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Late Pliocene Avifauna from the Hominid Bearing *Zinjanthropus* Land Surface at Olduvai Gorge, Tanzania

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ABSTRACT. Taxonomic and taphonomic data on 236 fossil bird bone specimens are applied to paleolandscape models and reconstructions developed by the Olduvai Landscape Paleoanthropology Project (OLAPP) for Late Pliocene (1.84 Ma) hominid bearing deposits in the FLK Complex at Olduvai Gorge, Tanzania. Shorebirds dominate the avifauna but the occurrence and densities of different avian ecotypes vary across the landscape in ways that corroborate OLAPP reconstructions of wetland, peninsular and riverine landscape facets in this area of the paleo-Lake Olduvai Basin. Taphonomic profiles are based on observations of modern bird bone in similar environments of Tanzania. The taphonomy suggests habitat patchiness within these delineated landscape facets. Results support the use of fossil bird assemblages, even small assemblages thereof, for aiding in and refining paleoenvironmental reconstructions.

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Olduvai Gorge is a bifurcated valley in the Eastern Serengeti Plains, part of the western margin of the Eastern Rift Valley of northern Tanzania. The Ngorongoro Volcanic Highlands to the south and east contributed ca. 100 m of volcaniclastic sediments spanning the last two million years at Olduvai (Hay, 1976). This produced extensive, fossiliferous deposits, dating from the late Pliocene through more recent times, which were later exposed by tectonic uplift and down-cutting that created the Gorge.

Olduvai Gorge is best known for its paleoanthropological richness, beginning with discoveries by Louis and Mary Leakey (e.g., L.S.B. Leakey, 1965; M.D. Leakey, 1971) of early hominid fossils in association with primitive, Oldowan stone tools. Since 1989, excavations at Olduvai have been undertaken by the Olduvai Landscape Paleoanthropology Project (OLAPP), an international and interdisciplinary team whose goals are to understand the subsistence ecology of these early hominids through detailed reconstructions of the paleoenvironments in which they made and used stone tools and butchered animal carcasses (e.g., Blumenschine & Masao, 1991; Peters & Blumenschine, 1995; Blumenschine & Peters, 1998; Blumenschine *et al*., 2008). OLAPP uses a landscape paleoanthropology approach in which numerous, relatively small scale excavations are placed across exposed portions (ca. 130 km^2) of the Olduvai Basin. Trench locations are based on accessibility of the target stratigraphic unit-regardless of artifact densities observed to have been eroded to the surface. This method produces samples of stone tools, fossils and other paleoenvironmental indicators across a full range of paleolandscape facets for a given depositional sequence.

A recent focus of OLAPP has been to develop landscape samples between and beyond two important Late Pliocene (1.84 Ma) sites in the FLK Complex (Fig. 1): Level 22 at

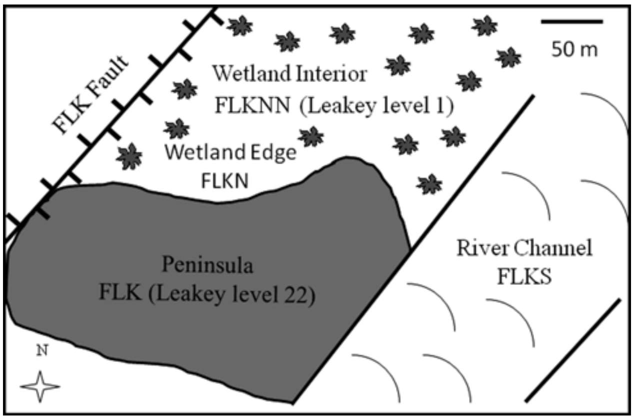

Figure 1. Schematic map depicting the spatial orientation of three major landscape facets in the FLK Complex, during Middle Bed I times (1.8 Ma). Landscape reconstructions are based on botanical, sedimentological and paleontological material recovered by OLAPP in the areas of FLK S (Tr. 143, 146, 148), FLK (Tr. 138, 140, 141), FLK N (Tr. 137, 144, 142, 147), and FLK NN (Tr. 134, 135, 145) (Blumenschine *et al*., in press) and by the M.D. Leakey's (1971) at FLK (Level 22) and FLK NN (Level 1). Birds were recovered from all trenches with the exception of 134, 141, 143 and 148.

FLK and Level 1 at FLK NN. These sites were excavated by the Leakeys in 1959–1962 and are known for their dense concentrations of Oldowan stone artifacts and vertebrate fossils, including hominid remains such as the type specimens of *Homo habilis* and *Paranthropus* (syn. *Zinjanthropus) boisei*, (L.S.B. Leakey, 1959; L.S.B. Leakey *et al*., 1964; Tobias, 1967). The FLK Complex spans a distance of ca. 0.5 km along the eastern lake margin, or floodplain, of paleo-Lake Olduvai, a closed, shallow, saline and alkaline lake that fluctuated in size between a maximum diameter of ca. 25 km during wet periods, and a perennial portion of ca. 10 km diameter during dry periods (Hay, 1976). The deposits of interest occur on what is referred to as the *Zinjanthropus* land surface, named for the famous *Zinjanthropus* skull discovered in 1959 from FLK, Level 22 (L.S.B. Leakey, 1959). This land surface is stratified between two volcanic tuffs, IB and IC, the latter of which buried and preserved the *Zinjanthropus* land surface, allowing for geologically precise dating of the *Zinjanthropus* land surface to landscape formation between 1.845 + 0.002 Ma and 1.839 + 0.005 Ma (based on dates in Blumenschine *et al*., 2003).

OLAPP has identified several paleolandscape facets along this half-kilometer stretch of the *Zinjanthropus* land surface (Fig. 1) on the basis of sedimentary facies analysis and supported by botanical and vertebrate fossils (Blumenschine *et al*., in press). These landscape facets include a 0.5–1.0 m high, lightly wooded Peninsula in the area of FLK, with a very low-gradient River Channel or Spillway to the south (FLK S) and a freshwater Wetland (FLK N and FLK NN), directed towards the lake shoreline to the north. The Wetland is divided into two sub-facets, an expansive Wetland Interior (FLK NN), located along the eastern lake margin, and the Wetland Edge (FLK N), a narrow zone occurring at the ecotone of the Wetland and Peninsula. These four landscape facets delimit for the first time the mosaic of marshland, woodland, bushland and grass/sedgeland environments evident from previous analyses of mammalian faunas from the two Leakey sites (e.g., Plummer & Bishop, 1994; Kappelman *et al*., 1997; Fernandez-Jalvo *et al*., 1998), as well as OLAPP's results (Blumenschine *et al*., in press).

The fossil avifauna from the *Zinjanthropus* land surface contributes two classes of paleoecological information to these landscape reconstructions. One is the taxonomic and ecotypic composition of avifaunal assemblages from each landscape facet. A second is comprised of taphonomic data from the same assemblages, the interpretation of which are guided by my observations in modern saline-alkaline lake environments in the Rift Valley of northern Tanzania (Prassack, dissertation in prep.). Here, I report these taxonomic and taphonomic data, providing details not reported in Blumenschine *et al*. (in press).

Materials and methods

Fossil bird bones (NISP [number of identified specimens present] = 236) were recovered from the *Zinjanthropus* land surface in nine of the thirteen trenches excavated by OLAPP during the 2006–2008 field seasons. Excavations were made by skilled OLAPP field workers using picks to break up the matrix followed by dry sieving using a 5 mm wire mesh sieve. For trenches 144–147, blocks of clay were taken back to the base camp where they were spread on plastic sheets, wetted, and allowed to dry in several cycles to break up the matrix, allowing the recovery of micro-faunal remains with low risk of breakage and higher likelihood of recovery. Taxonomic identifications are conservative and based on comparison to multiple osteological specimens from a full range of relevant modern taxa housed at the Florida Museum of Natural History and American Museum of Natural History. Specimens were not piece-plotted during excavation, such that in–situ specimen associations could not be made. As a result, I made no attempt to identify phalanges or vertebrae beyond that of Aves. Shorebird identifications are to the family level only until a more comprehensive comparative analysis can be made of these specimens.

Ericson's (1987) formula for measuring wing versus leg abundance is used to determine if taphonomic processes affected avian skeletal part survivorship and how this may have differed across the landscape. In this formula, the NISP of wing elements (humerus + ulna + carpometacarpus) is divided by the sum of wing and leg (femur + tibiotarsus + tarsometatarsus) elements, such that a percentage deviation of the quotient from 50% suggests taphonomic bias in skeletal part survivorship.

Taphonomic analysis involved careful examination of each specimen under a 100 W lamp using 10–20× magnification hand lenses. Flaking, cracking and corrosion of bone (Fig. 2) was used to assign bone to subaerial weathering stages (Table 2) following Behrensmeyer (1978) with proper adjustment for birds (Behrensmeyer *et al*., 2003). Evidence of carnivore tooth marks (Fig. 3a–b, Blumenschine *et al.,* 1996), rodent gnawing (Fig. 3c), medullary bone (Fig. 3d), and trample marks (Behrensmeyer *et al*., 1986; Fiorillo, 1989) was also noted. Bioerosion, defined here as the macroscopic alteration of bone's outer cortical surface by algae, fungi, aquatic invertebrates and/or insects (see Blumenschine *et al*., 2007 for review), was diverse and observed on specimens from all facets. Data on bioerosion will be presented in a forthcoming manuscript, comparing fossil marks to those observed during modern landscape studies in Tanzania (Prassack, dissertation in prep.).

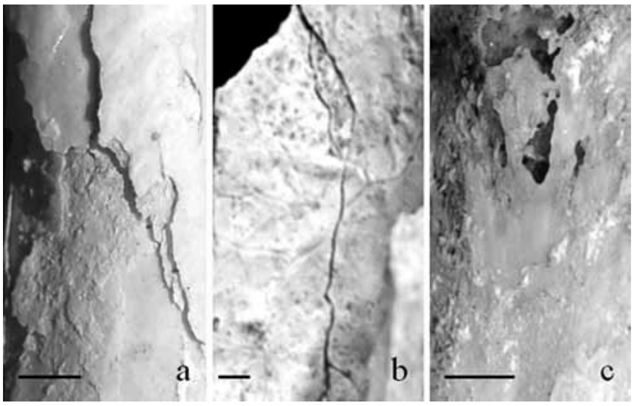

Figure 2. Flaking (*a*), cracking (*b*), and corrosion (*c*) to bird bone interpreted as the result of exposure to subaerial weathering. Scale bars are 5 mm (*a*), 1 mm (*b*), and 5 mm (*c*).

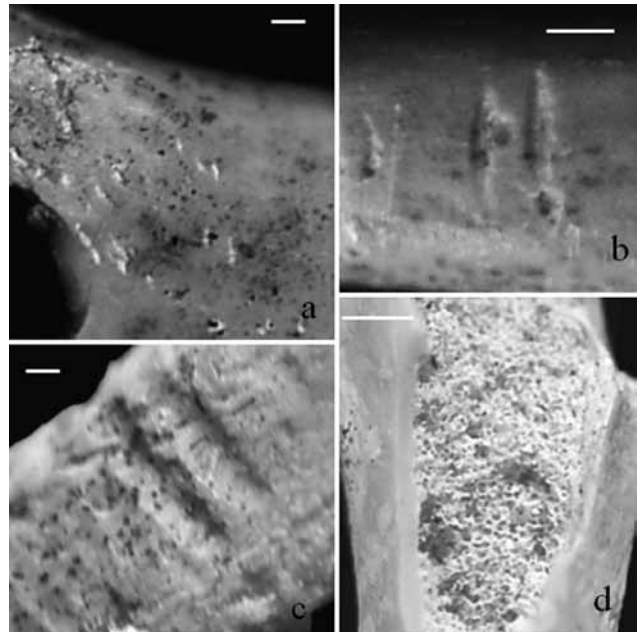

Figure 3. Taphonomic analysis of the FLK Complex birds revealed modifications by carnivores including (*a*) small tooth pits and (*b*) scores, in all landscape facets. Rodent-gnawed bones (*c*) also occurred in all facets, while medullary bone (*d*) was limited to the Wetland Interior and Wetland Edge. Scale bars are 1 mm.

Results

Table 1 lists the 236 fossil bird specimens recovered by OLAPP in the FLK Complex. The vast majority of specimens (70%) are too fragmented or lacking in sufficient diagnostic criteria for identification beyond Aves. Of the 70 specimens that could be identified further, shorebirds (Charadriiformes) are the most common ecotype (57%), and are found in all landscape facets. However, a variety of lake and wetland taxa, including grebes, rails and ducks and birds typical of bush, grass, and open wood land, are also represented. Shorebird medullary bone is present in the Wetland Interior and Wetland Edge.

Taphonomic results for each of the four landscape facets are presented in Table 2. Appendicular elements are more common than axial elements (56.8% of total assemblage), and wing bones are more common than those from the leg (65.7%). Weathering is low across all facets, with 72% of the FLK Complex avifauna being described to stage 0–1. The incidence of more heavily weathered specimens increases across the landscape from the Wetland Interior to the Channel, with 23.7% of Wetland Interior bones being at stage 2 or higher compared to a value of 46.2% in the Channel facet. Within the Wetland Interior, weathering is higher at Trench 145 than at Trench 135, and preservation was so poor that no bones could be identified beyond Aves. On the Peninsula, bones are slightly more weathered and corroded at Trench 140 than at Trench 138. Leg bones are both more likely to be weathered beyond stage 1 (34.8%) than wings (12.5%). Carnivore tooth-marked bones are found in all facets (27% total assemblage), but are most common on the Peninsula (39.3%). Legs are more commonly tooth-marked (38%) than wings (26.4%). Rodent gnawing (7.6%) and trampling (4.9%) are uncommon and primarily limited to the Peninsula and Channel. Bioerosion occurs in all facets but the type of modification varies across facets. Types of bioerosion observed include yellow oblong marks, clusters of tiny black dots, stained cracks, and both isolated and branching smooth-bottomed runnels that penetrate through the upper layer of the outer cortical surface. Dendritic-patterned stains produced by manganese dioxide are evident on specimens from all facets, but are most common on the Peninsula.

Discussion

The dominance of shorebirds among the *Zinjanthropus* land surface avifauna, and their occurrence in all landscape facets, may reflect the complex's proximity to the shoreline of paleo-Lake Olduvai, but shorebirds can be found in a wide range of habitats (i.e., shoreline, wetland edge, flooded grassland, and open savanna). Future refinement of the shorebird taxonomy for this complex is expected to better reflect known habitat preferences of each species. For example, shorebird density is highest in the Wetland Interior, comprised of small sandpipers and plovers, such as are typically found in modern near-shore marshes. Shorebird numbers decrease away from the Marsh Interior and are replaced by larger taxa, likely those associated with wetland and riverine systems (e.g., *Glareola, Limosa, Pluvialis*). Ducks, rails and grebes are also well represented in the complex but are primarily limited to the Wetland Edge and Peninsula, as would be expected given the habitat preferences of these taxa. Larger birds (e.g., flamingo, stork, cormorant, goose and pelican) were only found in OLAPP samples from the Channel facet (i.e., a large extinct goose-like duck and midshaft fragments of a large bird) although Matthiesen (1990) reports them at FLK Level 22 (Peninsula) and FLK NN Level 1 (Wetland Interior). I have also recovered larger birds from other Bed I strata.

Low overall weathering supports Behrensmeyer *et al.*'s (2003) suggestion that bird bone peaks at weathering stage 1, while mammal bone weathering typically peaks at stage 2. Differences across the landscape may reflect differences in vegetative ground cover and/or soil chemistry. Tooth-marked bird bones comprise 27% of the entire FLK Complex avian assemblage, a percentage similar to both modern, carnivore-ravaged bird bone assemblages and

Table 1. NISP (number of identified specimens present) for avifauna recovered from the four landscape facets reconstructed by OLAPP in the FLK Complex, Olduvai Gorge, Tanzania. Charadriiformes are only assigned to family level and general body size (i.e., *Calidris alba* and *Charadrius tricollaris* would be considered small sandpipers and plovers respectively). Numbers in parentheses denote NISP for taxa identified beyond that of Aves.

area in FLK Complex		FLK S Tr. 146	FLK Tr. 138, 140	FLK N Tr. 137, 142, 144, 147	FLK NN Tr. 135, 145	total NISP
landscape facet		Channel	Peninsula	Wetland Edge	Wetland Interior	
Charadriiformes indet.		—	2	6	2	10
Scolopacidae						
	small sandpipers	1	—	9	10	20
	large sandpipers	—	1	1	—	2
Charadriidae						
	small plovers	1	—	1	3	5
	large plovers	—	—	1	—	1
Recurvirostridae		—	—	2	—	2
Podicepidae						
	Tachybaptus ruficollis	—	—	5	—	5
	Anatidae					
	Anatidae indet.	1	1	1	—	3
	Anas crecca	—	1	2	—	3
	Aythyia sp.	—	1	—	—	1
Rallidae						
	Rallidae indet.	1	—	—	—	1
	Amaurornis flavirostris	—	—	1	—	1
	Sarothrura cf. sp.	—	—	1	—	1
	Porphyrio alleni	—	1	—	—	1
	Gallinula chloropus	—	—	1	—	1
Ardeidae						
	Ardeidae indet. (small)	—	—	1	—	1
Corvidae						
	Corvidae indet.	—	1	—	—	1
Columbidae						
	Streptopelia decipiens	1	1	3	1	6
Colidae						
	Colius cf. sp.	—	—	1	—	1
Pstittacidae						
	Agapornis cf. sp.	—	—	1	—	1
Passeriformes indet.		1	—	2	—	3
Aves indet.		7	19	118	22	166
NISP total		13 (6)	28 (9)	157 (39)	38 (16)	236 (70)

some other fossil assemblages at Olduvai. Tooth marks are small and were likely made by smaller carnivores such as mongoose, genet, jackal or serval, based on my direct observations of carnivore feeding episodes. Fossil wing bone specimens are both less weathered and less likely to be tooth-marked than leg specimens. Similar patterns of weathering (Prassack, in press) and carnivore damage (pers. obs.) have been observed in modern settings and suggest a link between these taphonomic agents and skeletal part bias, at least for the preferential survivorship of wings over legs.

Wetland Interior (FLK NN). The northernmost deposits in the FLK Complex are reconstructed as perennial wetlands based on the presence of extensive marsh plant mats consisting of *Typha* and *Phragmites* macrofossils on the surface of an olive waxy claystone, indicative of a previous lake inundation of the area (Blumenschine *et al*., in press).

The Leakey excavations at FLK NN (Levels 1–4) recovered over 3,000 specimens representing a range of avifauna. It is unknown what the actual numbers are for Level 1, but Matthiesen (1990) notes that shorebirds dominate, followed by ducks and rails, supporting the presence of wetlands, emergent vegetation and standing water. The much smaller OLAPP assemblage at FLK NN is not surprisingly much less diverse, predominately represented by small shorebirds, including examples of medullary bone suggesting that Lake Olduvai was a breeding ground for some shorebirds. Mourning Dove (*Streptopelia decipiens*) is not unexpected since these birds rely of fresh water for drinking and bathing and their carcasses have been observed along the edges of freshwater pools and saline-alkaline lake flats. The absence of typical wetland taxa (e.g., ducks, herons, rails) in OLAPP's assemblages is most likely an artifact of sample size (NISP =157). Alternatively though not determinable with this small sample, it attests to the patchiness of near-shore landscapes.

Two of the wetland interior trenches (145 and 134) are located on what appears to have been a small topo-high. No birds were recovered from Trench 134, and specimens from Trench 145 exhibit slightly heavier fragmentation and weathering than bones at Trench 135, which is hypothesized as deep marsh. This suggests prolonged exposure on the surface of the mound rather than quick burial. KAP has observed Blacksmith Plover (*Vanellus armatus*) carcasses lying atop clumps of sedge grass (*Cyperus laevigatus*) in near-shore, spring-fed wetlands at Lake Manyara, Tanzania (Prassack, unpublished). Clumping or a general lack of vegetation on the Wetland Interior topo-high may have left bone exposed to more prolonged subaerial weathering.

Table 2. Raw data and percentages for weathering and incidence of carnivore tooth markings, rodent gnawing, trampling, and microbial bioerosion across the *Zinjanthropus* equivalent landscape. Weathering and carnivore tooth-marks for wing and leg elements are emphasized. In parentheses are percentages for a given column. Note: Ten specimens from the Wetland Edge were not analyzed because they were small (< 5 mm) mid shaft fragments. This lowered the total assemblage size to 226, which is reflected in percentages for the Wetland Edge and FLK Complex totals for rodent gnawing, trampling, and bioerosion. It does not affect wing and leg percentages.

landscape facet	Channel	Peninsula	Wetland Edge	Wetland Interior	FLK Complex
taphonomic trace	FLKS	FLK	FLKN	FLKNN	total
wing : leg ratio	3:1 (75)	10:4 (71.4)	60:34 (64.5)	15:7 (68.2)	88:46 (66.2)
WS 0-1					
all elements	7 (53.8)	20 (71.4)	107 (72.7)	29 (76.3)	163 (72)
wings	0 (N/A)	3 (75)	22 (64.7)	7 (100)	30 (65.2)
legs	1 (7.1)	11 (39.3)	40 (27.2)	9 (23.7)	61 (25.8)
tooth-marked					
all elements	1 (7.7)	11 (39.3)	40 (27.2)	9 (23.7)	61 (27.0)
wings	0 (N/A)	6 (60)	15 (25)	2 (13.3)	23 (26.1)
legs	0 (N/A)	2 (50)	14 (41.1)	2 (28.6)	18 (39.1)
rodent-gnawed	1 (7.7)	4 (14.3)	13 (8.9)	0 (N/A)	18 (7.6)
trample-marked	1 (7.7)	3 (10.7)	5 (7.3)	2 (5.2)	11 (4.9)
bioerosion	3 (23.1)	8 (28.6)	11 (5.2)	2 (7.5)	24 (10.0)

Tooth-marked bird bones in this facet suggest only moderate damage by carnivores, although there is a dominance of wing bones. Conversely, the larger mammal assemblage shows a stronger, larger-carnivore signal in the form of low bone densities, an absence of limb bone ends, and many tooth-marked bones (*cf.* Blumenschine, 1995; Blumenschine *et al.*, in press).

Wetland Edge (FLK N). OLAPP reconstructs this facet as the edge of a perennial wetland abutting the topographically higher Peninsula to the south. A range of *in situ* sedge culms and stems of dicots are present, plus woody stems and branches, the latter of which were likely washed down slope from the Peninsula. Crocodiles and the presence of grebes and teals support proximity to open water while the rails and the small heron imply wetlands and emergent vegetation with sufficient cover. The ecotonal nature of this facet is evident from the occurrence of dove, mousebird, and lovebird, which implies trees or bushes in the vicinity, as also evidenced for the adjacent Peninsula facet. These brush/woodland birds likely utilized small pools of water at the Wetland Edge to drink and bathe, as is seen today at the Cheetah Marsh at Lake Ndutu, Tanzania (pers. obs.). This behavior may have exposed them to greater predation risk. The Wetland Edge provides the highest densities of fossil birds from the FLK Complex but this may be an artifact of screening methods since it was only for these trenches that wet/dry sorting was done. Low overall weathering supports this as an area with either sufficient vegetative ground cover and/or quick burial. The absence of skeletal remains of larger wetland birds (e.g., pelicans, geese, stork), commonly encountered in similar modern landscape settings, may be the result of water-logged cracking, where water is repeatedly leached from exposed drying bone (Trueman *et al.*, 2003; Prassack, in press). This is expected to occur, and has been observed by KAP along wetland edges that dry out along their outer margins seasonally. This phenomenon may have a greater affect on larger bones that may remain unburied and exposed on the surface longer than smaller bird bones (pers. obs.). Small carnivore activity, as seen in the incidence of tooth marking, is moderate compared to the other assemblages. In contrast, the larger carnivore signal on larger mammal specimens is low, with high survivorship of large mammal limb bone ends and few tooth-marked specimens occurring (Blumenschine *et al.*, in press). However, crocodile tooth marks occur on several large mammal bones and the high number of complete larger mammal bones in this facet is indicative of crocodile feeding (Njau & Blumenschine, 2006). Rodent gnawing lends further support of adequate vegetation that would have concealed rodents from aerial predators.

Peninsula (FLK). OLAPP excavations identify the presence of a patchily-treed narrow peninsula that rose approximately 0.5 to 1 m above the Wetland Complex to its north and the River Channel to its southeast (Blumenschine *et al.*, in press). Trees are inferred along its southern face, based on high densities of micro-mammal remains from FLK Level 22 (Fernandez-Jalvo *et al.*, 1998) and what has been inferred to be a depression created by an uprooted tree (M.D. Leakey, 1971). High densities of siliceous roots and their casts, in addition to grasses and sedges, are present, but an absence of micro-mammals and woody vegetation at Trench 138 are suggestive of open grassy habitat along part of the Peninsula facet (Blumenschine *et al.*, in press).

Mary Leakey's massive excavation at FLK produced dense concentrations of stone tools and vertebrate fossils, including cut-marked larger mammal bones, leading her and others to describe Level 22 as a hominid living site or home base (M.D. Leakey, 1971; Bunn, 1981; Potts, 1984). Many bones, however, are also tooth-marked by large carnivores and/or crocodiles (Njau & Blumenschine, 2006), suggesting heavy competition for carcass-scavenging and high predation risk to hominids. Carnivore tooth-marked larger mammal bone is abundant at Level 22 (Blumenschine, 1995), but uncommon elsewhere on the Peninsula (Blumenschine *et al.*, in press).

Over 2,000 avifaunal specimens were recovered from Level 22 by the Leakeys (Matthiesen, 1990). As at FLK NN, shorebirds, ducks and rails dominate but cormorants (Brodkorb & Mourer-Chauviré, 1984) and raptorial birds (Matthiesen, 1990) are also present, suggesting the presence of roosting trees or rocky outcrops in the vicinity. OLAPP trenches produced far fewer specimens but with moderate species diversity and excellent preservation allowing for 32% of specimens to be identified to family or genus (e.g., ducks, rails, several larger sandpipers, a dove and a small corvid).

A higher proportion of bird bones bear small carnivore tooth marks in this part of the complex. Carnivores commonly remove carcasses from open ground, as would be expected along a marsh edge, to areas to cover (i.e., a treed peninsula with a brush slope) to reduce kleptoparasitism risk from other carnivores. Allen's Gallinule (*Porphyrio alleni*) and the ducks might have been brought in from the adjacent wetland by a carnivore or the ducks may have fallen victim while nesting in the tall grass along the peninsula. This is supported by the presence of tooth marks on specimens of Common Teal (*Anas crecca*) and of *Aythya* sp. The higher ground of the Peninsula would have also provided a clearer view of danger. Accumulations of tooth-marked bird bone have been observed at the Ngorongoro Burial Mounds, a series of lightly vegetated hills ranging in size between 50 and 400 m and elevations as high as 50 m spread along ca. 2.5 km of an otherwise low grade, upper lacustrine plain in the Ngorongoro Crater of Tanzania. Those remains include Yellow-necked Spurfowl (*Francolinus leucoscepus*), which are expected along the upper grassy plains, but also pelican, which was likely transported from freshwater springs or the lake shore approximately 1 km away. Rodent gnawing is most common in this facet and correlates to the abundance of micromammal remains recovered at FLK (Fernandez-Jalvo *et al*., 1998; Blumenschine *et al*., in press).

Etching by filamentous fungi (Fernandez-Jalvo *et al*., 2002) and dendritic-patterned staining by manganese dioxide are common here and suggest a dry, low-light area where lichen is typically found (Fernandez-Jalvo *et al*., 2002; Thackery *et al*., 2005). Trample-marked bone at Trench 140 suggests an exposed high-traffic area with some cover, on a gritty sandy substrate (Fiorillo, 1989), as would expected in an area between two freshwater sources.

Channel/Spillway (FLK S). An anastomising river flowed parallel to the Peninsula in the area of FLK S (Blumenschine *et al*., in press). It was likely seasonal, as are many in the Rift Valley. Botanical data are limited to silicified rhizomes believed to be perennial sedges, which are common along river banks today. Larger mammal bone densities are low here, limb bone ends are absent, and carnivore tooth marked bones are found on 50% of larger mammal bones, suggesting that this, along with the Wetland Interior, were areas of heavy larger carnivore activity. The Peninsula likely provided shade along the northern banks of the River Channel, and lions, leopards, and hyenas frequent riverine habitats today to both hunt and rest, producing common kill-site bone assemblages along river banks in East Africa (pers. obs.).

Bird bone densities are also low here. Many larger birds (vulture, eagle, crowned crane) congregate at rivers to bathe, but African water birds prefer standing water (O'Keefe, 1986), and the flow of this river, while likely seasonal, may alone have been of sufficient velocity to restrict or limit avian activity. Surveys in modern landscape facets of Tanzania (Prassack, in prep.) yielded few avian remains in riverine settings at Lake Manyara and Ngorongoro Crater but strong evidence of carnivore activity, including scat, prints, hair balls, as well as hyena, jackal and lions resting in the shade along the banks. The small avifauna sample size makes it difficult to discuss this facet's taphonomy, but based on modern observations one can expect that high carnivore activity and fluvial transport, coupled with exposure to subaerial weathering, will result in low survivorship potential for bird bones in riverine environments.

Application to study of hominid land use at Olduvai. The Olduvai fossil birds provide additional supporting evidence of paleolandscape structure and ecology in the FLK Complex during Middle Bed I times, as well as novel environmental information lacking from other biotic proxies. For example, the proximity of the lake to the complex cannot be currently defined, but the abundance of small shorebirds (plovers and sandpipers) in the wetland interior suggests near shore environments and close proximity to mudflats. The presence of shorebird medullary bone implies that Olduvai was a breeding ground for at least some taxa. Diving birds (cormorant, teal and grebe) attest to lake depth, and marsh birds (moorhen, crake, swamphen, and flufftail) suggest suitable emergent vegetation, which is further supported by the paleobotanical evidence. Geomorphic data point to dry, higher ground in the area of FLK, which we interpret as a peninsula, and are directly supported by the occurrence of various perching and bush/grassland birds including the likelihood of nesting cormorants and predatory bird roosts.

The taphonomic analysis, even of specimens that could not be described beyond Aves or to skeletal element (i.e., midshaft fragments), provides additional data supporting OLAPP's landscape reconstructions. Weathering is lowest in the Wetland Interior where bones likely become mired in mud and are unaffected by solar radiation. Damage by carnivores is highest at the Peninsula, where they would have had sufficient access to cover as well as to birds nesting, drinking and/or bathing in nearby freshwater pools of the Wetland Edge. Rodent damage and trampling, while not common, also correlate to landscape facet, with rodent gnawing occurring in areas of adequate ground cover (Peninsula and Wetland Edge) and trampling along the Peninsula, where herds of large mammals would be expected to frequent. The bioerosion, while treated here anecdotally, does show similarities to modifications and staining seen in some modern habitats, justifying further study.

With these data, hominid land use patterns can be better ascertained. Hominids likely avoided much of the Wetland Interior owing to its inaccessibility and dangers from crocodiles, hippopotamus and larger mammalian carnivores. This is evident in the absence of stone tools or cut-marked mammal bones in the facet (Blumenschine *et al*., in press). Hominids may have accessed the Wetland Edge to harvest rootstocks, acquire large mammal carcasses left by carnivores, and to gather bird eggs and nestlings. The adjacent, treed Peninsula would have provided nearby arboreal refuge for hominids to escape terrestrial predators, and could have served as relatively safe foci for processing carcasses brought in from the nearby Wetland and Channel. The Peninsula may also have afforded hominids access to various fruiting trees lining the banks of abandoned channels crossing this facet. Such a reconstruction could explain the strong evidence of hominid activity, including the abundant stone tools and cut-marked mammal bones seen here. We did not find nor did we expect cut-marked bird bones, but if hominids were indeed processing larger bird carcasses, it is in facets such as the Peninsula that we would expect to find evidence. However, large carnivores frequent river banks in search of prey, and buffalo and elephant can be found traversing dried river banks (Prassack, pers. obs.), making this an unlikely place for prolonged hominid activity such as that imagined in the living-site scenario. This is attested to by evidence of mammalian carnivore and crocodilian tooth marks on hominid bones recovered from the Peninsula (Blumenschine *et al*., in press).

Conclusion

A relatively small avifaunal assemblage (NISP = 236) is shown to corroborate and strengthen OLAPP reconstructions of the paleolandscapes at the FLK Complex during the Late Pliocene. Our results support previous claims that fossil birds (Baird, 1989; Cheneval, 1989), even small assemblages (Behrensmeyer *et al*., 2003), can provide important paleoenvironmental data, particularly when recovered as part of an excavated landscape sample. In this instance we are better able to delineate hominid land use strategies as these relate to their subsistence and exposure to competition and predation hazards. The taphonomy of these fossils also proves useful for understanding site paleoecology and landscape distribution by providing fine scale detail on microhabitat and landscape heterogeneity that may not be apparent through the analysis of other proxies (e.g., mammalian fauna, botanical and sedimentological samples). These findings should encourage others to include avifaunal remains when studying site taphonomy but also promote the continuation of modern analogue studies across a wider range of depositional environments in order to increase the validity of taphonomic-based reconstructions at fossil sites. Earlier reports by Hay (1976), Brodkorb (1980), and Matthiesen (1990), coupled with the results from this study, suggest that the Olduvai birds will play an increasingly significant role in the understanding of Plio-Pleistocene avifaunas in Africa.

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References

Baird, R.F., 1989. Fossil bird assemblages from Australian caves: precise indicators of late Quaternary environments? *Palaeogeography, Palaeoclimatology, Palaeoecology* 69: 241–244.
http://dx.doi.org/10.1016/0031-0182(89)90167-3

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4: 150–162.

Behrensmeyer, A.K., K.D. Gordon, & G.T. Yanasi, 1986. Trampling as a cause of bone surface damage and pseudo cut marks. *Nature* 319: 768–771.
http://dx.doi.org/10.1038/319768a0

Behrensmeyer, A.K., C.T. Stayton, & R.E. Chapman, 2003. Taphonomy and ecology of modern avifaunal remains from Amboseli Park, Kenya. *Paleobiology* 29: 52–70.
http://dx.doi.org/10.1666/0094-8373(2003)029<0052:TAEOMA>2.0.CO;2

Blumenschine, R.J., 1995. Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 29: 21–51.
http://dx.doi.org/10.1006/jhev.1995.1046

Blumenschine, R.J., C.W. Marean, & S.D. Capaldo, 1996. Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. *Journal of Archaeological Science* 23: 493–507.
http://dx.doi.org/10.1006/jasc.1996.0047

Blumenschine, R.J., & F.T. Masao, 1991. Living sites at Olduvai Gorge, Tanzania? Preliminary landscape archaeology results in the basal Bed II lake margin zone. *Journal of Human Evolution* 21: 451–462.
http://dx.doi.org/10.1016/0047-2484(91)90095-D

Blumenschine, R.J., & C.R. Peters, 1998. Archaeological predictions for hominid land use in the paleo-Olduvai Basin, Tanzania, during lowermost Bed II times. *Journal of Human Evolution* 34: 565–607.
http://dx.doi.org/10.1006/jhev.1998.0216

Blumenschine, R.J., C.R. Peters, F.T. Masao, R.J. Clarke, A.L. Deino, R.L. Hay, C.C. Swisher, I.G. Stanistreet, G.M. Ashley, L.J. McHenry, N. Sikes, N.J. van der Merwe, J.C. Tactikos, A. Cushing, D.M. Deocampo, J.K. Njau, & J.I. Ebert, 2003. Late Pliocene *Homo* and hominid land use from western Olduvai Gorge, Tanzania. *Science* 299: 1217–1221.
http://dx.doi.org/10.1126/science.1075374

Blumenschine, R.J., K.A. Prassack, C.D. Kreiger, & M.C. Pante, 2007. Carnivore tooth-marks, microbial bioerosion, and the invalidation of Dominguez-Rodrigo & Barba's (2006) test of Oldowan hominin scavenging behavior. *Journal of Human Evolution* 53 420–426.
http://dx.doi.org/10.1016/j.jhevol.2007.01.011

Blumenschine, R.J., F.T. Masao, J.C. Tactikos, & J.I. Ebert, 2008. Effects of distance from stone source on landscape-scale variation in Oldowan artifact assemblages in the paleo-Olduvai Basin, Tanzania. *Journal of Archaeological Science* 35(1): 76–86.
http://dx.doi.org/10.1016/j.jas.2007.02.009

Blumenschine, R.J., I.G. Stanistreet, J.N. Njau, M.K. Bamford, F.T. Masao, R.A. Albert, H. Stollhofen, P. Andrews, K.A. Prassack, L.J. McHenry, Y. Fernández-Jalvo, E.L. Camilli, & J.I. Ebert, 2010 in press. Environments and activity traces of Oldowan hominins across the FLK Peninsula during *Zinjanthropus* times (1.84 Ma), Olduvai Gorge, Tanzania. Special issue: *Fifty Years after* Zinjanthropus*: Landscape Paleoanthropology of Plio-Pleistocene Olduvai Gorge, Tanzania*. *Journal of Human Evolution,* in press.

Brodkorb, P., 1985. Preliminary report on Pliocene/Pleistocene birds of East Africa. In *Acta XVIII Congressus Internationalis Ornithologici*, Moscow, August 16–24, 1982, vol. 1, pp. 174–177. Moskow: Nauka Editions.

Brodkorb, P., & C. Mourer-Chauviré, 1984. A new species of cormorant (Aves: Phalacrocoracidae) from the Pleistocene of Olduvai Gorge, Tanzania. *Geobios* 17: 331–337.
http://dx.doi.org/10.1016/S0016-6995(84)80098-4

Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature* 291: 547–577.
http://dx.doi.org/10.1038/291574a0

Cheneval, J., 1989. Fossil bird study, and paleoecological and paleoenvironmental consequences: examples from the Saint-gerandle-Puy deposits (lower Miocene, Allier, France). *Palaeogeography, Palaeoclimatology, Palaeoecology* 73: 395–309.
http://dx.doi.org/10.1016/0031-0182(89)90010-2

Ericson, P.G.P., 1987. Interpretations of archaeological bird remains: a taphonomic approach. *Journal of Archaeological Science* 14: 65–75.
http://dx.doi.org/10.1016/S0305-4403(87)80006-7

Fernández-Jalvo, Y., C. Denys, P. Andrews, T. Williams, & Y. Dauphin, 1998. Taphonomy and paleoecology of Olduvai Bed I (Pleistocene, Tanzania). *Journal of Human Evolution* 34: 137–172.
http://dx.doi.org/10.1006/jhev.1997.0188

Fernández-Jalvo, Y., B. Sánchez-Chillón, P. Andrews, S. Fernández-López, & L. Alcalá Martínez, 2002. Morphological taphonomic transformations of fossil bones in continental environments and repercussions on the chemical composition. *Archaeometry* 44(3): 353–361.
http://dx.doi.org/10.1111/1475-4754.t01-1-00068

Fiorillo, A.R., 1989. An experimental study of trampling: implications for the fossil record. In *Bone Modification*, ed. R. Bonnichen and R.H. Sorg, pp. 61–71. Orono: University of Maine, Center for the Study of the First Americans.

Hay, R.L., 1976. *Geology of the Olduvai Gorge*. Berkeley: University of California Press.

Kappelman, J., T. Plummer, L. Bishop, A. Duncan, & S. Appleton, 1997. Bovids as indicators of paleoenvironments in East Africa. *Journal of Human Evolution* 32: 229–256.
http://dx.doi.org/10.1006/jhev.1996.0105

Leakey, L.S.B., 1959. A new fossil skull from Olduvai. *Nature* 184: 491–493.
http://dx.doi.org/10.1038/184491a0

Leakey, L.S.B., 1965. *Olduvai Gorge 1951–61*. Volume 1: *A Preliminary Report on the Geology and Fauna*. Cambridge: Cambridge University Press.

Leakey, L.S.B., P.V. Tobias, & J.R. Napier, 1964. A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202: 7–9.
http://dx.doi.org/10.1038/202007a0

Leakey, M.D., 1971. Olduvai Gorge: Excavations in Bed I and II, 1960–1963. Cambridge: Cambridge University Press.

Matthiesen, D.G., 1990. *Prodromus of the paleoecology of the Plio-Pleistocene fossil birds from the early man sites of Omo and Hadar, Ethiopia, and Olduvai Gorge, Tanzania*. Paper presented at the International Conference for Archaeozoology, Washington D.C., June, 1990.

Njau, J.K., & R.J. Blumenschine, 2006. A diagnosis of crocodile feeding traces on large mammal bone with fossil examples from Plio-Pleistocene Olduvai Gorge, Tanzania. *Journal of Human Evolution* 50: 142–162.
http://dx.doi.org/10.1016/j.jhevol.2005.08.008

O'Keeffe, J.H., 1986. Ecological research on South African rivers-a preliminary synthesis. *South African National Scientific Programmes Report 121*. Pretoria: Council for Scientific and Industrial Research.

Peters, C.R., & R.J. Blumenschine, 1995. Landscape perspectives on possible land use patterns for early hominids in the Olduvai Basin. *Journal of Human Evolution* 29: 321–362.
http://dx.doi.org/10.1006/jhev.1995.1062

Plummer, T.W., & L.C. Bishop, 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *Journal of Human Evolution* 27: 47–75.
http://dx.doi.org/10.1006/jhev.1994.1035

Potts, R.B., 1984. Home bases and early hominids. *American Scientist* 72: 338–347.

Prassack, K.A., in prep. *Avian Taxonomy and Taphonomy from Bed I and Lower Bed II, Olduvai Gorge, Tanzania.* PhD dissertation, Center for Human Evolutionary Studies, Rutgers University of New Jersey.

Prassack, K.A., in press. The impact of weathering on bird bone at a saline-alkaline lake in Tanzania. *Journal of Archaeological Science,* in press 2010.

Thackery, J.F., F. Senegas, & G. Laden, 2005. Manganese dioxide staining on hominid crania from Sterkfontein and Swartkrans: possible association with lichen. *South African Journal of Science* 101: 1.

Tobias, P.V., 1967. *Olduvai Gorge*. Volume 2: *The Cranium of* Australopithecus (Zinjanthropus) boisei. Cambridge: Cambridge University Press.

Trueman, C.N.G., A.K. Behrensmeyer, N. Tuross, & S. Weiner, 2003. Mineralogical and compositional changes in bones exposed on soil surfaces in Amboseli National Park, Kenya: diagenetic mechanisms and the role of sediment pore fluids. *Journal of Archaeological Science* 31: 721–739.
http://dx.doi.org/10.1016/j.jas.2003.11.003