostic features of the anatomy. The resulting dataset was then compared to the faunal spectrum reported in the (archaeo)zoological literature.

**Results:** The rock art dataset provides evidence that the distributions of lesser kudu (*Tragelaphus imberbis*), wild camel, and African wild ass (*Equus africanus*) extended into the north-west of Arabia, and that the engravers may have had knowledge of aurochs (*Bos primigenius*).

**Main conclusions:** The presence of previously undocumented mammal species in Arabia provides new information regarding their distribution, as well as the types of habitat and vegetation that were available in prehistoric landscapes. Moreover, the presence of kudu on the Arabian Peninsula indicates that the identification of palaeo-distributions based exclusively on faunal remains may miss key species in the Afro-Eurasian faunal exchange.

**Key words:** African wild ass, aurochs, camel, Holocene environment, kudu, palaeoenvironment, palaeo-distribution, rock art, wild dromedary

INTRODUCTION

The Holocene and terminal Pleistocene biogeography and faunal record of the Levant, Anatolia, and the Zagros have been researched intensively over the past century. Within archaeology, research has strongly focused on hunting strategies and species targeted by Epipalaeolithic and Neolithic hunters, and on the distribution of the wild ancestors of domesticates. This focus on the contrast between pre-agricultural and agricultural periods has led to a situation where the distribution of animal species in the Fertile Crescent area of domestication is relatively well understood (see for example Martin 2016; Moore et al. 2000; Uerpmann 1987). However, with the exception of a small number of sites in Yemen, and along the Gulf coast, the Holocene faunal record of the Arabian Peninsula
remains largely unknown (Fedele 2008; Harrison & Bates 1991; Uerpmann 1987; 1991). This represents a substantial gap in our knowledge of the palaeo-distribution of taxa in the Middle East and limits our understanding of prehistoric habitats in the region.

In north-western Saudi Arabia, the lack of faunal remains is countered by a rich record of rock art, in which the prehistoric human populations of the area documented the fauna in their environment. Extensive rock art surveys carried out by the Palaeodeserts Project at the UNESCO world heritage rock art sites of Jubbah and Shuwaymis in Ha’il Province, Saudi Arabia, now provide a unique dataset with over 6000 animal depictions, which can be used in conjunction with the existing faunal record in Arabia to begin to close this gap.

While we can assume that the engravers and painters could only create naturalistic and anatomically accurate depictions of species they were familiar with, there are also a number of constraints that result from the ‘artistic filter’ that underlies the creation of these images. The frequency with which a particular species is depicted is culturally driven and probably relates to the symbolic value of the animal (Avner et al. 2016; Guagnin 2015; 2016; Rollefson et al. 2008). The rock art therefore allows a deduction of what species were present, but the frequency of the animal in the landscape and its economic importance can only be identified through skeletal remains of the animals themselves. Moreover, as we are dealing with mobile populations, we have to be able to show that the depicted species occurred locally, rather than reflecting animals seen elsewhere (see for example Masseti 2015).

To a large extent, these obvious limitations in the rock art can be countered by the use of large, systematic datasets, and by limiting the interpretation to those depictions that are clearly identifiable. Rock art also brings the additional benefit that patterns on the coat of the animals are often depicted and can be used to aid species identification. Similar approaches have successfully been used to identify animal species in the Sahara and in southern Africa (Gautier & Muzzolini 1991; Guagnin 2015; Loubser et al. 1990). Here we present compelling evidence from rock art for the identification of four novel large mammal species in the early and middle Holocene of north-western Arabia.

BACKGROUND

The oasis of Jubbah is located in the southern part of the Nefud desert, in the north-west of Saudi Arabia (Figure 1). Groundwater remains close to the surface and supports vegetation and irrigation agriculture today. During the Holocene humid period, increased precipitation and groundwater contributed to the formation of substantial palaeolakes in the Jubbah basin (Clark-Balzan et al. 2017; Engel et al. 2017). Hilbert and colleagues report an early phase of lake formation at ca 10,000 BC
Environmental evidence from the region suggests that the Holocene humid period peaked between 7000 and 6000 BC, when grasslands spread in the area and palaeolakes supported lush vegetation (Crassard et al. 2013; Dinies et al. 2015; Hilbert et al. 2014). Pollen records subsequently show a reduction in moisture availability; a more abrupt shift to aridity around 3900 BC is associated with changes in settlement patterns and an abandonment of landscapes in southeastern Arabia (Dinies et al. 2015; Preston et al. 2012).

No palaeoenvironmental records are currently known for the region around Shuwaymis, a landscape of relict wadi courses, flanked by sandstone escarpments. In wetter periods, the watercourses along these wadis were active and would have supported vegetation. A climate model for the area shows that during the Holocene humid period Shuwaymis was situated on the northern extent of the African Summer Monsoon (Guagnin et al. 2016).

Recent archaeological surveys and excavations in the Jubbah oasis have identified a number of sites that can be related to this emerging environmental record. An occupation site, dated to ca 8000 BC, was identified in the central part of the Jubbah oasis (Hilbert et al. 2014). El-Khiam and Helwan points, akin to those recorded in Pre-Pottery Neolithic (ca 9700-6250 BC) assemblages in the Levant (Crassard et al. 2013), and a large open-air site with artefacts relating to the Levantine Pottery Neolithic (ca 6250-5300 BC) (Guagnin et al. 2017b) were discovered on the edges of two smaller palaeolakes. Although settlement sites dating to the Bronze Age (ca 3500/3300-1200 BC) are not yet known from Jubbah, recent surveys have identified a body of Bronze Age rock art that is distinct from Neolithic and Iron Age imagery in stratigraphy, style and motif, and includes occasional representations of classic Bronze Age weaponry such as a double-convex bow and a lunate pommel sword (Figure 2; Guagnin et al. 2017a; see also Anati 1968; Newton & Zarins 2000). Bronze Age occupation at Jubbah was also confirmed through artefacts recovered from disturbed burial cairns, which include a perforated shell pendant radiocarbon dated to 2850 ± 80 calBC (Guagnin et al. 2017a). Although Iron Age settlements have yet to be identified in Jubbah, the rock art from this period is easily identifiable through the widespread use of so-called ‘Thamudic’ inscriptions, which accompany many figurative panels, and in the frequent depiction of domestic horse and camel (Figure 2; for a more detailed discussion of the rock art chronology see Guagnin et al. 2017a).

While direct absolute dating methods are not yet available for engraved rock art, it is possible to establish a relative chronology based on superimpositions, and changes in image content. Dated archaeological events such as the introduction of domesticated animal species, or the use of distinctive weapons are then used to correlate the rock art with dated archaeological contexts. We have consequently assigned the imagery discussed here to the early and middle Holocene (Figure 2). We cannot rule out that some engravings predate the Holocene. However, there is
currently no evidence in the archaeological record to suggest terminal Pleistocene occupation or rock art production.

In north-western Arabia cattle herding scenes are frequently superimposed on a body of earlier, “Pre-Neolithic” rock art that exclusively depicts wild animal species and hunting scenes with dogs (in the absence of established terminology we adopt Fedele’s (2008) term “Pre-Neolithic” here to describe the period preceding the adoption of food production). Since domestic cattle, sheep and goat were introduced before 6000 BC on the Arabian Peninsula (Drechsler 2007), the body of rock art that predates the presence of livestock must be older. Pre-Neolithic and Neolithic rock art also provide a reference to the landscapes of the Holocene humid period in representations of prey and carnivore species that are not supported in the current climatic regime (Guagnin et al 2015; 2016; 2017a; 2017c; see also Khan 2007; 2011; Olsen & Bryant 2013). Of the surveyed areas in Jubbah, ca 40% of individual animal depictions can be associated with the Holocene humid period (Guagnin et al 2017a); and on the western escarpment at Shuwaymis ca 24%

MATERIALS AND METHODS

Rock art data was collected between 2011 and 2016 in four survey seasons in Jubbah, and one in Shuwaymis (survey results and methodologies are reported in Guagnin et al. 2015; 2016; 2017a; Jennings et al. 2013; 2014). Specifically, the eastern escarpment at Shuwaymis, and 13 rocky hills (jebels) in the Jubbah oasis were systematically surveyed for rock art and associated archaeological sites (Figure 1).

To date, a combined dataset of 1405 rock art panels has been recorded, containing a total of 6618 individual animal depictions. These were registered in a specially designed Microsoft Access database, that links photographs of each motif with individual characteristics such as the animal species, level of preservation, and any details in the representation such as coat markings or horn shapes.

The resulting dataset was then compared to the faunal spectrum reported in the (archaeo)zoological literature. In general, there is a very close match between animal species recorded in the rock art and faunal remains (Guagnin et al. 2016). Here we present four species that were identifiable in the rock art, but had previously not been reported in north-western Arabia.

RESULTS

Lesser Kudu (*Tragelaphus imberbis*)
The lesser kudu (*Tragelaphus imberbis* Blyth 1869) is a large antelope with a shoulder height of up to 110cm, large ears, and a grey-brown coat with a white longitudinal stripe along the spine and vertical stripes along the body. Only the males have horns, which are long and have a characteristic double spiral twist. Lesser kudu are browsers, feeding on shrubs and trees; they extract sufficient moisture from their food but rely on succulent plants in the dry season and drink water where they can (Kingdon 1997).

Today, the distribution of the lesser kudu is limited to the Somali-Maasai Arid Zone of north-eastern Africa (IUCN Red List 2016; Kingdon 1997). In Arabia the lesser kudu is only known from two sets of horns that were recovered from hunted specimens in the 1960s (Harrison & Bates 1991; Figure 3). One was reputedly shot in south Yemen, and another in the mountainous area of western Saudi Arabia (Büttiker 1982). However, there is uncertainty as to whether the two Arabian specimens came from wild stock, because no other faunal remains or live animals of this species are known in Arabia (IUCN Red List 2016). Harrison and Bates (1991) suggest that the distance between the two locations in Arabia is larger than one would expect for introduced specimens.

In the rock art, representations of bovids with twisted horns were reported from the Yatib area near Hail, and from Jebel al Lawz north-west of Tabuk. However, in the absence of evidence for local bovid species with twisted horns, the representations were interpreted as stylized depictions of gazelles or cattle, rather than the representation of actual twisted horns (Khan 2007: 119pp). Animals with twisted horns were also reported from the eastern Badiah in Jordan, where they occur in small numbers in the rock art. Here, representations of addax (*Addax nasomaculatus*), greater kudu (*Tragelaphus strepsiceros*), and lesser kudu were considered (Rollefson et al. 2008). The addax is a large, white antelope with a shoulder height of 115cm, and long annulated horns that form loose spirals. In a stylized, two dimensional engraving addax are therefore indistinguishable from kudu, particularly where hide markings are omitted in favour of a fully pecked body, such as in the examples illustrated by Rollefson and colleagues (2008: 26).

**Evidence for lesser kudu in the rock art**

The Jubbah rock art survey now provides sufficient data to address uncertainties about the prehistoric distribution of lesser kudu. Of 4715 individual animal depictions, 91 were identified as kudu. There are a number of factors that contributed to this identification: A total of 18 animals were depicted with striped coats (Figure 4), and one image clearly shows the modular pattern of the longitudinal stipe and the vertical stripes that spring from it. Most importantly, STH 180 shows a herd of males on one face of a boulder and a herd of females with
calves and a single male on the adjacent face (Figure 5). This social organization of bachelor male groups and harem groups of females with offspring and a solitary male is typical of lesser kudu (Leuthold 1974). The females at this site are depicted without horns and show the large ears that are characteristic of this species. The coat markings, social organization, and absence of horns in females all suggest a depiction of kudu, rather than addax. Owing to the fact that two specimens of lesser kudu were reported from Arabia in the 1960s (Harrison & Bates 1991), we consider the images to be representations of the former.

In our sample of the rock art of Jubbah, kudu appear to be exclusively depicted in the earlier periods of rock art production, which are concurrent with the Holocene humid period. However, engravings reported by Khan (2007) on panels at Jebel al Lawz and the Tabuk area that can also be identified as kudu, may be later in date. Differences in style, weathering, and stratigraphic position indicate that within the Jubbah oasis kudu were depicted over multiple phases of rock art production (Figure 2), which suggests the portrayal of a local species.

Wild camel

The wild ancestor of the domestic dromedary remains somewhat elusive. Over the last two decades, excavations in south-eastern Arabia, largely in the territory of the United Arab Emirates, have produced faunal remains of ancient camels (Figure 6; Beech et al. 2009; von den Driesch & Obermaier 2007; Uerpmann & Uerpmann 2012). Based on osteological differences, principally a reduction in size and a change in the survival rates within dromedary populations, the shift from hunting to herding is dated to the transition between the Bronze and the Iron Age, between 1400 BC and 900 BC (Uerpman & Uerpmann 2012). However, it remains unknown if the camel was domesticated locally. The rest of the Arabian Peninsula, where the dromedary could feasibly have been domesticated, remains poorly documented from an archaeozoological perspective, thus knowledge about the biogeographical history of wild camel is incomplete. Faunal remains from coastal Yemen did not yield wild camel remains, leading Almathen and colleagues (2016, supplementary information) to hypothesize that the wild ancestor of the dromedary may already have been limited to south-eastern Arabia at the time of its domestication at the end of the Bronze Age. A small number of rock art panels in south-western Saudi Arabia are reported to show the hunting of wild camels, with the images attributed to the Bronze Age based on the weapons depicted in their hunt (Anati 1968; Macdonald 1990; Zarins et al. 1981). The wild dromedary likely became extinct towards the end of the Iron Age; excavations have so far not provided evidence for wild camels from younger sites (von den Driesch et al. 2008).
There is currently no valid scientific description of the wild dromedary, although *Camelus thomasi*, the extinct North African wild camel, and *Camelus “arabs”* have been proposed by various authors (von den Driesch & Obermaier 2007; Peters 1998; Uerpmann & Uerpmann 2012). Nothing is known about the diet or feeding behavior of wild camels (von den Driesch et al. 2008). Observations on free-grazing domestic dromedaries in the Sahara indicate that camels make periodic visits to areas with salty plants (halophytes) (Gauthier-Pilters & Dagg 1981). Likewise, veterinary studies on domestic camels suggest they require salt intake for their wellbeing, specifically for the prevention of diseases such as skin necrosis and arthritis (Peck 1939).

**Evidence for wild camel in the rock art**

In Jubbah nine camel depictions and one engraving of a camel footprint could be attributed to the initial Holocene on account of advanced patina and weathering, the position of the engravings underneath later petroglyphs, and the naturalistic style of the images which distinguishes them even from Pre-Neolithic hunting scenes and Neolithic herding scenes. The engravings in Figures 7, 8, and 9 show a clear variation in patina. While late engravings of domestic camels appear freshly pecked and light in colour (Figure 7), the petroglyph in Figure 8 shows that dark patina has formed over the pecked lines and suggests a much older age. The panel in Figure 9c in particular illustrates the relative difference in patina and preservation in a direct superimposition; later engravings are also engraved over the camel in Figure 8 (for a more detailed photograph see Figure 10). There is also a pronounced difference in the representation of camels in early and late engravings. While the former are larger and naturalistic, the latter tend to be small (10-30 cm) and highly stylized. Heavily patinated, naturalistic engravings of camels are thus associated with a very early period of rock art production. Since the domestication of the camel is currently dated between 1400 and 900 BC (Uerpmann & Uerpmann 2012), the recorded early engravings of camels predate domestication by several thousand years, therefore representing wild species (Figure 2).

**Aurochs (*Bos primigenius*)**

Similarities in osteomorphological features, in particular the post-crania, renders distinguishing between members of the tribe Bovini difficult. To date three species have been identified in the Middle East: Aurochs (*Bos primigenius* Bojanus 1827), wisent (*Bison bison*), and buffalo (*Bubalus* sp.) (Uerpmann 1987). While the buffalo was likely confined to the riverine habitats of the Mesopotamian lowlands, aurochs are well known across the Levant, Mesopotamia and beyond. On the Arabian Peninsula, evidence for the Holocene presence of aurochs was recently reported from eastern and southern Arabia (McCorriston & Martin 2009; see also Fedele...
2008). Aurochs can survive in a wide range of habitats, from wooded environments to open steppe, but require access to drinking water every few days. There is some evidence from rock art that African buffalo (*Syncerus caffer*) may also have extended into southern Arabia, but has not yet been confirmed by faunal remains (McCorriston & Martin 2009).

Early evidence for the domestication of cattle in the middle Euphrates region and the southern Levant has been dated to the seventh millennium BC (summarized in Drechsler 2007). In Anatolia cattle herding appears to have been well established by the eighth millennium BC (Peters et al. 2013), while in southern Arabia domestic cattle are known from the late sixth millennium BC (McCorriston & Martin 2009). In the more arid regions of eastern and southern Jordan livestock was dominated by caprine herding (Martin & Edwards 2013; see also Henry et al. 2003; Rollefson et al. 2014).

Evidence for aurochs in the rock art

In our sample only a single engraving in Jubbah from the naturalistic earliest phase of rock art creation appears to represent a member of the tribe Bovini. Below the engraved outline of the camel in Figure 8 an earlier, completely internally pecked engraving can be seen (Figure 10). Unfortunately, the engraved horns have exfoliated and are no longer distinguishable. However, the outline of the body is clearly visible. The shape of the neck and back, as well as the environment of the Jubbah oasis, suggest a representation of *Bos* rather than buffalo or bison. The stratigraphic position of this engraving, and the degree of naturalism in the outline, suggest the image pre-dates the Neolithic and belongs to the earliest rock art in Jubbah (Figure 2). We therefore consider it likely to be a representation of wild rather than domestic cattle. The only other securely identified engraving of an aurochs on the Arabian Peninsula was found at Kilwa, on the other side of the Nefud desert, close to the Jordanian border (Guagnin et al. 2015). It therefore appears that at least some of the inhabitants of Jubbah and the wider region were familiar with wild cattle. However, in the absence of further aurochs engravings and skeletal remains, it is not yet possible to establish if aurochs occurred locally or were seen by the engravers some distance away.

African wild ass (*Equus africanus*)

A small but growing body of data suggests the prehistoric presence of African wild ass (*Equus africanus* Heuglin & Fitzinger 1866) in the Levant and on the Arabian Peninsula (Cattani & Bökönyi 2002; Fedele 2008; Marshall 2007; Uerpmann 1991; Zarins 1986). At Ash Shumah in Yemen, 930 specimens of African wild ass were identified at a site radiocarbon dated to between 6684-6475 cal BC (Cattani &
Bökönyi 2002). At Ra’s al-Hamra in Oman, a number of bones were assigned to African wild ass and at Ain Qannas in Saudi Arabia 20 specimens were identified; remains at both sites were dated to around 5500 BC (Uerpmann 1991; see also Marshall 2007). The only other dataset from the Arabian Peninsula comes from Hili 8 in the United Arab Emirates, where 26 specimens were dated to the Bronze Age (3000 cal BC) (Uerpmann 1991; see also Marshall 2007; Figure 11).

The African wild ass is the ancestor of the domestic donkey (Equus africanus asinus), which was probably domesticated in north-east Africa (Beja-Pereira et al. 2004; Marshall & Weissbrod 2011; Rosenbom et al. 2015). There is some evidence that the morphology of early domestic donkeys remained undifferentiable from that of the wild ancestor for at least 1000 years (Marshall 2007; Marshall & Weissbrod 2011). Kimura and colleagues (2013) have therefore argued that the African wild ass remains in Arabia could be conflated with early domesticates (see also Marshall 2007). The earliest domesticated donkeys in North Africa are currently dated to around 4000 BC (Marshall & Weissbrod 2011; see also Grinder et al. 2006), and they may have spread into Arabia fairly rapidly. The identification of African wild ass in Natufian and Chalcolithic layers at three sites in Jordan (Marshall 2007; Uerpmann 1991), and a metatarsal dated to between 8000 and 7000 BC at Mureybit in Syria (Ducos 1986), confirms the presence of wild ass in southwest Asia. However, in the Levant the domestic donkey is not known before the Bronze Age. Here, the earliest evidence for the presence of domestic donkey currently dates to between 2800 and 3000 BC, and to the late 3rd to early 2nd millennium BC in Oman, although a slow rate of morphological change may make it difficult to identify early domesticates in the archaeological record (Marshall 2007).

A range of subspecies are recognized among the wild asses and there is no consensus in their identification and naming (see for example Kingdon 1997; Marshall 2007; Uerpmann 1987; Zarins 1986). The most common distinction is between two North African subspecies: Somali wild ass (E. a. somaliensis) with transverse barring on the legs, and Nubian wild ass (E. a. africanus), the likely ancestor of the domestic donkey, which has a shoulder stripe (Grinder et al. 2006; Kingdon 1997; Marshall 2007). Shoulder stripes are also reported from North African wild asses depicted in the rock art of the Atlas Mountains (Kimura et al. 2013).

African wild ass in the rock art of Jubbah and Shuwaymis

At Shuwaymis 10 of 31 wild equid depictions suggested a possible depiction of African wild ass. On one panel, an equid was re-engraved to enlarge the head and ears in proportion to the body in a possible modification of the animal from onager to African wild ass (Figure 12). However, the engraved outline of two such similar animal species cannot be taken as conclusive evidence (Guagnin et al. 2016) and...
subtle differences in the proportion of head and ears may reflect artistic license
rather than anatomical accuracy.

A recent survey in the Jubbah oasis provided the first evidence for the depiction of
African wild ass. On panel ORF 131A a large wild equid is clearly depicted with a
shoulder stripe (Figure 13). Shoulder stripes are absent in onager and therefore
serve as a secure distinction between both species. Moreover, the timing of the
image is comparatively well secured. The animal is superimposed by the earliest
known Chalcolithic or Bronze Age rock art in the Jubbah oasis. The fully patinated
elongated human figures visible on the panel are typical for the Neolithic of the area
(Khan 2007; 2011; Nayeem 2000; Olsen & Bryant 2013). However, the present panel
is the first recorded example that was engraved using a metal tool, and depicts
human figures with bronze or perhaps copper daggers. On the Arabian Peninsula the
beginning of the Bronze Age dates to the late 4th millennium BC (Magee 2014); the
earliest dates in the Levant are somewhat disputed but are thought to be between
3500 and 3300 BC (Regev et al. 2012) with the Chalcolithic dating back to the end of
the 5th millennium BC. If the engraved human figures with daggers date to the early
Bronze Age then the depiction of the African wild ass itself must date to the early 4th
millennium or earlier. On the other hand, if the human figures date to the
Chalcolithic, then the underlying wild ass may even have been engraved as early as
the 5th or 6th millennium BC. The engraving thus predates the earliest evidence for
domestic donkeys in the Levant (Figure 2), and presumably represents a wild
specimen. The presence of a shoulder stipe in the depicted individual indicates
similarity to the Nubian wild ass, rather than the Somali wild ass.

DISCUSSION

Our research has shown that rock art studies provide information on species palaeo-
distributions, particularly in areas where research on faunal remains is lacking. The
rock art data also demonstrated that even in areas with comparatively rich datasets,
such as in the archaeological and zoological records of the Levant, key species may
be missing in faunal lists. Additionally, the representation of herd compositions, and
coat markings in the rock art can provide information that is sometimes lacking in
skeletal remains and help to distinguish the presence of morphologically similar
species.

The relatively frequent depiction of bovids with twisted horns, often with vertical
stripes, their social organization in bachelor groups and harems, and the
representation of hornless females lead us to conclude that lesser kudu was present
in Saudi Arabia during the Holocene humid period. If the two specimens hunted in
the 1960s represent the last individuals of this population, kudu show remarkable
resilience in the face of aridification, and illustrate the considerable effect habitat
destruction and hunting have had on the diversity of mammals in Arabia (see Tsahar et al. 2009 for similar observations in the southern Levant).

Although kudu tend to maintain low population density, they must have been present in large enough numbers in the early Holocene to sustain their population longer term. The presence of palaeolakes is well attested at the oasis of Jubbah, with various lake phases dated to the early and middle Holocene, and palaeoecological reconstructions indicating well-vegetated environments (Hilbert et al. 2014; Crassard et al. 2013). Kudu are almost exclusively browsers (Estes 1991; Kingdon 1997), therefore there must have been trees and shrubs in the vegetation around the Jubbah palaeolakes.

It remains unclear when kudu arrived on the Arabian Peninsula and what route this dispersal followed. The complete lack of kudu identifications from Holocene faunal remains makes it difficult to trace any movements, although had they been common in the landscapes of North Africa and the Levant they would presumably have been noticed in the archaeological record. However, remains of *Tragelaphus* have been reported from the Middle Pleistocene site of Tighenif in northern Algeria (Geraads 2010) and confirm their dispersal during periods of wetter climate. The presence of lesser kudu in Saudi Arabia therefore raises the question whether they arrived during the Pleistocene and survived the Last Glacial Maximum in small refugia, yet in large enough numbers to sustain populations over some millennia. Alternatively, a dispersal of kudu during the Holocene humid period via the Sinai and Levant or the Red Sea is a possibility, as has been surmised for Middle and Late Pleistocene movements of other species (Breeze et al. 2016; Stimpson et al. 2016).

The distribution of wild camel remains currently known gives the impression that they were attracted to coastal environments and lagoons (Uerpmann & Uerpmann 2012). The presence of wild camel in the middle of the Nefud Desert confirms that their prehistoric distribution likely extended across all of the Arabian Peninsula, and that their habitat requirements, diet and feeding behavior may have been similar to those of the domestic camel. While domestic camel rely on humans to supply them with water (Gauthier-Pilters & Dagg 1981), wild camel would have been much more reliant on water sources in the form of springs and palaeolakes. Additionally, palaeolake deposits formed in multiple cycles of lake expansion and contraction (Hilbert et al. 2014; Crassard et al. 2013), may also have sustained the salty plants so sought after by camels (Gauthier-Pilters & Dagg 1981).

Although equid depictions are relatively common in Jubbah and Shuwaymis, only a single engraving had the body markings that enabled an attribution to *Equus africanus*. While the engravers and painters of Shuwaymis and Jubbah have so far been shown to depict local species (Guagnin et al. 2016), we cannot exclude the possibility that the African wild ass was seen somewhere else and then depicted in Jubbah. The archaeological record suggests wider reaching contacts (Crassard et al.
2013, Guagnin et al. 2017b; Hilbert et al. 2014) and at least some of the occupants of Jubbah would have been highly mobile. Similarly, we cannot be certain whether the depiction of an aurochs at Jubbah is the result of human or animal mobility. Nevertheless, the presence of large and medium-sized ungulates, such as kudu, onager, African wild ass, and aurochs reflects the extent to which the vegetation and rainfall regimes of the Holocene humid period opened up corridors across northern Arabia that enabled the movement of humans and animals.

The presence of lesser kudu, wild camel, and African wild ass shows that the Jubbah oasis was a focal point for animals from different habitats. Carnivores identified in the rock art include lions, leopards, and hyaenas. These carnivores were likely attracted to the Jubbah oasis by the rich available prey biomass (Guagnin et al. 2016). We note with interest that three of the previously undocumented species described here were present in Jubbah, but not in the Shuwaymis riverine zone. This opens up the possibility that oases like Jubbah may have provided refugia during periods of increased aridity, and provided stability and food security during episodes of drought. While we report four species that are identifiable in the rock art, our dataset also includes more ambiguous depictions. Engravings of mouflon or early domestic sheep are common and show horn shapes and hide markings. The distinction of wild and domestic sheep in the rock art requires more precise chronological controls than are currently available. However, in conjunction with the excavation and analysis of faunal remains, the rock art of north-western Saudi Arabia may provide further evidence on the palaeo-distribution of wild and early domesticated species in the future.

Prehistoric human populations documented many of the animals in their environments in paintings and engravings. Our data shows that faunal evidence from rock art contains valuable information that can be used to complement and strengthen datasets from skeletal remains. Rock art is found in most regions of the world and thus has an as of yet largely untapped potential to provide evidence on palaeo-distributions and biogeography.

REFERENCES


**FIGURE CAPTIONS**

**Figure 1** Satellite image of northern Saudi Arabia (top). White rectangles indicate the location of Shuwaymis (bottom left) and Jubbah (bottom right). Dashed lines indicate areas surveyed for rock art. All three satellite images are Google Earth,
Comparison of the chronology for rock art sites, individual engraved species, and archaeological contexts. Top: Darker shading represents more intensive rock art production. Representations of curvaceous women and of Bronze Age rock art were only identified in Jubbah (Guagnin et al. 2017a). Middle: Approximate timing of engraved species discussed in the text. Bottom: Domestic cattle and caprines were introduced to the Arabian Peninsula between 6,800 and 6,200 BC (Drechsler 2007); in the absence of dated early Neolithic sites in northwestern Saudi Arabia we have used 6,200 BC as a more conservative earliest date. Earliest evidence for domestic donkeys in the Levant currently dates to 3000 BC (Marshall 2007). Early dates for the presence of domestic camel and horse were documented in eastern Arabia (Magee 2014; Uerpmann & Uerpmann 2012) and we assume similar timing in Jubbah and Shuwaymis.

Current distribution of *Tragelaphus imberbis* (based on Kingdon 1997) shaded in grey. Locations of the two sets of horns found in Arabia indicated with stars (based on Harrison & Bates 1991). The hatched area indicates rock art representations of lesser kudu around the oasis of Jubbah.

Engraved scene from Jebel Umm Sanman (Jubbah) with a hunter and two lesser kudu (Panel JSM 60A; bottom left: original; bottom right: tracing). Coat markings and twisted horns are clearly visible in both kudu engravings. The image on the top shows the engraved rock surface with two large, stylized camels superimposed over the scene, and a scale.

Engraved boulder at Jebel Sateihah (Jubbah) with 12 male kudu on the west facing surface of the boulder (STH 180A, above) and one male, eight female and two young kudu on the south facing surface of the boulder (STH 180B, below). Engravings identifiable as kudu are traced in white, other engravings are traced in grey. A later engraving of a stylized camel and a wusum sign on panel STH 180A have not been traced. While the cellular markings on one of the females may represent a striped coat, this pattern is also frequently found on species that are not known to have coat markings, such as ibex.

Currently known Holocene distribution of wild dromedary (based on Uerpmann & Uerpmann 2012) shaded in grey. The hatched area indicates rock art representations of wild dromedary around the oasis of Jubbah.

Four late Holocene engravings of domestic camels from Jubbah. The engraving on the top left shows a saddle, while the engraving on the bottom left shows a rider. The camel on the bottom right is associated with an inscription.

Engraving of a large camel at Jebel Umm Sanman (JSM50). The boulder is approximately 3m in height and appears to have fallen over from its original
position. The depictions are therefore in a vertical position today. A number of later engravings can be seen superimposed over the top of the camel.

Figure 9 Engravings of wild camels at Jebel Umm Sanman in Jubbah. A: Detailed depiction of a camel’s head (JSM193) on a boulder directly in front of JSM50 (Figure 8). B: Eroded and patinated engraving of a camel footprint. C: Large and incomplete engraving of an almost live sized camel, superimposed by three engravings of later, domesticated camels (JSM211).

Figure 10 Left: Engraving of an aurochs at Jebel Umm Sanman (JSM50). The outline of the aurochs is traced in white, the superimposed camel is traced in grey. Right: detailed photograph of the superimposition of the camel hump and neck over the back of the aurochs.

Figure 11 Distribution of Somali wild ass (light grey) and Nubian/Saharan wild ass (dark grey) after Marshall (2007). Sites with faunal remains of African wild ass are marked with stars (after Marshall 2007; Uerpmann 1991). The hatched area indicates rock art representations of African wild ass at the sites of Jubbah and Shuwaymis.

Figure 12 Panel 105A at Shuwaymis showing an equid with a young being attacked by hunting dogs. The head of the adult equid was modified in prehistory to increase its proportion relative to the body.

Figure 13 Panel ORF 131A from Jebel Oraf in the jubbah oasis (above) and close up of the shoulder area of the equid (below). Pecked areas are traced in faded white. To the right of the equid three human figures are clearly visible. An additional figure is engraved on the belly of the animal, and a spear held by the figure is also superimposed on the animal. A fourth human figure can be seen to the left of the equid.
Figure 1
Figure 2
Figure 7
Figure 8
Figure 13

BIOSKETCH
Maria Guagnin is an archaeologist specialising in rock art research, with a particular focus on the relationship between the depicted animal species and the prehistoric environment and landscape. This study was carried out as part of her postdoctoral position with the Palaeodeserts project (www.palaeodeserts.com), a multidisciplinary team that examines the effect of environmental change on prehistoric human and animal populations in the Arabian Desert.

STATEMENT OF AUTHOR CONTRIBUTIONS

M.G. performed the analyses and wrote the manuscript with contributions from C.S., M.S., F.O. and M.D.P. All authors collected data in the field. A.A. facilitated collaboration with King Saud University and support in the field, and S.D. contributed panel identifications from her PhD research in Jubbah. M.D.P is the grant holder and PI of the ERC funded Palaeodeserts project and secured research permits and collaboration with the Saudi Commission for Tourism and National Heritage.