The paleoecology of Pleistocene birds from Middle Bed II, at Olduvai Gorge, Tanzania, and the environmental context of the Oldowan-Acheulean transition

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Abstract

Fossil bird data (community composition and taphonomic profiles) are used here to infer the environmental context of the Oldowan-Acheulean transitional period at Olduvai Gorge, Tanzania. This is the first comprehensive report on the Middle Bed II avifauna and includes fossils excavated by the Olduvai Geochronology and Archaeology Project (OGAP) and recently rediscovered fossils collected by Mary Leakey. Crane, ibis, darter, owl, raptor, crow, and vulture are reported from Bed II for the first time. The presence of these taxa, absent earlier in this Bed, point to a general opening and drying of the landscape with grassland and open woodland expansion. Taxa associated with dense, emergent wetland vegetation, such as dabbling ducks and rails, are uncommon and less diverse than earlier in Bed II. This suggests more mature wetlands with clearer waters. Cormorants continue to be common, but are less diverse. Cormorants and other roosting taxa provide evidence of trees in the area. Compared to lowermost Bed II, the Middle to Upper Bed II landscape is interpreted here as more open and drier (but not necessarily more arid), with matured wetlands, scattered trees, and a greater expansion of grasslands.

Introduction

The Pleistocene birds of Olduvai Gorge, Tanzania, remain the largest and richest avifaunal assemblage known in Africa (Wetmore, pers. comm., in Leakey, 1965; Brodkorb, 1985) and provide important data on avian evolution and community change on that continent (e.g., Harrison, 1980a; Brodkorb, 1985; Prassack, 2010, 2014). The Olduvai birds are also important to the field of paleoanthropology, as they come from a dynamic period of hominin evolution at a site internationally recognized for its paleoanthropological significance (Leakey et al., 1964; Leakey, 1965, 1971; Tobias, 1967, 1991; Blumenschine et al., 2003; Clarke, 2012; Domínguez-Rodrigo et al., 2013). In this article, avifaunal data from the uppermost Lower, Middle, and lowermost Upper Bed II are used to reconstruct environmental conditions at Olduvai during the Oldowan-Acheulean stone tool transition. These birds come from excavations made by the Olduvai Geochronology and Archaeology Project (OGAP; de la Torre et al., 2012), which currently investigates the behavioral and/or environmental causalities behind the important and highly visible shift in the archaeological record from an archaic, core-and-flake Oldowan stone tool industry to the large handaxes that characterize the Acheulean.

Traditionally, the Oldowan has been associated with *Homo habilis*, while the emergence of the Acheulean is linked to *Homo erectus*/*ergaster* (e.g., Leakey, 1975). However, the behavioral ecologies and taxonomic affinities of the hominins involved in this transition, at Olduvai and elsewhere, and the role, if any, played by a changing environment remain unclear (Beyene et al., 2013; de la Torre and Mora, 2014; Diez Martin et al., 2015). For example, the appearance of *Homo erectus*/*ergaster*, sometime between 1.65–1.7Ma (McDougall et al., 2012), coincides with the emergence of the Acheulean, but this technology also temporally overlaps in part with *Homo habilis* (Spoor et al., 2007) and *Paranthropus boisei* (Domínguez-Rodrigo et al., 2013). The purpose here is to provide an ecological framework from which to address the causalities behind this technological transition.

Geology and Early Stone Age archaeology at Olduvai Gorge

Olduvai Gorge is located on the eastern Serengeti Plains of northern Tanzania. The Gorge is part of the eastern branch of the East African Rift, an intra-continental ridge system that extends from Ethiopia through Kenya and into northern Tanzania. Fossil and artifact-rich exposures extend 20km along an east-west trending Main Gorge and southerly-directed Side Gorge, which meet at a fossiliferous "junction" (Leakey, 1971; Hay, 1976). Olduvai's deposits date from approximately 1.98Ma to 15,000BP (Hay, 1976; McHenry et al., 2007).

Early excavations at Olduvai focused on dense archaeological and fossiliferous deposits termed hominin "living floors" (e.g., Leakey, 1971). A methodological shift occurred in 1989, when the Olduvai Landscape Archaeology and Paleoanthropology Project (OLAPP) initiated a landscape mode of excavation to address environmental, community, and behavioral changes across temporally refined but spatially expansive paleolandscapes (Peters and Blumenschine, 1995; Blumenschine and Peters, 1998; Blumenschine et al., 2003, 2012a). OLAPP excavations sampled areas across the landscape, regardless of fossil or artifact densities, with a focus on understanding *Homo habilis* behavior and its use of Oldowan technologies during Bed I and lowermost Bed II times. Olduvai at that time was lacustrine-dominated, and localities occur primarily along what would have been the eastern lacustrine plain of saline-alkaline Paleolake Olduvai (Hay, 1976). Cyclical lake fluctuations (Stanistreet, 2012) coupled with frequent volcanic activity (McHenry et al., 2008; Stollhofen et al., 2008; Stollhofen and Stanistreet, 2012), facilitated burial and preservation of artifacts and faunal remains. Until the last few years, Middle Bed I and lowermost Bed II have been the focus of most archaeological research at Olduvai (e.g., Bunn and Kroll, 1986; Binford et al., 1988; Potts, 1988; Blumenschine et al., 2003, 2012b,c; Domínguez-Rodrigo et al., 2010; Pante et al., 2012; Reti, 2016).

Middle/Upper Bed II

Well-refined dates are available for Bed I and lowermost Bed II (Deino, 2012; McHenry, 2012), but Middle and Upper Bed II have a complex stratigraphy punctuated by four reworked, laterally discontinuous, and poorly dated tuffs (Tuff IIA–D: Hay, 1976; Stanistreet, 2012; McHenry et al., 2016; McHenry, submitted; Stanistreet et al., submitted). This has limited tephrostratigraphic and lithological facies control and the ability to reconstruct fossil landscapes and their representative faunal communities. Tuff IIA is variably dated from 1.66+0.01Ma (Manega, 1993) to 1.72Ma (Curtis and Hay, 1972), and McHenry (submitted) has updated these dates (incorporating a more recently accepted decay constant for ^{40}K) to 1.677Ma and 1.756Ma, respectively. Tuff II A was originally considered the boundary between Lower and Middle Bed II (Leakey, 1971), but Stanistreet et al. (submitted; see also McHenry et al., 2016, McHenry, submitted) reassign this boundary higher up at a wide-spread disconformity between the Lemuta Member and overlying Lower Augitic Sandstone (Fig. 1), providing a lithostratigraphic boundary for these two sub-beds. The Bird Print Tuff (BPT in Fig. 1) has a unique geochemical fingerprint (McHenry et al., 2016) and remains useful as a local marker bed despite exhibiting some compositional heterogeneity (McHenry, submitted). Diez-Martin et al. (2015) produced a date of 1.664Ma for a tuff, which Uribelarrea et al. (in press) place 25cm below the actual BPT. Tuff IIB is not a true tuff and has yet to provide a reliable date (McHenry et al., 2016). Leakey (1971) placed the Middle-Upper Bed II boundary at Tuff IIC, but Tuff IIC is less widespread

(McHenry, submitted) than previously thought (Hay, 1976). There is no clear lithostratigraphic boundary for separating Middle and Upper Bed II, but OGAP (Stanistreet et al., submitted) maintains Leakey's (1971) Tuff IIC boundary for lack of a better marker. A Tuff IID date of 1.3386±0.024Ma (Domínguez-Rodrigo et al., 2013) is used here. The Bed II/III transition dates to at least 1.15Ma (Hay, 1976; McHenry et al., 2007) and marks a change from a lake to a river-dominated system and a community shift reflecting greater aridity (Hay, 1976; Gentry and Gentry, 1978; Brodkorb, 1985).

Building on past avifaunal studies

Avifaunal data can provide a snapshot of local environmental and ecosystem composition and health (Pearson, 1994; Hawkins et al., 2007; Chambers, 2008). The establishment of many extant genera dating back to the Miocene, and even Oligocene (Brodkorb, 1971; Stewart and Beech, 2006; Louchart, 2008a; Louchart et al., 2008), also facilitates their utility as paleoenvironmental indicators (Miller, 1937; Cheneval, 1989; Eastham, 1997; Finlayson et al., 2011; Peresani et al., 2011; Prassack, 2014) and can provide important data on long-term environmental and climate change (Brodkorb, 1985; Emslie and Morgan, 1994; Emslie et al., 1998; Meijer et al., 2013; Prassack, 2014).

Fossil studies need to take a community-level approach and consider taphonomic bias, but our understanding of Olduvai's avifaunal communities was previously limited to some species descriptions (Harrison and Walker, 1976,1979; Brodkorb and Mourer-Chauviré, 1982, 1984a, b; Haarhoff, 1993) and various, short species-list reports (Harrison, 1980a,b; Brodkorb, 1985). Work in the 1980's by Diane Matthiesen, promised a community based ecological focus with reports of 29,662 birds representing 41 families, in addition to the Passeriformes. This work was never completed, and the only available information on these birds come from Ms. Matthiesen's detailed presentation notes (including tables and figures) from two conferences presented in 1990. One of these, from a talk given at the International Conference for Archaeozoology (ICAZ) meetings, is used here (herein noted as Matthiesen, unpublished conference notes) as it remain the only known "complete" source of species information for the Olduvai birds. These notes are available from the first author (KAP) by request. These birds, known colloquially as the "Leakey birds," remain in Ms. Matthiesen's private collection; she does not respond to inquiries and the collections remain inaccessible to researchers.

An ecotaphonomic approach to the study of Olduvai's avifaunal communities was applied by Prassack (2010, 2014) to the study of OLAPP excavated birds. When combined with data from other environmental proxies (e.g., Plummer and Bishop, 1994; Kappelman et al., 1997; Fernández Jalvo et al., 1998; Liutkus et al., 2005; Werdelin and Lewis, 2005; Bamford et al., 2006; Sikes and Ashley, 2008; Bennet et al., 2012; Blumenschine et al., 2012a, b; Ungar et al., 2012; Kovarovic et al., 2013), this type of approach can allow for greater accuracy in inferences made as to the potential causalities behind observed changes in hominin behavioral ecology and land use (i.e., distributions and types of stone tools, butchered animal bones, and hominin fossils) at Olduvai (Blumenschine et al., 2012a, b; Pante and de la Torre, submitted).

Materials and methods

Fossil site localities

This study reports on fossil birds (*n*= 682) collected between 2009 and 2015 by OGAP (Supplementary Material 1). These fossils are housed at the National Museum of Tanzania in Dar es Salaam, Tanzania. Olduvai localities are grouped into acronym-based site complexes based on geographic locations within recently formed gullies called korongos (e.g., MNK, Mary Nicol Korongo; FLK, Frida Leakey Korongo). These avifaunal-bearing localities are separated here into three avifaunal assemblages (Fig.1) from oldest to youngest: Assemblage IIA (pre-Tuff IIB)—HWK EE, MNK Skull, FLK West Trench 73; Assemblage IIB (Tuff IIB to Tuff IIC)—FC West (all trenches), FC East (all trenches), MNK Main, MNK Trench 5; and Assemblage IIC (post Tuff IIC to Tuff IID)—EF-HR, FLK West Trench 69. Assemblage IIA spans the uppermost section of Lower Bed II and the lower portion (pre-Tuff IIB) of Middle Bed II. Assemblage IIB lies within Middle Bed II between Tuff IIB and Tuff IIC. EF-HR (Assemblage IIC) was previously placed in Middle Bed II (Leakey, 1971; Hay, 1976), but belong in the lower part of Upper Bed III (de la Torre et al., submitted "a"; McHenry, submitted). Assemblage IIC receives limited attention here with only two bird fossils. Included in this analysis is a small (*n*=77) assemblage collected by Mary Leakey at HWK EE (Assemblage IIA) during the 1970's. This previously undescribed collection was recently discovered in a storage building at Olduvai and is reported on here for the first time (Supplementary Material 1).

OGAP specimen catalogue numbers are referenced by korongo, trench, level, and identification number (e.g., FC East T34-L89-75). Leakey HWK EE specimens are referenced as either HWK EE LC (Leakey Clay) or HWK EE LSC (Leakey Sandy Conglomerate). The LC and LSC correlate to the Lemuta Member and Lower Augitic Sandstone, respectively (de la Torre et al., submitted "b"; Pante and de la Torre, submitted). Both levels correlate to Assemblage IIA, but the LC is placed within the upper part of lowermost Bed II with the LSC above it in Middle Bed II (Stanistreet et al., submitted; Fig. 1). Olduvai bird specimens from OLAPP excavations are noted in the text as either OLAPP (Middle Bed II, Prassack, 2010) or OAS (lowermost Bed II, Prassack, 2014).

Modern osteological comparative collections

Museum acronyms are as follows: FMNH, Field Museum of Natural History; HAFO, Hagerman Fossil Beds National Monument; KAP, the first author's personal collection; LACM, Los Angeles County Museum; YPM, Yale Peabody Museum. The modern osteological comparative specimens used in this study were: Accipitridae—*Accipiter cooperii* HAFO 1809; *Accipiter striatus* HAFO 25460; *Aquila chrysaetos* HAFO 25456, HAFO 25457; *Aquila rapax* YPM 105273; *Buteo jamaicensis* HAFO 25451; *Buteo swainsoni* HAFO 25459; *Circus cyaneus* HAFO 122, HAFO 15461; *Haliaeetus leucocephalus* HAFO 25454, HAFO 25455; *Haliaeetus vocifer* YPM 105274; *Gyps africanus* KAP 005. Anatidae—*Anas crecca* AMNH 16716; *Anas acuta* HAFO 25493, HAFO 25486; *Anas discors* KAP 001; *Anas platyrhynchos* HAFO 25499; *Aix sponsa* HAFO 25506; *Nettapus auritus* LACM 102949, YPM 105270; *Cygnus olor* HAFO 25505; *Branta canadensis* HAFO 25506; *Dendrocygna* sp. HAFO 25498; *Alopochen aegyptiacus* AMNH 4262; *Sarkidiornis melanotos melanotos* AMNH 15667, LACM 112242. Ardeidae—*Ardea herodias* HAFO 25439, HAFO 25440, HAFO 2544; *Nycticorax nycticorax* HAFO 25443, HAFO 7306. Corvidae—*Corvus albus* YPM 103186, YPM 103182; *Corvus brachyrhynchos* HAFO 25575; *Corvus capensis* 103195; *Corvus corax* HAFO 25577, HAFO 25578; *Corvus rhipidurus* YPM 103189, YPM 103190; *Pica pica* HAFO 702. Falconidae—*Falco sparverius* HAFO 25462. Gruidae—*Balearica regulorum* HAFO 25481; *Grus canadensis* HAFO 25482. Haematopodidae—*Haematopus ostralegus* AMNH 27056. Pandionidae—*Pandion haliaetus haliaetus* HAFO 25458. Pelecanidae—*Pelecanus erythrorhynchos* HAFO 25426, 25412; *Pelecanus onocrotalus* FMNH 368756; *Pelecanus rufescens* FMNH 368757. Phalacrocoracidae—*Phalacrocorax africanus* FMNH 368740, FMNH 368741, FMNH 368742, FMNH 368743; *Phalacrocorax carbo* FMNH 368739, FMNH 368737, FMNH 368738.

Phoenicopteridae—*Phoeniconaias minor* KAP 007, KAP 008; *Phoenicopterus antiquorum* FMNH 105184; *Phoenicopterus ruber roseus* FMNH 105184. Podicipedidae—*Podilymbus podiceps* HAFO 25574. Rallidae—*Fulica americana* HAFO 25483, HAFO 25484, HAFO 25488; *Gallinula chloropus pyrrhorrhoa* YPM 102591; *Amaurornis* (*Limnocorax*) *flavirostra* LACM 103561; *Porphyrio madagascariensis madagascariensis* FMNH 368815, FMNH 368816; *Rallus limicola* HAFO 25487, HAFO 25490. Recurvirostridae—*Recurvirostra avocetta* AMNH 28666, YPM 111284. Scolopacidae—*Gallinago gallinago* KAP 003. Strigidae—*Asio flammeus* HAFO 25472, HAFO 25476; *Asio otus* KAP 006; *Athene cunicularia* HAFO 25479; *Bubo virginianus* HAFO 25467; *Megascops kennicottii* HAFO 25477. Threskiornithidae—*Bostrychia hagedash* HAFO 25436. Tytonidae—*Tyto alba* HAFO 25469, HAFO 25470.

We also used fossil taxa previously identified by the first author from other deposits at Olduvai (e.g., Prassack, 2010, 2014, unpublished observation) and published images and measurements to assist in the identification of these birds. These are noted in the text.

Phylogenetic classifications and osteological nomenclature

Osteological terminology followed Baumel and Witmer (1993). Phylogenetic classification followed that of Hackett et al. (2008) for the separation of the Ciconiiformes (a polyphyletic grouping, Olson, 1979; Ericson et al., 2006) into the Pelecaniformes (Pelecanidae, Ardeidae, and Threskiornithidae) and Suliformes (Phalacrocoracidae, Anhingidae, Sulidae, and Fregatidae) with the order Ciconiiformes reserved for the Ciconiidae (true storks). Accipitriformes (eagles, hawks, kites, harriers, and Old World vultures) were distinguished from Falconiformes (falcons), following Hackett et al. (2008). Members of the Gruidae (cranes) formerly assigned to *Bugeranus* (*B. carunculatus*) and *Anthropoides* (*A. virgo* and *A. paradisea*) were placed within the *Grus* genus following Yu et al. (2011). Fossils were identified to the lowest taxonomic level possible. The focus of this paper is on the environmental data provided by these birds; osteological descriptions focus on taxa uncommon or not previously recorded at Olduvai.

Quantitative methods in community ecology

Species-level data can provide a more refined reconstruction of a changing community, but species-estimate reports for even modern ecosystems are likely to be underestimated (Gotelli and Colwell, 2011), and assignment of fossil taxa to the species level is rarely attainable in avifauna. Fortunately, higher ordinal richness is often correlated with high species richness (Louys et al., 2012), and using familial data allows for the inclusion of more taxa and can allow for more inclusive, qualitative-based ecological assessments. Therefore, statistical analysis here focuses on familial changes in community composition, with reference to specific taxa (i.e., genera, species) where appropriate. Number of Identifiable Specimens Present (NISP) provides information on the number of fossils and/or taxa represented at a site. Minimum Number of Individuals (MNI), coupled with ecological and behavioral data, can provide greater insight into a site’s taphonomic history, the relative abundance of specific taxa, and the likelihood that a given taxon is representative of that locality’s environment or if it is allochthonous (i.e., a stopover or brought in by some taphonomic agent). Table 1 provides an occurrence matrix showing total abundances (in NISP and MNI) of taxa for each locality, with the ecological affinities of these taxa provided in Table 2.

Several community indices were calculated in PAST (Hammer et al., 2001; Table 3) using MNI data from Table 1 to assess changes in Olduvai’s avifauna community during Middle

Bed II times. Numbers are low across taxonomic groupings and preclude assessment of relative abundance shifts across time and space (beta diversity), but several measures of alpha diversity were used. The Simpson's Index reflects the likelihood that any two specimens collected at random will belong to the same taxon. The Shannon-Wiener Index (entropy) considers both richness and evenness at a site, with a single taxon assigned a rank of zero and higher values indicative of greater diversity. It assumes sampling was random from an infinitely large community and is used here under the assumption that bones are fossilized by chance occurrences and represent a subset of a time-averaged community. This raw diversity index is converted into the effective number of families to provide the alpha diversity at each site (evenness). Pielai's Equatability Index is a normalized measure of species evenness between 0 (one taxon dominates) to 1 (evenness across taxa). Chao 1 is used in ecology to estimate actual richness by correcting for collection or observation bias due to rare species, where n_1 is the number of singletons (species captured or recorded only once) and n_2 is the number of doubletons (species captures twice). It was applied here to account for potential preservation and collection bias against small and/or solitary taxa, especially in the absence of wet screening.

Taphonomic profiling

The taphonomic histories of avifaunal remains provide information that, in conjunction with the community profile, can be used to make stronger inferences about a site's environmental context (Emslie et al., 1996; Behrensmeyer et al., 2003; Cruz, 2007; Prassack, 2010, 2011, 2014). The taphonomic agents most likely to alter the community profile through differential destruction and/or transport of a birds bones are weathering, carnivoran feeding, and fluvial transport. Other traces that can provide information on the depositional environment include corrosion, rounding, trampling, and rodent gnawing. All fossils were studied under bright, indirect light using a Meiji binocular microscope at variable power to assist in the identification of such trace evidence. Weathering (cf. Behrensmeyer, 1978) follows Prassack's (2014) simplified weathering scale for birds (A, no to low weathering; B, moderate to high; and C, indeterminate due to small size or corrosion). Carnivore damage was identified if a tooth puncture, tooth pit, or score was present. Notches on bone can indicate gnawing, but notches can be ambiguous and are not included here. Trampling and fluvial transport ("abrasion" in Table 4) can produce linear scratches on bone. Fluvial transport can also produce rounding of broken ends, for which there was no evidence of here. Abrasion can be distinguished from tooth scores in being V-shaped, rather than U-shaped, in cross section (Behrensmeyer et al., 1986). Cut marks, produced by stone-tool wielding hominins, are less likely to occur on bird bones as bird carcasses can be often processed with little to no cutting (Steadman et al., 2002; Serjeantson, 2009; Prassack, unpublished observation). Profiles of completeness, defined as a bone that may exhibit minor damage but is otherwise complete, and fragmentation (mid shaft fragments, mid shafts, and isolated epiphyseal ends) are provided in Table 4. These data are only reported as percentages due to small sample sizes and low incidence of unambiguous modifications to the cortical surface of the fossils.

Wing (humerus, ulna, and carpometacarpus) over leg (femur, tibiotarsus, and tarsometatarsus) abundance was used to infer skeletal part bias resulting from some taphonomic phenomenon (otherwise wings/wings+legs=0.5; Ericson, 1987). Wing abundance is often attributed to anthropogenic causes (Gotfredsen, 1997; Bovy, 2002), but carnivores can produce a similar profile (Livingston, 1989; Oliver and Graham, 1994; Prassack, 2011). Prassack (2011) further shows that bone shaft thickness, pneumaticity, shape, and collagen fiber orientation may affect a bone's susceptibility to weathering, and especially weather-related cracking, and that this can skew skeletal part profiles of avifaunal assemblages by disproportionately destroying distal limb elements. Bone density also has a high likelihood of affecting taxon-specific differential survivorship (Livingston, 1989; Prassack, 2011), but quantitative data on density-mediated differential survivorship across taxa is limited to non-African birds (Dirrigl, 2001; Cruz and Elkin, 2003; Dumont, 2010; Ksepka et al., 2015). Body size, locomotion type, and other variables may also have an effect on resulting skeletal part profiles. This is a taxonomically diverse assemblage with relatively small sample sizes of relevant skeletal elements, so skeletal part survivorship (wings versus legs) is only considered here for the larger samples from Assemblage IIA (HWK EE) and Assemblage IIB (MNK, FC West and FC East), and only at the level of the Class of Aves.

Results and preliminary discussion

Avian taxonomy

Phalacrocoracidae (cormorants) Cormorants are diving, piscivorous birds that feed on a range of smaller vertebrates (Nelson, 2005). Five species of cormorant are found in Africa today, with the great cormorant (*Phalacrocorax carbo*) and long-tailed (reed) cormorant (*Phalacrocorax africanus*) found in Tanzania. Cormorants are well represented in the African Miocene of Namibia (Mourer-Chauviré, 2008), Tunisia (Rich, 1974), Chad, and Ethiopia (Louchart et al., 2008), and in the Pliocene of Chad (Louchart et al., 2004), Ethiopia (Louchart, 2014), and South Africa (Olson, 1985a; Manegold et al., 2013). Four species of cormorant are known from Olduvai: *Phalacrocorax carbo*, *P. africanus*, and the extinct cormorants *Phalacrocorax owrei* (Brodkorb and Mourer-Chauviré, 1984a) and *Phalacrocorax tanzaniae* (Harrison and Walker, 1979). Cormorants are common at Olduvai and occur in the oldest fossil bearing sites there through to at least the lower part of Upper Bed II.

Cormorants are easily distinguished osteologically from most other families, but sexual dimorphism and high intrageneric variability preclude easy differentiation between cormorant species of similar size (Nelson, 2005). *Phalacrocorax africanus* is the smallest cormorant at Olduvai. *Phalacrocorax owrei* is slightly larger and more robust (Brodkorb and Mourer-Chauviré, 1984a), but some skeletal parts cannot be readily distinguished from *P. africanus*. Both are distinct from the much larger *P. carbo*. *Phalacrocorax tanzaniae*, a species limited to Bed II at Olduvai and, potentially, to the Pleistocene of Konso, Ethiopia (Louchart, 2014), may be synonymous with the South African Cape cormorant, *Phalacrocorax capensis* (Louchart, 2014; Prassack, 2014). Data on *Phalacrocorax kuehneanus*, (Schlüter, 1991, in Louchart, 2014) from the Plio-Pleistocene of Tanzania is not readily available, but it is thought to have been similar in size to, but distinct from, *P. owrei* (Louchart, 2014).

Cormorants are the most common taxon present during both Assemblage IIA (27%) and IIB (77%). The majority can likely be assigned to *P. owrei*, which is also the most common cormorant in Bed I (Brodkorb and Mourer-Chauviré, 1984a). *Phalacrocorax africanus* also appears to be present in both Intervals, in much smaller numbers. *Phalacrocorax africanus* and *P. owrei* are combined in Table 1 as *Phalacrocorax owrei*/*africanus* (see also Fig. 2 A-C). *Phalacrocorax carbo* is restricted to MNK during Assemblage IIB. Lowermost Bed II was more diverse, with four species (Prassack, 2014). Only *P. carbo* and *P. africanus* are reported above Tuff IID (Brodkorb and Mourer-Chauviré, 1984a) and onlt these two taxa occur in Tanzania today. The habitat preference of *P. owrei* is not known, but it was likely similarly piscivorous and either roosting in trees or outcrops, as observed with modern cormorants.

Anhingidae (anhingas and darters) The Anhingidae can be separated into two groups: New World anhingas (*Anhinga anhinga*) and Old World darters (*Anhinga melanogaster)*. The *Anhinga melanogaster* group is further split into an Asian *A. melanogaster*, a sub-Saharan African *Anhinga rufa*, and an Australian *Anhinga novaehollandiae* (Kennedy et al., 2005; Schodde et al., 2012). *Anhinga* sp. occurs in the late Miocene of Kenya (Harris and Leakey, 2003) and Abu Dhabi (Stewart and Beech, 2006), and in the Pliocene of Ethiopia (Louchart et al., 2009). *Anhinga pannonica* is known from the middle-late Miocene of Tunisia (Rich, 1974), Kenya (Dyke and Walker, 2008), and, potentially, from the late Miocene of Chad and Libya (Louchart, 2008b), as well as in Europe (Lambrecht, 1916). *Anhinga hadarensis* occurs in the late Pliocene of Ethiopia (Brodkorb and Mourer-Chauviré, 1982) and at Olduvai, where it was placed ancestral to *A. rufa* (Brodkorb and Mourer-Chauviré, 1982). Extant darters of the *A. melanogaster* group also occur in the Pliocene of Chad (Louchart et al., 2004), Kenya (Harris et al., 2003), and possibly Ethiopia (Louchart et al., 2009), and from the Pleistocene of Ethiopia (Louchart, 2008b; Louchart, 2014).

A complete ulna (Fig. 2D) from Assemblage IIA at HWK EE can be assigned to *Anhinga* based on several traits. This includes a large, ventrally projecting tuberculum ligamenti collateralis ventralis, which is placed immediately below the rim of the cotyla ventralis in anhingas and more distally in line with the impression brachialis in cormorants (Campbell, 1996). The specimen falls within the width and depth size range for *A. rufa* and *A. hadarensis* (Table 1 in Brodkorb and Mourer-Chauviré, 1982). The specimen exhibits a more rounded, but not distally expansive, tuberculum ligamenti collateralis ventralis than seen in *A. hadarensis* (Fig. 1 in Brodkorb and Mourer-Chauviré, 1982). Brodkorb and Mourer-Chauviré (1982) did not provide length measurements, but describe *A. hadarensis* as short limbed and robust compared to

A. rufa and *A. anhinga*, while this Middle Bed II specimen appears to be more robust than *A. hadarensis*. It is assigned here only to the genus *Anhinga* until additional material becomes available. Darters are morphologically similar to cormorants, and it is possible that some of the more fragmentary specimens assigned to *Phalacrocorax* may belong in this family.

According to Matthiesen (unpublished conference notes), darters only made up 0.03% of the Leakey birds. She placed them within the Phalacrocoracidae when reporting locality data, so it is not clear which beds or localities contained darters. Darters are otherwise not known from Lower Bed I (Prassack, unpublished observation), Middle Bed I (Prassack, 2010), or lowermost Bed II (Prassack, 2014), and must have been rare, where present, in those deposits.

Darters roost in mixed colonies with other water birds, but are solitary feeders. Darters can overlap with cormorants in habitat, but darters are less buoyant (Rijke et al., 1989), feed in shallower waters (Ryan, 2007), and prefer fresher waters and areas with dense mangroves or brushy shorelines (Nelson, 2005).

<u>Ciconiidae (storks)</u> The Ciconiidae comprises “true” storks and is the only family to remain in the once polyphyletic Ciconiiformes (Hackett et al., 2008). Storks typically roost in trees near water and can be found in mixed colonies with ibis, pelican, or heron (Hancock et al., 1992). Their diet varies across species, but storks are largely omnivorous, with most feeding on insects, fish, and amphibians (Hancock et al., 1992). African storks appear in the Eocene (Miller et al., 1997) and are found in the Oligocene (Rasmussen et al., 1987) and Miocene (Miller et al., 1997) of Egypt and the Miocene of Tunisia (Harrison, 1974), Libya (Mlíkovský, 2003), Kenya (Hill and Walker, 1979; Harris and Leakey, 2003), Chad (Louchart et al., 2008), and South Africa (Haarhoff, 1988). Storks are also present in the Pliocene (Louchart et al., 2004) and Pleistocene

(Louchart et al., 2005a) of Chad and the Plio-Pleistocene of Kenya (Harrison, 1980a; Harris et al., 2003; Dyke and Walker, 2008; Mayr, 2014), Morocco (Mourer-Chauviré and Geraads, 2010), and Ethiopia (Louchart et al., 2005, Louchart, 2008, 2014).

Storks are rare at Olduvai (Matthiesen, unpublished conference notes), but *Ciconia* and *Anastomus* occur in lowermost Bed II (Prassack, 2014) and a species of *Leptoptilos,* presumably, the marabou stork (*Leptoptilos crumeniferus*) is cited for an unknown locality at Olduvai (Brodkorb, 1985). At HWK EE, the anterior portion of a right coracoid, broken posterior of the scapular facet but preserving part of the shaft, is assigned to a medium-sized stork, such as *Ciconia*. It is distinguished from herons (Ardeidae) by traits in the procoracoid (i.e., shape and orientation of the facies articularis humeralis and the cotyla scapularis).

<u>Pelecanidae (pelicans)</u> The great white pelican (*Pelecanus onocrotalus*) and the pink-backed pelican (*Pelecanus rufescens*) occur today across the African continent, including in Tanzania. *Pelecanus* is known from Miocene fossils (Harris and Leakey, 2003; Mayr, 2014) and Pleistocene fossil trackways (Roach et al., 2016) in Kenya, and from the Pleistocene of Ethiopia (Louchart, 2008b). *Pelecanus rufescens* can be distinguished from *P. onocrotalus* by its notably smaller size. It can be further distinguished (relevant to this study) by an elongated, rather than boxy, styloid process and narrow head of the radius, and a reduced process pisciformis and more abruptly angled process extensorius of the carpometacarpus.

Pelicans were uncommon at Olduvai during Bed I (Matthiesen, unpublished conference notes), but *P. rufescens* was present in Lower Bed I (Prassack, unpublished observation). Both *P. rufescens* and *P. onocrotalus* occur in lowermost Bed II (Prassack, 2014) and Middle Bed II, but *P. rufescens* appears to be restricted to Assemblage IIA (HWK EE, Fig. 2E). Harrison and

Walker (1976) described an extinct pelican, *Pelecanus aethiopicus*, at Olduvai from “Bed II,” as being slightly smaller than *P. onocrotalus*. Pelicans are sexually dimorphic and *P. aethiopicus* is not considered here to be a valid taxon (see also Brodkorb, 1985).

Pelecanus onocrotalus occurs throughout the Palaearctic and Africa today, with both sedentary and Palaearctic wintering populations in East Africa. They are colonial ground nesters and prefer inland waters (Nelson, 2005). *Pelecanus rufescens* is an African resident that feeds on small fish in the shallows; it can occur in habitats unable to sustain *P. onocrotalus*, including small, ephemeral or seasonally flooded wetlands, and shallow lakes and ponds with exposed shorelines (Nelson, 2005). *Pelecanus rufescens* occurs in smaller numbers than *P. onocrotalus* and roost in trees, often in mixed colonies with other taxa (Nelson, 2005).

Threskiornithidae (ibis and spoonbills) African threskiornithids are represented today by the African sacred ibis (*Threskiornis aethiopicus*), glossy ibis (*Plegadis falcinellus*), hadada ibis (*Bostrychia hagedash*), wattled ibis (*Bostrychia carunculata*), and southern bald ibis (*Geronticus calvus*), with one member of the sub-family Plataleinae; the African spoonbill (*Platalea alba*). Threskiornithids occur in the Oligocene (Rasmussen et al., 1987) and Miocene (Smith, 2013) of Egypt, the Pliocene of Ethiopia (Louchart et al., 2009), Kenya (Dyke and Walker, 2008), Morocco (Mourer-Chauviré and Geraads, 2010), and South Africa (Olson, 1985b; de Ruiter et al., 2010), and in the Pleistocene of South Africa (Manegold and Brink, 2011) and Ethiopia (Louchart, 2014).

The brief mention of an *Ibis* sp. for an unknown Bed by Brodkorb (1985) is the only previous record of this family at Olduvai. In Middle Bed II, two tarsometatarsi from HWK EE (Assemblage IIA) and one coracoid from MNK (Assemblage IIB) can be assigned to the

Threskiornithinae. The HWK EE specimens are of the approximate size of *Bostrychia hagedash*, but with a more robust shaft and narrower trochlear breadth (Fig. 2F). The sternal portion of a coracoid is broken below where the foramen nervi supracoracoidei would be, if present. It exhibits several features that align it with the northern bald ibis (*Geronticus eremita*; Fig. 2c in de Pietri, 2013). *Geronticus eremita* is restricted today to Syria and Morocco (Serra et al., 2009), but it had a greater historical range that extended into northern Africa (Collar and Stuart, 1985), and the extinct ibis, *Geronticus olsoni,* was present in Morocco during the Pliocene (Mourer-Chauviré and Geraads, 2010). The distribution range of *Geronticus* may have been broader in the past, as has been reported for other African bird taxa (e.g., Louchart et al., 2005b, 2008; Prassack, 2014).

Most threskiornithids are tree nesters and omnivorous, shallow-water feeders found associated with flooded grasslands, wetlands, and lake shores (Archibald et al., 1980). Bald ibis (*G. eremita*) prefer drier open grassland environments (Manry, 1982), are largely insectivorous, and prefer to nest on cliffs. Relict populations of *G. eremita* in Syria are migratory and have a foraging range of up to 25 km (Serra et al., 2009).

<u>Anatidae (ducks, geese, and swans)</u> The Anatidae are a large and diverse family with over sixty species from eight tribes found in Africa (Johnsgard, 1978). Anatids are not common in the African fossil record, but do occur in the early Miocene of Namibia (Mourer-Chauviré, 2008), the late Miocene of Ethiopia (Louchart et al., 2005,2008) and Libya (Louchart et al., 2005b), and the Pliocene of Chad (Louchart et al., 2004), Morocco (Mourer-Chauviré and Geraads, 2010), and South Africa (Manegold et al., 2013). Fossil anatids become more abundant during the

Middle and Late Stone Age (Pleistocene) in South Africa (e.g., Avery and Underhill, 1986; Klein et al., 1999, 2004; Manegold and Brink, 2011).

Matthiesen (unpublished conference notes) reported 2283 specimens of anatid. She did not provide any further taxonomic information, but others report on shelduck (*Tadorna cana*), teal (*Anas capensis*/*crecca*; Harrison, 1980a, b, see also Brodkorb, 1985), and goose (*Plectropterus gambensis*; Brodkorb, 1985) from Bed I. No anatids were identified from the OLAPP excavations in Middle (Prassack, 2010) or Upper (Prassack, unpublished observation) Bed I, but a teal (*Anas capensis*/*crecca*), a swan (cf. *Cygnus olor*; see also Harrison, 1980b), and several geese (*Nettapus auritus*, *Alopochen aegyptiacus*, *Sarkidiornis melanotos*, and *Thalassornis leuconotus*) were present during lowermost Bed II times (Prassack, 2014).

Anatids can be difficult to assign taxonomically (Olson and Rasmussen, 2001), but a small teal (c.f. *Anas crecca*/*capensis*) and at least one species of goose-like anatid occur at both HWK EE and MNK. The Eurasian teal (*Anas crecca*) and Cape teal (*A. capensis*) are of similar size and difficult to distinguish from each other. Both species occur in Tanzania today.

Anatids are invariably associated with water, but they exhibit a range of habitat preferences that can include lakes, rivers, streams, swamps, ephemeral pools, and even wet and dry grasslands and woodlands (Brickell, 1988). Teals exhibit a lower niche breadth than some other anatids and require shallower waters with adequate emergent/flooded vegetation, which can include flooded grasslands (Rizzo and Battisti, 2009).

<u>Gruidae (cranes)</u> Cranes are widespread today, but most of the 15 species are geographically restricted. The black-crowned crane (*Balearica regulorum*) and gray-crowned crane (*Balearica pavonina*) of the subfamily Balearicinae, and the wattled crane (*Grus carunculatus*), demoiselle

crane (*Grus virgo*), and blue crane (*Grus paradisea*) of the Gruinae are found in Africa today, but only *B. regulorum* and *G. carunculatus* occur in Tanzania. The fossil record of cranes prior to the Pleistocene is sparse. The subfamily Balearicinae dates to the Eocene of Europe with *Balearica* known from the Miocene of Egypt (Smith, 2013) and Chad (Louchart et al., 2008). The Gruinae (*Grus*) have a late Miocene, Eurasian origin (Brodkorb, 1967; Göhlich, 2003), with African cranes dating to the Pliocene (Manegold et al., 2013) and Middle Pleistocene (Manegold and Brink, 2011) of South Africa and the Late Pleistocene of Zambia (Harrison, 1980a).

A “few bones of crane” (Brodkorb, 1985) and a single specimen (subfamily not noted, in Matthiesen, unpublished conference notes) are the only previous accounts of crane at Olduvai. A coracoid (Fig. 2G) from FC West (Assemblage IIB) is missing the bicipital attachment but preserves the glenoid (humeral) facet and retains part of the sterno-coracoid fossa and sternal facet. It is assigned to the Gruinae and distinguished from *Balearica* by the presence of a large pit with the foramen centered in the sterno-coracoidal fossa, shape of the scapular facet and glenoid facet, and the presence of an enlarged foramen nervi supracoracoidei. *Grus paradiseus*, a small crane, was not available for study, but the FC West specimen is slightly more robust and shorter than *Grus canadensis*, which is a large crane. It can likely be assigned to *G. carunculatus*, the largest African crane and the second largest extant crane. *Grus carunculatus* feeds in shallow wetlands on the tubers and rhizomes of water lilies and sedges, along with a variety of small vertebrates, but prefers wetlands surrounding drier grasslands (Meine and Archibald, 1996).

<u>Rallidae (coots, rails, and moorhens)</u> There are 142 species of rail today, with 12 species from nine genera in Tanzania (Sibley and Monroe, 1990). Coots and moorhens are gregarious and

found in open waters, but crakes, gallinules, and rails are solitary, secretive, and more terrestrial, with most preferring the dense, emergent vegetation of freshwater systems (Taylor, 1998). Rails occur in the Oligocene of Egypt (Rasmussen et al., 1987), the Pliocene of Ethiopia (Louchart et al., 2009), Morocco (Mourer-Chauviré and Geraads, 2010), and South Africa (Manegold et al., 2013), and in the early Pleistocene of Eritrea (Rook et al., 2013). Outside of some islands (e.g., Steadman, 1986; Kirchman and Steadman, 2007), the Rallidae are represented by mostly modern genera in the Pliocene and modern species by the Pleistocene (Brodkorb, 1967). A notable exception at Olduvai is a possible new (undescribed) genus of rail from Lower and Middle Bed I (Prassack, 2010).

Rails were abundant throughout Bed I with 3539 specimens (Matthiesen, unpublished conference notes), including *Crex crex* (Harrison, 1980b), *Gallinula chloropus* (Harrison, 1980b*;* Prassack, 2010), *Porphyrio alleni*, and *Amaurornis flavirostris* (Prassack, 2010). Brodkorb (1985) cited an absence of rails for Bed II, but OLAPP excavations in lowermost Bed II recovered specimens of *Gallinula*, *Fulica*, and *Rallus* cf. *caerulescens* (Prassack, 2014). Rails are uncommon but present in Middle Bed II. A small rallid, smaller than the Virginia rail (*Rallus limnicola*) occurs at HWK EE (Assemblage IIA). Fossils from Assemblage IIB at MNK are tentatively assigned to *Fulica* (coot), while a second, slightly smaller rail at MNK shows similarities to *Gallinula chloropus* (moorhen). Rails are morphologically similar and can be difficult to distinguish (Olson, 1973), but *Fulica atra* is larger than *Gallinula* and most other African rails, and its tarsometatarsus differs from the larger *Porphyrio madagascariensis* (swamp hen) in the shape of the trochlea metatarsi II and IV. African rails are speciose and not all relevant specimens (e.g., *Crex crex* and *Porphyrio alleni*) were available for direct comparison, but OLAPP fossil specimens of *C. crex* from lowermost Bed II (OAS-043) and *P. alleni* from

Middle Bed I (OLAP-1107) and lowermost Bed II (OAS-1107) were utilized (Prassack, 2010; 2014). The Middle Bed II rails are poorly preserved and not overly diagnostic, such that a broader comparative analysis is unlikely to resolve their identities.

Phoenicopteridae (flamingos) The greater flamingo (*Phoenicopterus roseus*) and lesser flamingo (*Phoeniconaias minor*) occur throughout East Africa today. Flamingos are well documented in the fossil record. The earliest African flamingos are the late Oligocene/early Miocene *Palaelodus* from the extinct Palaelodidae family (Rasmussen et al., 1987; Mourer-Chauviré, 2008). The genus *Phoenicopterus* first appears in the Miocene of Kenya (*Phoenicopterus* [*Leakeyornis*] *aethiopicus*; Harrison and Walker, 1976; Rich and Walker, 1983; Dyke and Walker, 2008), but it is attributed as ancestral to the lesser flamingo (Rich and Walker, 1983), which is now considered a separate genus. However, *Phoenicopterus roseus* is established by the late Miocene/early Pliocene (e.g., Namibia, Pickford et al., 2009; Egypt, Smith, 2013). In addition to some slight morphological differences in the postcranial skeleton (Miller, 1963), *Phoenicopterus* and *Phoeniconaias* can be readily differentiated by size.

Matthiesen (unpublished conference notes) notes flamingo as a “minor component” at Olduvai, though it is not clear to which species or Bed (Bed I or lowermost Bed II) she is referring. *Phoeniconaias minor* (Fig. 3A) appears to be restricted to Bed II (Brodkorb, 1985), while both it and *Phoenicopterus roseus* were present during lowermost Bed II (Prassack, 2014) and Middle Bed II (Table 1) times. Flamingos are more common during Assemblage IIA (16.30%) than Assemblage IIB (<5%), and *Phoenicopterus roseus* is notably more common than *Phoeniconaias minor* during both lowermost Bed II and Middle Bed II.

Phoenicopterus roseus eats a variety of small aquatic invertebrates (Jenkin, 1957) and frequents nearshore wetland habitats (Samraoui et al., 2006). *Phoeniconaias minor* is a blue-green algae specialist, so its presence is highly dependent on local environmental conditions, including food availability (Tuite, 2000; Krienitz and Kotut, 2010). These flamingos are a conspicuous sight on East African lakes today, with millions breeding at Lake Natron along the Kenyan border of Tanzania. The rarity of *P. minor* may be taphonomic, based on its preference for mud flats or shallow lake shorelines where wet-dry cracking can compound weathering (Prassack, 2011).

Podicipedidae (grebes) Grebes are diving birds that prefer shallow, open waters for feeding but require emergent vegetation for nesting (Athamnia et al., 2015). The least grebe (*Tachybaptus ruficollis capensis*), black-necked grebe (*Podiceps nigricollis gurneyi*), and great crested grebe (*Podiceps cristatus*) occur in Africa today. *Podiceps* dates to the late Miocene (Louchart et al., 2008) and Pleistocene of Ethiopia (Louchart, 2014) and early Pliocene of South Africa (Olson, 1994). *Tachybaptus ruficollis* occurs in the Pliocene of South Africa (Olson, 1994; de Ruiter et al., 2010) and Pleistocene of Ethiopia (Louchart, 2014). Grebes are not common at Olduvai, representing only 1.5% of birds studied by Matthiesen (unpublished conference notes), but *T. ruficollis* is known from Middle Bed I (Prassack, 2010) and lowermost Bed II (Prassack, 2014; see also Brodkorb, 1985). Relevant Middle Bed I (OLAP-1070, 1157, 1243, and 1255) and lowermost Bed II (OAS-885 and 175) fossils were used to identify 13 specimens of *T. ruficollis* from Middle Bed II (Fig. 3B). *Tachybaptus ruficollis* occurs in both assemblages but is more common in Assemblage IIB (10 of 13 specimens). A tarsometatarsus from MNK (Assemblage

IIB) is slightly larger and more robust than *T. ruficollis*, and may belong to *Podiceps* sp., but it is corroded and poorly preserved.

Charadriiformes (shorebirds) The Charadriiformes are a large order comprising over 340 species of small to medium sized shore birds (del Hoyo et al., 1996). Shorebirds can be found feeding along lake and ocean shorelines, and in the shallows of calm lakes, ponds, and in other areas of standing water, but some taxa occur in open wet or dry grasslands or riverine settings. Shorebirds occur during the Pliocene of Tanzania (Louchart, 2011), South Africa (Rich, 1980; Olson and Eller, 1989; Manegold et al., 2013), and Morocco (Mourer-Chauviré and Geraads, 2010), and in the Pleistocene of South Africa (Pocock, 1969; Plug and Clark, 2008).

Shorebirds were the most common group of birds from Bed I, with over 8,000 specimens assigned to the Scolopacidae, Rostratulidae, Charadriidae, Recurvirostridae, Glareolidae, Burhinidae, Numididae, and Laridae families (Matthiesen, unpublished conference notes). The number of species can make further taxonomic assignment of fragmentary shorebird material difficult (de Pietri et al., 2013), but a lapwing (*Vanellus senegallus*; Harrison, 1980a), a small plover (*Charadrius* sp.), and a whimbrel (*Numenius phaeopus*; Harrison, 1980b) have been recorded, though not described, from Bed II. Prassack's (2010) analysis of OLAPP birds from Middle Bed I did not assign shorebirds beyond family, but scolopacids, charadriids, and recurvirostrids were present. No shorebirds were identified from Upper Bed I (Prassack, unpublished observation), and only a single specimen each of recurvirostrid (*Recurvirostra avocetta*) and small sanderling (*Calidris* sp.) were identified from lowermost Bed II (Prassack, 2014).

Shorebirds are rare in Middle Bed II and restricted to HWK EE. A humerus is assigned to a larger member of the Scolopacidae, based on traits noted in Ballmann (2004). An ulna is tentatively assigned to *Haematopus* (Haemetopodidae), although it shares some traits with *Recurvirostra avocetta*, which is known from older deposits (Prassack, 2010, 2014). Two other specimens cannot be assigned beyond Charadriiformes, but are small, about the size of the sanderling, *Calidris alba*.

Tytonidae (barn owls) Owls are specious in Africa, with 49 species from 10 genera. All but one genera are in the family Strigidae, with the family Tytonidae represented by four species of *Tyto*. Many of these owls are endemic to particular islands or mountain ranges in Africa, while others, like *Tyto alba*, the barn owl, are cosmopolitan. At least 16 species of owl occur in a range of habitats throughout Tanzania today (Stevenson and Fanshawe, 2006).

The earliest African owls are known from the Miocene of Kenya (Walker and Dyke, 2006). Pliocene owls occur in Tanzania (Louchart, 2011), South Africa (Pavia et al., 2015), Ethiopia (Louchart et al., 2009), and Morocco (Mourer-Chauviré and Geraads, 2010). The record for Pleistocene owls is largely restricted to South Africa (Pocock, 1969; Watson, 1993; Plug and Clark, 2008), which may be a taphonomic/recovery factor given a strong cave-based paleoanthropological record there and the likelihood of owls inhabiting caves in between hominin occupations (e.g., Avery, 2001). Owls, as with other raptorial birds, are uncommon at Olduvai, but members of the family Strigidae (*Bubo leakeyae* and *Bubo* cf. *lacteus*) and Tytonidae (*Tyto alba* cf. *affinis*; Brodkorb and Mourer-Chauviré, 1984b) are present. Pavia et al. (2015) erroneously cited the presence of African grass owl (*Tyto capensis*) at Olduvai, but Harrison (1980a) was referring to the site of Kabwe (formerly Broken Hill) in Zambia.

An owl ulna (Fig. 3C) from Assemblage IIB is assigned to the Tytonidae. It can be distinguished from the Strigidae based on a condylus dorsalis ulnaris that is oblique in ventral view with an anterior edge almost flush with the shaft; condylus ventralis ulnaris tapered, well pronounced and slightly protruding over the tuber carpal; and tuber carpal tapered with a rounded dorsal face. It shows strong affinity to the barn owl (*Tyto alba*), which is a geographically widespread owl that exhibits a great range in body size. It is smaller than the North American specimens of *Tyto alba* available for comparison, but its measurements fall within the range of *T. alba* cf. *affinis* (Table 4 in Brodkorb and Mourer-Chauviré, 1984b), while *Tyto capensis* is larger (Table 2 in Pavia et al., 2015). This is the first evidence of owls from Bed II.

<u>Accipitridae (eagles, hawks, kites, Old World vultures)</u> The Accipitridae are one of four sub-families of the Accipitriformes, an order previously subsumed under the Falconiformes (falcons and caracaras) but now considered separate (Hackett et al., 2008). This is a diverse family of small to large sized raptorial birds mostly associated with dry, open grasslands near permanent water sources. They are further separated into one of nine sub-families, including Aegypiinae (Old World vultures), Aquilinae (true eagles), Haliaeetinae (fish eagles), and Accipitrinae (true hawks). Raptors are known from the Miocene of Chad (Louchart et al., 2008) and Kenya (Walker and Dyke, 2006), the Pliocene (Louchart et al., 2009; White et al., 2006) and Pleistocene (Louchart, 2014) of Ethiopia, the Pliocene of Tanzania (Louchart, 2011) and South Africa (Manegold et al., 2014), and the late Pleistocene of Zambia (Harrison, 1980a).

Matthiesen (unpublished conference notes) reports an NISP of 170 for the Accipitridae, but with none identified beyond family. Three accipitrids occur at HWK EE (Assemblage IIA).

The anterior portion of a coracoid, preserving the intermuscular line on its ventral face with only minor damage to the process lateralis and angulus medialis, is assigned to a medium-sized hawk, possibly the African goshawk (*Accipiter tachiro*) based on comparison to Cooper's hawk (*Accipiter cooperi*). A distal tibiotarsus from HWK EE (Fig. 3D), preserving the sulcus extensorius, is most similar to the tawny eagle (*Aquila rapax*), but much smaller. At MNK, a right medial phalanx (Fig. 3E) missing the trochlea is the size of a fish eagle (*Haliaeetus* sp.), but differs in the shape and orientation of the medial and lateral articular facet, and is more like *Aquila* in that regard. The vulture sub-family, Aegypiinae, is represented at HWK EE by a coracoidal sulcus of a sternum (Fig. 3F); it lacks the dorsal manubrial spine but retains both the dorsal and ventral lips. *Aegypius* (vulture) is known from the early Pliocene of South Africa (Manegold et al., 2014) and early Pleistocene of Ethiopia (Louchart, 2014).

<u>Struthionidae (ostrich)</u> Ostrich (*Struthio camelus*) are the largest land birds with a wide distribution across Africa. Ostrich date to the Miocene in Africa (Mourer-Chauviré and Geraads, 2008) and occur as fossils or eggshell fragments at a variety of Pliocene and Pleistocene sites throughout Africa (Harris et al., 2003; Harrison and Msuya, 2005; Leonard et al., 2006; Manegold and Brink, 2011). Ostrich fossils are rare at Olduvai (Lowe, 1933; Leakey, 1971), but ostrich eggshell is common in Bed I (Leakey, 1971). A single eggshell piece was recovered at HWK EE. It is identified as ostrich based on its thickness and porosity (Bibi et al., 2006).

<u>Passeriformes (perching birds</u>) The earliest African Passeriformes date to the late Oligocene of Egypt (Rasmussen et al., 1987), early Miocene of Kenya (Mayr, 2014), and middle Miocene of Tunisia (Mourer-Chauviré, 2003, 2008), but they are generally uncommon in African deposits.

Two notable exceptions are in the early Pliocene at Langebaanweg, South Africa (Rich and Haarhoff, 1985; Manegold et al., 2013), and at Olduvai. Passeriformes are one of the most common groups at Olduvai during Bed I (NISP: 3683 in Matthiesen, unpublished conference notes), with at least 11 families including the Hirundinidae, Sturnidae, Muscicapidae, Turdidae, Sylviidae, Nectariniidae, and Fringillidae, as well as the Ploceidae (Brodkorb, 1985), Corvidae (Prassack, 2010), Apodidae (*Tachymarptis* cf. *equatorialis*, Charles T. Collins, pers. comm., 2017), and Coliidae (Haarhoff, 1993; Prassack, 2010). Middle Bed II Passeriformes are limited to Assemblage IIA at HWK EE: a tiny tibiotarsus is assigned to an indeterminate member of the Passeriformes and a coracoid is assigned to the Corvidae.

Of the Corvidae, eight species of *Corvus* (crows and ravens), two species of *Pyrrhocorax* (choughs), and *Zavattariornis stresemanni* (bush crow) occur in Africa today, along with one species each of jay, magpie, and piapiac. Prassack (2010) identified a piapiac (*Ptilostomus afer*) from Middle Bed I, but this specimen is larger and the approximate size of *Corvus rhipidurus.* It has a rugose bicipital muscle attachment, as seen in *Corvus*, but the facies articularis humeralis is slightly more elongate and the coracohumeral surface is less strongly curved medially. Corvids are difficult to distinguish at the species level, but this specimen belongs in the genus *Corvus* based on its size and collection of traits.

Avian quantitative ecology

Most OGAP trenches produced avifaunal remains, but their abundance and richness vary greatly across localities. Combined with the Leakey fossils, 468 of 759 specimens could be identified to family, with 16 non-passerine and at least one passerine family represented (Table 1). Table 3 provides data on the quantitative ecology of Middle Bed II sites with a total MNI (family level) greater than two (HWK EE, MNK, FC West, and FC East). Using MNI greatly reduces the number of taxa for each locality, but provides a more accurate measure of taxonomic occurrences. No one taxon dominates, despite the high number of cormorants (NISP: 177) compared to the next most common, pelicans (NISP: 29). HWK EE is the richest, especially compared to FC East, and along with the other localities, has a high degree of diversity (evenness). Chao 1 provides a higher predictive estimate of richness for every site, most notably at FC East with a richness of six, despite its small sample size (MNI=3).

Avian taphonomy

Wings are only slightly more abundant than legs at HWK EE (51%), but more noticeably so at MNK (66%). About 1/3 of fossils could not be confidently assigned a weathering stage either due to heavy corrosion or because the fossil cortical surface area was insufficient for assignment. Those specimens are omitted from the weathering tallies (Table 4). Overall, the Middle Bed II birds exhibit moderate to heavy weathering with the lowest incidence at MNK. Carnivore modification and rodent gnawing are much lower than was observed for Middle Bed I (Prassack, 2010) or lowermost Bed II (Prassack, 2014). A tooth puncture on a pelican carpometacarpus from HWK EE provides the only evidence of larger carnivore involvement, while other marks are primarily tooth scores that are likely from smaller-bodied carnivorans (e.g.,viverrid, herpestid, or small canid; Prassack, unpublished observation). No definitive evidence of hominin-modification was observed on any specimens. Specimens do not exhibit rounding at breaks as might occur during fluvial transport, but abrasion at HWK EE and MNK was extensive, when present.

Discussion

Avifauna at other Oldowan-Acheulean age sites

The Olduvai avifauna represents one of the largest and most diverse African fossil bird deposits and is one of only a few known from the Oldowan or Acheulean stages of hominin evolution. No birds are known from age-equivalent deposits in the Koobi Fora Formation (i.e., upper KBS Member [1.87–1.56Ma]) or Nariokotome (1.30–1.24 Ma) in Kenya, or Member J (1.76–1.53Ma) of the Shungura Formation, Lower Omo Valley, in Ethiopia (dates from McDougall et al., 2012). In South Africa, Sterkfontein Member 5E and Swartkrans Members 1–3 contain Oldowan-Acheulean horizons (Avery, 2001), but that bird material is understudied and primarily limited to bones from owl pellets from younger (~1Ma) deposits (Pocock, 1969; Watson, 1993).

At Konso, Ethiopia, *Homo erectus* and Acheulean tools have been recovered (Beyene et al., 2013), along with a small assemblage of birds (*n*=36) dating to ~1.45–1.25Ma (Louchart, 2014). This assemblage shares several water-associated taxa with Olduvai (e.g., *Podiceps, Tachybaptus*, *Phalacrocorax*, and *Anhinga*), as well as taxa that reflect the presence of trees and shrub-grasslands (*Aquila*, *Numida*, *Francolinus,* and potentially *Geronticus*). High avifaunal congruence across these two sites is not surprising, as many of the taxa present are cosmopolitan with strong fossil records. The scarcity of fossils from deposits (Louchart, 2014) comparable to the ages of Bed I and lowermost Bed II prevent the Konso assemblages from being used to imply evidence of wider-spread environmental changes during the Oldowan-Acheulean transition.

Olduvai birds as environmental indicators/community assessment

The Bed II avifaunal community suggests a shift from the wetland and lacustrine dominated system of lowermost Bed II (Prassack, 2014) to a habitat mosaic of open waters lacking in emergent vegetation, and a more open mix of dry and wet grasslands and open woodlands through Middle and lowermost Upper Bed II.

The high diversity of anatids during lowermost Bed II was used by Prassack (2014) to infer an extensive network of small, eutrophic wetlands capable of sustaining a variety of water birds (sensu Herremans, 1999). Low anatid diversity in Middle Bed II suggests lower nutrient yields, which may indicate clearer permanent waters that would have supported fish and piscivorous birds at the expense of dabbling ducks and other algae feeders. Rails are common and diverse during lowermost Bed II times (Prassack, 2014), but decline in Middle Bed II and appear to be restricted to open water taxa (gallinules and moorhens), with those preferring thick, emergent vegetation noticeably absent. This suggests an open permanent water source with an exposed shoreline. The paucity of shorebirds may be the result of preservation bias. The presence of crane, especially if it can be assigned to *Grus carunculatus*, would support the presence of open grasslands. This grassland signal is noted elsewhere in this volume by the predominance of C_4 grazing mammals (Uno et al., submitted) and grass phytoliths (de la Torre et al., submitted). The ibis, *Geronticus eremita,* provides an additional drier-grassland habitat signal that was missing earlier in the Bed. These are isolated specimens of *Grus* and *Geronticus* (MNI=1) and may reflect a stopover mortality during migration, but coupled with a decline in wetland taxa, support a drier grassland/woodland signal more akin to Middle Bed I (Prassack, 2010) than lowermost Bed II (Prassack, 2014). Cormorant numbers fluctuate and are most common in Assemblage IIB (MNI=16), less common in Assemblage IIA (MNI=4) and absent from Assemblage IIC. Most Assemblage IIB cormorants occur at MNK, a locality which may have sustained suitable roosting trees. The number of other perching and roosting taxa (i.e., owls, raptors, corvids, pelican) further supports the presence of at least isolated roosting trees or lightly wooded areas, but a dense woodland/forest signal is absent.

Assemblage IIA HWK EE exhibits high diversity with an avian environmental signal, suggesting trees and flooded grasslands with a body of water deep and fresh enough to sustain a variety of fish. This differs only slightly from the HWK Complex during lowermost Bed II (Prassack, 2014) in that a stronger tree and weaker emergent wetland signal are now evident. This environmental shift appears to begin in the upper portion of Lower Bed I (Leakey Clay), with the occurrence of vulture, raptor, and crow. These results are in agreement with sedimentary features (de la Torre et al., submitted "b"), fish and mammal community structure (Bibi et al., submitted), and diatoms (Pante et al., submitted) observed at the site. Weathering is highest here, suggesting a more exposed environment.

A grebe from FLK West (T73) and a duck from MNK Skull were identified, but both localities are nearly devoid of fossil birds and only a small alcelaphine was identified from MNK Skull (Bibi et al., submitted). It is therefore not clear what type of environment these two sites represent.

Assemblage IIB Assemblage IIB has three sites, all of which produced adequate avifaunal assemblages for analysis. The largest Middle Bed II assemblage comes from MNK T5 with an NISP of 365, but diversity is lower than at HWK EE because of the number of cormorants (NISP: 134, MNI: 9).

Cormorants similarly dominated HWK E and HWK W during lowermost Bed II (Prassack, 2014) and DK during Lower Bed I (Prassack, unpublished observation). However, those sites also contained both juvenile and medullary bone, indicative of breeding colonies, while neither type of bone was recovered at MNK. The cormorant bones may represent a roosting colony that accumulated at MNK outside of the breeding season. FC West and FC East assemblages are much smaller, but FC West is the site of owl and crane, and may represent a lightly wooded grassland. This is supported by higher incidence of rodent modification of bird bones at both FC West and FC East, compared to elsewhere at Olduvai, and the lower incidence of weathering seen at FC West and MNK. This high rodent/low weathering signal suggests greater ground cover.

<u>Assemblage IIC</u> Only two fossil bird bones were recovered from Assemblage IIC (Upper Bed II), but both were diagnostic with a cormorant at EF-HR and a duck at FLK West T69. The Acheulean locality of EF-HR is interpreted as a fluvially biased site with extremely poor preservation of bone (de la Torre et al., submitted “a”; de la Torre and Wehr, submitted). Cichlid fish are present at FLK West T69 in small numbers (*n*=3), but *Clarias* (catfish) are absent (Bibi et al., submitted). No fish were recovered from EF-HR, but a small alcelaphine, *Giraffa* cf. *stillei*, *Megalotragus isaaci*, *Hippotragus gigas*, *Hippopotamus gorgops*, *Equus oldowayensis*, and a premolar root fragment of a possible hominin were identified from that locality (Bibi et al., submitted). This suggests a more-open landscape, such as an ephemeral riverbank. This type of environment would hold lower avian diversity (sensu McIntyre and Wiens, 1999) and potentially lower preservation potential due to lower ground vegetation cover and greater exposure to the

elements (Behrensmeyer et al., 2003; Prassack, 2011), either of which may explain the scarcity of bird fossils here.

The environmental context of the Oldowan-Acheulean transition

OGAP studies using other environmental proxies show no major environmental/faunal turnover across the Oldowan-Acheulean transition and denote only minor faunal shifts (Bibi et al., submitted), with a trend towards slightly drier conditions based on isotopic (Rivals et al., submitted) and microwear (Uno et al., submitted) data (see also Cerling and Hay, 1986). There is also no major avifaunal turnover, but changes in the Bed II avian community are notable and provide evidence that the Olduvai landscape was opening up, as grasslands expanded and the lake and its associated wetlands retreated. However, similar environmental flux is also observed in older deposits, with a landscape mosaic during Middle Bed I (Prassack, 2010; Blumenschine et al., 2012b) shifting to an arid phase in Upper Bed I, to the return of extensive wetlands during lowermost Bed II times (Blumenschine et al., 2012c; Prassack, 2014).

We do not know the spatial or temporal scale at which the Olduvai hominins viewed their landscape (c.f. Wiens et al., 1993), and our data collections and observations are perhaps not yet made at a scale that allows for accurate interpretations of ecologically significant behavioral shifts (Peters and Blumenschine, 1995; Blumenschine and Peters 1998; Behrensmeyer et al. 2007). The driving force behind the Oldowan/Acheulean technological shift may relate to how habitats (and the resources they contained) were differentially distributed (i.e., landscape patchiness and connectivity) across time and space and, therefore, based more on localized hydrology, topography, and other environmental factors rather than the types of large-scale environmental shifts or faunal turnovers that are more readily recognized in the fossil record and (apparently) absent during this technological shift.

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Figure legends

Figure 1. Schematic diagram (not to scale) of Bed II, Olduvai Gorge. Birds from each assemblage are discussed in the text. Stratigraphic placements come from Stanistreet et al. (submitted) and McHenry (submitted). The Tuff IID date comes from Domínguez-Rodrigo et al. (2013). BPT stands for the Bird Print Tuff. The BPT date comes from Diez-Martin et al. (2015), but Uribelarrea et al. (in press) note that the dated tuff is 25cm below the actual BPT. This date may therefore be slightly older that the actual BPT.

Figure 2. Fossil birds from Middle Bed II, Olduvai Gorge. A) *Phalacrocorax owrei*/*africanus* (MNK T5-L10-3207), cranial aspect of distal left humerus. B) *Phalacrocorax owrei*/*africanus* (MNK SF-69), caudal aspect of proximal left humerus. C) *Phalacrocorax owrei*/*africanus* (MNK T5-L12-495), ventral aspect of distal left ulna. D) (left) *Anhinga* sp. (HWK EE LC-61530), ventral aspect of complete right ulna compared to (right) complete left ulna modern *Anhinga* sp. (FMNH 368757). E) *Pelecanus rufescens* (HWK EE Main-L10-2078), medial/posterodorsal aspect of complete right quadrate. F) (left) plantar aspect of distal right tarsometatarsus of a modern *Bostrychia hagadash* (HAFO 25436) compared with (right) Threskiornithidae indet. (HWK EE Main-L6-1752). G) Dorsal aspect of distal left coracoids of (left) *Grus canadensis* (HAFO 25482), (center) *Grus* cf. *carunculatus* (FC West T63-L62-333), and (right) *Balaerica regulorum* (HAFO 25481). Scale bars at 5mm for A–C, E and 10mm for D.

Figure 3. Fossil birds from Middle Bed II, Olduvai Gorge. A) *Phoeniconaias minor* (HWK EE T28-L46-464), cranial aspect of distal left tibiotarsus. B) *Tachybaptus ruficollis* (MNK T5-L10-193), cranial aspect of distal right tibiotarsus. C)Ventral aspect of distal right ulna of (left) cf.

Tyto alba (MNK T5-L12-506) compared to (right) *Tyto alba* (HAFO 25469) D) affinis Aquilina (HWK EE LC-61444), cranial aspect of distal left tibiotarsus. E) cf. Accipitrinae (MNK T5-L12-505), ventral aspect of medial right phalanx. F) cf. Aegypiinae indet. (HWK EE T27-L32-618), cranial aspect of sternum. Scale bars at 5mm for A and 10mm for B–F.