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Applying habitat suitability modelling to establish the species identity of ambiguous animal depictions in archaeology: new insights into the wild bovids of ancient Egypt

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ABSTRACT

For researchers studying wildlife distributions of the past, the assignment of faunal depictions and remains to species can often present considerable challenges. Regrettably, many studies do not systematically consider all options and sources of evidence and, as a result, questionable identifications are widespread in the literature, which compromises the trustworthiness of meta-analyses of human-animal interactions in an environmental context. Here we present a cross-disciplinary 3-step approach to species identification of ancient animal depictions and remains featuring habitat suitability modelling from the discipline of spatial ecology. By applying the protocol in a case study of selected images of wild bovids from Predynastic and Dynastic Egypt, we provide evidence that the zoogeographic origin of the faunal elements now locally extinct were in the Mediterranean and Sudanian bioregions without the need to invoke also the more distant Somalian and Zambezian bioregions as previously suggested. Such more moderate range shifts may primarily have promoted cultural exchange between Egypt and neighbouring communities in the Levant and Nubia, which is consistent with the archaeological evidence. The study highlights the potential of habitat suitability modelling to contribute to the identification of ambiguous species representations and faunal remains from the past, which in turn can allow testing of hypotheses on a wide range of central archaeological questions pertaining to introduction of animals and indigenous domestication, cultural exchange and trade, as well as human migration and dispersal.

1. Introduction

Present-day wildlife distributions are often poor indicators of past environments due to historic climate change and human impacts such as overhunting and habitat loss. Careful zoogeographic analysis is therefore critical to accurately reconstruct faunas of the past, which in turn is essential to understand interactions between ancient societies and the environment that they inhabited. (Pre-)historical depictions and remains of animals provide valuable information in this regard, but the interpretation of such material faces several challenges.

A significant obstacle is that the evidence may not be assigned easily to species. Depictions can be ambiguous due to stylistic conventions, idiosyncratic artistic expression, inferior craftmanship or poor preservation. Faunal remains, while often providing clearer evidence, have their own difficulties, in particular species identification is frequently complicated by significant overlap between species in morphological measurements of bones, with juveniles often indistinguishable from adults of smaller, related species. Moreover, both direct and contextual cues to dating of evidence can be elusive - and even where species identity and dating are unambiguous, the evidence may not always reflect the local wildlife populations if exotics were held in captivity or body parts imported as raw materials or trophies. In addition, macroecological studies of historical wildlife communities are also affected by the accident of archaeology, coined in the oft-quoted tenet that ‘the

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absence of evidence is not evidence of absence': biases in the preservation of evidence may result in some species formerly present having left no trace at all. Faced with all these potential sources of error, a key task for researchers of past animal distributions is to critically assess all the evidence available to weigh up alternative interpretations. In the literature, however, depictions are not rarely assigned to species without a justification that considers all relevant options (as we will demonstrate below).

Here we evaluate the usefulness of applying habitat suitability modelling (HSM) from ecology to distinguish between alternative species candidates when faunal records from the past are ambiguous. HSM exploits data on the current distribution of species to identify their environmental requirements (climate, topography, etc.) and, on this basis, extrapolates the suitability of habitats in other areas and/or time periods from which the necessary environmental information is available, either as data or simulations (Guisan et al., 2017). HSM is widely used in ecology and conservation both to identify current areas of suitable habitat, especially for threatened species (e.g. Segal et al., 2021), and to forecast how habitat suitability is likely to respond to predicted climatic changes (e.g. Payne and Bro-Jørgensen, 2016). In archaeology, HSM has so far been used only rarely and then primarily with the aim of hindcasting the distribution of human populations (e.g. pre-Columbian people, Sales et al., 2022; Neanderthals, Benito et al., 2017) and their domestic plant and animal species (buckwheat *Fagopyrum esculentum*, Krzyzanska et al., 2022; millet, Shao et al., 2024; cattle, Conolly et al., 2012; Phelps et al., 2020; for an example using HSM to predict the location of archaeological artefacts, see Gillespie et al., 2016). However, HSM can also offer revealing insights into the likely distribution of wildlife species in the past by modelling their ecological niches and potential dispersal corridors as a function of paleoclimatic simulations. This information can then be used to assess the likelihood of morphologically plausible alternative species identifications for enigmatic faunal records.

The long-term record of faunal depictions and remains from Holocene Northeast Africa presents an exceptional opportunity to investigate links between climate change, biodiversity and sociocultural development (Yeakel et al., 2014). Increasing rainfall caused sub-Saharan savannah landscapes to spread northwards, and Mediterranean vegetation southwards, during the African Humid Period (13000-3000BC), but this Green Sahara phase eventually came to an end when North Africa witnessed the most dramatic climatic tipping point recorded since the Last Glacial Maximum - at the same time as one of the earliest civilizations was developing by the Nile Valley (Kuper and Kröpelin, 2006; Trauth et al., 2024). Although this scenario offers exciting possibilities for research, the confidence that can be placed in studies of the causes and consequences of the associated biodiversity change depends on the reliability of the underpinning species identifications. Rock art (i.e, petroglyphs and paintings) includes unambiguous representations of some savannah species such as giraffes (*Giraffa camelopardalis*) and African savannah elephants (*Loxodonta africana*) (Polkowski, 2021), but alternative interpretations are possible for many other simplified depictions of quadrupeds, often with obviously distorted proportions. From scientific dating, the zoomorphic rock art tradition in Egypt is known to go back to at least 15000BC, the late Pleistocene (Huyge et al., 2011), and it continues throughout the Holocene; however, dating of rock art is notoriously difficult, often relying on patination, varnishing or assignment to style periods (Judd, 2009; Polkowski, 2021). From the Predynastic Period (c. 5300-3100BC), wild animals are represented frequently also on objects such as pottery and palettes and, exceptionally, on tomb walls. These representations are often highly stylised and schematic, which can complicate species identification. From the Dynastic Period (c. 3100-332BC), wildlife is commonly depicted in hunting, offering, and tribute scenes in tombs and temples and on objects, until around 1000BC when wildlife images become exceedingly rare. Dynastic depictions are more detailed than those of the Predynastic Period, but ambiguity still surrounds the species identity of several critical images. Moreover, the species depicted may not always represent local wildlife, and the archaeological context of some faunal remains – even from the Predynastic Period – has been interpreted as evidence for menageries of exotic animals (Keimer, 1954; Hornung, 1967; Friedman et al., 2011, 2017). Also, the extent to which wildlife products, such as elephant ivory and pelts from big cats, were imported is not always clear. Dating is more straightforward for Dynastic than earlier depictions; however, the copying of scenes from earlier dynasties can in some cases undermine their value as evidence of the contemporary wild fauna, as can deification of certain species whose iconic representation thus became decoupled from an environmental context (Evans, 2015). All these complexities stress the importance of cautious analysis of the rich pictorial heritage from the region.

In this study, we present a novel cross-disciplinary approach to zooarchaeological species identification that introduces ecological habitat suitability modelling to facilitate the distinction between species candidates where the material itself is ambiguous. For illustration, we apply a 3-step protocol in a reassessment of key enigmatic representations of wild bovids from Predynastic and Dynastic Egypt. The Bovidae (antelopes, gazelles, goats, sheep, oxen) is a species rich family that abounds in Egyptian art, from the earliest prehistoric rock art to prolific Dynastic hunting scenes. This makes bovids an ideal study taxon, especially as their ecological diversity renders them well-suited also as indicators of environmental change. In Step 1, we describe the distinctive features of the ambiguous image(s). In Step 2, we produce a list of all plausible species candidates. First, we list all known species identifications suggested in the literature together with their (presumed) justifications. Next, we add to this list apparently overlooked alternative candidates by systematically comparing the image's distinctive quantitative and qualitative traits (from Step 1) to those on an exhaustive list of all relevant species, in this case considering all bovids from Africa, the Levant and the Mediterranean. For each of these candidate species, we extract evidence of their former presence in the study area, i.e. all records of faunal depictions and remains, from a comprehensive database covering Egypt and Nubia in the Holocene. In Step 3, we produce habitat suitability models that project the habitat suitability for each candidate species in Northeast Africa at the time of the depiction as well as at present, and we note the species' actual current distribution. We then conclude on the likelihood that the depiction represents each of the candidate species in an integrated qualitative analysis of all the information from Steps 1–3. According to the scientific principle of parsimony ('Occam's razor'), we assume that depictions *ceteris paribus* are more likely to represent a species (i) if HSM hindcasts suitable habitat for it within Egypt/Nubia at the relevant time, and (ii) if zooarchaeological evidence of its presence exists.

2. Materials and methods

2.1. Study objects

We selected as test cases four ambiguous representations (single images or sets of closely matching images) of wild bovids from the Predynastic and Dynastic Period. From broad literature searches, we recorded previous species identifications of these images, a major source being *The Mammals of Ancient Egypt* (Osborn and Osbornová, 1998), a compilation of representations of wild mammals from Predynastic and Dynastic Egypt that is widely used in later studies as an authoritative inventory of wildlife species present in ancient Egypt (e.g. Strandberg, 2009; Yeakel et al., 2014). As the species candidates were well suited as indicator species for the key biogeographic regions in Africa (Fig. 1A; Linder et al., 2012), the test cases allowed us also to explore geographic patterns in biodiversity change.

2.2. Traits list

We produced a list of distinctive qualitative and quantitative traits

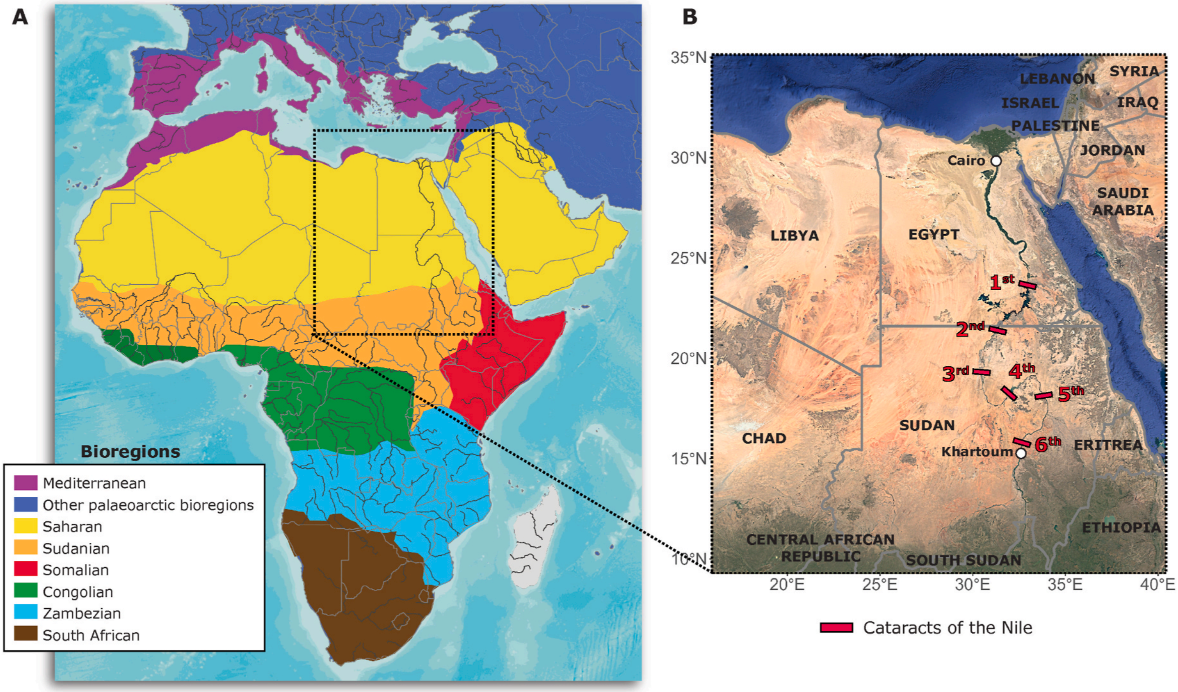

Fig. 1. The study area. (A) Biogeographical regions of Africa (based on sub-Saharan bioregions for mammals in Linder et al., 2012, with the Mediterranean biome from Dinerstein et al., 2017). (B) Location of the Nile cataracts.

for the animal depictions themselves and, for comparison, all their candidate species (Table 1). The qualitative traits, for which information relied chiefly on Kingdon and Hoffmann (2013) and Castello (2016), included: horn shape (in lateral or front view), general build, colour, facial and body markings, hair appendages and tail morphology. The quantitative traits, measured in ImageJ version 1.48 (https://imagej.net/software/imagej/), included relative horn and tail lengths (i.e. absolute measures divided by shoulder height at withers) and, where horns were depicted in profile, horn insertion angle and curvature. When comparing real-life and depicted traits, we took into account the characteristics of Egyptian art: (i) quantitative measures may deviate considerably due to deliberate distortion of depicted proportions, especially horn length is often exaggerated, leg length sometimes grotesquely shortened, and the relative size of animal species modified to produce harmonic scenes, (ii) qualitative traits may be absent due to a tendency to depict only the most obvious features, (iii) whereas bovids like other animals are generally depicted in profile, horns can be depicted either in lateral or front view depending on the angle perceived as most distinct, (iv) image-specific depiction principles can become apparent by comparing similarities of individual animals across a scene, and (v) artist errors may occur, e.g. due to unfamiliarity with the subject.

2.3. Reference database

From extensive searches of the archaeological literature (journal articles, books, conference proceedings, published and unpublished reports), we compiled a database of provenanced and dated records of faunal remains (primarily bones and teeth) and depictions (mainly from tombs, temples, rock art and artefacts including palettes etc.), covering Egypt and Nubia as far south as Khartoum from the Last Glacial Maximum (~20kya) to the end of the Ptolemaic Period (30BC). This database, which includes all wild and domestic terrestrial species above 4 kg, enabled us to analyse the images in light of the evidence from a wider spatiotemporal context. The final database (December 2024) comprise 6685 entries from 425 sites for animal remains and 2726 entries from 259 sites for animal depictions; the subset of the dataset used in this study is available in Supplementary Table S1 & S2 (faunal remains and depictions, respectively).

2.4. Habitat suitability modelling

We generated habitat suitability projections following standard species distribution modelling techniques (Araújo et al., 2019) as outlined below; for a more detailed description of our workflow, see Lazagabaster et al. (2024).

2.4.1. Environmental data

Climate data for current and past climatic scenarios were obtained from a transient simulation conducted with the MPI-ESM1.2 Earth System Model. This climatic simulation of the last 7850 years has a raster cell size of 1.8° × 1.8° (~200 km^2) and demonstrates a strong concordance with Holocene precipitation reconstructions derived from pollen records in northern Africa (Dallmeyer et al., 2020). The variables used include mean annual precipitation (MAP, in mm), mean annual temperature (MAT, in °C), mean temperature of the coldest month (TCM, in °C), and mean temperature of the warmest month (TWM, in °C).

We also used the CHELSA-Trace21k paleo-orographic simulations (Karger et al., 2023) to calculate four topographic variables, aspect, elevation, roughness and slope. We further generated a variable 'distance to water' by calculating the distance to water bodies using the function rgeosgDistance in R (Bivand et al., 2017). The water bodies' vectorial data for the Late Holocene from 5500BP to the present were derived from World Data Bank II (https://doi.org/10.3886/ICPSR08376.v1) by smoothing and adjusting the river and lake outlines to fit a shaded relief generated. The water bodies data for the African Humid Period until 5500BP were generated by vectorising the map from Larrasoaña et al. (2013).

The study area from 15°W to 40.5°E longitude and 9°S to 36°N latitude was selected to encompass the area of influence of the ancient Egyptian empire at its greatest extent, and all climatic, topographic, and environmental rasters were cropped accordingly.

Table 1
Quantitative and qualitative traits for focal animal depictions and the candidate species.

Species	Horn shape	Horn length: shoulder height (♂)	Horn insertion angle[a]	Horn curvature[a]	Other diagnostic features	Tail length: shoulder height
Case 1: **Two dog palette**	Front view: nearly horizontally diverging, upward-curving and converging at the tips	44 %	NA	NA	Sturdy build; shoulder hump; prominent penis sheath; vertical shoulder stripes; tail tuft? [uncoloured]	75 %
Common wildebeest (*Connochaetes taurinus*)	Front view: diverging horizontally (slightly downwards), then upward curving	50 %	–	–	Sturdy build; slight shoulder hump; modest penis sheath; vertical stripes on neck, shoulder and flanks; black facial blaze; mane (erect or lax); beard from chin to forelegs; very long horse-like tail tuft	76 %
Aurochs (*Bos primigenius*)[b]	Front view: diverging horizontally (slightly upwards), then curving upwards and inwards	43 %	–	–	Heavy build; shoulder hump; penis sheath often conspicuous in oxen; no markings recorded; tail tuft	78 %
African buffalo (*Syncerus caffer*)	Front view: diverging laterally (from slightly downwards to drooping), then upward curving	56 %	–	–	Heavy build; shoulder hump; prominent penis sheath; tail tuft	47 %
Case 2: **Idut's tomb**	Front view: diverging upwards gradually to converge at tips; pedicel	55 %	NA	NA	Cow-like build; shoulder hump; elongated head; colour yellowish; no markings; black tail tuft	56 %
Soemmerring's gazelle (*Nanger soemmerringii*)	Front view: diverging upwards, first modestly then markedly, then curving upwards with tips pointing directly inwards	48 %	–	–	Gazelline build; colour pale fawn; white countershading; black facemask; tapered tail with minimal tuft	26%
Dama gazelle (*Nanger dama* subsp. *ruficollis*)	Front view: initially running upwards, then nearly horizontally diverging, with tips curving upwards and inwards	32 %	–	–	Gazelline build with elongated neck and limbs; slight shoulder hump; colour white with neck, shoulders and sometimes upper body rufous; minimal tail tuft	31 %
Dorcas gazelle (*Gazella dorcas* subsp. *isabella*)	Front view: diverging, then converging, upwards moderately	53 %	–	–	Gazelline build; colour pale fawn; white countershading; dark face- and side-stripes; no tail tuft	29 %
Hartebeest (*Alcelaphus buselaphus* subsp. *buselaphus*)	Front view: diverging upwards, then converging, sometimes diverging again	44 %	–	–	Build somewhat cow-like; shoulder hump; head elongated into pedicel; colour pale brown; only lightly countershaded with no conspicuous markings; long tail tuft	41 %
Case 3: **Unas' causeway**	Profile: convex arch; weak annuli	96 %	42°	−135°	Sturdy build; shoulder hump; elongated ears; short mane; possible neck fringe; long terminal tail tuft [paint lost]	54 %
Case 3: **Ibi's tomb**	Profile: convex arch	66 %	53°	−170°	Sturdy build; colour reddish; tail tuft [severely damaged]	46 %
Roan antelope (*Hippotragus equinus*)	Profile: convex arch; annuli	57 %	34°	−100°	Sturdy build; shoulder hump; ears long and narrow; colour reddish sandy-brown; black facemask; short, erect mane; shaggy coat underneath throat; terminal tail tuft	48 %
Nubian ibex (*Capra nubiana*)	Profile: convex arch; pronounced transversal ridges	116 %	30°	−260°	Stout, compact build; colour tan to greyish; variable black markings (legs, side stripe, face); beard under chin; dorsal crest from nape to tail; no tail tuft	12 %
Scimitar-horned oryx (*Oryx dammah*)	Profile: convex arch; weak annuli	99 %	1°	−85°	Sturdy build; shoulder hump; colour white with rufous colouration on neck, shoulders, upper legs and face; long tail tuft	41 %
Case 4: **Silsila engraving**	Profile: forward-pointing	53 %	26°	140°	Slight to gracile build; tail lifted without tuft? [uncoloured]	38 %?
Case 4: **Painted tomb**	Profile: forward-pointing	52 %	28°	130°	Slight build; colour blackish; no tail tuft	25 %
Dibatag (*Ammodorcas clarkei*)[c]	Profile: forward-pointiing	24 %	10°	95°	Gracile build; elongated neck; colour cinnamon-brown to silver-grey; white countershading; erectile tail without terminal tuft	39 %
Kob (*Kobus kob*)	Profile: backward- and then upward-curving	68 %	33°	−60°, then 95°	Sturdy build; colour reddish; white countershading and eye-ring; tail tuft	14 %
Bohor reedbuck (*Redunca redunca*)	Profile: forward-pointing	47 %	4°	115°	Slight build; colour sandy; white countershading; subauricular black patch; no tail tuft	25 %
Waterbuck (*Kobus ellipsiprymnus*)	Profile: forward-curving	62 %	−10°	62°	Sturdy build; colour russet; white rump; tail tuft	29 %

[a] For images with horns in profile only.
[b] Based on remains and Charles Hamilton Smith's rendition of the Augsburg aurochs (Nehring, 1898).
[c] For dama gazelle, see Case 2.

2.4.2. *Presence-absence data*

Occurrence data for each candidate species were generated from PHYLACINE natural ranges, which represent estimations of the potential modern distribution of each species in the absence of human impacts (Faurby et al., 2018). In a comparison with alternative sources of occurrence data, i.e. GBIF/iNAT point data and IUCN range maps, we have found PHYLACINE ranges to be effective for generating accurate habitat suitability projections for African large mammals (Lazagabaster et al., 2024). The presence data were aligned to match the resolution of the climatic rasters, ensuring one presence point per pixel, and an equal number of absence points were generated by randomly sampling the area outside the defined ranges (Barbet-Massin et al., 2012).

2.4.3. Variable selection

Initially, we excluded covariates (sec. 2.4.1) where Variance Inflation Factors (VIF) exceeded 10 to prevent collinearity. Our models are founded on Bayesian additive regression trees (BART) and following Carlson (2020), we next removed the least significant variables based on the root mean square error (RMSE) by applying the automated stepwise reduction approach available through the *embarcadero* R-package, using 200 model iterations and 20 trees. The variables retained for each species are listed in Supplementary Table S3. The variables MAP, TCM, and TWM were included in all models, consistent with the established predominance of precipitation and temperature on vegetation productivity in tropical regions (Andrews and O'Brien, 2000; Ogutu and Owen-Smith, 2003; Chamaillé-Jammes and Fritz, 2009).

2.4.4. Model implementation and evaluation

We utilized the MaxEnt algorithm, applying standard parameters as implemented in the flexSDM package in R (Velazco et al., 2022). The fitness of each model was evaluated using two commonly used evaluation metrics: the true skill statistic (TSS) and the Area Under the Curve (AUC). The evaluation results are summarized in Supplementary Table S4. Environmental suitability maps were produced for specific historical periods (5500BP or 4500BP, depending on depiction age) and compared against current conditions. In addition, a threshold that maximised TSS was calculated for each MaxEnt model and used to generate binary suitability maps.

3. Results

Case 1. Two dog palette, Hierakonpolis, c. 3300–3100 BC (Predynastic Period, Naqada III)

Context: The 42.5 × 22cm siltstone palette, found in the Horus temple of the then capital of Upper Egypt, is an example of the large,

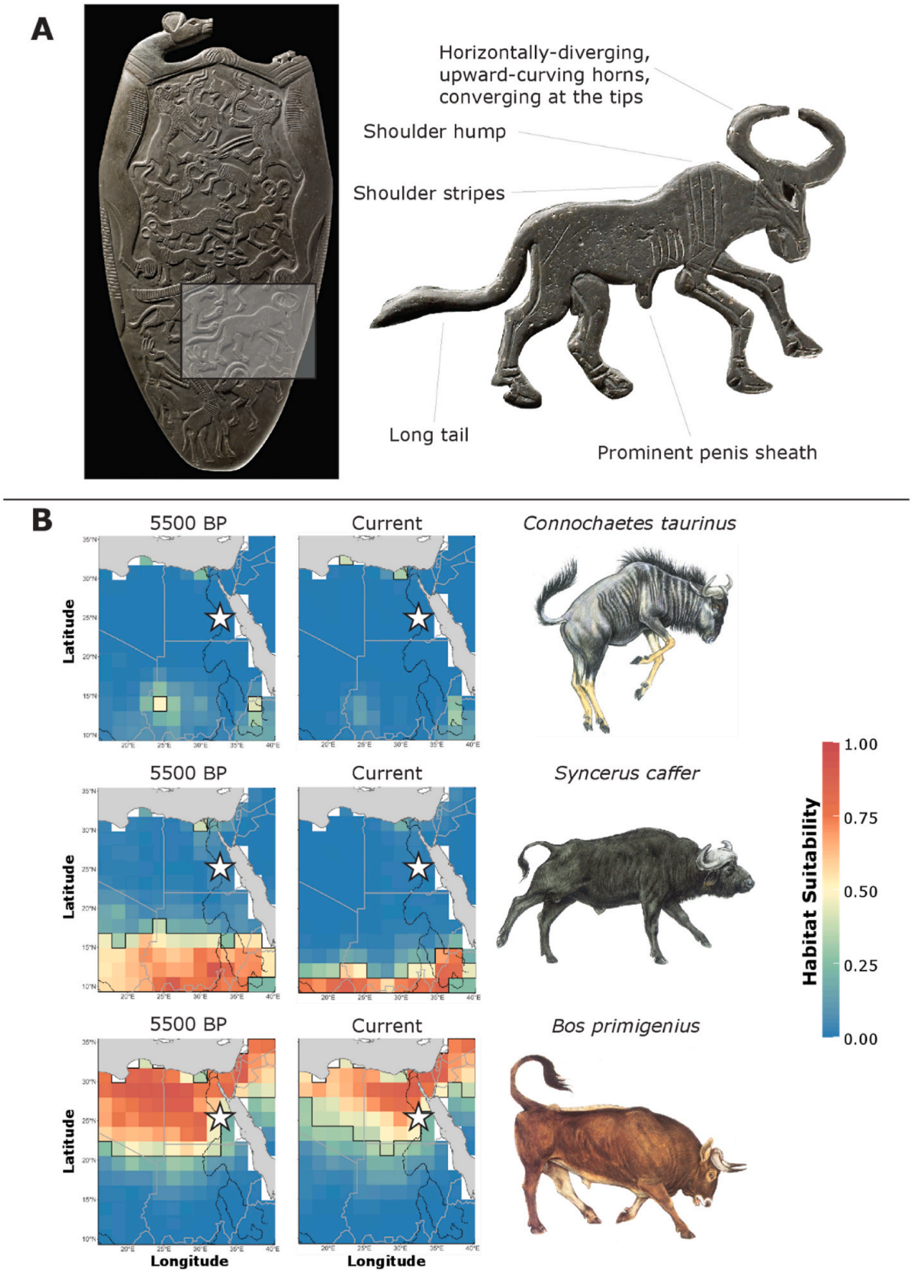

Fig. 2. Case 1. (A) The two dog palette (Hierakonpolis, *c.* 3300-3100BC) with cut-out of the focal bovid (© Ashmolean Museum). (B) Habitat suitability for the candidate species projected for 5500BP and the present. Bovid illustrations by Jonathan Kingdon.

late-Predynastic palettes believed to function as ritual objects, with symbols of kingship dominating their decoration. The focal image is on the reverse side of the palette, where the contemporary wild fauna of Egypt is comprehensively depicted alongside some fabulous creatures.

Step 1 *Image description (*Fig. 2*A;* Table 1*):* The focal image shows a sturdily built bovid with upward-curving, crescent-shaped horns (front view), a prominent penis sheath mid-ventrally (absent from other bovids on the palette), vertical shoulder stripes, and a very long tail reaching the fetlocks.

Step 2 *Candidate species (*Fig. 2*B;* Table 1*)*

- (i) *From the literature:* Identified as a common wildebeest (*Connochaetes taurinus*) by Osborn and Osbornová (1998), presumably due to the vertical shoulder stripes, long tail, and horn shape. Identified by Legge (1909) as either a 'buffalo' or a 'wild bull' ('*Bos africanus*'), which we assume in the modern taxonomy refer to the African buffalo (*Syncerus caffer*) and aurochs (*Bos primigenius*), respectively; presumably these identifications are based on the horn shape, build, penis sheath and tail.
- (ii) *Other morphologically plausible alternatives:* None.
- (iii) *Evidence of local presence:* The common wildebeest is not documented from Northeast Africa, either in faunal remains or depictions. Bones reliably identified as African buffalo are reported from southern Upper Nubia just south of the Nile's 5th cataract from c. 7-5000BC and from the 6th cataract from c. 4-3000BC (Peters, 1992, Fig. 1B), with a single astragalus (ankle bone) from the 2nd cataract in southernmost Lower Nubia dating to c. 22kya (Yeshurun, 2018). A single, tentative, artefact identification, of a nondescript Old Kingdom figurine from the Dakhla Oasis (Boutantin, 2001), as African buffalo is unconvincing. Faunal remains attributed to aurochs are recorded from Egypt throughout our study period, from the Late Pleistocene (e.g. 25kya in Abadiya, Upper Egypt; van Neer, 2000) to the Roman Period (Tell el-Fara'in; von den Driesch, 1997); a record from just north of the 2nd cataract in Nubia dates to c. 3500BC (Gautier, 1968; Wendorf et al., 1979). Aurochs are frequently depicted in Egyptian rock art and tomb/temple scenes, dating from the late Pleistocene (Qurta, Upper Egypt; Huyge et al., 2007; 2011) to 1175BC (Medinet Habu, Upper Egypt; Murnane, 1980).

Step 3 *Habitat suitability modelling (*Fig. 2*B):* Consistent with the faunal records, HSM suggests that the habitat in Egypt and Nubia around 3500BC was unsuitable for the common wildebeest and limited to the extreme south by the 6th cataract for the African buffalo, whereas suitable habitat was found in both Egypt and Lower Nubia for the aurochs. Today, the closest extant population of the common wildebeest are in southern Kenya and of the African buffalo in southeastern Sudan. Beierkuhnlein (2015) estimates that the aurochs went locally extinct in Egypt during the early part of the first millennium BC, which however conflicts with the bone identifications from the Roman Period mentioned above; global extinction of aurochs occurred in 1627AD due to overhunting, in Poland.

Conclusion: The image very likely represents an aurochs because (i) hindcasts show suitable habitat for this species in Egypt at the time of depiction, but not for the African buffalo or common wildebeest, and (ii) its presence is supported by a rich pictorial and zooarchaeological record in Egypt, contrasting with the absence of credible pictorial and zooarchaeological records of the wildebeest and, except for remains from southernmost Nubia, the African buffalo. We note that vertical shoulder stripes are depicted on all the other ungulates on the palette, none of which have shoulder stripes in real life (i.e. dorcas gazelle *Gazella dorcas*; hartebeest *Alcelaphus buselaphus*; aoudad *Ammotragus lervia*; scimitar-horned oryx *Oryx dammah*; Nubian ibex *Capra nubiana*; giraffe). These stripes thus do not represent markings but are probably a stylistic device to indicate the shoulders and ribs. Our conclusion is further supported by the observation that, except for the addax (*Addax nasomaculatus*), all other wild bovids thought to have been relatively common in Predynastic Egypt are represented on the palette and a depiction of an aurochs may therefore be expected.

Case 2. Mastaba of Princess Idut, Saqqara, c. 2250BC (Old Kingdom, 5th-6th Dynasty)

Context: Situated on the east wall in the northernmost chamber of her tomb, the bas-relief shows Pharaoh Unas' daughter being presented with a comprehensive selection of local wild bovids, i.e. scimitar-horned oryx, Nubian ibex, addax, dorcas gazelle, and the focal animal (upper register), alongside cattle (lower register).

Step 1 *Image description (*Fig. 3*A [note for ease of comparisons, cut-outs all face right];* Table 1*):* The focal image shows a bovid of cow-like build, with a long tail ending in a black tuft reaching the hocks; skull elongated into a pedicel for the horns that diverge gradually to converge sharply at the tips (front view); colour yellowish without countershading (both traits contrasting with the adjacent bovid depiction). The animal is labelled with the otherwise unattested Old Egyptian word gsꜣ, which is translated simply as 'antelope' in Erman and Grapow (1931, 206[2]).

Step 2 *Candidate species (*Fig. 3*B;* Table 1*)*

- (i) *From the literature:* Identified as a Soemmerring's gazelle (*Nanger soemmerringii*) in Osborn and Osbornová (1998), Strandberg (2009) and Khalil et al. (2014) based on horn shape. Identified by Macramallah (1935) as the subspecies of the dorcas gazelle found east of the Nile, the Isabelline gazelle (*G. d. isabella*), presumably again due to the inward pointing horn tips (Kingdon and Hoffmann, 2013).
- (ii) *Other morphologically plausible alternatives:* Gradually diverging horns that converge distally in front view are consistent also with the northern subspecies of hartebeest, the bubal (*A. b. buselaphus*). The following depicted traits are consistent with the hartebeest only (not the gazelles): the elongation of the skull into a pedicel, the long tail with black tuft, the bovinesque rather than gazelline build and, specifically for the bubal subspecies, the yellowish colour and absence of conspicuous countershading (cf. Sclater and Thomas, 1894).
- (iii) *Evidence of local presence:* The assignments of bones from Jebel Uweinat (Predynastic Period; van Noten, 1978) and, listed with a question mark, Elephantine (Old Kingdom-Middle Kingdom; Boessneck & von den Driesch, 1982) to Soemmerring's gazelle are likely wrong. For Jebel Uweinat, the identification has been convincingly rejected by Peters (1987) in favour of the closely related (yet distinctive) dama gazelle (*Nanger dama*). With Jebel Uweinat located 550 km west of the Nile, it is worth noting that the congeneric Soemmerring's and dama gazelles are confined to non-overlapping areas east and west of the Nile respectively, and that dama gazelles, which were present in northwestern Sudan until recently (Newby et al., 2010; IUCN SSC Antelope Specialist Group, 2016), are also represented by bone records from the Western Desert of Lower Nubia and Upper Egypt in our zooarchaeological database. For Elephantine, Boessneck & von den Driesch (1982) tentatively assigned three bones to Soemmerring's gazelle by default; they dismissed the dama gazelle as a possibility due to its larger size, which seemingly ignores that the bones could be from a subadult. Bones from just north of Khartoum dating to c. 4000-2800BC have been assigned to either Soemmerring's or dama gazelle (Peters, 1992). Boessneck & von den Driesch (1982) invoke a gazelle depicted with converging horns in front view in Ptahhotep II's mastaba (Saqqara; 5th Dynasty) as evidence of the Soemmerring's gazelle's former presence in Egypt; however, this horn shape is consistent also with other gazelles. Remains attributed to the dorcas gazelle are

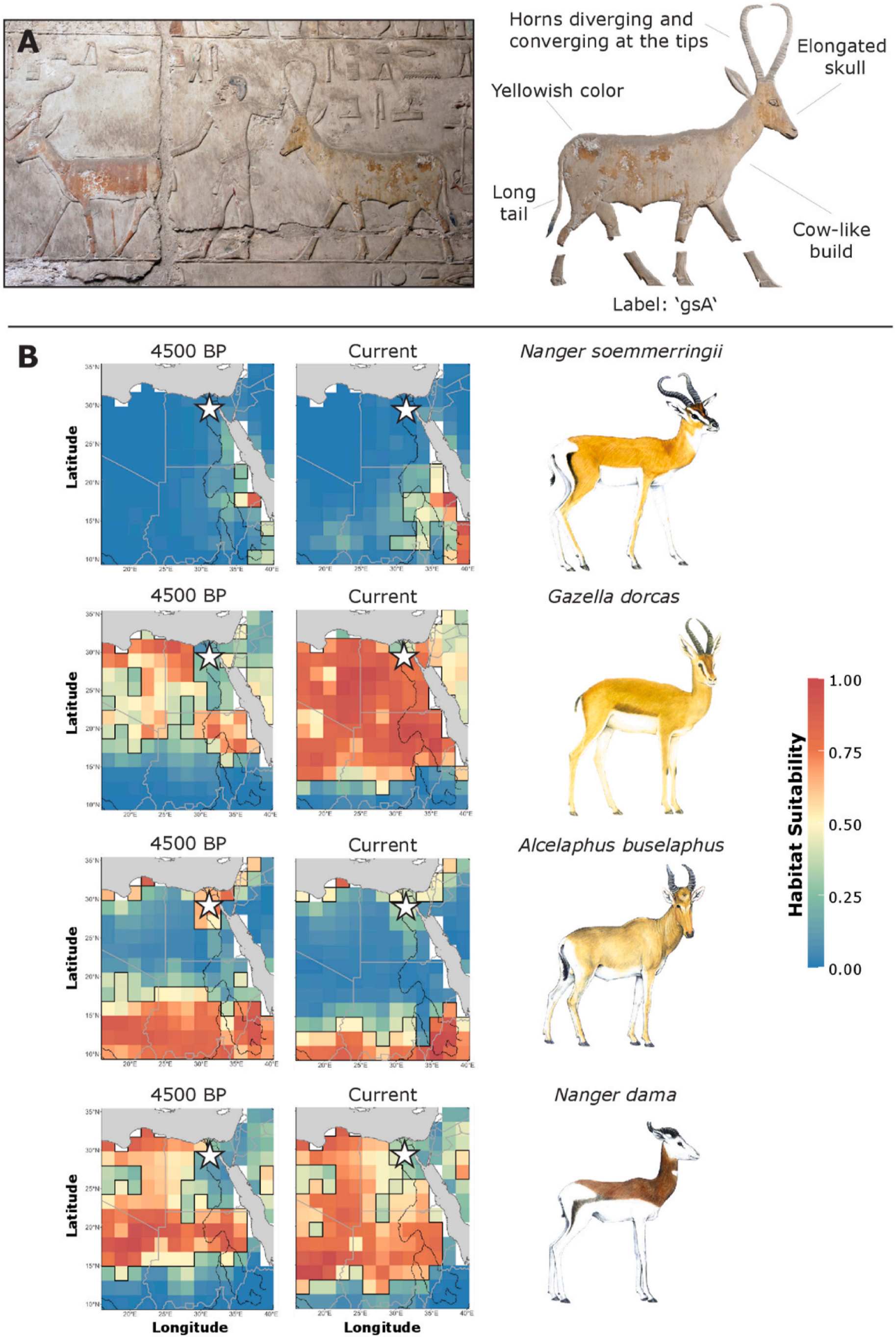

Fig. 3. Case 2. (A) Relief from Princess Idut's mastaba (Saqqara, *c.* 2250BC) with cut-out of the focal bovid (photo: Jakob Bro-Jørgensen). (B) Habitat suitability for the candidate species projected for 4500BP and the present (western hartebeest *A. b. major* shown as the extant subspecies most resembling the extinct bubal, although the marked countershading is unrepresentative). Bovid illustrations by Jonathan Kingdon.

present in Egypt throughout the study period (e.g. Linseele and van Neer, 2009; Morand, 2021). Depictions of wild gazelles most likely representing *G. dorcas* range from late Pleistocene rock art (Qurta; Huyge and Ikram, 2009) to Dynastic images until the end of the New Kingdom (Medinet Habu); a 26th Dynasty hunting scene in Theban Tomb 36 is a copy of an Old Kingdom original (Baike, 1932; Decker and Herb, 1994) and thus unreliable as evidence of the contemporary fauna. Hartebeest remains are reported from Egypt throughout the study period, from the late Pleistocene (Linseele and van Neer, 2009) to the Ptolemaic Period (Morand, 2021). A modest number of rock art depictions has been interpreted as hartebeest, starting from the late Pleistocene (Qurta; Huyge and Ikram, 2009), and numerous, unambiguous depictions (with conventional S-shaped horns in front view) date from the Predynastic Period until at least the 20th Dynasty (Decker and Herb, 1994). Depictions unambiguously identified as the dama gazelle are so far lacking.

Step 3 *Habitat suitability modelling (*Fig. 3*B):* HSM did not hindcast suitable habitat for the Soemmerring's gazelle in Egypt and Nubia around 2500BC, and the closest extant population is today found in north-western Ethiopia. By contrast, suitable habitat was found for the dama gazelle in Egypt's Western Desert and Nubia at the time, with the closest extant population of this heavily hunted species located in central Chad. For the still extant dorcas gazelle, HSM hindcasts suitable habitat in Egypt west of the Nile around 2500BC (although curiously not east of the Nile where the Isabelline subspecies occurs). For hartebeest, HSM also identified suitable habitat in Lower and Northern parts of Upper Egypt around 2500BC. The bubal subspecies, which went globally extinct around the mid-20th century, only disappeared from Egypt during the mid-19th century (Haltenorth and Diller, 1980); the tora (*A. b. tora*) in north-western Ethiopia possibly constitutes the closest extant hartebeest population although it may now also be globally extinct (IUCN SSC Antelope Specialist Group, 2019).

Conclusion: HSM identifies suitable habitat for the hartebeest in Lower Egypt at the time of the depiction, with supporting zooarchaeological evidence, and since only this species is consistent with the elongated skull, long tail, cow-like build and, arguably, colouration, we conclude that the image very likely represents this species. This is further supported by the observation that gsꜣ is likely a misspelling of the word for hartebeest šsꜣ(w) (Erman and Grapow, 1930, 543[5]) caused by confusing the hieroglyphs š (𓈙) and g (𓎼), either because both are roughly quadrate or, conceivably, because the artist used a hieratic draft: in hieratic both š () and g () comprise horizontal elements at the top and bottom and three vertical elements in between (hieroglyphs: Rosmorduc, 2014; hieratic forms: Roberson, 2018). The credibility of such occasional errors is supported e.g. by the misspelling of the label gḥs(t) ('(dorcas) gazelle'; Erman and Grapow, 1931, 191[1]) as ḥsg and gsḥt in the mastabas of Wernu and Mereruka, respectively (Saqqara; 6th Dynasty). We note that the horn shape differs from the conventional depictions of hartebeest horns as S-shaped in front view;

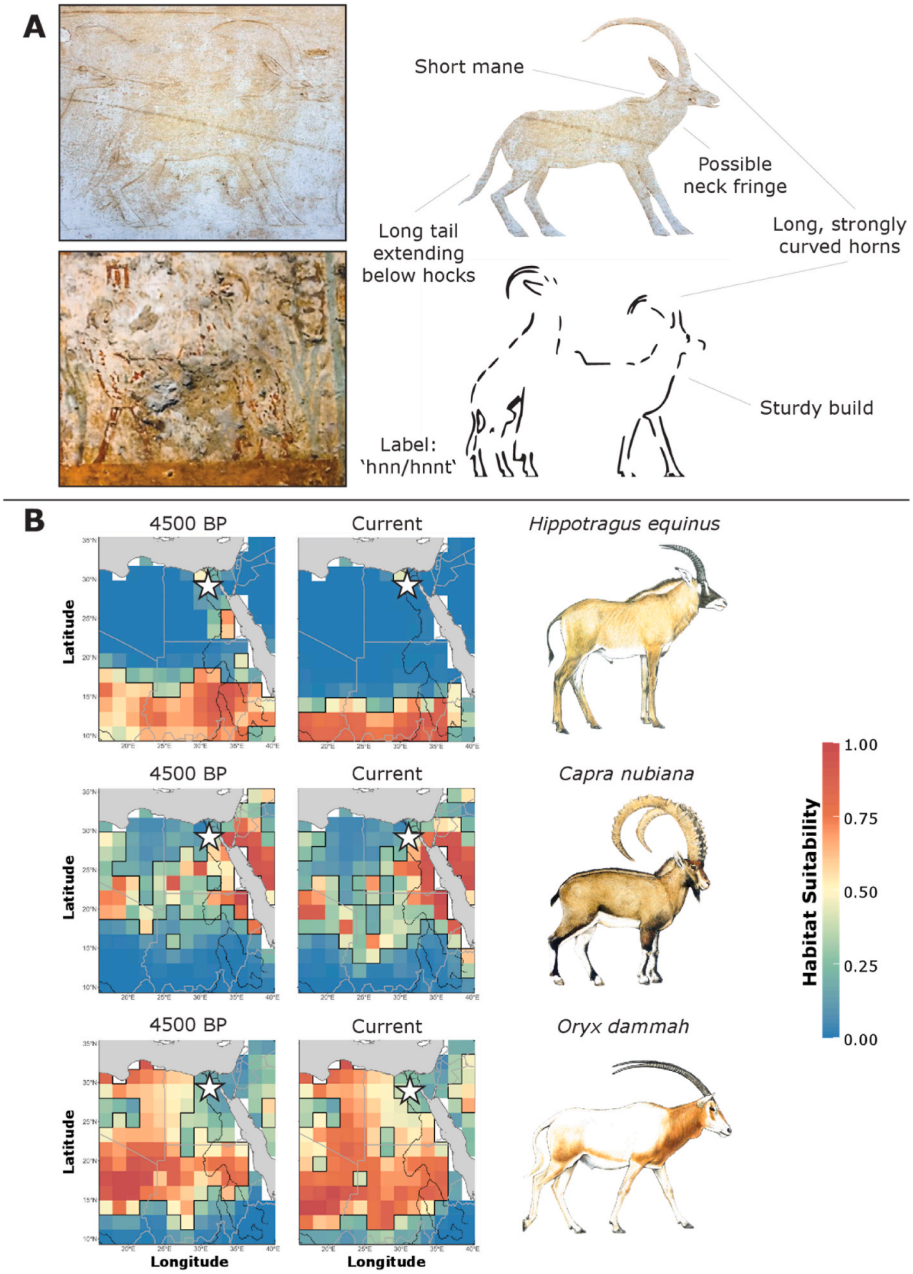

Fig. 4. Case 3. (A) (*top*) Relief from Unas' causeway (Saqqara, *c.* 2300BC; photo: Jakob Bro-Jørgensen) and (*bottom*) wall painting from Ibi's tomb (Deir el-Gebrawi, *c.* 2200BC; photo courtesy of Naguib Kanawati) with cut-out and line drawing of the focal bovids. (B) Habitat suitability for the candidate species projected for 4500BP and the present. Bovid illustrations by Jonathan Kingdon.

however, this is consistent with natural variation within the bubal subspecies. Speaking against the other candidates, HSM hindcasts unsuitable habitat for the Soemmerring's gazelle, the label gsꜣ contrasts with the already established Old Egyptian name for the dorcas gazelle, gḥs, and the dama gazelle is an exceptionally poor fit morphologically.

Case 3. Causeway of Unas' pyramid complex, Saqqara, c. 2300BC (Old Kingdom, 5th Dynasty) & Tomb of Ibi, Deir el-Gebrawi, c. 2200BC (Old Kingdom, 6th Dynasty)

Context: The Saqqara relief is located roughly midway on the 750m causeway linking the valley and mortuary temples of Unas' pyramid complex, on the southside. The Gebrawi image is painted on plaster on the north wall of the chapel in the rock-cut tomb of the nomarch, probably of Abydos, Ibi (Kanawati, 2007). Both scenes are fragmentary and show hunting in the 'desert', presumably of local wildlife.

Step 1 *Image description (*Fig. 4*A;* Table 1*):* Both focal images show sturdily built bovids with long, strongly curved horns in lateral view, inserted at an obtuse angle, elongated ears and long tails ending in long tufts extending below the hocks. On the Saqqara image, a short mane and possibly a neck fringe are present. On the Gebrawi image, which is damaged, the male of the mating couple is labelled hnn, the female hnnt, which usually denote the Persian fallow deer (*Dama mesopotamica*) (Erman and Grapow, 1928, 495[20]), a species incompatible with the depiction due to its antlers.

Step 2 *Candidate species (*Fig. 4*B;* Table 1*)*

(i) *From the literature:* The Saqqara image is identified as roan antelope (*Hippotragus equinus*) by Keimer (1943) and Osborn and Osbornová (1998), which is consistent with the horns (although shorter in roan), elongated ears, mane (although longer in roan), long tail (although usually ending above the hocks in roan), and the possible neck fringe. The Gebrawi image is also identified as roan antelope by Osborn and Osbornová (1998), but as Nubian ibex by Davies (1902) and, tentatively, by Decker and Herb (1994), presumably based on a similarity in horn shape as pointed out by Kanawati (2007).

(ii) *Other morphologically plausible alternatives:* Long backward-curved horns are also present in the scimitar-horned oryx (*Oryx dammah*) for which the tail and, arguably, mane are better fits.

(iii) *Evidence of local presence:* A bone attributed to a roan antelope from around 3000BC has been recorded from Abu Tabari in Wadi Howar close to the Dongola Reach south of the 3rd cataract in Upper Nubia. A horn core fragment from Piramesse in the Nile Delta dated to the 19th-20th Dynasty was also assigned to roan antelope by Bossneck & van den Driesch (1982), who however assumed that the water-dependent species could not survive in Egypt at the time and that the bone originated from a menagerie, or else a trophy from Nubia. Occasional depictions with sharply curved horns inserted at an obtuse angle have been interpreted as roan antelope, with potential for confusion with Nubian ibex or scimitar-horned oryx. Ibex bones are reported from Egypt's Eastern Desert from the Paleolithic (30kya; Vermeersch et al., 1994) through to the Roman Period (1st century AD; van Neer and Lentacker, 1996), and thus throughout our study period (Linseele and van Neer, 2009). Ibex depictions, which have been reported from Epipaleolithic rock art, become common during the Predynastic Period, including in mobiliary art and, during the Dynastic Period until the New Kingdom, also in reliefs and paintings in tombs and temples (Osborn and Osbornová, 1998; Gatto et al., 2009; Polkowski, 2021). Scimitar-horned oryx remains are reported from Egypt dating from the early Holocene (Western Desert; Gehlen et al., 2002) to the first millennium BC (Eastern Delta; Grezak, 2020), and images of this species in the wild span from mid-Holocene cave art (Western Desert; Claßen et al., 2009) to a 19th Dynasty ostracon (Deir el-Medina; Osborn and Osbornová, 1998).

Step 3 *Habitat suitability modelling (*Fig. 4*B):* HSM suggests that around 2500BC the habitat was suitable for roan antelope in the Delta and Upper Egypt east of the Nile, for the Nubian ibex in the Eastern Desert, Nile Valley, southern parts of the Western Desert, and northern Nubia, and for the scimitar-horned oryx in the Western Desert and Nubia. The roan antelope only recently went extinct from Eritrea, and the closest extant roan antelope populations are today found in north-western Ethiopia and southern Sudan. The Nubian ibex is still extant in Egypt east of the Nile. Formerly widespread west of the Nile, the scimitar-horned oryx was last sighted in Egypt in 1975 (Osborn and Helmy, 1980), followed by extinction in Sudan around 1980, and globally (in the wild) during the 1990s, all due to overhunting (Woodfine and Gilbert, 2016); following recent successful reintroduction in Chad, it is now downlisted to 'endangered' (IUCN, 2024).

Conclusion: Our HSM reveals that suitable habitat for all three species may have been present in Egypt at the time of the depictions, and hence all three are credible candidates from this perspective. As such, morphological and other contextual data may be more relevant. In this instance, we conclude that the roan antelope is the most parsimonious identification for both depictions. Speaking against the Nubian ibex are its short tail, beard, and compact build. Speaking against the scimitar-horned oryx are (i) its horn insertion angle which follows the plane of the nasal ridge, (ii) its Old Egyptian name mꜣ-ḥḏ (Erman and Grapow, 1928, 11[4]), which is at variance with hnn, and (iii) the presence in both scenes also of conventional scimitar-horned oryx depictions, which contrast with the focal images.

Case 4. West Bank of Gebel el-Silsila, estimated c. 4000–3350BC (Predynastic Period, Naqada I/II) & Tomb 100 ('Painted Tomb'), Hierakonpolis, c. 3400BC (Predynastic Period, Naqada II)

Context: The Silsila image is a solitary engraving on a boulder at a site rich in rock art, dating from the Epipaleolithic to present (Nilsson et al., 2023). The Hierakonpolis image is part of a c. 115 × 500cm scene with boat, fighting and animal subjects, painted on a plastered mudbrick wall in the tomb possibly of a king (Kemp, 2018); the focal animals are depicted around a circular structure, possibly a leg trap (Osborn and Osbornová, 1998).

Step 1 *Image description (*Fig. 5*A;* Table 1*):* Both focal images show bovids of slight build with forward-pointing horns in profile. The more gracile Silsila bovid may display a long, lifted tail, i.e. if the posterior line is not an erroneous continuation of the belly line which could explain the unnaturally low insertion point. The Hierakonpolis bovid has a short tail.

Step 2 *Candidate species (*Fig. 5*B;* Table 1*)*

(i) *From the literature:* A tentative identification of the Silsila image as dibatag (*Ammodorcas clarkei*) is suggested by Nilsson et al. (2023), consistent with its forward-pointing horns, gracile build and possible long, lifted tail (a peculiar trait of the dibatag). The Hierakonpolis image is identified as kob (*Kobus kob*) by Osborn and Osbornová (1998), the justification for which is unclear. Finally, Schreiber & Striedter (2022) suggest that a rock image of gazelle-like animals with forward-curving horns from the Dakhla Oasis are juvenile dama gazelles, which share this horn shape.

(ii) *Other morphologically plausible alternatives:* Forward-pointing horns is consistent also with the bohor reedbuck (*Redunca redunca*), which is slightly built, and the waterbuck (*Kobus ellipsiprymnus*), which is sturdily built with more moderately forward-curving horns; both have a relatively shorter tail than the dibatag.

(iii) *Evidence of local presence:* No remains of dibatag have been reported, but bones from the other species have been reported from

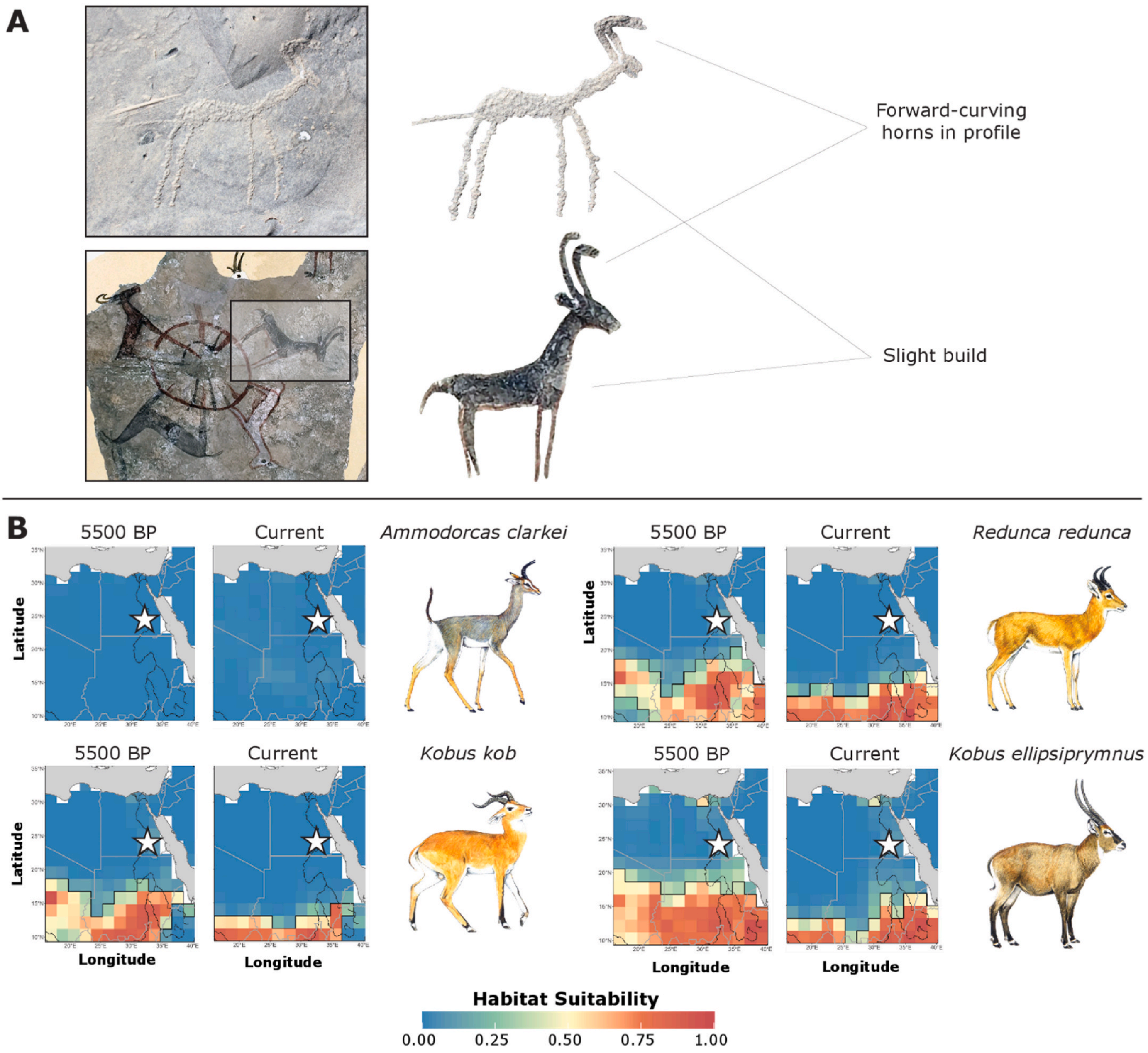

Fig. 5. Case 4. (A) (*top*) Rock engraving (Gebel el-Silsila, *c.* 4000-3350BC; photo: Jakob Bro-Jørgensen) and wall painting from Painted tomb (no. 100) (Hierakonpolis, *c.* 3400BC; photo courtesy of Bianca Madden and Simon Connor) with cut-outs of the focal bovids. (B) (*bottom*) Habitat suitability for the candidate species projected for 5500BP and the present. Bovid illustrations by Jonathan Kingdon.

Upper Nubia as follows: kob from the 6th cataract with dates spanning the interval c. 7-3000BC (Peters, 1992), bohor reedbuck from Abu Tabari in Wadi Howar west of the Dongola Reach between the 3rd and 4th cataract dating to c. 3000BC (Pöllath, 2011) as well as from between the 5th and 6th cataract with dates spanning the interval c. 7-3000BC (Peters, 1992), and waterbuck from between the 3rd and 4th cataract dating to c. 7000BC (Osypiński et al., 2023) as well as from the 6th cataract dating to c. 7000-5000BC (Peters, 1992). For dama gazelle, see Case 2. No depictions have unambiguously been assigned to any of these species so far.

Step 3 *Habitat suitability modelling (*Fig. 5*B):* HSM shows that the habitat around 3500BC was not suitable for the dibatag, an endemic to eastern Ethiopia/Somalia, whose restricted range is separated from the Nile by the Ethiopian highlands. By contrast, HSM hindcasts suitable habitat in southern parts of Upper Nubia for both the kob, the bohor reedbuck and the waterbuck consistent with the faunal record. The closest extant populations of these species are in South Sudan for the kob, in southern and southeastern Sudan for the reedbuck and limited to a more confined area of southeastern Sudan for the waterbuck. For dama gazelle, see Case 2.

Conclusion: Despite shortcomings of the two simplistic images from an identification perspective, both show very clear forward-pointing horns. This, combined with the lack of zooarchaeological evidence from Egypt, makes the lyre-horned kob unlikely as the subject. In spite of the good morphological fit, the dibatag is also unlikely because the HSM – consistent with the lack of remains - fails to hindcast suitable conditions for this species in the region at the time (or indeed now). A more plausible identification is the bohor reedbuck, for which the hindcast shows suitable habitat in Upper Nubia; other images of more sturdily built bovids with long, forward-curving horns might represent the waterbuck. That suitable habitat was not identified in Egypt itself for the reedbuck and waterbuck at the time may reflect that the local effect of the Nile is not fully captured by the HSM. We find obscure the reason why specifically juveniles of the dama gazelle would have been depicted; however, a conceivable interpretation favouring the dama gazelle, but perhaps even more the dorcas gazelle, is that artists for some reason perceived the forward curvature of their horn tips as more distinctive than the more prominent backward curvature, and therefore focused on depicting this. In summary, we propose as most parsimonious that the images represent the bohor reedbuck, or else conceivably a gazelle.

4. Discussion

Our case studies from Egyptian archaeology demonstrate how the integration of HSM into historical species identification analysis in some cases can provide important insights that strengthen the inference favouring one potential identification over another. Our findings are compatible with a pattern where the ungulates whose ranges extended into Egypt during the African Humid Period originated from the Mediterranean/Near-eastern fauna (bubal, aurochs) and from the savannah communities immediately to the south along the Nile (roan antelope, bohor reedbuck); we found no reason to invoke immigration from the more distant communities in the Horn of Africa and East Africa as previously suggested, with the presence of dibatag, common wildebeest, and Soemmerring's gazelle found unlikely. This pattern is supported by additional pictorial and zooarchaeological evidence from Northeast Africa, which suggests that the Mediterranean/Near-eastern communities were further represented by the presence of Persian fallow deer and wild boar (*Sus scrofa*), and the Sudanian communities by giraffe, African savannah elephant and rhinoceros (Osborn and Osbornová, 1998; however, for fallow deer, see also Kitagawa, 2008). The pattern is also in line with the evidence-based suggestion that the straight-horned oryx present in the Eastern Desert during the Dynastic Period was most likely the Arabian oryx (*Oryx leucoryx*; Manlius, 2000), which was present in Sinai until recently (IUCN SSC Antelope Specialist Group, 2017), rather than - as alternatively suggested - the beisa oryx (*Oryx beisa*) from the Horn and eastern parts of Africa (Yeakel et al., 2014).

The moderate shifts in the bioclimatic envelopes underlying wildlife distributions may have had a limiting effect also on the range shifts of nomadic hunter-gatherers and thus cultural interactions between more distant tribes in sub-Saharan Africa and Egyptian communities during the mid-late Holocene transition. Cultural exchange with Nubia and the Levant, however, may have been promoted by the ecological changes through their effect on subsistence, and this is consistent with the distribution of pottery, Mesopotamian influence in Predynastic and Early Dynastic Art (e.g. subject on the Two Dog Palette and in the Painted Tomb adjacent to Case 1 and 4, respectively), and archaeological evidence of trade with the A-group and Levantine communities (Wengrow, 2006). One could also argue that a less prolific wildlife fauna to sustain hunters agrees with the proposed local domestication of cattle in Egypt's Western Desert in the mid-Holocene; however, such a third domestication event, in addition to those in the Fertile Crescent and the Indus Valley, remains controversial (Pitt et al., 2019).

The case studies also illustrate how our 3-step approach can lead to more specific insights that advance our cultural understanding. How the modern observer may be misled by the stylistic conventions dictating how animals should be depicted is demonstrated by Case 1, where the shoulder stripes result in a superficial similarity to wildebeest. Case 2 shows that these stylistic conventions sometimes offered more than a single option for how a species should be depicted (similar alternative representations of hartebeest horns are found e.g. in Kagemni's mastaba at Saqqara, 6th Dynasty). Linguistically, the likely use of hnn for roan antelope in Case 3 could indicate a perceived commonality with another uncommon artiodactyl, i.e. the fallow deer, in the ancient zoological classification system; alternatively, the label could be an artist error, another example of which is the likely spelling mistake identified in Case 2, of gsꜣ for šsꜣ. Finally, the probable local presence of roan antelope in Egypt highlights the need for a review of the evidence for Pharaonic menageries of exotic animals, which may have been less common than sometimes assumed (Keimer, 1954; Boessneck & von den Driesch, 1982; Herb and Förster, 2009).

Although we hope the findings of this study showcase the potential of HSM to inform species identification in archaeology, its usefulness depends on several factors. A first limitation is that uncertainty in dating differs between different media, with rock art particularly difficult. However, in principle HSM has the potential to inform dating of rock art as well: if some species depictions are unambiguous (e.g. giraffes or elephants), accurate HSM hindcasts for these species could help narrow down the possible time window for when the images were created, thereby strengthening the potential of HSM to discriminate between candidate species for contemporary depictions that are ambiguous. Second, HSM relies on the assumption that depictions represent local fauna and the justification for this should always be considered carefully; for instance, it is conceivable that some rock art depicted familiar species because of their absence rather than their presence. Third, HSM is more likely to result in convincing discrimination when candidate species differ markedly in their bioclimatic envelopes (compare e.g. Case 1 to the difficulty in discriminating between reedbuck and waterbuck in Case 4).

Also, it should be acknowledged that HSM projections are often associated with a significant degree of uncertainty due to technical challenges in constructing the models. Hindcasts may depend both on the specific environmental factors used to construct the models, and on the quality of the available data. Currently, simulations of paleoclimatic variables come with considerable uncertainty, and specifically for Northeast Africa, climatologists have faced difficulties to fully capture the higher rainfall during the African Humid Period in simulations (Pausata et al., 2020). Another source of uncertainty is the inaccuracy inherent in the current species distribution data used to derive the HSM-models. We used PHYLACINE because it compensates for human-caused absences; however, the PHYLACINE creators acknowledge that their methodology may not work equally well for all species (Faurby et al., 2018), extinct species likely to be especially taxing. Because of these sources of error, caution must be exercised when balancing the reliance on HSM outputs against other evidence; e.g., we found the roan antelope the most likely subject in Case 3, and the reedbuck in Case 4, due to pictorial analysis in spite of their more marginal HSM hindcasts. These challenges emphasize the importance of a truly cross-disciplinary approach to improve the analysis of the zooarchaeological record, guided by the recognition that "all models are wrong, but some are useful".

5. Conclusion

Our findings suggest that although considerable shifts occurred in the wildlife distributions of Northeast Africa during the Mid-Holocene, the biodiversity changes in Egypt and Nubia since the Predynastic Period may primarily have occurred along the axis of the catchment area of the Nile. We hope that our 3-step approach introducing HSM to identify species in archaeological material will be useful to other researchers working on faunal evidence in similar contexts of significant historical climate change. In this study we concentrated on depictions, however HSM is likely to be equally useful to inform species identification of ambiguous faunal remains, as zooarchaeologists often struggle to discriminate related species from the bones preserved. Future studies could also benefit from focusing on larger datasets to interpret changes in biodiversity at the community level using an integrated probabilistic approach to species identities: by formally leveraging contextual information in this way, confidence in both individual species identifications and proposed community-level changes may be strengthened.

CRediT authorship contribution statement

Jakob Bro-Jørgensen: Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Salima Ikram:** Writing – review & editing. **Juliet V. Spedding:** Writing – review & editing, Data curation. **Chris D. Thomas:** Writing – review & editing, Methodology. **Steven Snape:** Writing – review & editing. **Maria Nilsson:** Writing – review & editing. **Ignacio A. Lazagabaster:** Writing – review & editing, Methodology, Formal analysis.

Data availability statement

The data that support the findings of this study are openly available in the Open Science Framework at https://osf.io/8b6fp/?view_only=561d6cde25cd4cec801b6ba54329b4aa.

Reproducible results

The Associate Editor for Reproducibility downloaded all materials and could reproduce the results presented by the authors.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2025.106239.

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