

Ecomorphology and ecology of the grassland specialist, *Rusingoryx atopocranion* (Artiodactyla: Bovidae), from the late Pleistocene of western Kenya

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Abstract

Rusingoryx atopocranion is an extinct alcelaphin bovid from the late Pleistocene of Kenya, known for its distinctive hollow nasal crest. A bonebed of *R. atopocranion* from the Lake Victoria Basin provides a unique opportunity to examine the nearly complete postcranial ecomorphology of an extinct species, and yields data that are important to studying paleoenvironments and human-environment interaction. With a comparative sample of extant African bovids, we used discriminant function analyses to develop statistical ecomorphological models for 18 skeletal elements and element portions. Forelimb and hindlimb element models overwhelmingly predict that *R. atopocranion* was an open-adapted taxon. However, the phalanges of *Rusingoryx* are remarkably short relative to their breadth, a morphology outside the range of extant African bovids, which we interpret as an extreme open-habitat adaptation. It follows that even recently extinct fossil bovids can differ in important morphological ways relative to their extant counterparts, particularly if they have novel adaptations for past environments. This unusual phalanx morphology (in combination with other skeletal indications), mesowear, and dental enamel stable isotopes, demonstrate that *Rusingoryx* was a grassland specialist. Together, these data are consistent with independent geological and paleontological evidence for increased aridity and expanded grassland habitats across the Lake Victoria Basin.

Keywords: Alcelaphin; Bovid; Discriminant function analysis; Ecomorphology; Grassland; Kenya; Late Pleistocene; Rusinga Island; *Rusingoryx*; Wakondo

INTRODUCTION

Researchers have only recently begun to understand the late Pleistocene faunas of eastern Africa, despite their critical role for interpreting the paleoenvironmental context of a time and place central to the diversification and dispersal of early modern humans (*Homo sapiens*) (Henn et al., 2018; Scerri et al., 2018; Tryon, 2019). The late Pleistocene large mammal communities were composed of numerous extinct taxa, some of which were dominant members of the region's

faunas until the onset of the Holocene (MacInnes, 1956; Marean and Gifford-Gonzalez, 1991; Marean, 1992; Faith, 2014; Faith et al., 2015; Lesur et al., 2016; Tryon et al., 2016). This emerging perspective has been reinforced by ongoing research in the Kenyan portions of the Lake Victoria Basin since 2008, which has documented numerous extinct taxa (*Rusingoryx atopocranion*, *Damaliscus hypsodon*, *Kolpochoerus*, and others) in late Pleistocene sediments, including new species or those formerly thought to have disappeared from eastern Africa during the middle Pleistocene (e.g., Tryon et al., 2010, 2012, 2016; Faith et al., 2011, 2014, 2015; Jenkins et al., 2017). These new data show that *Homo sapiens* in eastern Africa evolved among non-analog faunal communities (e.g., Faith et al., 2016), as has long been recognized for southern Africa (e.g., Klein, 1980).

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A better understanding of the paleoecology of the extinct species that were a part of these communities is critical to paleoenvironmental and archaeological research. Developing a robust understanding of dietary ecology, habitat preferences, and locomotor strategy is an essential step in the use of fossil taxa as paleoenvironmental indicators (Faith and Lyman, 2019). In turn, such knowledge facilitates the study of human-environment interactions, and provides insight into hunting and subsistence methods, potential proxies for past human mobility, population density, and cognitive ability (e.g., Marean, 1997; Klein and Cruz-Urbe, 2000; Faith, 2008; Wadley, 2010). However, a challenge in developing a fuller and more detailed paleoecological understanding of extinct species from African Pleistocene sites (and earlier) is that most are known almost exclusively from taxonomically diagnostic craniodental remains. Sites with large assemblages of reliably associated postcranial remains or taxa with diagnostic features in many postcranial elements are rare. An important exception is the Bovid Hill archaeological site at Wakondo on Rusinga Island within Lake Victoria (Fig. 1) (see also Marean, 1990, 1992, 1997), which preserves a large, monospecific bonebed that resulted from the targeted hunting of a herd of the extinct bovid *R. atopocranion* (Jenkins et al., 2017).

Rapid burial in fluvial and alluvial sediments at Bovid Hill led to the preservation of a large amount of associated skeletal material with both cranial and postcranial elements of *R. atopocranion*. The Bovid Hill assemblage thus affords a rare opportunity to provide a more holistic understanding of its ecology. In addition to the bonebed accumulation at Bovid Hill, remains of the alcelaphin bovid *Rusingoryx* have been recovered from other late Pleistocene sediments (~100–36 ka) around the Kenyan Lake Victoria Basin, including both Rusinga and Mfangano islands and mainland sites Luanda West and Karungu (Faith et al., 2011; O'Brien et al., 2016; Tryon et al., 2016; Blegen et al., 2017; Jenkins et al., 2017).

Rusingoryx atopocranion is the most abundant species recovered from many of these late Pleistocene deposits, indicating its important role for understanding the paleoecology and paleoenvironments of the Lake Victoria Basin (Faith et al., 2015; Tryon et al., 2016). Importantly, fossils of *R. atopocranion* co-occur with hominin fossils attributed to *H. sapiens* (Grine, 2016; Pearson et al., 2020) and Middle Stone Age (MSA) artifacts (Tryon et al., 2010, 2012, 2014; Faith et al., 2015; Blegen et al., 2017; Jenkins et al., 2017), the latter providing the archaeological context of early modern humans in eastern Africa (Tryon and Faith, 2013; Tryon, 2019). Past work in the Lake Victoria Basin has documented the expansion of Serengeti-like grasslands across the region in the late Pleistocene (e.g., Tryon et al., 2010, 2012, 2016; Faith et al., 2015; Garrett et al., 2015), likely in response to increased aridity and desiccation of the lake (e.g., Beverly et al., 2015a, 2017, 2020). This interpretation has been heavily influenced by the fossil faunas, including inferences based on the dominance of *R. atopocranion*, which was assumed to have had an affinity for open grassland habitats similar to extant alcelaphins (e.g., Faith et al., 2011; Faith,

2014). However, the craniodental remains of this species are unusual compared to other bovids and, indeed, are without parallel among other mammals—it has a large, hollow nasal crest otherwise known only from lambeosaurine hadrosaur dinosaurs (O'Brien et al., 2016). That the postcranial anatomy and other behavioral aspects of *Rusingoryx* are comparable to those of other alcelaphin bovids represents a series of assumptions or untested hypotheses. By relying solely on the untested assumption of taxonomic uniformitarianism, we cannot evaluate how the past might have differed from the present (e.g., Behrensmeier et al., 2007). With this in mind, our goal here is to provide an assessment of the habitat preferences of *R. atopocranion* through an ecomorphological analysis of the large postcranial sample from Bovid Hill.

Rusingoryx atopocranion

Rusingoryx atopocranion was described by Pickford and Thomas (1984) on the basis of a partial cranium from the Wakondo locality on Rusinga Island. Because most of the face was not preserved, they did not anticipate the nasal dome that has since been observed on more complete specimens (O'Brien et al., 2016). This resulted in incorrect anatomical orientation of the type specimen (e.g., the dorsal cranium was thought to be anterior), leading Pickford and Thomas (1984) to infer an aberrant morphology that included dramatic shortening of the face and the presence of a proboscis—hence the species name *atopocranion* (= strange skull). Harris (1991) later observed similarities between the cranial architecture of the type specimen and *Megalotragus* from Koobi Fora, and suggested that *Rusingoryx* be considered a junior synonym of *Megalotragus*. This opinion prevailed for the next two decades, until Faith et al. (2011) provided morphological and systematic analyses of new material recovered from Rusinga Island that suggested *Rusingoryx* could not be accommodated within *Megalotragus*. Subsequent analyses of complete crania recovered from the Bovid Hill site on Rusinga Island supported this taxonomic assessment, though it is clear that *Rusingoryx* is a recent offshoot of *Megalotragus* (O'Brien et al., 2016). O'Brien et al. (2016) demonstrated that unlike any other known mammals, *R. atopocranion* has a hollow nasal crest comparable to those of some lambeosaurine hadrosaur dinosaurs, a bizarre morphology hypothesized to facilitate the production of low-frequency vocalizations in open and grassy habitats. Thus, *Rusingoryx* does indeed have a strange skull, although not for the reasons initially suggested by Pickford and Thomas (1984).

In terms of its masticatory anatomy, the combination of extreme hypsodonty and a reduced premolar row suggested that *R. atopocranion* was a hyper-grazer (Faith et al., 2011). This is supported by stable carbon isotopic evidence indicating a diet dominated by C₄ plant biomass (Faith et al., 2015; Garrett et al., 2015; Tryon et al., 2016), consistent with the diet of its living (*Connochaetes taurinus*) and fossil (*Megalotragus*) relatives (Kingdon and Hoffman, 2013; Cerling et al., 2015). Analyses of ancient soils, associated fossil taxa, and

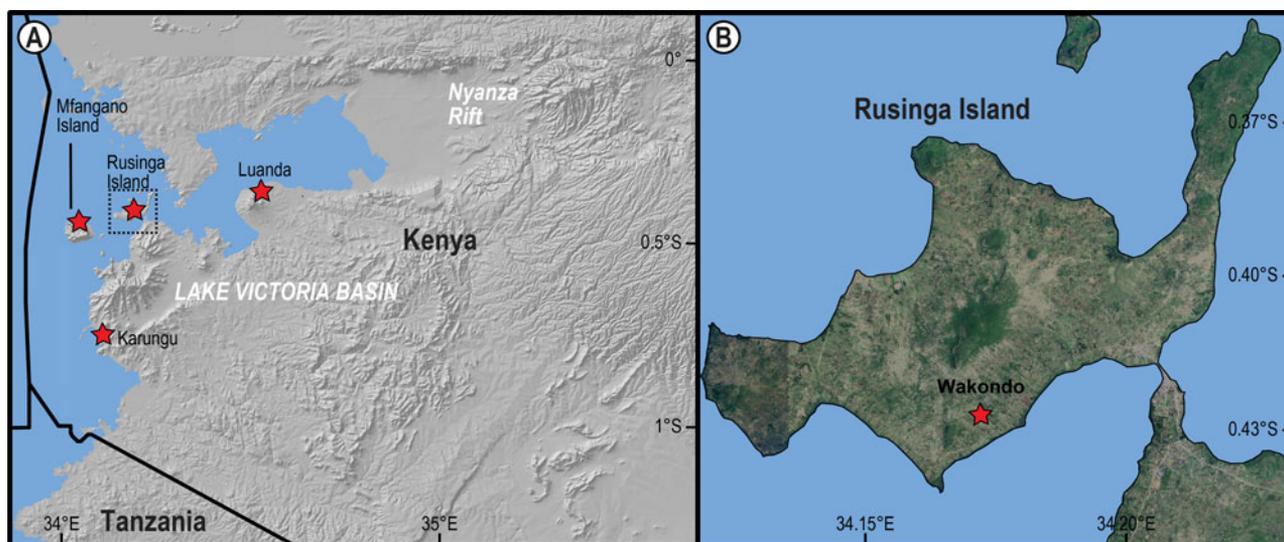


Figure 1. (color online) (A) Map of Lake Victoria showing fossil localities discussed in the text, denoted by a star. (B) Wakondo Bovid Hill within Rusinga Island's Pleistocene Wasiriya Beds.

bathymetric reconstructions suggest that open and grassy habitats were widespread throughout much of the late Pleistocene in the Lake Victoria Basin. The region was considerably drier than modern times from ~100–36 ka, which probably resulted in the complete desiccation of Lake Victoria and an expansion of a Serengeti-like ecosystem across the basin (Tryon et al., 2014, 2016; Beverly et al., 2015a, b, 2017, 2020; Faith et al., 2015).

With no postcranial remains definitely attributed to the species until recovery of the Bovid Hill assemblage, nothing could be said about its behavior or ecology from the perspective of postcranial skeletal morphology. Here, we provide such an assessment through analysis of a large assemblage of postcranial remains from Bovid Hill at Wakondo, on Rusinga Island, within Lake Victoria. At Bovid Hill, remnants of a herd of *R. atopocranion* were recovered from a shallow channel deposit where rapid sedimentation preserved a large sample of nearly complete elements of individuals from a range of ages (Jenkins et al., 2017). As one of the dominant species in the basin, the postcranial anatomy, locomotor patterns, and adaptations of *R. atopocranion* play an important role in further assessing the palaeoecology of Pleistocene Lake Victoria region, as well as the evolutionary history of eastern African bovids.

Rusingoryx ecomorphology

Skeletal adaptations to physical environmental conditions, or ecomorphologies, are commonly studied aspects of mammalian anatomy. Long bones, phalanges, and even some carpals and tarsals are effective indicators of the physical characteristics of the habitat that animals in multiple families exploit (e.g., van Valkenburgh, 1987; Kappelman, 1988; Plummer and Bishop, 1994; DeGusta and Vrba, 2005; Kovarovic and Andrews, 2007; Curran, 2012; Meloro et al., 2013; Barr, 2014). This is particularly the case with bovids whose

taxonomic, geographic, and behavioral diversity have resulted in nuanced differences in their skeletal elements that reflect their ecology, which in turn reflects differences in their habitats. Multiple studies have demonstrated that, for example, a highly cursorial species living in open environments that relies on outrunning predators can be distinguished from species inhabiting closed habitats with significant vegetation cover that favor camouflage or hiding as a means of predator defence (Kappelman, 1988; Köhler, 1993; Plummer and Bishop, 1994; Barr, 2014). The array of ecomorphologies displayed by an entire fossil community can be assessed in order to develop a composite picture of the habitat types that once supported the community, making this a useful method of paleoenvironmental reconstruction (e.g., Kovarovic and Andrews, 2007). However, ecomorphological studies are also typically used to evaluate the behavior of a particular species where this is not well understood (e.g. Faith et al., 2012; Fabre et al., 2015; Barr, 2018).

Wakondo “Bovid Hill” Site

While *Rusingoryx* is now recognized from many sites in the eastern Lake Victoria Basin, specimens used in this study come from the type site for *Rusingoryx atopocranion*, Wakondo, a Pleistocene locality on Rusinga Island (Pickford and Thomas, 1984) (Fig. 1). A dense bonebed of *Rusingoryx* specimens was the focus of surface collections in 2007–2009 at a sub-locality of Wakondo named “Bovid Hill” (O’Brien et al., 2016), which was likely the same area collected by Pickford and Thomas (1984). Preliminary excavations in 2009 established the in situ nature of the Wakondo deposits and the stratigraphic position of the Bovid Hill site within the Wasiriya Beds (Tryon et al., 2010). In 2011, targeted archaeological excavations at Bovid Hill totaling 19 m² uncovered additional *Rusingoryx* specimens (MNI = 11) with associated MSA stone tools and cut-marked specimens

(Jenkins et al., 2017). Unusually, the excavation includes a number of individuals where crania and post-crania can be directly associated, with a large portion of the skeleton represented in the composite sample from the site (see Fig. 2). The bonebed rests in a coarse-grained, cut and fill fluvial deposit atop a partially eroded Vertisol. OSL dates from the Bovid Hill excavation indicate an age of 68 ± 5 ka for the bonebed (Blegen et al., 2015).

Skeletal part frequencies from the 2011 Bovid Hill excavations point to a density-mediated and fluvially winnowed assemblage, where low-density elements and portions of elements are relatively rare (Jenkins et al., 2017). Mortality profiles based on dental remains from both surface finds and the excavated collection indicate a prime-dominated assemblage (Jenkins et al., 2017). Sexual dimorphism is not well understood in *Rusingoryx*, but given the lack of very young juveniles (individuals under 12 months) at Bovid Hill, it is possible that the assemblage represents a bachelor herd (O'Brien et al., 2016; Jenkins et al., 2017).

The excavated monospecific assemblage, taphonomic characteristics, prime-dominated mortality profiles, stone tools, and geologic context suggest that the assemblage may represent the remains of a mass kill site where MSA hunters employed tactical hunting techniques that used features of the landscape, such as topographic lows or water features, to corral and disable large portions of animals herds (Jenkins et al., 2017). Alternatively, the site may represent a scavenged mass drowning from a flash flood starting in the adjacent highlands of Rusinga, although the low competency of the reconstructed paleo-channel make this latter explanation less likely (Jenkins et al., 2017).

Given the high quality of the Bovid Hill sample of multiple *Rusingoryx* individuals, and the relative rarity of extinct Pleistocene African mammals associated with postcranial elements, we are in the unique position to be able to investigate the ecological niche of this unusual species using a suite of skeletal elements and adaptive characters. Here we present an ecomorphological analysis of the entirety of the appendicular skeleton available for *Rusingoryx*.

MATERIALS AND METHODS

Skeletal elements and measurements

Complete long bones provide some of the best ecomorphological predictors of habitat, but they are uncommon in the fossil record. We therefore focused only on elements or portions of elements that are present in the Bovid Hill *Rusingoryx* sample. Studied long bones include the distal humerus, radius, metacarpal, proximal femur, distal femur, proximal tibia, and metatarsal. We also studied four carpals (magnum, unciform, lunar, and cuneiform) and four tarsals (astragalus, calcaneus, naviculo-cuboid, and the external and middle cuneiform). Proximal, intermediate, and distal phalanges were analyzed without consideration of their location on the fore- or hindlimb, due to the difficulty of identifying isolated phalanges to their correct limbs in the fossil record.

Additionally, previous research has not found any difference between habitat assignments based on limb position of the phalanges (Louys et al., 2013).

The measurements taken on each element or element portion are adapted from a previously published bovid ecomorphological study (Kovarovic and Andrews, 2007). They include many standard archaeological and palaeontological measures of length and the diameters of the distal and proximal ends, as well as measurements targeted at capturing dimensions of the articular surfaces (Supplementary Material 1 and Supplementary Material 2, Figs. S1–S18). We note that it is far likelier that a fossil long bone will preserve its functional length (length between the proximal and distal articular surfaces) rather than the total length, so this measure was used. All measurements were taken with digital Mitutoyo calipers (instrument accuracy = 0.02 mm) or a Paleo-Tech osteometric board.

Analysis and statistical considerations

Ecomorphological analyses typically involve the use of multivariate predictive statistics to indicate which habitats fossil individuals were likely adapted to based on comparisons with a sample of extant known-habitat individuals. Discriminant function analysis (DFA) is commonly employed in this regard (e.g., Kovarovic et al., 2011; Faith and Lyman, 2019). Each individual in the comparative sample is assigned to an ecological category (e.g., habitat preference) given what is known of the species' behavior, and the measurements of each element are the predictor variables used to determine the linear dimensions along which these habitat groups can be discriminated. The groups are clustered around a centroid (i.e., mean discriminant score). A probability is calculated for group membership based on proximity to each centroid; naturally, the extant individuals can be mis-classified to the incorrect habitat group. The success of a DFA model is thus based on the overall number of individuals correctly assigned to their known habitat category. Models with high success rates can then be used to predict the group affiliation of unknown individuals which, in this study, are the *Rusingoryx* fossil elements.

There are several important assumptions inherent to DFA. The number of predictor variables cannot exceed the number of individuals in the smallest group, for example, nor can they be collinear. The method also suffers from a problem with over-fitting whereby group predictions are usually better than expectations based on "chance" alone, even when the predictor variables bear no relationship to group membership (DeGusta and Vrba, 2003; Kovarovic et al., 2011; Luo et al., 2011). For example, in a case where there are five groups, we would expect that there is a 1 in 5, or a 20%, chance of the assignments being correct, but in fact the overall proportion of correct assignments always surpasses this level. Success rates are also influenced by the number of groups, the total number of individuals in each group, and the number of predictor variables. For a detailed exploration of the issues arising from the application of DFA in archaeological and

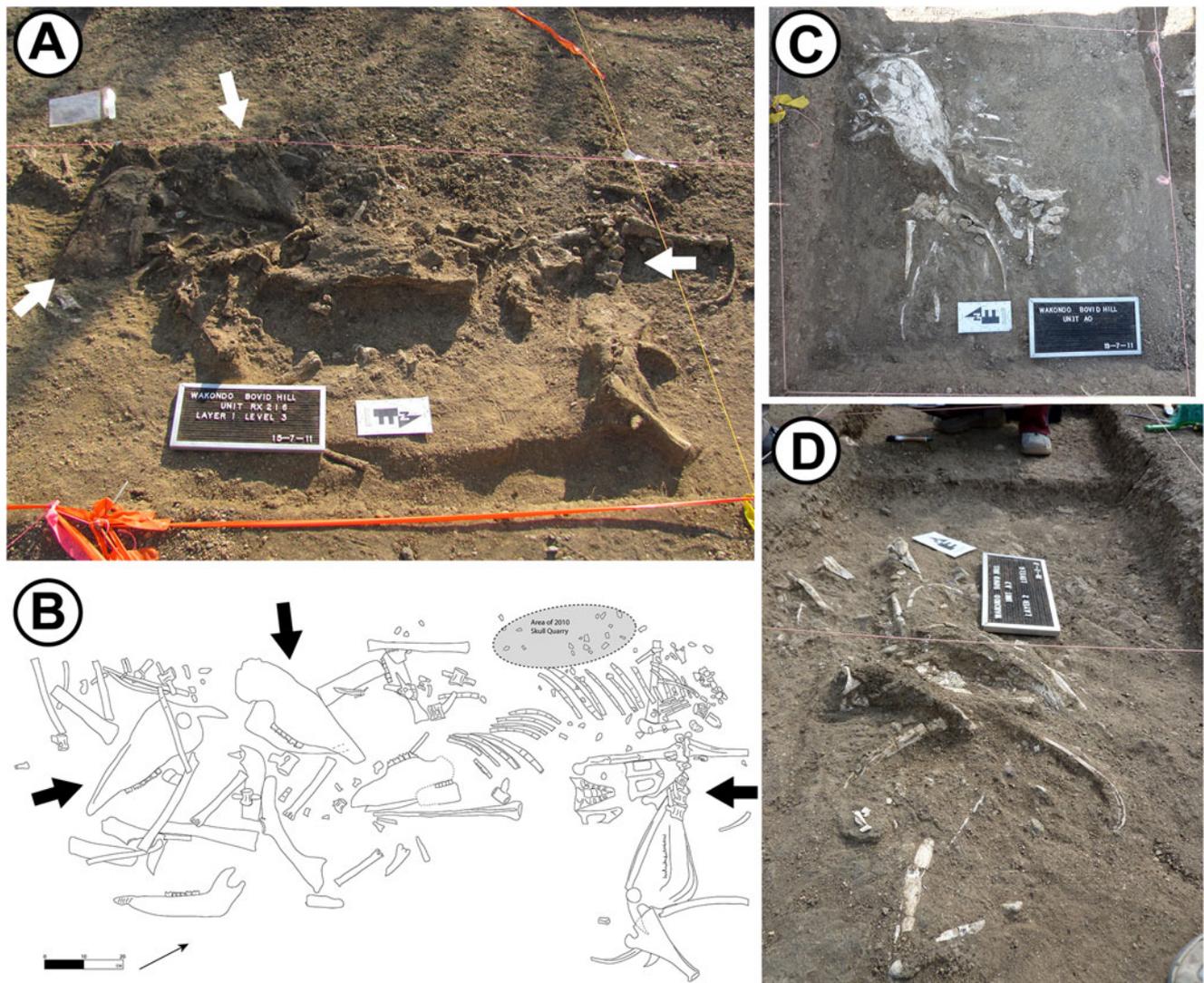


Figure 2. (color online) Field photos and sketch map of *Rusingoryx* bonebed at the Wakondo locality on Rusinga Island. (A) Field photo of excavation Grid 1 showing a partially articulated juvenile of *Rusingoryx*, as well as skeletal elements from multiple other individuals. White arrows indicate elements, also indicated in (B), for reference. (B) Sketch map of excavation Grid 1 showing a partially articulated juvenile *Rusingoryx* and bones of other individuals. Black arrows indicate elements, also indicated in (A), for reference. Figure is modified from Jenkins et al. (2017). (C) Field photograph of excavation Grid 3 showing a *Rusingoryx* skull and other skeletal elements. (D) Field photograph of excavation Grid 3 showing an example of the bone bed with multiple elements of multiple individuals of *Rusingoryx* preserved together.

palaeontological contexts we refer readers to Kovarovic et al. (2011). We follow their use of the Tau statistic in evaluating the relative success of each DFA model. Tau is a chance-corrected measure that does not control for the number of predictor variables, but takes group numbers and unequal group sizes into account. It is defined as:

$$\text{TAU} = (N_c - \sum_{i=1,G} P_i \times N_i) / (N - \sum_{i=1,G} P_i \times N_i)$$

where: N = total sample size; N_c = total number of cases correctly assigned by the DFA; P_i = prior probability of group membership in the i -th of the G groups; N_i = number of cases in the i -th group (Klecka, 1980; McGarigal et al., 2000). When converted to a percentage, Tau provides a

metric for assessing how many fewer misclassifications are made when compared to chance assignments.

We also report cross-validated results, which calculate the success rates of models based on a leave-one-out (i.e., jack-knife) approach. Each individual case is held out of the calculation of the discriminant functions and then tested against the resulting model to see if it correctly assigns the case. The classification rate in this instance is the proportion of cases correctly assigned to the right group when they have not contributed information to the model, whereas the basic resubstitution results report the percentage of cases correctly assigned when they have been included. The cross-validated results indicate how well a model can be generalized; where the resubstitution and cross-validated success rates are similar, they are particularly robust.

Here we apply DFA to each skeletal element or element portion available in the *Rusingoryx* sample. However, not every element is as good as the next in predicting habitat affiliation. Complete long bones, phalanges, the astragalus, and calcaneus are particularly useful elements (Kappelman, 1988; Plummer and Bishop, 1994; DeGusta and Vrba 2003, 2005; Barr, 2014), but the fossil record is replete with epiphyseal portions and smaller, irregular elements such as carpals that are somewhat less habitat-sensitive. This has important implications for the habitat schemes used in our analysis, which must be broad enough to be detected in the anatomy, while remaining sufficiently narrow to provide useful ecological information (Faith and Lyman, 2019). Because different elements and portions thereof vary in the amount of ecological information they provide concerning an animal's habitat adaptations, we considered a five- (most refined), four-, and three-category (least refined) system. These and the comparative species classifications are described in more detail below (see *Habitat categories and assignments*). We considered the best DFA model for each element to be the one that used the highest number of habitat categories where the resulting success rate was > 60% and the difference between the resubstitution and cross-validated rates was < 10%. These criteria are helpful in determining which DFA model was the best for each element, but Tau provides a statistical means for evaluating the success of all of our models despite variations in the number of habitat groups or unequal sample sizes per group. This approach allows us to survey the entire available *Rusingoryx* skeleton, while accounting for the fact that elements differ in sensitivity of the adaptive information they provide.

All measurements were log₁₀-transformed for analysis. Variables determined to be multicollinear via a tolerance test were excluded from the calculations of the discriminant functions. In particular, a variable whose variance inflation factor is greater than 10 was excluded. Tau was calculated in Excel 2013. The tolerance test and DFAs were conducted in SPSS Version 22.

Bovoid data

Comparative sample

The modern comparative bovid sample consists of African species; the total number of modern specimens differed in each DFA, ranging from n = 121 to n = 350 (see Supplementary Data 1). Effort was made to include a consistent number of specimens from the eight African bovid tribes (Alcelaphini, Cephalophini, Neotragini, Antilopini, Reduncini, Tragelaphini, Hippotragini, and Aepycerotini) and the habitat groups, but numbers of specimens in each group were constrained by their availability in museum collections. Data were collected at: The Natural History Museum, London, UK (NHM); Powell-Cotton Museum, Birchington-on-Sea, UK (PC); American Museum of Natural History, New York City, New York, USA (AMNH); National Museum of Natural History, Washington, DC, USA

(NMNH); Field Museum, Chicago, Illinois, USA (Chic); Zoological Museum, Copenhagen, Denmark (Copen); Swedish Museum of Natural History, Stockholm, Sweden (Stock); Natural History Museum Vienna, Austria (Vienna); Naturalis, Leiden, The Netherlands (Leiden); Museum of Natural History, Berlin, Germany (Berlin); Royal Museum of Central Africa, Tervuren, Belgium (RMCA); and Hungarian Natural History Museum, Budapest, Hungary (Buda) (institutional abbreviations are used to denote the locations of the individual specimens in the raw data file; see Supplementary Data 1). All of the specimens are adult, non-pathological, and were caught in the wild.

Fossil sample

Fossil collections from Rusinga Island are housed in the Palaeontology Department at the National Museums of Kenya (NMK) in Nairobi, where metric data were collected. The samples used in the current study are derived solely from the Bovid Hill bonebed assemblage and include both excavated and surface material (Jenkins et al., 2017). A total of 58 *Rusingoryx* specimens were sufficiently complete to be included here (Table 1).

Habitat categories and assignments

We use three different habitat category systems. The five-category system is the most refined and relates most clearly to specific habitat types. The four- and three-category systems largely describe the broad physical characteristics of the overall amount of cover provided by the vegetation. All of the habitat types present differences in the physical environments that animals must navigate during activities that affect survival, particularly predator avoidance.

The five-category habitat system is adapted from Kovarovic and Andrews (2007) where detailed descriptions of the habitat types can be found (and references therein). Brief definitions of each habitat are below:

Grassland/treeless (G/T) includes grasslands and deserts. Scattered woody cover may be present, but it does not exceed 2% of the overall surface.

Wooded-bushed grassland (WBG) are areas dominated by grasses, but also have trees and shrubs providing 2–40% cover. They are often ecotonal and the tree/shrub cover may be inconsistently distributed. This category also includes semi-desert habitats that are similar in the distribution of shrub and bush cover, but have seasonally fluctuating amounts of grass and herbaceous ground cover.

Light woodland-bushland (LWB) and *heavy woodland-bushland* (HWB) are categories distinguished largely by the amount of woody vegetation present. Light woodland-bushland equates to 40–60% woody cover and heavy woodland-bushland equates to 60–75%. Grasses may be present, but are inconsistently distributed and tend to decrease as the amount of tree and bush cover increases.

Forest (F) is where herbs and shrubs dominate the ground cover with few grasses. Woody vegetation is dense, more or

Table 1. Wakondo “Bovoid Hill” *Rusingoryx atopocranion* specimens included in the ecomorphological analyses. Material is housed in the National Museums of Kenya, Paleontology Department. RU = Bovoid Hill surface collection from 2006 and 2007; RUP = Bovoid Hill surface collection from 2010; BH = Bovoid Hill excavated specimen.

Element	Number	Specimen No.
<i>Forelimb (n = 20)</i>		
humerus (distal)	3	RU06-74 RU06-75/85 BH EX-1077
radius	3	BH EX-674 BH EX-1286 BH-EX-1323.005
metacarpal	2	BH EX-134 BH EX-1063
magnum	3	RUP10-285 RUP10-312 BH-EX-1324.018
unciform	3	BH EX-638 BH EX-1266 BH-EX-1324.011
lunar	2	BH-SB-001 BH-EX-1324.001
cuneiform	4	RU07-BHE-12 BH EX-635 BH EX-731 BH-EX-1324.024
<i>Hindlimb (n = 13)</i>		
femur (distal)	1	BH-EX-1323.004
femur (proximal)	1	BH SC-293
tibia (proximal)	1	BH-EX-1319.001
metatarsal	1	BH EX-876
astragalus	5	BH EX-474 BH EX-881 BH EX-1226 RUP12-20 BH-EX-1324.029
calcaneus	1	BH EX-779
naviculo-cuboid	1	RU06-79
external & middle cuneiform	2	BH EX-1004 BH-EX-1324.022
<i>Phalanges (n = 25)</i>		
proximal phalanges	7	RU2007-799 BH EX-259 BH EX-718 BH EX-1291 BH-EX-1323.001 BH-EX-1324.002 BH-EX-1324.026
intermediate phalanges	13	RU06-78 RU2007-BHE-30 RU2007-BHE-45 RU2007-BHE-46 RUP10-10003 BH EX-256 BH EX-333

(Continued)

Table 1. Continued.

Element	Number	Specimen No.
		BH EX-788
		BH-EX-1324.003
		BH-EX-1319.004
		BH-EX-1324.012
		BH-EX-1324.013
		BH-EX-1324.025
distal phalanges	5	RU2007-BHE-16 RUP10-297 RUP10-305 RUP10-307 BH EX-634

less continuous, and the canopy can be comprised of interlocking crowns and multistoried trees with 75–100% woody cover.

The four-category habitat system is similar to the habitat system in other bovid ecomorphological studies. It subsumes the open/treeless and wooded-bushed grassland categories into one open-cover category (O). Light cover (LC), heavy cover (HC), and forest (F) are equivalent to LWB, HWB, and F, respectively, in the five-category system.

The three-category system recognizes a rather coarse difference between the amounts of vegetation cover overall, and is not strictly tied to well-defined habitat types. The differences among the three categories—open (O), intermediate (INT) and closed cover (C)—are much more approximate. The intermediate category is particularly broad, encompassing most woodlands, bushlands, and ecotones (*sensu* Plummer and Bishop, 1994).

Habitat assignments for each of the modern species were based on observations of the living species and interpretations of the habitats where each species spends the majority of its time, even if they may be occasionally observed elsewhere. The majority of the observational and behavioral information that informed habitat assignments was found in Kingdon (2015), Nowak (1999), and MacDonald (2001). Each species' habitat assignment within each of the three habitat category systems can be found in Appendix 1.

RESULTS

Forelimb elements

The results of the forelimb DFAs are presented in Table 2, where they are ranked according to their Tau statistic values. The cross-validated results range from 55.8% (cuneiform) to 66.2% (unciform). The Tau statistic ranges from 29.3% (cuneiform) to 52.5% (metacarpal). The metacarpal analysis dropped four measurements because they failed the tolerance test for multicollinearity. These include the measure of the distance between the medial and lateral epicondyle at the most distal point (MC14), the antero-posterior and transverse mid-shaft diameters (MC15 and MC16), and the transverse

Table 2. Forelimb element results. Habitat category abbreviations are as follows: (G/T) grassland/tree-less; (WBG) wooded-bushed grassland; (LWB) light woodland-bushland; (HWB) heavy woodland-bushland; (F) forest; (O) open cover; (LC) light cover; (HC) heavy cover; (C) closed cover; (INT) intermediate cover. DFA models are organized according to the highest value of Tau. *Four measurements have been dropped from the model because they fail a tolerance test: MC14, MC15, MC16, and MC20.

Element	Habitat system	No. of extant specimens	% correct (resubstitution)	% correct (cross-validated)	Tau	<i>Rusingoryx</i> predictions	Probability	Specimen no.
Metacarpal* n = 2	4	Total n = 220 O = 88 LC = 50 HC = 46 F = 36	75.0	65.9	52.5	open	0.93198 0.61072	BH EX-134 BH EX-1063
Radius n = 3	5	Total n = 225 G/T = 27 WBG = 62 LWB = 50 HWB = 50 F = 36	66.7	60	49.1	2 = grassland/treeless 1 = wooded-bushed grassland	0.73424 0.58886 0.46517	BH EX-674 BH-EX-1323.005 BH EX-1286
Unciform n = 3	3	Total n = 219 O = 89 INT = 94 C = 36	70.8	66.2	45.8	open	0.72910 0.74357 0.97880	BH EX-1266 BH EX-638 BH-EX-1324.011
Lunar n = 2	3	Total n = 213 O = 88 INT = 90 C = 35	67.6	62.4	39.8	open	0.99610 0.99958	BH-SB-001 BH-EX-1324.001
Magnum n = 3	3	Total n = 218 O = 88 INT = 94 C = 36	64.7	58.7	33.7	open	0.83055 0.94486 0.83256	BH-EX-1324.018 RUP10-312 RUP10-285
Humerus (distal) n = 3	3	Total n = 215 O = 79 INT = 100 C = 36	59.5	56.3	29.6	open	0.59620 0.69086 0.85896	RU06-75/85 RU06-74 BH EX-1077
Cuneiform n = 4	3	Total n = 215 O = 88 INT = 91 C = 36	57.7	55.8	29.3	open	0.84149 0.81594 0.74729 0.74937	RU07-BHE-12 BH EX-635 BH EX-731 BH-EX-1324.024

diameter of the distal shaft (MC20) (see Figure S3). These variables are not included in the calculation of the final discriminant functions, but this analysis is the most successful according to the Tau statistic, which is the highest (52.5%). It also has a cross-validated success rate of 65.9%, second only to the unciform (66.2%).

In these forelimb element DFA models, all but one of the 20 *Rusingoryx* specimens are predicted to the most open habitat category (Table 2). One of the three radii is predicted to belong to the wooded-bushed grassland (WBG) category. Probabilities of assignment are moderate to high in the long bones (0.589–0.932), except for the one radius, which is predicted to WBG (0.465) (Figure 3). Probabilities of assignment are high in the carpals (0.729–1.000) (Figure 3).

Hindlimb elements

Hindlimb DFA results are ranked by Tau (Table 3). Cross-validated success rates range from 58.7% (proximal tibia) to 68.6% (metatarsal). The Tau statistic mirrors these results, identifying the best model as the metatarsal with 56.3%, and the worst as the proximal tibia with a value of 33.2%. Also note that the metatarsal model, like the metacarpal, suffers from multicollinearity. Six measurements fail the tolerance test and are therefore not included in the calculation of the final discriminant functions: the measure of the distance between the medial and lateral condyle at the most proximal (MT15) and the most distal point (MT16), the antero-posterior and transverse midshaft diameter (MT17 and

MT18), and the antero-posterior and transverse diameter of the distal shaft (MT21 and MT22) (see Figure S7 in Supplementary Material).

All of the *Rusingoryx* hindlimb fossil specimens, except for the one distal femur, are assigned to the most open habitat (Table 3). The distal femur is predicted to the intermediate cover category, but this prediction is associated with a rather low probability (0.425). Only the single metatarsal has a lower probability (0.403). The remaining probabilities are moderate to high, ranging from 0.542 (a proximal tibia) to 0.963 (a naviculo-cuboid) (Figure 3).

Phalanges

The results of the three phalanges DFAs are in Table 4 ranked by Tau statistic values. The cross-validated success rates range from 59.1% (proximal phalanges) to 65.5% (distal phalanges). The Tau statistic indicates that the best model is the distal phalanges (55.1%) and the worst is the proximal phalanges (43.3%).

Rusingoryx phalanges are predicted to habitats that range from open to forest in each category system (Table 4). Of the 25 available phalanges, 11 of them are predicted to belong to the most open habitat category. Their associated probabilities are not very high, ranging from 0.387 to 0.624. Of the remaining 14 specimens, six are assigned to light-cover categories with probabilities ranging from 0.362 to 0.706 and eight to heavy cover or forest with probabilities ranging from 0.471 to 0.696.

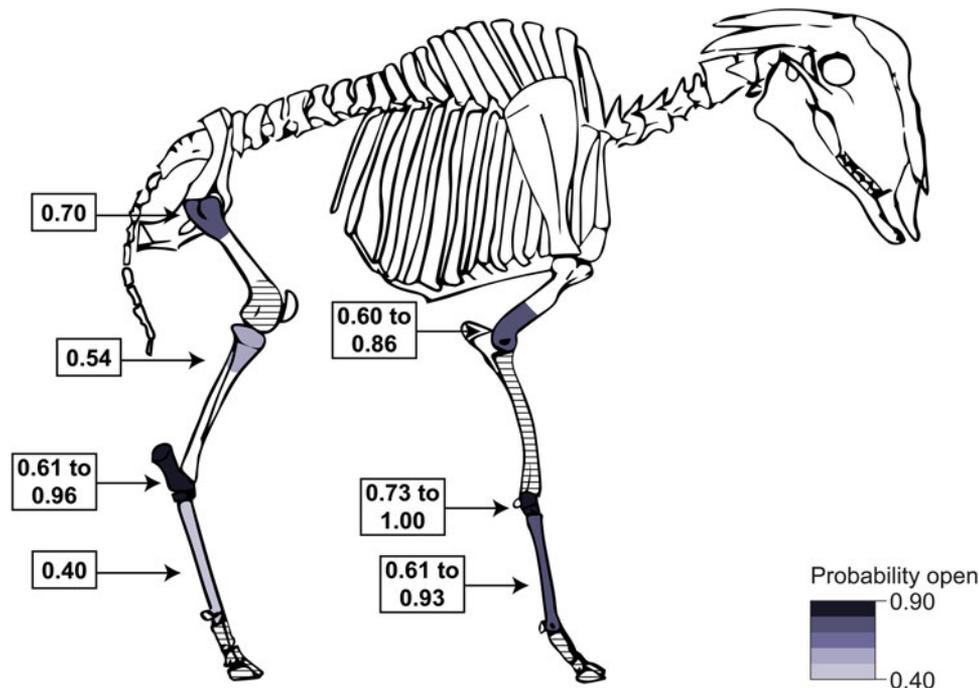


Figure 3. Illustration of postcranial elements used in this study. Specimens are shaded according to the mean probability of assignment to the most open habitat category. Shading for carpals and tarsals represents the mean value for all carpals and tarsals included in the analysis. If an element has a lined pattern, this indicates that it was not always assigned to the most open habitat category.

Table 3. Hindlimb element results. Habitat category abbreviations are as follows: (G/T) grassland/tree-less; (WBG) wooded-bushed grassland; (LWB) light woodland-bushland; (HWB) heavy woodland-bushland; (F) forest; (O) open cover; (LC) light cover; (HC) heavy cover; (C) closed cover; (INT) intermediate cover. DFA models are organized according to the highest value of Tau. *Six measurements have been dropped from the model because they fail a tolerance test: MT15, MT16, MT17, MT18, MT21, and MT22.

Element	Habitat system	No. of extant specimens	% correct (resubstitution)	% correct (cross-validated)	Tau	<i>Rusingoryx</i> predictions	Probability	Specimen no.
Metatarsal* n = 1	4	Total n = 223 O = 89 LC = 51 HC = 47 F = 36	78.9	68.6	56.3	open	0.40297	BH EX-876
Naviculo-cuboid n = 1	4	Total n = 223 O = 91 LC = 49 HC = 47 F = 36	74.4	66.4	52.9	open	0.96311	RU06-79
Femur (proximal) n = 1	4	Total n = 221 O = 81 LC = 53 HC = 51 F = 36	68.8	66.1	48.3	open	0.70300	BH SC-293
Astragalus n = 5	4	Total n = 223 O = 89 LC = 52 HC = 46 F = 36	68.6	60.6	45.0	open	0.73060 0.88587 0.89290 0.94158 0.64178	BH EX-1226 BH EX-474 BH EX-881 BH-EX-1324.029 RUP12-20
Femur (distal) n = 1	3	Total n = 221 O = 81 INT = 104 C = 36	66.5	64.7	42.9	intermediate	0.42534	BH-EX-1323.004
Calcaneus n = 1	3	Total n = 221 O = 86 INT = 99 C = 36	66.1	61.1	36.8	open	0.94844	BH EX-779
Ext & mid cuneiform n = 2	3	Total n = 212 O = 89 INT = 91 C = 32	63.7	59.9	35.0	open	0.60683 0.89169	BH EX-1004 BH-EX-1324.022

(Continued)

Table 3. Continued.

Element	Habitat system	No. of extant specimens	% correct (resubstitution)	% correct (cross-validated)	Tau	<i>Rusingoryx</i> predictions	Probability	Specimen no.
Tibia (proximal) n = 1	3	Total n = 230 O = 90 INT = 104 C = 36	61.3	58.7	33.2	open	0.54239	BH-EX-1319.001
Element	Habitat system	No. of extant specimens	% correct (resubstitution)	% correct (cross-validated)	Tau	<i>Rusingoryx</i> predictions	Probability	Specimen no.
Metatarsal* n = 1	4	Total n = 223 O = 89 LC = 51 HC = 47 F = 36	78.9	68.6	56.3	open	0.40297	BH EX-876
Naviculo-cuboid n = 1	4	Total n = 223 O = 91 LC = 49 HC = 47 F = 36	74.4	66.4	52.9	open	0.96311	RU06-79
Femur (proximal) n = 1	4	Total n = 221 O = 81 LC = 53 HC = 51 F = 36	68.8	66.1	48.3	open	0.70300	BH SC-293
Astragalus n = 5	4	Total n = 223 O = 89 LC = 52 HC = 46 F = 36	68.6	60.6	45.0	open	0.73060 0.88587 0.89290 0.94158 0.64178	BH EX-1226 BH EX-474 BH EX-881 BH-EX-1324.029 RUP12-20
Femur (distal) n = 1	3	Total n = 221 O = 81 INT = 104 C = 36	66.5	64.7	42.9	intermediate	0.42534	BH-EX-1323.004
Calcaneus n = 1	3	Total n = 221 O = 86 INT = 99 C = 36	66.1	61.1	36.8	open	0.94844	BH EX-779

(Continued)

Table 3. Continued.

Element	Habitat system	No. of extant specimens	% correct (resubstitution)	% correct (cross-validated)	Tau	<i>Rusingoryx</i> predictions	Probability	Specimen no.
Ext & mid cuneiform n = 2	3	Total n = 212 O = 89 INT = 91 C = 32	63.7	59.9	35.0	open	0.60683 0.89169	BH-EX-1004 BH-EX-1324.022
Tibia (proximal) n = 1	3	Total n = 230 O = 90 INT = 104 C = 36	61.3	58.7	33.2	open	0.54239	BH-EX-1319.001

DISCUSSION

Although there is a general correspondence between the ranking of the best DFA models indicated by the cross-validated success rates and Tau, only the Tau statistic can be compared equally across them because it accounts for differences in group numbers and group sizes. Converted to a percentage, Tau indicates how many fewer mistakes the DFA makes when compared to chance assignments. Comparing Tau and the success rate of the cuneiform DFA (Table 2), for example, the value of Tau becomes apparent; this model yields almost 56% correct habitat predictions, but it is only 29.3% better than chance. Although it is clear from the results that some DFA models are better than others, amongst the forelimb and hindlimb elements the complete long bones (radius, metacarpal, metatarsal, see Table 2 and Table 3) are the best and are the most ecologically nuanced, utilizing a four- or five-habitat classification system. Carpals, tarsals, and long bone portions are less ecologically sensitive, and have generally lower rates of success and Tau values.

Strikingly, despite variations in the sensitivity of the different elements, an overwhelming majority of the *Rusingoryx* forelimb and hindlimb specimens (31 out of 33) are predicted to belong to the most open cover habitat category, with the exception of one radius and one distal femur, which are assigned to the wooded-bushed grassland and intermediate cover categories, respectively. The associated probabilities of prediction for that radius and distal femur are, however, not high (radius = 0.465; distal femur = 0.425). Given that the overwhelming majority of the *Rusingoryx* material is assigned to the open cover habitats, it is likely that these two predictions are incorrect assignments. This could be related to measurement error or natural variation in morphology that is not adequately captured in the extant sample. An additional possibility is that the specimens in question belong to another species, but this is unlikely given that all of the taxonomically diagnostic craniodental remains from the excavation belong to *Rusingoryx*, and only a small number of surface-collected specimens from elsewhere at Bovid Hill belong to other bovid species (nine specimens = 7%) (Jenkins et al., 2017). It is interesting to note that the majority of these additional specimens from other bovid species also belong to open-habitat lineages, namely bovids of the tribe Alcelaphini (Jenkins et al., 2017).

Rusingoryx is an alcelaphin, a bovid tribe that today includes multiple gregarious species, such as the hartebeest (*Alcelaphus buselaphus*), that are associated with open and very lightly covered habitats, and wildebeest (*Connochaetes taurinus*), which are generally found in open grasslands and shrubland plains over which some populations traverse hundreds of miles in well-documented annual migrations. Alcelaphins are considered some of the most open and arid-adapted bovid taxa; their general cursorial morphologies, such as long metapodials (Hildebrand, 1974) and oblong femoral heads (Kappelman, 1988), are associated with an increased stride length, hindlimb propulsion during rapid locomotion, and the restriction of locomotion to the parasagittal plane. This behavior is necessary for fleeing

Table 4. Phalanges results. Habitat category abbreviations are as follows: (G/T) grassland/tree-less; (WBG) wooded-bushed grassland; (LWB) light woodland-bushland; (HWB) heavy woodland-bushland; (F) forest; (O) open cover; (LC) light cover; (HC) heavy cover; (C) closed cover; (INT) intermediate cover. DFA models are organized according to the highest value of Tau.

Element	Habitat system	No. of extant specimens	% correct	% correct (cross-validated)	Tau	<i>Rusingoryx</i> predictions	Probability	Specimen no.
Distal phalanges n = 5	5	Total n = 120 G/T = 13 WBG = 36 LWB = 27 HWB = 25 F = 19	70.0	65.5	55.1	1 = grassland/treeless	0.48340	RUP10-297
						4 = light woodland-bushland	0.36198	BH EX-634
							0.41877	RU2007-BHE-16
							0.42680	RUP10-307
							0.58868	RUP10-305
Intermediate phalanges n = 13	4	Total n = 223 O = 97 LC = 48 HC = 50 F = 28	67.7	64.6	49.3	7 = [?] open	0.38716	RU06-78
							0.62423	RU2007-BHE-30
							0.51258	BH-EX-1324.013
							0.64706	BH-EX-1324.025
							0.56188	BH EX-788
							0.40634	BH EX-256
							0.41816	RU2007-BHE-46
						2 = heavy cover	0.52956	BH EX-333
							0.58519	BH-EX-1324.003
						4 = forest	0.69614	RUP10-10003
							0.50886	RU2007-BHE-45
							0.52057	BH-EX-1319.004
							0.48841	BH-EX-1324.012
Proximal phalanges n = 7	4	Total n = 350 O = 139 LC = 78 HC = 71 F = 62	62.9	59.1	43.3	3 = open	0.61578	BH EX-1291
							0.61982	BH-EX-1323.001
							0.52064	BH-EX-1324.026
						2 = light cover	0.51754	BH EX-259
							0.70628	RU2007-799
						1 = heavy cover	0.47085	BH EX-718
						1 = forest	0.60532	BH-EX-1324.002

predators across an open landscape or towards ecotonal areas where cover may be sought.

Morphology and habitat preference are phylogenetically conserved in bovids and, as such, our results are not strictly “taxon-free.” Depending on which species are included in the comparative sample of the DFA (and other analytical approaches we have not employed), phylogeny can affect the ecomorphological analyses to a certain degree (Barr, 2014; Barr and Scott, 2014; Scott and Barr, 2014; Laza-gabaster et al., 2016). Our analyses may therefore somewhat overfit the data, but the ecological signal was remarkably clear regardless. Phylogenetic comparative methods arguably would not have provided any greater clarity in our interpretation of *Rusingoryx*. Our survey of its available forelimb and hindlimb skeleton in fact suggests that it was an alcelaphin *par excellence* in terms of its locomotion, exceptionally well adapted to open habitats, much like modern wildebeest (*Connochaetes taurinus*). The picture does become less clear when we consider the results of the pooled-limb phalanges analyses (Table 4). Only 11 of the available 25 phalanges are assigned to the most open habitat, with relatively low associated probabilities of correct assignment. The remainder

of the phalanges are assigned to habitats across the spectrum of vegetation cover, from light woodland-bushland to forest. We suspect this relates to the remarkably short phalanges of *Rusingoryx*, shown in Figure 4, which illustrates phalanx length and breadth relative to overall phalanx size (= the geometric mean of all measurements) for *Rusingoryx* and the bovids in our extant comparative sample. The fact that *Rusingoryx* falls at or beyond the limits of similarly sized bovids means that its morphology is not well represented by the modern taxa used to create the DFA models, which likely contributes to the varied habitat assignments with relatively weak probabilities (Table 4). Given the large size and ecological breadth of our comparative sample of extant bovids, these differences suggest postcranial features or adaptations without a clear modern analog.

The ecological significance of the *Rusingoryx* phalanx morphology is harder to explain in the absence of modern bovid analogs, although others have noted that relatively short phalanges relative to width are typical of both open and heavy-cover taxa (see DeGusta and Vrba, 2005, fig. 4). Short phalanges are generally associated with open-country species, while the opposite morphology—relatively long

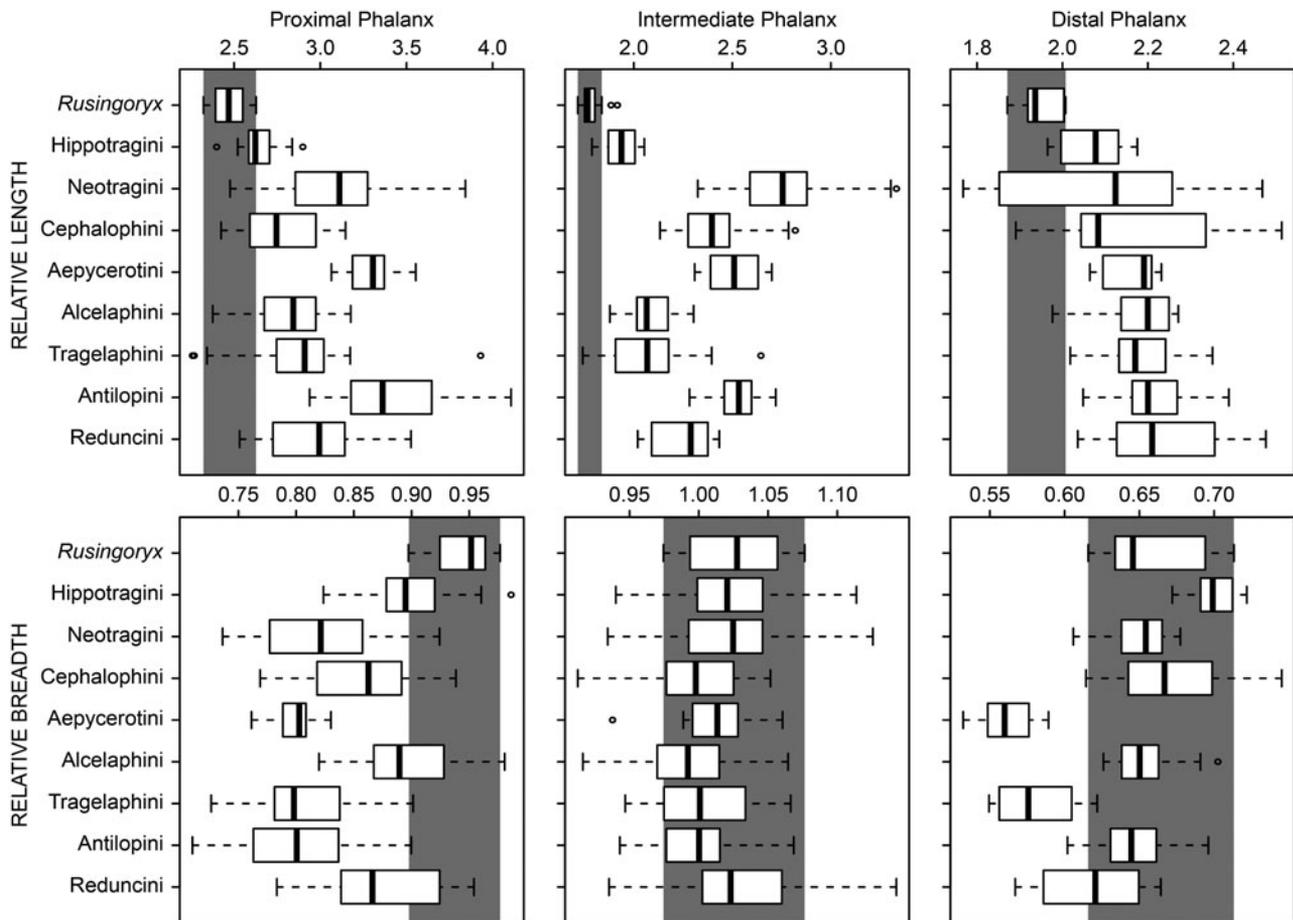


Figure 4. Phalanx length and breadth relative to overall phalanx size (i.e., the geometric mean of all measurements) for *Rusingoryx* and the bovids in our extant comparative sample. *Rusingoryx* has relatively short proximal, intermediate, and distal phalanges, and relatively wide proximal phalanges. Shading encompasses the range of values for *Rusingoryx*.

and splayed phalanges—is today found in species such as *Tragelaphus spekei* (sitatunga) (DeGusta and Vrba, 2005; Kingdon, 2015), which prefers swampy areas, where phalanx morphology is considered an adaptation to waterlogged terrain. The greater surface area of longer phalanges provides support in swampy conditions, but inhibits efficient running on stable surfaces (Kingdon, 2015). In contrast, cursorial animals tend to have reduced phalanges (e.g., Coombs, 1978), perhaps in part because lighter hooves allow for greater speed and reduced energetic costs of locomotion (e.g., Clifford, 2010; McHorse et al., 2017). We posit that phalanx morphology of *Rusingoryx* is functionally significant, rather than adaptively neutral, and when coupled the overwhelming evidence from the rest of the postcrania of *Rusingoryx*, suggests that the shortened phalanges are an extreme open-habitat adaptation beyond the range of extant species.

Interestingly, given the extremely shortened phalanges, which result in a small surface area of the hooves in contact with the ground, water-logged environments were likely challenging for *Rusingoryx*. This in turn may have made *Rusingoryx* particularly vulnerable to predators or human hunters when drinking from springs and streams on the landscape, such as at Bovid Hill assemblage, which is interpreted a kill

site where hominins strategically ambushed the herd in a riverine setting (Jenkins et al., 2017).

The availability of multiple skeletal elements for our study has provided a far more comprehensive picture of the locomotor behavior and ecology of *Rusingoryx* than single-element analyses are capable of providing. Taken together, our ecomorphological survey of the skeleton of *Rusingoryx* suggests a species that was very well adapted for open and probably dry habitats, perhaps even more so than its closest living relatives. This plausibly explains its dominance in late Pleistocene deposits in the Lake Victoria Basin, which sampled expanded grassy plains in an arid climate (Tryon et al., 2014, 2016; Beverly et al., 2015a, b, 2017; Faith et al., 2015). This accords well with other indicators of the behavior of *Rusingoryx* and paleoecological proxies. Its grazing diet is indicated by the general skeletal morphology, mesowear patterns (Faith et al., 2011), and stable carbon isotopic analyses of its teeth (Faith et al., 2015; Garrett et al., 2015; Tryon et al., 2016), suggesting that, like extant alcelaphins, it was a grazer that consumed primarily C_4 grasses, perhaps supplementing only occasionally with shrubs or broad leaves. Its nasal dome is also interpreted as a communication device that propagated sound in open habitats (O'Brien et al., 2016).

Rusingoryx is found throughout the late Pleistocene sequence at Bovid Hill (~100 ka to 36 ka) in western Kenya (Faith et al., 2015; O'Brien et al., 2016; Tryon et al., 2016), after which there is no further Pleistocene sedimentary record from terrestrial deposits within the Lake Victoria Basin. As yet, and despite its local abundance in the fossil record, the taxon is currently unknown outside the Lake Victoria Basin. This may reflect an accurate measure of its former geographic range or perhaps a reflection of the limited paleontological research on the late Pleistocene of eastern Africa, as there are few late Pleistocene assemblages with detailed systematic descriptions (e.g., Rowan et al., 2015). In the absence of younger sediments around Lake Victoria and a more clear understanding of when *Rusingoryx* made its last appearance in the basin, it is difficult to pin down the reasons for its demise. However, we note that given its clear affinity for open habitats, it is likely that *Rusingoryx* inhabited the grassy plains that were exposed by the reduction of Lake Victoria due to the dry conditions that persisted throughout the ~100–36 ka interval (Tryon et al., 2014, 2016; Beverly et al., 2015a, b, 2017, 2020; Faith et al., 2015).

There are several currently undated terraces around the margins of Lake Victoria, some up to ~18 m above current lake levels, which indicate the occurrence of previous highstands in the lake (Doornkamp and Temple, 1966; Temple, 1966; Bishop, 1969; Stager and Johnson, 2008). We propose that at some point during the late Pleistocene, Lake Victoria began to refill and expanded to its maximum highstand, causing a shift in depositional patterns that mark the end of the formation of the Wasiriya Beds. Based on comparisons with Holocene and recent analogs (Andrews, 1973; Stager and Johnson, 2008; Tryon et al., 2016), the potential highstand would have caused an increase in humidity and precipitation, changing the regional environment. The increase in moisture would have eliminated much of the formerly grassy plains in the central basin and contributed to grassy habitats along the margin of the lake becoming compressed or replaced with more closed habitats unsuitable to *Rusingoryx*. In fact, the loss of *Rusingoryx* near the end of the Pleistocene fits in with the overall loss of open-grassland specialists across Africa during the late Pleistocene (Faith, 2014) and a long-term decline of grazers in eastern Africa over the last million years (Faith et al., 2019).

CONCLUSION

Rusingoryx atopocranion is an extinct alcelaphin bovid found across multiple sites of late Pleistocene age in the eastern portions of the equatorial Africa's Lake Victoria Basin, where at least locally, it is one of the dominant large herbivores in the fossil record. This taxon, therefore, plays an outsized role in our understanding of past ecological communities in the region, communities that are particularly important for providing the context for the diversification and dispersal of early modern humans (*Homo sapiens*). Although taxonomic, functional, and isotopic analyses of fossil fauna are routinely used to characterize past environments, these

analyses are usually based on craniodental material alone, in part because of the difficulty of identifying bovid postcrania to lower taxonomic levels. However, postcrania can be particularly informative about the paleoecology of fossil species, and we used the fortuitous preservation of a mass death assemblage of *Rusingoryx* from the Bovid Hill site on Rusinga Island to provide fuller reconstruction of its ecology.

Our ecomorphological analyses consistently point to morphological adaptations to open habitats, including extreme adaptations, such as short phalanges, that are not present among modern bovids. These results contribute to a greater understanding of the mosaic of features that characterized *R. atopocranion* in general, and serve to highlight the ephemeral nature of Lake Victoria. While the lake is the largest in Africa as measured by surface area today, it is shallow and was probably absent throughout much of the late Pleistocene (Beverly et al., 2020) and replaced by some form of grassland habitat occupied by species such as *R. atopocranion*, fundamentally altering the dispersal potential of early *H. sapiens* and other floras and faunas in the region.

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SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/qua.2020.102>.

REFERENCES

- Andrews, P., 1973. Vegetation of Rusinga Island. *Journal of the East Africa Natural History Society and National Museum* 142, 1–8.
- Barr, W.A., 2014. Functional morphology of the bovid astragalus in relation to habitat: controlling phylogenetic signal in ecomorphology. *Journal of Morphology* 275, 1201–1216.
- Barr, W.A., 2018. Ecomorphology. In: Croft, D., Simpson, S., Su, D. (Eds.), *Methods In Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities*. Springer Vertebrate Paleobiology and Paleoanthropology Series. Cham, Switzerland, pp. 339–349.
- Barr, W.A., Scott, R.S., 2014. Phylogenetic comparative methods complement discriminant function analysis in ecomorphology. *American Journal of Physical Anthropology* 153, 663–674.
- Behrensmeyer, A.K., R. Bobe, Z. Alemseged. 2007. Approaches to the analysis of faunal change during the East African Pliocene. In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K. (Eds.), *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence*. Springer, Dordrecht, pp. 1–24.
- Beverly, E.J., Driese, S.G., Peppe, D.J., Arellano, L.N., Blegen, N., Faith, J.T., Tryon, C.A., 2015a. Reconstruction of a semi-arid late Pleistocene paleocatena from the Lake Victoria region, Kenya. *Quaternary Research* 84, 368–381.
- Beverly, E.J., Driese, S.G., Peppe, D.J., Johnson, C.R., Michel, L.A., Faith, J.T., Sharp, W.D., 2015b. Recurrent spring-fed rivers in a Middle to late Pleistocene semi-arid grassland: implications for environments of early humans in the Lake Victoria basin of Kenya. *Sedimentology* 62, 1611–1635.
- Beverly, E.J., Peppe, D.J., Driese, S.G., Blegen, N., Faith, J.T., Tryon, C.A., Stinchcomb, G.E., 2017. Reconstruction of late Pleistocene paleoenvironments using bulk geochemistry of paleosols from the Lake Victoria region. *Frontiers in Earth Science* 5:93. <https://doi.org/10.3389/feart.2017.00093>.
- Beverly, E.J., White, J.D., Peppe, D.J., Faith, J.T., Blegen, N., Tryon, C.A., 2020. Rapid Pleistocene desiccation and the future of Africa’s Lake Victoria. *Earth and Planetary Science Letters* 530, 115883. <https://doi.org/10.1016/j.epsl.2019.115883>.
- Bishop, W.W., 1969. Pleistocene Stratigraphy in Uganda. *Geological Survey of Uganda, Entebbe* 10, 1–128.
- Blegen, N., Faith, J.T., Mant-Melville, M., Peppe, D.J., Tryon, C.A., 2017. The Middle Stone Age after 50,000 years ago: new evidence from the late Pleistocene sediments of the eastern Lake Victoria basin, Western Kenya. *PaleoAnthropology* 2017, 139–169.
- Blegen, N., Tryon, C.A., Faith, J.T., Peppe, D.J., Beverly, E.J., Li, B., Jacobs, Z., 2015. Distal tephtras of the eastern Lake Victoria Basin, equatorial East Africa: correlations, chronology and a context for early modern humans. *Quaternary Science Reviews* 122, 89–111.
- Clifford, A.B., 2010. The evolution of the unguligrade manus in artiodactyls. *Journal of Vertebrate Paleontology* 30, 1827–1839.
- Coombs, W.P., Jr., 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *The Quarterly Review of Biology* 53, 393–418.
- Curran, S.C., 2012. Expanding ecomorphological methods: geometric morphometric analysis of Cervidae post-crania. *Journal of Archaeological Science* 39, 1172–1182.
- DeGusta, D., Vrba, E., 2003. A method for inferring paleohabitats from the functional morphology of bovid astragali. *Journal of Archaeological Science* 30, 1009–1022.
- DeGusta, D., Vrba, E., 2005. Methods for inferring paleohabitats from the functional morphology of bovid phalanges. *Journal of Archaeological Science* 32, 1099–1113.
- Doornkamp, J., Temple, P., 1966. Surface, drainage and tectonic instability in part of southern Uganda. *The Geographical Journal* 132, 238–252.
- Fabre, A., Salesa, M.J., Cornette, R., Antón, M., Morales, J., Peigné, S., 2015. Quantitative inferences on the locomotor behaviour of extinct species applied to *Simocyon batalleri* (Ailuridae, Late Miocene, Spain). *The Science of Nature* 102, 30.
- Faith, J.T., 2014. Late Pleistocene and Holocene mammal extinctions on continental Africa. *Earth-Science Reviews* 128, 105–121.
- Faith, J.T., Choiniere, J.N., Tryon, C.A., Peppe, D.J., Fox, D.L., 2011. Taxonomic status and paleoecology of *Rusingoryx atopocranion* (Mammalia, Artiodactyla), an extinct Pleistocene bovid from Rusinga Island, Kenya. *Quaternary Research* 75, 697–707.
- Faith, J.T., Lyman, R.L., 2019. *Paleozoology and Paleoenvironments: Fundamentals, Assumptions, Techniques*. Cambridge University Press, Cambridge, 398 pp.
- Faith, J.T., Potts, R., Plummer, T.W., Bishop, L.C., Marean, C.W., Tryon, C.A., 2012. New perspectives on middle Pleistocene change in the large mammal faunas of East Africa: *Damaliscus hypsodon* sp. nov. (Mammalia, Artiodactyla) from Lainyamok, Kenya. *Palaeogeography, Palaeoclimatology, Palaeoecology* 361–362, 84–93.
- Faith, J.T., Rowan, J., Du, A., 2019. Early hominins evolved within non-analog ecosystems. *Proceedings of the National Academy of Sciences of the USA* 201909284. <https://doi.org/10.1073/pnas.1909284116>.
- Faith, J.T., Tryon, C.A., Peppe, D.J., 2016. Environmental change, ungulate biogeography, and their implications for early human dispersals in equatorial East Africa. In: Jones, S.C., Stewart, B.A. (Eds.), *Africa from MIS 6-2: Population Dynamics and Paleoenvironments*. Springer, Dordrecht, pp. 233–245.
- Faith, J.T., Tryon, C.A., Peppe, D.J., Beverly E.J., Blegen, N., 2014. Biogeographic and evolutionary implications of an extinct late Pleistocene impala from the Lake Victoria Basin, Kenya. *Journal of Mammalian Evolution* 21, 213–222.
- Faith, J.T., Tryon, C.A., Peppe, D.J., Beverly, E.J., Blegen, N., Blumenthal, S., Chritz, K.L., Driese, S.D., Patterson, D., 2015. Paleoenvironmental context of the Middle Stone Age record from Karungu, Lake Victoria Basin, Kenya, and its implications for

- human and faunal dispersals in East Africa. *Journal of Human Evolution* 83, 28–45.
- Garrett, N.D., Fox, D.L., McNulty, K.P., Faith, J.T., Peppe, D.J., Van Plantinga, A., Tryon, C.A., 2015. Stable isotope paleoecology of late Pleistocene Middle Stone Age humans from the Lake Victoria basin, Kenya. *Journal of Human Evolution* 82, 1–14.
- Grine, F.E., 2016. The late Quaternary hominins of Africa: the skeletal evidence from MIS 6-2. In: Jones, S.C., Stewart, B.A. (Eds.), *Africa from MIS 6-2: Population Dynamics and Paleoenvironments*. Springer, Dordrecht, pp. 323–381.
- Harris, J.M., 1991. Family Bovidae. In: Harris, J.M. (Ed.), *Koobi Fora Research Project. Volume 3. The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments*. Clarendon Press, Oxford, pp. 139–320.
- Henn, B.M., T. E. Steele, T.E., T. D. Weaver, T.D., 2018. Clarifying distinct models of modern human origins in Africa. *Current Opinion in Genetics and Development* 53, 148–156.
- Hildebrand, M., 1974. *Analysis of Vertebrate Structure*. John Wiley & Sons, Inc, New York, 710 pp.
- Jenkins, K.E., Nightingale, S., Faith, J.T., Peppe, D.J., Michel, L.A., Driese, S.G., McNulty, K.P., Tryon, C.A., 2017. Evaluating the potential for tactical hunting in the Middle Stone Age: insights from a bonebed of the extinct bovid, *Rusingoryx atopocranion*. *Journal of Human Evolution* 108, 72–91.
- Kappelman, J., 1988. Morphology and locomotor adaptations of the bovid femur in relation to habitat. *Journal of Morphology* 198, 119–130.
- Kingdon, J., 2015. *The Kingdon Field Guide to African Mammals*, 2nd edition. Bloomsbury Publishing, London, 640 pp.
- Kingdon, J., Hoffman, M., 2013. *Mammals of Africa. Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids*. Bloomsbury, New York, 704 pp.
- Klecka, W.R., 1980. *Discriminant analysis. Sage University Paper series. Quantitative Applications in the Social Sciences, Series No. 07-019*. Sage Publications, Beverly Hills and London, 72 pp.
- Klein, R.G., Cruz-Urbe, K., 2000. Middle and Later Stone Age large mammal and tortoise remains from Die Kelders Cave 1, Western Cape Province, South Africa. *Journal of Human Evolution* 38, 169–195.
- Köhler, M., 1993. Skeleton and habitat of recent and fossil ruminants. *Munchner Geowissenschaftliche Abhandlungen* 25, 1–88.
- Kovarovic, K., Aiello, L.C., Cardini, A., Lockwood, C.A., 2011. Discriminant function analyses in archaeology: are classification rates too good to be true? *Journal of Archaeological Science* 38, 3006–3018.
- Kovarovic, K., Andrews, P., 2007. Bovid postcranial ecomorphological survey of the Laetoli paleoenvironment. *Journal of Human Evolution* 52, 663–680.
- Lazagabaster, I.A., Rowan, J., Kamilar, J.M., Reed, K.E., 2016. Evolution of craniodental correlates of diet in African Bovidae. *Journal of Mammalian Evolution* 23, 385–396.
- Lesur, J., Faith, J.T., Bon, F., Dessie, A., Ménard, C., Bruxelles, L., 2016. Paleoenvironmental and biogeographic implications of terminal Plesitocene large mammals from the Ziway-Shala Basin, Main Ethiopian Rift, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 449, 567–579.
- Louys, J., Montanari, S., Plummer, T., Hertel, F., Bishop, L.C., 2013. Evolutionary divergence and convergence in shape and size within African antelope proximal phalanges. *Journal of Mammalian Evolution* 20, 239–248.
- Luo, D., Ding, C., Huang, H., 2011. Linear discriminant analysis: new formulations and overfit analysis. *Proceedings of the Twenty-Fifth AAAI Conference on Artificial Intelligence* 417–422.
- MacDonald, D. (Ed.), 2001. *The New Encyclopedia of Mammals*. Oxford University Press, Oxford, 961 pp.
- MacInnes, D., 1956. Fossil Tubulidentata from East Africa. *Fossil Mammals of Africa* 10, 1–38.
- Marean, C.W., Gifford-Gonzalez, D., 1991. Late Quaternary extinct ungulates of East Africa and palaeoenvironmental implications. *Nature* 350, 418–420.
- McGarigal, K., Cushman, S., Stafford, S., 2000. *Multivariate Statistics for Wildlife and Ecology Research*. Springer-Verlag, New York, 283 pp.
- McHorse, B.K., Biewener, A.A., Pierce, S.E., 2017. Mechanics of evolutionary digit reduction in fossil horses (Equidae). *Proceedings of the Royal Society B*, 28420171174. <https://doi.org/10.1098/rspb.2017.1174>.
- Meloro, C., Elton, S., Louys, J., Bishop, L.C., Ditchfield, P., 2013. Cats in the forest: predicting habitat adaptations from humerus morphometry in extant and fossil Felidae (Carnivora). *Paleobiology* 39, 323–344.
- Nowak, R.M. (Ed.), 1999. *Walker's Mammals of the World*, 6th edition. Johns Hopkins University Press, Baltimore, Maryland, 1936 pp.
- O'Brien, H.D., Faith, J.T., Jenkins, K.E., Peppe, D.J., Plummer, T.W., Jacobs, Z.L., Li, B., Joannes-Boyau, R., Price, G., Feng, Y., Tryon, C.A., 2016. Unexpected convergent evolution of nasal domes between Pleistocene bovids and Cretaceous hadrosaur dinosaurs. *Current Biology* 26, 503–508.
- Pearson, O.M., Hill, E.C., Peppe, D.J., Van Plantinga, A., Blegen, N., Faith, J.T., Tryon, C.A., 2020. A Late Pleistocene human humerus from Rusinga Island, Lake Victoria, Kenya. *Journal of Human Evolution* 146, 102855. <https://doi.org/10.1016/j.jhevol.2020.102855>.
- Pickford, M., Thomas, H., 1984. An aberrant new bovid (Mammalia) in subrecent deposits from Rusinga Island, Kenya. *Proceedings of the Koninklijke Nederlandsche Akademie van Wetenschappen B87*, 441–452.
- Plummer, T. Bishop, L.C., 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *Journal of Human Evolution* 27, 47–75.
- Rowan, J., J. T. Faith, J.T., Y. Gebru, Y., J. F. Fleagle, J.F., 2015. Taxonomy and paleoecology of fossil Bovidae (Mammalia, Artiodactyla) from the Kibish Formation, southern Ethiopia: implications for dietary change, biogeography, and the structure of the living bovid faunas of East Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 420, 210–222.
- Scerri, E.M.L., Thomas, M.G., Manica, A., Gunz, P., Stock, J.T., Stringer, C., Grove, M., Groucutt, H.S., Timmermann, A., Rightmire, G.P., d'Errico, F., Tryon, C.A., Drake, N.A., Brooks, A.S., Dennell, R.W., Durbin, R., Henn, B.M., Lee-Thorp, J., deMenocal, P., Petraglia, M.D., Thompson, J.C., Scally, A., Chikhi, L., 2018. Did our species evolve in subdivided populations across Africa, and why does it matter? *Trends in Ecology & Evolution* 33, 582–594.
- Scott, R.S., Barr, W.A., 2014. Ecomorphology and phylogenetic risk: implications for habitat reconstruction using fossil bovids. *Journal of Human Evolution* 73, 47–57.
- Stager, J.C. Johnson, T.C., 2008. The late Pleistocene desiccation of Lake Victoria and the origin of its endemic biota. *Hydrobiologia* 596, 5–16.
- Temple, P.H., 1966. *Evidence of Changes in the Level of Lake Victoria and Their Significance*. Ph.D., Dissertation, University of London, London, United Kingdom.

- Tryon, C.A., 2019. The Middle/Later Stone Age transition and the cultural dynamics of late Pleistocene East Africa. *Evolutionary Anthropology* 28, 267–282.
- Tryon, C.A., Faith, J.T., 2013. Variability in the Middle Stone Age of Eastern Africa. *Current Anthropology* 54(S8), S234–S254.
- Tryon, C.A., Faith J.T., Peppe, D.J., Beverly, E.J., Blegen, N., Blumenthal, S.A., Chritz, K.L., Driese, S.G., Patterson, D., Sharp, W.D., 2016. The Pleistocene prehistory of the Lake Victoria Basin. *Quaternary International* 404(B), 100–114.
- Tryon, C.A., J. T. Faith, J.T., D. J. Peppe, D.J., D. L. Fox, D.L., K. P. McNulty, K.P., K. Jenkins, K., N. Garrett, N., H. M. Dunsworth, H.M., W. E. H. Harcourt-Smith, W.E.H., 2010. The Pleistocene archaeology and environments of the Wasiriyi Beds, Rusinga Island, Kenya: *Journal of Human Evolution* 59, 657–671.
- Tryon, C.A., Faith, J.T., Peppe, D.J., Keegan, W.F., Keegan, K.N., Jenkins, K.H., Nightingale, S., Patterson, D., Van Plantinga, A., Driese, S., Johnson, C.R., and Beverly, E.J., 2014. Sites on the landscape: Paleoenvironmental context of late Pleistocene archaeological sites from the Lake Victoria Basin, equatorial East Africa. *Quaternary International* 331, 20–30.
- Van Valkenburgh, B., 1987. Skeletal indicators of locomotor behaviour in living and extant carnivores. *Journal of Vertebrate Paleontology* 7, 162–182.