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Bird fossils from Ankilitelo Cave: Inference about Holocene environmental changes in Southwestern Madagascar

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Abstract

The identifications of non-permineralized fossil bird bones recovered from Ankilitelo Cave in southwestern Madagascar are presented. Among the more than 560 elements recovered, 29 different taxa were identified, the vast majority being species that still occur in this region of the island. Eggshell remains from the extinct elephant bird (Family Aepyornithidae) and assigned to *Aepyornis* sp. were found at the site. Two identified extant taxa, *Scopus umbretta* and *Monias benschi*, no longer occur in the area immediately surrounding the cave. The available radiocarbon measurements of collagen from fossil bird bones and avian eggshell carbonate of recovered from the cave range from 13,270 Cal yr BP to modern times. Hence, the presumed ecological shifts that took place resulting in the disappearance or range contractions of these three taxa is within the Holocene and are presumed to be associated with natural climatic change and in more recent centuries associated human pressures. Information is also presented on the origin of guinea fowl (*Numida*) and inference on the period of colonization of *Corvus albus* on Madagascar.

Key words: Ankilitelo Cave, birds, *Aepyornis*, *Monias benschi*, *Numida meleagris*, fauna, environmental shifts, C14 dates

Résumé

Les identifications des os d'oiseaux fossiles récupérés dans la Grotte d'Ankilitelo dans le Sud-ouest de Madagascar sont présentées ici. Parmi les 560 éléments et plus récupérés, 29 taxa différentes ont été identifiées dont la majorité sont des espèces qui se trouvent encore dans cette région de l'île. Des restes de coquilles d'œuf de l'oiseau-éléphant éteint (famille des Aepyornithidae) et affecté à *Aepyornis* sp. ont été trouvés sur le site. Par ailleurs, deux taxa actuels, *Scopus umbretta* et *Monias benschi*, ont été identifiés mais ne se rencontrent plus à proximité de la grotte. Sur la base des mesures disponibles de radiocarbone de fossiles d'oiseaux récupérés dans la grotte, le matériel le plus ancien est daté à 11 310 ± 40 ^{14}C BP et le plus récent à l'époque moderne. Par conséquent, les changements écologiques présumés, ayant entraîné la disparition ou la restriction de la zone de répartition de ces trois taxons, ont eu lieu dans l'histoire récente. Ces changements sont probablement associés à perturbations climatiques naturelles et aux pressions humaines ultérieures. Des informations sont aussi présentées sur l'origine de la pintade (*Numida*) et l'inférence sur la période de la colonisation de *Corvus albus* à Madagascar.

Introduction

There is good evidence to suggest that since the start of the Holocene some rather dramatic environmental changes have taken place on Madagascar (Burney *et al*. 2004). These vicissitudes have had considerable impact on the

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native and highly endemic vertebrate fauna of the island and resulted in notable levels of extinction or local extirpation (Goodman & Jungers in press). Non-permineralized bones excavated from different paleontological and archeological sites on the island have provided important data to interpret these changes.

The causes of these modifications can be divided into two separate factors. Firstly, those associated with natural climatic change and correlated with drier meteorological conditions, which in turn impacted natural ecosystems and their component species (Goodman & Rakotozafy 1997; Gasse & van Campo 2001; Virah-Sawmy *et al*. 2010). Little is known about the paleoecology of southwestern Madagascar prior to the Late Holocene (Burney *et al*. 2004), at which time aridification is well documented, with desiccation starting ca. 4000 Cal BP and peaking ca. 1000 Cal BP (Burney 1993; Goodman & Rakotozafy 1997; Virah-Sawmy *et al*. 2010). Given modern biotic clines across southern Madagascar, with increasing aridity towards the west, Quaternary climate shifts likely had significant impacts on the composition and evolutionary history of the regional biota. Secondly, those modifications that directly relate to human-induced environmental degradation, include hunting and the clearing of natural habitats (Burney *et al*. 2003; Perez *et al*. 2005; Dewar *et al*. 2013; Goodman & Jungers in press). Human arrival to Madagascar has been extended to approximately 4000 Cal BP (Dewar *et al*. 2013). The earliest evidence of butchery of extinct animals comes from the southwest at approximately 2300 Cal BP (MacPhee & Burney 1991; Perez *et al*. 2005). However, at several sites there is mounting evidence that synergistic combinations of these two factors came into play (Burney *et al*. 2004, Goodman & Jungers in press).

While a considerable literature exists on lemur fossil remains to infer the impact of these changes on the extinct and extant primate communities of Madagascar (e.g., Jungers *et al*. 2002; Godfrey & Irwin 2007; Godfrey *et al*. 2010; Gommery & Ramanivosoa 2011), less attention has been given to fossil material of other land vertebrates, such as birds (Burney *et al*. 1997; Goodman & Rakotozafy 1997; Goodman 1999; Mlíkovský 2006). Based on the uniqueness of the island's avifauna, of which about half of the 208 nesting species are endemic, birds are likely a useful group to study in juxtaposition the impacts of natural climatic vs. anthropogenic factors on extinctions or shifts in the distributions of extant species. The purpose of this paper is to report on bird fossils recovered from the base of a deep shaft entrance to a cave in the southwest of Madagascar and, based on the species represented, infer aspects of possible habitat shifts and distributional changes in very recent geological time.

Material and methods

Site description. During the southern winters of 1994, 1997-99, and 2003, Elwyn Simons (Duke University) and colleagues, including those from the Université d'Antananarivo, conducted excavations at a pitfall cave to the northeast of Toliara, southwestern Madagascar, known as Ankilitelo Cave (Simons 1997; Simons *et al*. 2004). The site, located at 22°54.8199'S, 43°52.6109'E and 550 m elevation, occurs on the Mikoboka Plateau, composed of Eocene limestone, and in close proximity to the village of Manamby (Fig. 1). The only known entrance into the cave is a relatively narrow vertical shaft, 10 m in diameter and 145 m deep (Simons *et al*. 2004; Muldoon *et al*. 2009). The shaft and cavern of Ankilitelo formed underground as the limestone of the Mikoboka Plateau dissolved through the action of surface water. As the cave grew, the roof of the shaft became unstable and collapsed, forming a rather vertical shaft open at ground level (Muldoon *et al*. 2009). The bottom of the shaft opens into a large room with a sloping floor, which continues to the known end of the cave, approximately 230 m vertical distance below the entrance. At the base of the shaft and in lower areas of the cave, considerable quantities of terrestrial animal bones were found. To date, work has been published on the primate and non-primate mammal fossil remains and associated inferences of ecological reconstruction (Muldoon *et al*. 2009; Muldoon 2010).

The southwestern portion of Madagascar, specifically in the general area of the cave, has an annual rainfall of about 350 mm per year (Toliara) and a very pronounced dry season that can last up to 10 months (Donque 1975). There is a notable evapotranspiration deficit in this area, producing distinctive bioclimatic conditions (Cornet 1974). By consequence, the native flora is composed of highly adapted xerophytic plants, with a high-level of endemism (Phillipson 1996).

The majority of the nearly 5000 fossils collected at Ankilitelo Cave are from a large concentration of bones from an assortment of vertebrates, found at the bottom of the entrance shaft; much of the material is well preserved. The entrance to Ankilitelo is on a raised plateau, distant from any watercourse, suggesting that transportation of material from run-off discharge into the mouth of the cave is unlikely. The cave entrance probably acted as a natural pitfall trap, with terrestrial animals tumbling from the ground surface into the shaft and dying upon impact. For volant birds, the narrowness and depth of the shaft probably acted as a terminal trap, particularly for more heavy-bodied species. Ledges and crevices in the shaft walls served as nesting and roosting sites for different birds, including raptors that would have dropped mishandled prey remains or regurgitated pellets, forming a portion of the recovered bone material.

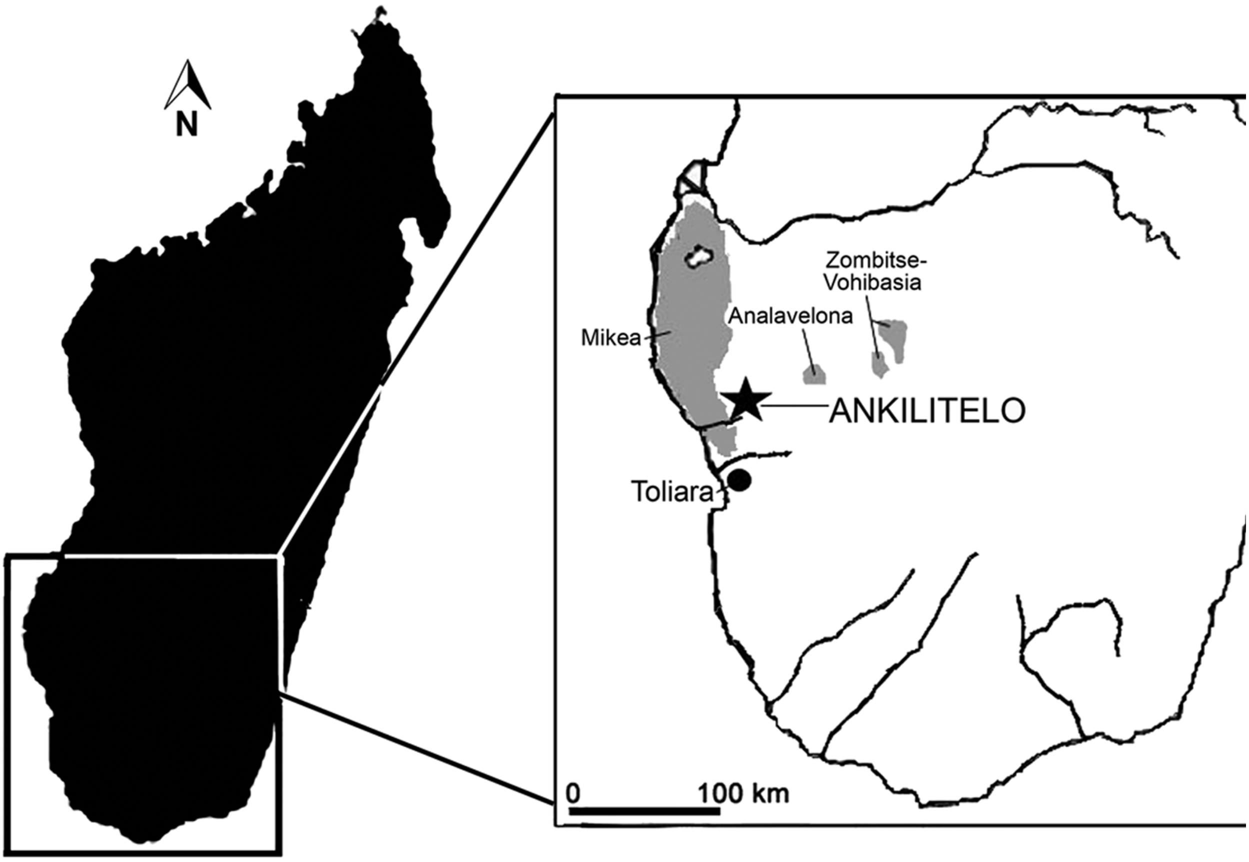

FIGURE 1. Map of southwestern Madagascar, including the location of Ankilitelo Cave and other sites mentioned in the text.

Site collection. Pitfall caves, such as Ankilitelo, pose considerable problems for fossil collection because of technical difficulties and physical rigor of access, which can only be accomplished by experienced cavers. Excavation at Ankilitelo involved daily controlled rope descents/ascents through the opening shaft by a group of specialized field collectors. In the later seasons of fieldwork, specimen collection at the site involved controlled sampling from the surface cortex of the conical talus deposit at the base of the vertical entrance and fossils were collected according to a series of areal zones on the talus cone surface. Stratigraphic investigations of the soil at stratigraphic depth into the talus cone did not reveal any bone material.

Individual specimens or associated remains received a field number in the format: year collected - "M" for Madagascar - and chronological number of specimen identified for the season. In most cases, non-associated material received a common field number based on their close proximity. As part of a research accord between the Duke University Lemur Center Division of Fossil Primates (DLC) and the Département de Paléontologie et Anthropologie Biologique, Université d'Antananarivo (DPAB), the fossil collections from Ankilitelo was divided between these institutions. The material described herein (Appendix 1) was transferred to Duke University where it was accessioned and catalogued. Not all of the Ankilitelo Cave material sent to DLC has been sorted (G. Gunnell pers. comm.)

Dating. Previously published radiocarbon dates based on bone remains from Ankilitelo Cave within the range of 630–510 ^{14}C yr BP (585–475 Cal BP) (Simons 1997; Muldoon *et al*. 2009; Crowley 2010; Muldoon 2010; Table 1). While this period is notably after human colonization of the island, which is now thought to have taken place over 4000 years BP (Dewar *et al*. 2013), there is no evidence that people were directly associated with the deposition of the Ankilitelo fossils. Herein we report on notably older dates from the cave based on bird bone and eggshell fossil remains (Table 1).

TABLE 1. Radiocarbon dates from Ankilitelo Cave based on standard AMS dating techniques. Insufficient material was obtained from one cf. *Aepyornis* eggshell (DLC 18878) for accurate radiocarbon dating.

Genus and species	Material	^{14}C BP	± 1σ	2σ calibrated age	Calibration curve	^{14}C lab number	Source
Megaladapis edwardsi	bone	630	50	520–650	SHCal04	not given	Simons (1997)
Palaeopropithecus ingens	bone	510	80	320–630	SHCal04	not given	Simons (1997)
Cryptoprocta sp.[1]	bone	560	40	500–620	SHCal04	Beta-201844	Muldoon *et al*. (2009)
Numida meleagris (DLC 18875)	bone (collagen)	8970	40	10230–9940	IntCal04	Beta-355565	This study
Numida meleagris (DLC 18875)	bone (collagen)	11310	40	13270–13130	IntCal04	Beta-355564	This study
Numida meleagris (DLC 18157)	bone (collagen)	290	30	450–290	IntCal04	Beta-355563	This study
Corvus albus (DLC 17265)	bone (collagen)	8420	40	9520–9330	IntCal04	Beta-355562	This study
cf. *Aepyornis* (DLC 18916)	eggshell (organics)	11220	50	13210–13080	IntCal04	Beta-355561	This study
cf. *Aepyornis* (DLC 18082)	eggshell (organics)	6150	40	7160–6940	IntCal04	Beta-355559	This study

[1] Note that Beta-201844 was erroneously attributed to *Lemur catta* in Crowley (2010).

Comparisons and counts. The Ankilitelo bird fossils were sent on loan from the DLC to The Field Museum of Natural History, which has an extensive skeletal collection of extant Malagasy birds. The remains were identified to the most precise taxonomic level possible. Paired osteological elements of any taxon recovered with the same field catalog number were separated and the largest number of elements from either the left or right side was considered the minimum number of individuals (MNI). Based on the DLC catalog numbers, we also counted the unique number of elements (NE). As mentioned above, no clear stratigraphic information is available on the excavated bird remains, however, given that most are from surface deposits, precise information on the position of the different remains is not critical for the analyses presented herein.

Results

Faunistics. We identified 29 taxa of birds from Ankilitelo Cave, including at least 25 different species, based on approximately 570 different fossil elements (Table 2, Appendix 1); a few taxa without definitive identifications are not included in this species total (cf. *Anhinga melanogaster*, cf. *Milvus aegyptiacus*, cf. *Streptopelia picturata*). The collection is dominated by remains of the Greater Vasa Parrot, *Coracopsis vasa*, whether measured by MNI (n = 100, 50% of the collection) or NE (n = 362, 64% of the collection). Across portions of Madagascar, this species occurs in sympatry with the Lesser Vasa Parrot, *C. nigra*; these two parrot species are distinguishable based on external (Perrin 2013) and skeletal measurements (Table 3). *Coracopsis vasa* is the only member of this genus identified from the cave, although *C. nigra* is known today from the immediate area (Goodman and Raherilalao 2013). The absence of *C. nigra* in the bone remains can be explained by it being tree-cavity dwelling (Goodman & Raherilalao unpub. data), while *C. vasa* often perches and nests on cliffs and rock ledges, including caves such as Ankilitelo.

TABLE 2. Listing of different bird taxa identified from Ankilitelo Cave, including minimum number of individuals (MNI) and number of elements (NE) represented within the DPC and field catalog groupings. All identifications are based on bone remains, with the exception of aepyornithid eggshells, for which MNI and NE was not determined. Scientific names preceded by asterisk represent endemics to Madagascar and those with † are extinct. The habitat types used by each species presented in parentheses are denoted as FD = forest dwelling and NFD = non-forest dwelling. The habitat utilization classification is after Goodman & Raherilalao (2013).

	MNI	NE
†Order Aepyornithiformes		
Family Aepyornithidae		
cf. *Aepyornis* sp. eggshells	-	-
Order Suliformes		
Family Anhingidae		
cf. *Anhinga melanogaster* (NFD)	1	1
Order Ciconiiformes		
Family Scopidae		
Scopus umbretta (NFD)	1	1
Family Threskiornithidae		
**Lophotibis cristata* (FD)	2	3
Order Falconiformes		
Family Accipitridae		
**Accipiter madagascariensis* (FD)	1	1
**Buteo brachypterus* (FD)	3	4
cf. *Milvus aegyptius* (NFD)	1	1
Order Galliformes		
Family Numididae		
Numida meleagris (NFD)	2	3
Order Gruiformes		
Family Mesitornithidae		
**Monias benschi* (FD)	1	1
Order Charadriiformes		
Family Turnicidae		
**Turnix nigricollis* (NFD)	9	15
Order Columbiformes		
Family Pteroclididae		
**Pterocles personatus* (NFD)	5	16
Family Columbidae		
Oena capensis (NFD)	1	1
Treron australis (FD)	2	2
cf. *Streptopelia picturata* (FD)	1	1
Order Psittaciformes		
Family Psittacidae		
Coracopsis vasa (FD)	100	362
Coracopsis cf. *vasa*	3	5
Order Cuculiformes		
Family Cuculidae		
**Coua cristata* (FD)	1	1
**Coua* cf. *cristata*	2	2
**Coua cursor* (FD)	1	1

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TABLE 2. (Continued)

	MNI	NE
**Coua gigas* (FD)	5	8
**Coua* cf. *gigas*	1	1
**Coua ruficeps* (FD)	3	3
Order Strigiformes		
Family Tytonidae		
Tyto alba (NFD)	29	43
cf. *Tyto alba*	4	9
Family Strigidae		
**Asio madagascariensis* (FD)	8	12
cf. **Asio madagascariensis*	1	1
**Otus rutilus* (FD)	3	3
**Ninox superciliaris* (FD)	1	1
cf. **Ninox superciliaris*	1	1
Order Coraciiformes		
Family Coraciidae		
Eurystomus glaucurus (NFD)	1	1
Family Leptosomidae		
**Leptosomus discolor* (FD)	1	1
Family Upupidae		
**Upupa marginata* (FD)	4	4
Order Passeriformes		
Family Hirundinidae		
Phedina borbonica (NFD)	1	1
Family Corvidae		
Corvus albus (NFD)	1	1
Family Ploceidae		
Ploceus sakalava (NFD)	1	1
Unidentified bird bones	57	
Study totals	202	569

After parrots, the best-represented group of birds in the fossil remains are raptors (hawks and owls), which represent 25% of the MNI and 14% of the NE. The second most commonly represented species is the Barn Owl, *Tyto alba*, with a MNI = 29 (14%) and NE = 43 (8%). This species occurs today in southwestern Madagascar, and can be found nesting on rock ledges and in cave crevices (Goodman & Raherilalao unpub. data). Hence, in parallel to *C. vasa*, aspects of the natural history of this owl can explain why its remains are common amongst the Ankilitelo fossils. Further, a considerable number of incompletely ossified bone remains of these two taxa are represented in the Ankilitelo remains, further supporting their nesting in and around the upper portions of the vertical shaft. A considerable number of small mammal bones were found in the Ankilitelo deposits (Muldoon *et al*. 2009) and, in part, probably represent raptor food remains.

Eggshell remains allocated to the Family Aepyornithidae represent the only extinct form recovered from the Ankilitelo Cave bird fossils. On the basis of visually estimated thickness and the inferred curvature of the eggshells, we allocate these remains to the genus *Aepyornis*. Using Brodkorb's (1963) summary of elephant bird taxonomy and distribution of fossil remains, the large *Aepyornis* reported from the southwestern region of the island is *A. maximus*; hence, the eggshells reported herein may be referable to that species. However, elephant bird taxonomy is in a state of disorder, with holotypes of numerous taxa based on isolated osteological elements or eggshell remains (some having been destroyed) and with limited morphological means to assess correctly possible synonymies. To date, molecular tools have not been successful in isolating high-quality DNA from elephant bird remains (Cooper *et al*. 2001). When such information is available, combined with morphological characters, important questions can be addressed such as the number of species that existed, as has been resolved for New Zealand moas (Order Dinornithiformes) (e.g. Allentoft *et al*. 2010; Oskam *et al.*, 2010).

TABLE 3. Comparison of different bone measurements between *Coracopsis vasa* and *C. nigra*. Measurement acronyms include: TL—total length, PW—proximal width, DW—distal width.

Species	Humerus TL	Humerus PW	Humerus DW	Ulna TL	Femur TL	Femur PW	Femur DW
C. nigra	53.4 ± 1.02, 52.2–54.7, n=4	13.1 ± 0.63, 12.3–13.9, n=5	10.9 ± 0.36, 10.4– 11.4, n=5	63.2 ± 1.29, 62.0–64.8, n=5	39.6 ± 0.85, 38.7–40.4, n=5	8.0 ± 0.34, 7.6–8.5, n=5	8.1 ± 0.38, 7.6–8.4, n=5
C. vasa	64.9 ± 3.11, 61.2–67.6, n=4	17.7 ± 0.44, 17.1–18.1, n=4	13.6 ± 0.54, 12.9–14.1, n=4	79.2 ± 1.80, 77.2–81.3, n=4	47.6 ± 2.27, 45.1–50.4, n=4	10.2 ± 0.19, 9.9–10.3, n=4	10.1 ± 0.48, 9.4–10.5, n=4

TABLE 3. (Continued)

Tibiotarsus TL	Tibiotarsus PW	Tibiotarsus DW	Tarsometatarsus TL	Tarsometatarsus PW	Tarsometatarsus DW	Carpometacarpus TL
57.8 ± 1.72, 55.9–59.7, n=4	6.3 ± 0.15, 6.1–6.4, n=4	6.7 ± 0.22, 6.4–7.0, n=5	22.4 ± 1.28, 21.1–23.9, n=5	7.5 ± 0.31, 7.3–8.0, n=5	9.0 ± 0.32, 8.5–9.3, n=5	38.8 ± 1.09, 37.2–39.9, n=5
71.4 ± 2.10, 69.0–74.1, n=4	8.2 ± 0.15, 8.0–8.3, n=3	8.4 ± 0.24, 8.2–8.7, n=4	27.6 ± 0.68, 27.0–28.5, n=4	9.6 ± 0.48, 9.2–10.3, n=4	11.8 ± 0.29, 11.4–12.1, n=4	49.6 ± 1.30, 47.9–51.0, n=4

Within the fossil bird remains, two species were identified that no longer occur in the immediate vicinity of the cave (Table 4). The first is the Subdesert Mesite, *Monias benschi*, which today is restricted to a narrow zone in the southwestern coastal area, up to 60 km inland and 200 m in elevation, with an extent of occurrence estimated to be less than 4,200 km² (Seddon & Tobias 2013; Goodman & Raherilalao 2013). The presence of this strictly forest-dwelling species at Ankilitelo Cave indicates that its distribution in recent times extended about 20 km further to the east and several hundred meters higher in elevation. Mesites belong to an endemic family and this species is considerable Vulnerable by the IUCN (2012). In addition, remains of the Hamerkop, *Scopus umbretta*, were identified from the cave. This tree-nesting species is mainly distributed today in more mesic areas of the island, notably in the Central Highlands and other areas to the east (Langrand 1990).

Another species of note is the Madagascar Forest Ibis, *Lophotibis cristata*, which still occurs in the immediate region of the cave, most notably in large tracts of forest, such as those towards the summital zone on the Analavelona Massif (1350 m) (Fig. 1), which contains distinctly more mesic forests than surrounding areas in southwestern Madagascar. At least four species of coua, *Coua* spp., were identified from the fossil remains in the cave, all of which are known to occur today in the regional forests (Table 4) and indicates stability in recent geological time in aspects of the local bird community composition. At least two large-bodied species of *Coua* have gone extinct in western Madagascar in the past two millennia (Goodman & Rakotozafy 1997), but these taxa were not represented among the Ankilitelo fossils.

With the exceptions noted above, all of the species identified from the fossils still occur in areas of southwestern Madagascar and more specifically in the general vicinity of Ankilitelo Cave; some of these are strictly forest dwelling and others are not (Table 4). Given that little forest remains today in the immediate vicinity of Ankilitelo Cave, we chose three sites, all subjects of recent ornithological inventories, in order to make faunistic comparisons between the modern regional forest dwelling avifauna and that represented by the fossil remains (vegetation classification is after Moat & Smith 2007): Analavelona Massif – a notably remote orographic "mist-oasis", probably a vestige of former Pleistocene habitats in this portion of the island (Goodman & Jungers in press), and about 45 km to the northeast of the cave; Mikea Forest – a transitional western dry deciduous-spiny forest-thicket forest about 50 km west of the cave; and Zombitse-Vohibasia Forest – a sub-humid formation to the east of the Mikoboka Plateau, about 70 km from the cave, and with floristic remnants characteristic of more humid forests to the east (Table 4).

TABLE 4. Comparisons of the regional modern avifauna at three sites in southwestern Madagascar to that of Ankilitelo Cave based on presence-absence data. Species names in **bold** are of forest-dwelling species and those preceded by an asterisk identified in the cave remains. Sites and sources of information for modern inventory data include: Analavelona (Raherilalao & Goodman unpublished data), Zombitse-Vohibasia (Langrand & Goodman 1997), and Mikea (Raherilalao *et al*. 2004). Forest types after Moat & Smith (2007).

Forest type	Analavelona Western humid forest	Zombitse-Vohibasia Sub-humid forest	Mikea Transitional western dry-deciduous spiny forest-thicket
Species			
***Lophotibis cristata**	+	+	+
Aviceda madagascariensis	-	+	-
Circus marcoceles	-	+	-
**Milvus aegyptius*	+	+	+
Polyboroides radiatus	+	+	+
Accipiter francesii	-	+	+
Accipiter henstii	+	+	-
***Accipiter madagascariensis**	+	+	+
***Buteo brachypterus**	+	+	+
Falco eleonorae	-	-	+
Falco newtoni	+	+	+
Falco concolor	-	+	+
Falco zoniventris	-	+	-
Margaroperdix madagarensis	+	+	-
Coturnix delegorguei	-	+	-
***Numida meleagris**	+	+	+
***Monias benschi**	-	-	+
**Turnix nigricollis*	-	+	+
**Pterocles personatus*	+	+	+
Sarothrura insularis	+	-	-
***Streptopelia picturata**	+	+	+
**Oena capensis*	+	+	+
***Treron australis**	+	+	+
***Coracopsis nigra**	-	+	+
***Coracopsis vasa**	+	+	+
Agapornis cana	+	+	+
Cuculus rochii	+	+	+
***Coua gigas**	+	+	+
***Coua cristata**	+	+	+
Coua coquereli	-	+	+
***Coua cursor**	-	-	+
***Coua ruficeps**	-	+	+
Centropus toulou	+	+	+
**Tyto alba*	-	+	-
***Otus rutilus**	+	+	+
***Ninox superciliaris**	+	+	+
***Asio madagascariensis**	+	+	+
Caprimulgus madagascariensis	-	+	+
Zoonavena grandidieri	-	+	-
Cypsiurus parvus	-	+	+
Apus melba	+	+	-
Apus balstoni	+	+	+
Alcedo vintsioides	-	+	-
Corythornis madagascariensis	+	+	-
Merops superciliosus	+	+	+

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TABLE 4. (Continued)

Forest type	Analavelona Western humid forest	Zombitse-Vohibasia Sub-humid forest	Mikea Transitional western dry-deciduous spiny for
Eurystomus glaucurus	+	+	+
Uratelornis chimaera	-	-	+
****Leptosomus discolor***	+	+	+
**Upupa marginata*	+	+	+
Mirafra hova	+	+	+
**Phedina borbonica*	-	+	-
Motacilla flaviventris	+	+	-
Coracina cinerea	+	+	+
Bernieria madagascariensis	+	+	+
Xanthomixis zosterops	+	-	-
Xanthomixis apperti	+	+	-
Thamnornis chloropetoides	-	+	+
Cryptosylvicola randrianasoloi	+	-	-
Hypsipetes madagascariensis	+	+	+
Copsychus albospecularis	+	+	+
Saxicola torquata	+	+	-
Monticola sharpei	+	-	-
Nesillas lantzii	+	+	+
Cisticola cherina	-	+	-
Neomixis tenella	+	+	+
Neomixis striatigula	+	+	+
Terpsiphone mutata	+	+	+
Nectarinia notata	+	+	+
Nectarinia souimanga	+	+	+
Zosterops maderaspatana	+	+	-
Artamella viridis	-	+	+
Calicalicus madagascariensis	+	+	+
Schetba rufa	+	+	+
Vanga curvirostris	+	+	+
Xenopirostris xenopirostris	-	-	+
Falculea palliata	-	+	+
Leptopterus chabert	-	+	+
Cyanolanius madagascariensis	-	+	-
Tylas eduardi	+	-	+
Newtonia archboldi	-	-	+
Newtonia brunneicauda	+	+	+
Dicrurus forficatus	+	+	+
Acridotheres tristis	+	+	-
**Corvus albus*	+	+	+
Hartlaubius auratus	-	+	-
Ploceus sakalava	-	+	+
Foudia madagascariensis	+	+	+
Lonchura nana	+	+	-

Dating. Seven bird fossils were submitted for radiocarbon dating to the Beta Analytic Laboratory, four bone samples and three eggshell samples, of which all with the exception of one of the eggshell fragments yielded dates (Table 1). These six dates covered a period from 11,310 ± 50 ^{14}C yr BP to 60 ± 30 ^{14}C yr BP (13,270 Cal yr BP to 450 Cal yr BP); hence, encompassing the period before human colonization of the island until the modern era. Amongst the analyzed remains are two specimens of elephant bird eggshells, which provided dates of 11,220 ± 50 ^{14}C yr BP (13,210 – 13,080 Cal yr BP) and 6150 ± 40 ^{14}C yr BP (7160 – 6940 Cal yr BP). Recent research on such material excavated from coastal and near-coastal sites in southwestern Madagascar indicates an important discordance between radiocarbon dates derived from elephant bird eggshells and wood remains in the same stratigraphic deposits (Parker Pearson *et al*. 2010). The averaged discrepancy between dates for eight paired samples (eggshell-wood remains) fell between 185 and 1190 years older for the eggshells. A correction factor of 740 ± 125 years has been proposed to equalize these differences (Parker Pearson *et al*. 2010). If the same artifact applies to more inland sites, such as the area surrounding Ankilitelo Cave, the two eggshell dates we report here should be corrected to approximately 10,570 BP and 5410 BP.

Discussion

With few exceptions, the bird species identified from the Ankilitelo fossils represent taxa that still occur in the general area of the cave, specifically at nearby sites that have notably different vegetation types (Table 4). Amongst the 25 extant species identified from the remains, 10 are forest dwelling and 15 are non-forest dwelling (Table 2). Two points are important to underline:

1) Given the avifauna composition and associated habitat signal based on the extant taxa, it can be inferred that the habitat that occurred in the vicinity of the cave during the past 11,000 years (see below) was a succession of forest and more open habitats; the latter perhaps best associated with wooded grassland showing structural parallels to Miombo woodlands in the southern portion of Africa (Goodman & Jungers in press). Given the presence of taxa such as *Monias benschi* and *Coua cursor*, characteristic species of southwestern spiny forest-thicket, elements of this vegetational type also occurred in close proximity to the cave. Excluding these two exceptions, the majority of other extant forest-dwelling species identified from the remains are habitat generalists. Hence, the assemblage of birds, as well as a wide assortment of terrestrial and arboreal fossil mammals known from the site (Muldoon & Simons 2007; Muldoon *et al*. 2009; Muldoon 2010), would have utilized a variety of locally occurring habitats. Due to our scale of analysis, this reconstruction is likely overly simplistic, as it does not take into account any anthropogenic impacts on the local vegetation of the past few centuries, a period when at least a portion of the bone remains were deposited, such as probable opening up of the forest and associated colonization of non-forest dwelling species.

2) The level of extinction or major distributional shifts amongst the species represented in the Ankilitelo fossil avifauna is minor as compared to the terrestrial mammal fauna, which included five species of extinct lemur, all larger than any living species (Muldoon 2010). The only extinct bird identified from the cave is the aepyornithid elephant bird. Two other taxa (*Monias benschi* and *Scopus umbretta*) show some range shifts. Hence, based on the collections studied herein, it can be surmised that birds were relatively less impacted by local ecological and habitat vicissitudes than terrestrial mammals, at least in the general region surrounding the cave. The fact that the extant regional birds occur in a considerable variety of forest types (Table 4) is indicative of non-specialized aspects of their life-history strategies and their capacity to adapt to different ecological conditions.

Of the nearly 570 bird fossils from Ankilitelo Cave, 29 different taxa including minimally 25 species were identified. With the exception of three of these taxa, one being extinct, all occur today in the immediate region of the cave. Hence, the fossil and modern fauna show less than a 10% turnover in species representation. In contrast, amongst the terrestrial mammals and bats, 32 native species were identified from the cave remains (Muldoon *et al*. 2009). To place this in perspective, in the nearby Zombitse-Vohibasia forests, 24 species of native mammals have been documented during surveys (Goodman & Rasoloarison 1997; Goodman *et al*. 1997). Hence, the level of species turnover between the fossil and modern faunas is substantially higher for mammals than for birds. This is presumably associated with considerable specialization of certain extinct mammal taxa.

One of the intriguing aspects of the avian remains recovered from Ankilitelo Cave is the presence of elephant bird eggshells at the base of the vertical entrance. Two possibilities can be suggested: 1) females with shelled eggs in their oviduct fell into the cave; however, no elephant bird osteological remains were amongst the fossils we studied from the cave, or 2) elephant birds formerly nested in close proximity to the cave rim and the eggs either accidentally rolled into the cave or were pushed or carried over the edge by predators or flash floods. Given the early date of these remains, many millennia before the initial human colonization of the island, people cannot be implicated in their deposition.

Amongst the bird species identified among the Ankilitelo Cave fossils are two species that also occur on mainland Africa, *Numida meleagris* and *Corvus albus*. For the former, it has been suggested to have been introduced to Madagascar, perhaps from Mozambique (Benson 1984; Langrand 1990; Safford 2013) – this continental zone and Madagascar share the same subspecies, *N. m. mitrata*. Hitherto, the earliest evidence of guinea fowl on Madagascar is archeological remains recovered in the northwest and dated to the 11th to 14th-centuries (Rakotozafy 1996) and the southwest from the 13th to 15th-centuries (Rakotozafy & Goodman 2005). The *Numida* radiocarbon dates presented herein from Ankilitelo Cave from over 11,000 BP clearly indicate that wild populations of this species naturally colonized the island as they long predate the earliest evidence for humans. Given that the Malagasy vernacular name for this bird (*akanga*) has a distinct Bantu root, it can be assumed that domestic varieties were subsequently carried to the island, with individuals going feral and perhaps interbreeding with natural populations. Excluding this etymological aspect, it is also possible that natural populations of *Numida* were domesticated on Madagascar. Both morphological and molecular genetic comparisons need to be made between the older Ankilitelo material of this taxon and modern specimens to better understand the history of the domestic strains occurring on Madagascar.

The other species of interest in this regards is *Corvus albus*, which shows no clear morphological difference between African and Malagasy populations. The radiocarbon dates presented herein from Ankilitelo Cave (8420 ± 40 ^{14}C yr BP) indicates that this species has been present on Madagascar since the early portion of the Holocene and its local colonization was not associated, for example, as a ship stow-away, as known for other corvids.

There is evidence, based on data from palynological analyses and excavated bones, that southwestern Madagascar underwent a period of drastic aridification between 5,000-2,500 years BP, which resulted in notable vegetational shifts and the disappearance of animals relying on permanent freshwater ecosystems (Burney 1993, 1997; Goodman & Rakotozafy 1997). Previously reported radiocarbon dates from Ankilitelo were notably recent, the oldest being less than 630 ± 50 yr ^{14}C BP (Table 1). Hence, it was presumed that the collapse of the cave shaft roof was very recent and the faunal remains deposited during a very narrow temporal window. However, based on several of the dates reported herein, this was not the case and material was deposited over an interval of at least 11,000 years, spanning periods before and after human colonization of the island. Interestingly, a number of large-bodied and now extinct lemur species are represented in the Ankilitelo deposits and, based on radiocarbon dates (Table 1), they were able to persist for at least two millennia after pronounced regional natural climatic shifts (Simons 1997; Muldoon 2010). A study conducted on the small-bodied primates recovered from Ankilitelo and still occurring in the region, indicates that, in general, these primates fit an ecoregional model of size variation, whereby remains of species recovered from the cave are comparable in size to living forms inhabiting zones near the cave today (Muldoon & Simons 2007). Because highly seasonal environments may produce strong selective pressures for smaller adult body size, given that the dry season in most forests in Madagascar is characterized by low availability of high protein foods, this suggests that Malagasy primates have been subjected to similar patterns of resource seasonality for at least 500 years.

The human element is critical to piece together what was happening in the area about 650 years BP, the period of radiocarbon dates of extinct primates recovered from Ankilitelo Cave. On the basis of the archeological record, two settlement sites are known from the general area, Rezoky and Asambalahy, the former about 115 km northeast of the cave and dating from the 12th to 15th-centuries (Vérin 1971; Dewar & Wright 1993). Some of the first dog remains known from the island were recovered from these two sites, and these animals may have been trained to hunt wild game. Hence, it is not a coincidence that in the midden remains from these villages are bones of native animals, including extant lemurs and extinct dwarf hippos (Rakotozafy & Goodman 2005). While the ancient inhabitants of Rezoky and Asambalahy were out of immediate striking distance from the Ankilitelo Cave region, other villages, yet unknown to archeologists, may have occurred in closer proximity. Associated with expanding agriculture and cattle breeding, the period starting in about the 12th-century would have seen the commencement of habitat degradation, specifically clearing of forest or wooded savannas, as well as the imposition of other anthropogenic pressures on natural ecosystems. Given the gradual decline of populations of extinct fossil animals (Crowley 2010), and human implications for hunting and habitat degradation (Burney *et al*. 2004), the synergistic combination of natural climatic and human-induced factors is the best explanation for the changes that have taken place in the area surrounding Ankilitelo Cave.

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APPENDIX 1. Listing of bird fossils studied from Ankilitelo Cave and separated by year of field excavations. See Methods section for description of catalog system. In parentheses after each taxon is presented MNI/NE.

1994 excavations

94M-136 (DLC 13686) *Coracopsis vasa* (1/3); 94M-228 (DLC 13732) *C. vasa* (1/4); 94M-228 (DLC 13732) unidentified bird (0/2); 94M-292 (DLC 13764) *C. vasa* (1/1), (DLC 1376) *Lophotibis cristata* (1/2).

1997 excavations

97M-118 (DLC 17208) *Coracopsis vasa* (1/3), radius fractured and healing; 97M-124 (DLC 17211) *C. vasa* (1/9); 97M-134 (DLC 17216) cf. *Tyto alba* (2/5), *T. alba* (1/1), *C. vasa* (2/5), 1 adult and 1 subadult; 97M-194 (DLC 17246) *Buteo brachypterus* (1/1), cf. *T. alba* (1/1), *C. vasa* (1/2); 97M-212 (DLC 17255) *C. vasa* (3/8), cf. young *Tyto* or *Asio madagascariensis* (1/5), unidentified bird (0/1); 97M-232 (DLC 17265) cf. *Milvus aegyptius* (1/1), cf. *T. alba* subadult (1/3), *T. alba* (1/2), *Corvus albus* [radiocarbon dated] (1/1); 97M-238 (DLC 17268) cf. *Coracopsis vasa* (1/3), *C. vasa* (4/8), *Coua ruficeps* (1/1), *Turnix nigricollis* (1/1), *Tyto alba* (2/2); 97M-246 (DLC 17272) *Coracopsis vasa* (2/3), *T. alba* (1/1); 97M-268 (DLC 17283) *Monias benschi* (1/1), *A. madagascariensis* (1/1), *C. vasa* (3/5); 97M-296 (DLC 17297) *C. vasa* (1/1); 97M-298 (DLC 17298) *C. vasa* (1/4), *Treron australis* (1/1), *Turnix nigricollis* (1/3), *Tyto alba* (1/1), unidentified bird (1/1); 97M-302 (DLC 17300) *Asio madagascariensis* (1/2), *C. vasa* (3/8), *Scopus umbretta* (1/1), *Tyto alba,* subadult (1/1), unidentified nestling raptor (1/1); 97M-43 (DLC 17170) *Asio madagascariensis* (1/1), *C. vasa* (1/1), unidentified bird (0/1); 97M-76 (DLC 17187D) *T. alba* (1/1); 97M-80 (DLC 17189) *Lophotibis cristata* (1/1), *Turnix nigricollis* (1/3), *Treron australis* (1/1), *C. vasa* (3/14), *Tyto alba* (2/4), unidentified bird (0/3).

1998 excavations

98M-1 (DLC 18041) *Coua gigas* (1/1), *Coracopsis vasa* (3/18); 98M-5 (DLC 18043) *Asio madagascariensis* (1/1), *C. vasa*, includes distal tibiotarsus notably larger than typical for this species (4/13); 98M-115 (DLC 18098) *Turnix nigricollis* (1/1), *Pterocles personatus* (1/2), *Coua cristata* (1/1), *C. gigas* (1/1), *Coracopsis vasa* (4/17), unidentified bird (0/6); 98M-117 (DLC 18099) *P. personatus* (1/1), *C. vasa* (3/16), *Tyto alba* (2/2); 98M-119 (DLC 18100) *Asio madagascariensis* (1/3), *C. vasa* (1/5), unidentified bird (0/3) ; 98M-121 (DLC 18101) *P. personatus* (1/1), *C. vasa* (2/10); 98M-123 (DLC 18102) *C. vasa* including at least one subadult (2/11), *T. alba* including at least one subadult (2/3), unidentified young raptor (1/1), unidentified bird (0/5); 98M-125 (DLC 18103) *Accipiter madagascariensis* (1/1), *Buteo brachypterus* (1/1), *Turnix nigricollis* (1/1), *T. alba* at least one young (2/8), *Asio madagascariensis* (1/1), *Ninox superciliaris* (1/1), cf. *C. vasa* probably nestling (1/1), *C. vasa* (2/14), *Upupa marginata* (1/1), *Phedina borbonica* (1/1); 98M-129 (DLC 18105) *Oena capensis* (1/1), *C. vasa* (1/5), *T. alba* (1/1), unidentified bird (0/5); 98M-180 (DLC 18131) *Turnix nigricollis* (1/1), *Pterocles personatus* (1/1), *C. vasa* (2/10), unidentified bird (0/2); 98M-224 (DLC 18157) *T. nigricollis* (1/3), *Numida meleagris* [radiocarbon dated] (1/1), *Coua* cf. *cristata* (1/1), *Coracopsis vasa* (2/7), *Tyto alba* (1/3), unidentified bird (0/3); 98M-226 (DLC 18758) *T. alba* (1/1), *C. vasa* (1/20); 98M-260 (DLC 18775) *C. vasa* (1/2); 98M-270 (DLC 18780) *Coua gigas* (1/3), *Coracopsis vasa* (3/10); 98M-276 (DLC 18783) *Buteo brachypterus* (1/2); 98M-3 (DLC 18042) *C. vasa*, at least one subadult (4/9), *Otus rutilus* (1/1), *Leptosomus discolor* (1/1), unidentified bird (1/1); 98M-305 (DLC 18797) *Coua gigas* (1/2), *C.* cf. *gigas* (1/1), *C.* cf. *cristata* (1/1), *C. ruficeps* (1/1), *Coracopsis vasa* (3/19), unidentified bird (0/2)

1999 excavations

99M-46 (DLC 18888) *Asio madagascariensis* (1/2), *Coracopsis vasa* (2/3), unidentified bird (0/2); 99M-48 (DLC 18889) *C. vasa* (1/5); 99M-58 (DLC 18894) *C. vasa* (1/2), unidentified bird (0/3); 99M-60 (DLC 18895) cf. *Anhinga melanogaster*, young bird (1/1), *Turnix nigricollis* (1/1), *C. vasa* (2/5), unidentified bird (0/3); 99M-70 (DLC 18890) *C. vasa* (1/1), *Upupa marginata* (1/1); 99M-76 (DLC 18903) *C. vasa* (2/6); 99M-78 (DLC 18904) *C. vasa* (2/8); 99M-82 (DLC 18906) cf. *Streptopelia picturata* (1/1), *C. vasa* (1/1), *Tyto alba* (2/2), unidentified bird (0/2); 99M-88 (DLC 18909) *C. vasa* (1/1), *T. alba* (1/1), *Upupa marginata* (1/1), unidentified bird (0/1); 99M-113 (DLC 18921) *Turnix nigricollis* (1/1), *C. vasa* (1/1), cf. *C. vasa* (1/1), *Tyto alba*, at least one subadult (2/3), unidentified bird (0/1); 99M-151 (DLC 18940) *C. vasa* (2/7); 99M-153 (DLC 18941) *C. vasa* (2/5); 99M-155 (DLC 18942) *C. vasa* (3/7); 99M-157 (DLC 18943) *C. vasa* (2/10); 99M-159 (DLC 18944) *Pterocles personatus* (1/1), *C. vasa* (2/11), *T. alba* (1/1), unidentified bird (0/2); 99M-161 (DLC 18945) *C. vasa* (2/8), *Otus rutilus* (1/1); 99M-163 (DLC 18946) *C. vasa* (1/5), *T. alba* (1/1), cf. *Ninox superciliaris* (1/1), *Upupa marginata* (1/1), unidentified bird (0/3); 99M-207 (DLC 18968) *C. vasa* (1/1); 99M-207 (DLC 18875) *Numida meleagris* [two different bones radiocarbon dated] (1/2), *C. vasa* (1/1), unidentified bird (0/2); 99M-217 (DLC 18973) cf. *Asio madagascariensis*, subadult (1/1); *Otus rutilus* (1/1), *C. vasa* (2/8), unidentified bird (1/1); 99M-22 (DLC 18876) *Coua gigas* (1/1), *C. vasa* (1/1), *T. alba*, at least one nestling (2/3), *Eurystomus glaucurus* (1/1).