Subfossil birds from a submerged cave in southwestern Madagascar

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Abstract

The Mahafaly karst of southwestern Madagascar is rich with subfossil deposits. Vintany Cave (also known as Aven Cave), a submerged cave at Tsimanampesotse National Park, is the most subfossil-dense submerged cave known in the world. In particular, the cave has yielded abundant remains of birds, including some that are extinct. Among 1077 bird specimens recovered under water from the cave floor and from excavated sediments at this site, 35 different taxa were identified. Taxonomic attributions were made through comparative morphological analysis, using comparative osteological museum collections. The majority of these species still occur inside the park. Five extinct taxa were recovered from the cave, including one species of elephant bird (Aepyornithidae, *Mullerornis modestus*), two species of giant endemic ground couas (Cuculidae, *Coua* cf. *berthae* and *C.* cf. *primaeva*), a shelduck (*Alopochen sirabensis*, Anatidae), and a lapwing (Charadriidae, *Vanellus madagascariensis*). Two extant taxa, *Haliaeetus vociferoides* (Accipitridae) and *Threskiornis bernieri* (Threskiornithidae) are locally extirpated, but exist at other localities in Madagascar. Remains of Greater Vasa Parrots (Psittaculidae, *Coracopsis vasa*) are predominant. Some of the identified extinct and locally extirpated taxa from Vintany Cave have an aquatic dependence, most specifically freshwater, that suggests that there has been environmental modification such as reduction of the important water sources in the region of Tsimanampesotse, and wetter conditions in the area in the past.

Key words: Aves, extinction, Vintany Cave, Tsimanampesotse, comparative morphological analysis

Résumé détaillé

Le plateau karstique Mahafaly de la partie Sud-ouest de Madagascar est une zone riche en gisements subfossilifères. Les formations karstiques, tels que les gouffres et les grottes, situées au sein du Parc National de Tsimanampesotse témoignent de l'importance en subfossiles de la région. Cette étude se focalise particulièrement sur la grotte de Vintany (ou Aven Cave) localisée à l'intérieur du parc. Le site est riche de plusieurs subfossiles de vertébrés immergés dont l'abondance est unique sur le plan mondial. La période de collecte des spécimens s'est étendue sur quatre années, 2015, 2016, 2018 et 2019 pendant les mois de mai et de juin. La collecte a été effectuée par des plongeurs. Les restes subfossiles ont été par la suite catalogués par attribution de numéros de terrain et de laboratoire. Pour l'identification taxonomique, une analyse morpho-comparative a été réalisée en utilisant les collections ostéologiques de différents musées et laboratoires.

Les résultats de cette étude ont permis d'identifier, parmi les 1077 spécimens de subfossiles d'oiseaux récupérés dans les sédiments inondés de la grotte, 35 espèces différentes dont la majorité de ces espèces d'oiseaux figure encore parmi l'avifaune moderne du parc. Toutefois, cinq taxons sont reconnus comme éteints, incluant une espèce d'oiseaux-éléphants (*Mullerornis modestus*), deux espèces endémiques de couas terrestres (*Coua* cf. *berthae* and *C.* cf. *primaeva*), une espèce de tadorne (*Alopochen sirabensis*) et une espèce de vanneau (*Vanellus madagascariensis*). Deux taxons actuels, *Haliaeetus vociferoides* et *Threskiornis bernieri* ont disparu de cette région, mais existent encore dans d'autres localités à Madagascar. La collection osseuse de la

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grotte de Vintany est prédominée par des ossements du Grand Perroquet Vasa (*Coracopsis vasa*). La plupart des espèces éteintes ou localement disparues de l'avifaune de Tsimanampesotse présentaient une dépendance aux milieux aquatiques, pratiquement adaptés aux eaux douces, laissant donc penser à une modification environnementale ou une diminution des sources en eau importante dans la région et suggérant la présence des conditions plus humides de la région dans le passé.

Mots clés : Aves, extinction, analyse morpho-comparative, Grotte de Vintany, Tsimanampesotse

Introduction

Madagascar is the 4th largest island in the world. It is one of eight most important biodiversity hotspots in the world based on the species richness and uniqueness of its fauna and flora superimposed on the level of human-induced habitat modification (Ganzhorn *et al*., 2013). This level of uniqueness can be explained by its long history of isolation in deep geological time from other landmasses, its habitat diversity, and considerable climatic variation across the island (Dewar & Richard, 2007). Madagascar also stands out because of its unique and diverse vertebrate communities with extraordinary levels of endemism at higher taxonomic levels (genera and families) (Myers *et al*., 2000), although faunal diversity today is notably reduced as compared to that present in the Pleistocene (2.6 million years ago – 11,700 years ago) and Holocene (11,700 years ago to today). There is considerable evidence that during the last three millennia, significant changes occurred that transformed the island's ecosystems and the associated composition of the fauna. Many dozens of species have disappeared, including all large-bodied endemic fauna (hippopotami, "giant" lemurs, tortoises, and elephant birds). By 1000 years ago, few of these vertebrates remained.

The causes associated with the disappearance of these animals have been the subject of considerable debate over the past decades (Goodman & Jungers, 2013). Several hypotheses have been posited to explain the important demise of the fauna during the Late Holocene. These range from some aspects of climatic change (Mahé & Sourdat, 1972; Virah-Sawmy *et al*., 2009, 2010) to human activities (Burns *et al*., 2016; Crowley *et al*., 2017; Godfrey *et al*., 2019) to synergistic effects of both human impacts and climatic shifts (Burney *et al*., 2003, 2004). Researchers that advocate for climate change as the cause of the extinctions suggest that an island-wide drought took place at the end of Holocene, which induced major habitat modification and stressed portions of the endemic fauna to the point of extinction. This aridification hypothesis has been called into question because most extinct species persisted under intensely dry climate conditions (Crowley, 2010), and because, in the northwestern part of Madagascar, the decline of fauna occurred during a wet period (Burns *et al*., 2016; Scroxton *et al*., 2017; Godfrey *et al*., 2019). Indeed, prolonged Late Holocene drought is known only in the southwestern part of Madagascar (Vallet-Coulomb *et al*., 2006; Crowley *et al*., 2017; Faina *et al*., 2021).

In contrast, several authors have favored human actions as the primary trigger for the loss of large-bodied animals (often referred to as the "megafauna") on the island during the Late Holocene. Different versions of this hypothesis have focused on over-hunting, habitat modification, the use of fire, the introduction of zoonotic diseases, the introduction of domestic and invasive species, agropastoralism, the influx of new settlers, or the expansion of the Indian Ocean trade network (Dewar, 1984; MacPhee & Marx, 1997; Pérez *et al*., 2003, 2005; Burney & Flannery, 2005; Burns *et al*., 2016; Crowley *et al*., 2017; Godfrey *et al*., 2019). The synergy hypothesis proposes that a combination of anthropogenic activities and natural climatic change was responsible for the Holocene faunal decline (Burney *et al*., 2003, 2004). This theory posited that aridification increased the vulnerability of the large-bodied species to human activities, but that the latter (particularly the hunting of terrestrial megaherbivores and consequent spread of fire) were primarily responsible for the transformation of habitats. Debate on this subject continues.

Most prior studies focused on the large-bodied fauna despite the fact that bones of many other smaller animals have been found in subfossil deposits alongside the larger species. This includes lemurs, carnivorans, rodents, tenrecs, and birds (Goodman & Ravoavy, 1993; Goodman & Rakotozafy, 1997; Goodman, 1999; Muldoon *et al*., 2009, 2012; Goodman *et al*., 2013; Rosenberger *et al*., 2015; Samonds *et al*., 2019). In the case of the avifauna, little attention has been given to the nearly 100 bird species known from subfossil deposits, of which 16 are extinct or extirpated on the island (Safford *et al*., in press); the major exception is that of the elephant birds (Aepyornithidae) (Hansford & Turvey, 2018). The sensitivity of many bird species to shifts in ecosystems provides an excellent means to use their subfossil remains as a source of information on environmental vicissitudes. For example, Late Holocene communities can be compared with modern communities to assess faunistic change through time. Vintany Cave in the Tsimanampesotse National Park in extreme southwestern Madagascar has a substantially large and diverse sample of bird subfossils that provide the means to reconstruct based on known or inferred habitat preferences change. This study focuses on the identification of subfossil birds from the paleontological site of Vintany Cave. We include a preliminary assessment of what may have caused changes in the local avifauna in recent geological time.

Materials and methods

In 2013 Ryan Dart, a cave diver and amateur paleontologist, explored several underwater caves in southwest Madagascar for recreational purposes. He reported the presence of fossils in a submerged cave located inside Tsimanampesotse National Park to Phillip Lehman, another cave diver, who in turn informed Alfred Rosenberger of this find. Rosenberger is an anthropologist with experience at the excavating submerged fossil remains. He contacted Kathleen M. Muldoon and Laurie R. Godfrey, who had already established research collaborations with Université d'Antananarivo. A partnership between the Université d'Antananarivo, the University of Massachusetts, and Madagascar National Parks (a parastatal organization overseeing the management of protected areas) was created, in collaboration with divers from various institutions, and an exploratory expedition was conducted in 2014 (Rosenberger *et al*., 2015). During subsequent expeditions in 2015, 2016, 2018, and 2019, the field team collected subfossil remains at Vintany Cave, respecting the designated number authorized by Madagascar National Parks and three ministries (Ministère de l'Enseignement Supérieur et de la Recherche Scientifique, Ministère de la Culture et de la Communication, and Ministère des Mines et des Ressources Stratégiques).

Site description

Tsimanampesotse National Park

Tsimanampesotse National Park is located in the southwestern part of Madagascar, 85 km south of Toliara (Figure 1). It is situated between 24.05889° and 24.20889°S and 43.77472° and 43.84139°E. The area within and just outside the park is characterized by dune deposits in the west and Eocene limestone (the Mahafaly Plateau) in the east. The protected area is dominated by three topographical features: a vast plain from the coast inland and adjacent to Lake Tsimanampesotse, a transitional area between the plain and limestone Mahafaly Plateau, and the extensive karst habitat on the Mahafaly Plateau.

Inside the park, fresh groundwater fills some of the caves, emerging at their entrances. However, Lake Tsimanampesotse is filled with high mineralized (salinity > 41000 µS/cm) and moderately alkaline (pH~8,0) water (André *et al*., 2005; Rasoloariniaina, 2017). It is mainly frequented by flamingos adapted to brackish water, specifically *Phoenicopterus roseus* and *P*. *minor*.

The climate is sub-arid with irregular rainfall averaging 389 mm annually and a much-extended dry season without measurable rainfall, which typically lasts eight or nine months from March to October or November. The average annual minimum temperature is 19.2°C and maximal is 30.7°C (Ratovomanana *et al*., 2011; Goodman *et al*., 2018). The area has a flora with many species adapted to the local climatic conditions and mainly composed of xerophytic plants; 81.1% of the species are endemic to the island (Goodman *et al*., 2018). Dry spiny thicket is the principal vegetation type and dominated by the families Burseraceae, Didiereaceae, and Euphorbiaceae. However, there are numerous other succulent plant groups, as well as baobabs (Ratovomanana *et al*., 2011; Goodman *et al*., 2018).

Vintany Cave

Vintany Cave is located in the northern part of Tsimanampesotse National Park, at the geographic position of 24.043772°S and 43.755328°E. The cave is in the limestone of the Mahafaly Plateau and is the result of the ancient dissolution of limestone. Fresh water filled the cave when the water table rose during the last deglaciation period associated with increased sea levels and in the Pleistocene, there has been considerable fluctuation the water table in the flooded caves of Tsimanampesotse. The only entrance to Vintany Cave is a sinkhole 25 m in circumference at its rim; the opening widens below. The water table today is between 10 and 12 m below the rim. Water fills the cave to a depth of over 30 m. A sediment debris mound is found in the middle of the sinkhole forming a small island completely surrounded by water (Rosenberger *et al*., 2015). The rim of the entrance has a large *Ficus* tree with aerial

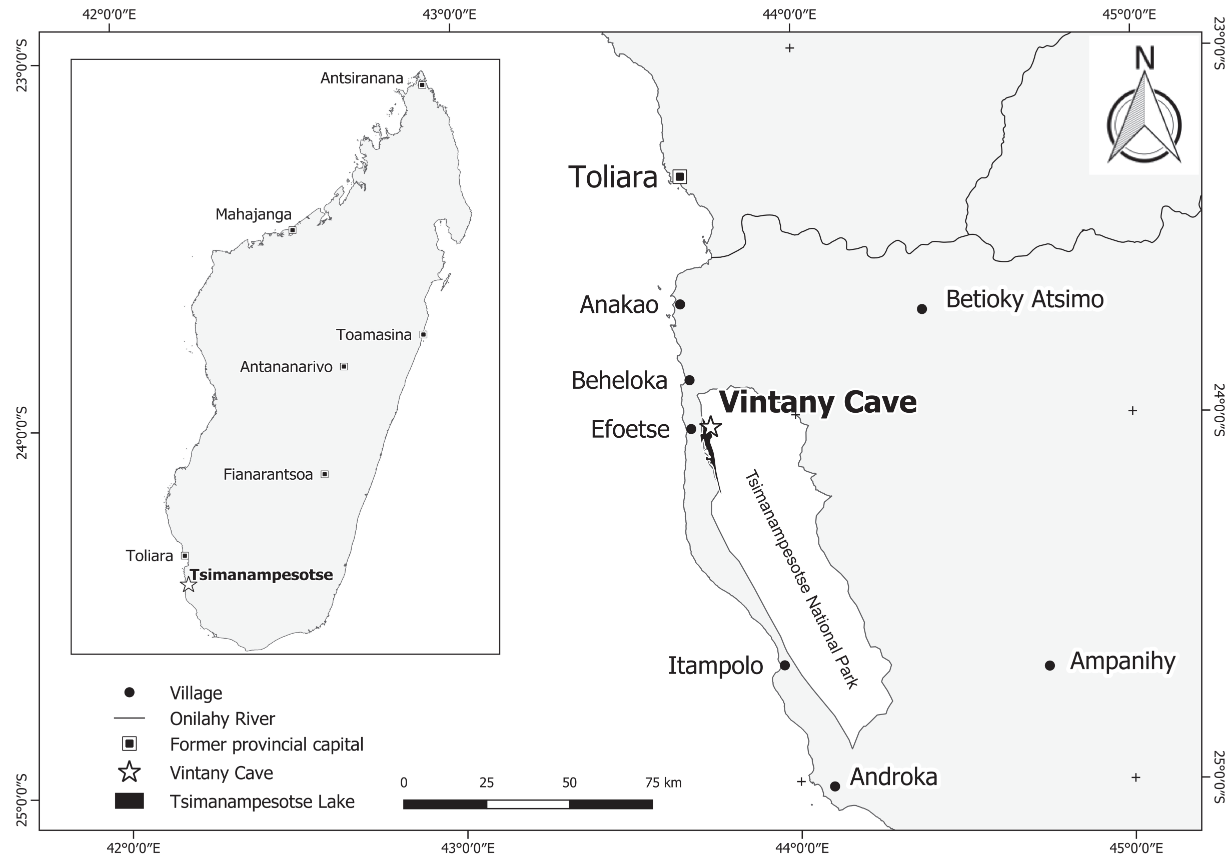

Figure 1. Map showing the position of Tsimanampesotse National Park and Vintany Cave.

roots descending down to the bottom of the sinkhole. This emergent tree forms a prominent feature of the landscape and attracts today a range of different animals, such as birds and ring-tailed lemurs (*Lemur catta*), due to its shade, seasonal fruits, and its prominent look-out position.

Collections

Subfossils were collected by a team of divers, directed by Zachary Klukkert, Phillip Lehman, Ryan Dart, and Patrick Widmann during the 2015, 2016, 2018, and 2019 field seasons (Godfrey *et al*., 2021). The specimens, individual or associated remains, were assigned field catalog numbers, with the prefix TNP for Tsimanampesotse National Park, followed by the year of expedition and a sequential number. The material was subsequently transferred to the laboratory of the Mention Bassins sédimentaires Evolution Conservation, Université d'Antananarivo, and cataloged with definitive museum numbers using the prefix UABEC followed by the collection year and chronological entry number. Provisional taxonomic determination showed a variety of mammals (including primates, carnivorans, artiodactyls, bats, and rodents), reptiles (including crocodiles and tortoise), and birds (including elephant birds). Herein, we use the systematic order, taxonomy, and English vernacular names proposed by Safford *et al*. (in press) for Malagasy birds.

Comparative morphological analysis

The taxonomic identification is based on a comparative morphological analysis using bird osteological collections at the Field Museum of Natural History, Chicago, and at the Laboratoire de Primatologie et de Paléontologie de Vertébrés, Université d'Antananarivo.

The Minimum Number of Individuals (MNI) refers to the number of individuals of a given taxon identified in the assemblage and is used to estimate the relative abundance of species or forms (Klein & Cruz-Uribe, 1984; Lambacher *et al*., 2016). The MNI is calculated based on the bone element with the maximum number of identified specimens, including unpaired or paired elements, allocated to a taxonomic category, generally at the species or genus level. The Number of Elements (NE) is the count of the skeletal remains assigned to a taxonomic category, once again generally at the species or genus level.

Results

Vintany Cave differs from most other subfossil cave deposits on Madagascar because the bones were submerged under water prior to being collected. Among the 1077 bird specimens collected from at the site, 35 taxa have been identified (Table 1) and 175 (16.3%) bone elements remain unidentified. Furthermore, the material recovered from Vintany Cave is just a small representation of the bones at the site. With the exception of *Mullerornis modestus*, *Vanellus madagascariensis*, *Alopochen sirabensis*, *Coua* cf. *primaeva*, and *C*. cf. *berthae*, all of the bird species identified in the studied collections still occur in the park or in southwestern Madagascar.

The collection is dominated by remains of the Greater Vasa Parrot (*Coracopsis vasa*); 43% of the material collected (NE) belong to this species. This is not surprising as it is known to perch and nest on cliffs and rock ledges around the cave site. Among the material from the cave referred to the order Passeriformes, those of the Sakalava Weaver (*Nelicurvius sakalava*) is the most common, but some less well-represented taxa in the subfossil remains have been also identified, such as the Madagascar Fody (*Foudia madagascariensis*) and Mascarene Martin (*Phedina borbonica*). These species are common in the park and occasionally nest in caves, as is the case for *Phedina borbonica* inside Mitoho Cave, located near Vintany Cave (Eve & Pers, 2014).

Five different species of endemic cuckoos (Cuculidae) occur in the subfossil collection, of which two, *Coua* cf. *primaeva* and *C*. cf. *berthae*, are extinct; both are distinctly larger in body size than any extant members of this genus, with *C*. *berthae* being the larger of the two. The three living species, Giant Coua (*C*. *gigas*), Crested Coua (*C*. *cristata*), and Red-capped Coua (*C*. *ruficeps*), still occur inside the park (Goodman *et al*., 2018). Among the coua remains, the extinct species are the most common and the majority of referred material are elements of the appendicular skeleton (humerus, ulna, femur, tibiotarsus or tarsometatarsus). A more detailed study is required to determine the specific identification of the large extinct couas, as the holotypes of *C*. *berthae* are a pelvis and a tarsometatarsus and that of *C*. *primaeva* are a tibiotarsus and tarsometatarsus. Hence, detailed comparisons based on allometry and relative size and proportions of extant couas is needed to statistically determine if these bones represent the two named extinct taxa or other unnamed species.

A variety of diurnal and nocturnal raptors were identified from the Vintany Cave bone remains: Henst's Goshawk (*Accipiter henstii*), Madagascar Buzzard (*Buteo brachypterus*), Madagascar Fish-eagle (*Haliaeetus vociferoides*), Yellow-billed Kite (*Milvus aegyptius*), Madagascar Harrier-hawk (*Polyboroides radiatus*), Madagascar Kestrel (*Falco newtoni*), White-browed Owl (*Athene superciliaris*), Madagascar Scops-owl (*Otus rutilus*), and Barn Owl (*Tyto alba*). Several of these species nest or roost along the rims of caves or use prominent tree perches for resting or hunting. Also, some bird subfossil material may have been the remains of prey that were consumed by these raptors and deposited in the cave as portions of cadavers or regurgitated pellets.

Eleven of the recognized species are known to occur (or reconstructed as having occurred) in aquatic habitats; extinct species are indicated by a "†" symbol: †*Alopochen sirabensis*, unidentified duck (*Anas* sp.), Greater Flamingo (*Phoenicopterus roseus*), Red-knobbed Coot (*Fulica cristata*), Black-winged Stilt (*Himantopus himantopus*), †*Vanellus madagascariensis,* Madagascar Heron (*Ardea humbloti*), Glossy Ibis (*Plegadis falcinellus*), Madagascar Sacred Ibis (*Threskiornis bernieri*), and Madagascar Fish-eagle (*Haliaeetus vociferoides*); about half of these species no longer occur inside the park (†*Alopochen sirabensis*, †*V*. *madagascariensis, Ardea humbloti*, *T*. *bernieri,* and *H*. *vociferoides*). Bones of one species of elephant bird (Aepyornithidae), a family of large terrestrial birds that is now extinct, were also found at Vintany Cave. †*Mullerornis modestus* is represented by a few juvenile specimens and a tibiotarsus of one adult. The presence of *M*. *modestus* in the cave remains, although rare based on current sampling, can be interpreted as evidence that this species at least on occasion occurred on the Mahafaly Plateau or a carnivoran predator brought its prey up to the area around Vintany Cave. We have found no evidence of carnivoran predation on the specimens retrieved from the cave in the form of toothmarks or other telltale signs.

Discussion

Taxonomic determination of the bird remains recovered from Vintany Cave shows that 8 species (23% of the identified species) have completely disappeared from the modern avifauna of the park and for the most part from southwestern Madagascar. Below we present some specific details about

Table 1. List of bird subfossils identified from Vintany Cave in Tsimanampesotse National Park, including Minimum Number of Individuals (MNI) and Number of Elements (NE). Taxa preceded by an asterisk represent those that are endemic to Madagascar, taxa preceded by † are extinct, and taxa in **bold** are introduced. The habitat types used by each species are presented in parentheses and include A = aquatic, FD = forest-dwelling, and NFD = non-forest dwelling. Some species occur in different habitats and for extinct species these designations are inferred and presented in brackets. The taxonomic order is after Safford *et al.* (in press).

	MNI	NE
Order Aepyornithiformes		
Family Aepyornithidae		
†**Mullerornis modestus* [FD]	5	7
Order Anseriformes		
Family Anatidae		
†**Alopochen sirabensis* [A]	1	1
Anas sp. (A)	2	2
Order Galliformes		
Family Numididae		
Numida meleagris (FD/NFD)	4	5
Order Phoenicopteriformes		
Family Phoenicopteridae		
Phoenicopterus roseus (A)	2	2
Order Columbiformes		
Family Columbidae		
Oena capensis (FD/NFD)	3	3
**Nesoenas picturata* (FD)	12	33
cf. Columbidae	1	1
Order Pterocliformes		
Family Pteroclidae		
**Pterocles personatus* (NFD)	8	17
Order Cuculiformes		
Family Cuculidae		
**Coua gigas* (FD)	4	4
**Coua cristata* (FD)	4	7
**Coua ruficeps* (FD)	3	5
†**Coua* cf. *berthae* [FD]	14	35
†**Coua* cf. *primaeva* [FD]	24	85
Order Caprimulgiformes		
Family Caprimulgidae		
Caprimulgus madagascariensis (FD/NFD)	4	4
Family Apodidae		
Apus balstoni (FD/NFD)	8	20
Order Gruiformes		
Family Rallidae		
Fulica cristata (A)	1	1
cf. Rallidae	1	1
Order Charadriiformes		
Family Recurvirostridae		
Himantopus himantopus (A)	1	1
Family Charadriidae		
†**Vanellus madagascariensis* [A]	1	1
Family Turnicidae		
**Turnix nigricollis* (FD/NFD)	1	2
Order Pelecaniformes		
Family Ardeidae		
Ardea humbloti (A)	1	1
Family Threskiornithidae		
Plegadis falcinellus (A)	1	1
Threskiornis bernieri (A)	2	2
Order Accipitriformes		
Family Accipitridae		
**Accipiter henstii* (FD)	4	6
cf. *Accipiter henstii* (FD)	2	3
**Buteo brachypterus* (FD/NFD)	8	17
**Haliaeetus vociferoides* (A)	1	1
Milvus aegyptius (NFD)	4	5
**Polyboroides radiatus* (FD)	4	6
cf. Accipitridae	1	1
Order Strigiformes		
Family Strigidae		
**Athene superciliaris* (FD)	2	3
cf. *Athene superciliaris* (FD)	5	6
**Otus rutilus* (FD)	1	1
Family Tytonidae		
Tyto alba (FD/NFD)	9	17
Order Falconiformes		
Family Falconidae		
Falco newtoni (FD/NFD)	13	44
Order Psittaciformes		
Family Psittacidae		
Coracopsis vasa (FD)	63	463
Order Passeriformes		
Family Ploceidae		
**Foudia madagascariensis* (NFD)	7	12
**Nelicurvius sakalava* (NFD)	29	74
*Family Hirundinidae		
Phedina borbonica (NFD)	2	2
Unidentified bird bones		175
Study total	**263**	**1077**

certain of these species, focusing on the extinct taxa and those no longer occurring in and around Tsimanampesotse.

Extinct species

Mullerornis modestus Müller's Elephant Bird

Mullerornis was the smallest-bodied member of the now extinct order Aepyornithiformes, known from Madagascar (Grealy *et al*., 2017). The recent revised taxonomy showed that this genus has only one species, *M. modestus* (Hansford & Turvey, 2018). Remains of the family Aepyornithidae have been recovered at many subfossil sites on Madagascar. *Mullerornis modestus* was widely distributed across the island and occurred sympatrically with the larger-bodied elephant birds *Vorombe titan* and *Aepyornis maximus* across the south, southwest, and the Central Highlands (Goodman & Jungers, 2013; Hansford & Turvey, 2018).

Alopochen sirabensis Malagasy or Sirabe Shelduck

Bone remains of this extinct waterfowl are common to abundant at certain subfossil sites. It was described on the basis of subfossil material collected near Antsirabe (Andrews, 1897). This taxon was distributed across different portions of the Central Highlands (Goodman, 1999; Samonds *et al*., 2019) and has been found at sites in the southwest and central west, such as Beavoha, Beloha Anavoha, Belo-sur-Mer, Lamboharana, and Manombo (Goodman & Rakotozafy, 1997).

Coua cf. *primaeva and C.* cf. *berthae* giant couas

Coua primaeva and *C. berthae* are the largest couas known to have occurred on Madagascar. *Coua primaeva* was described from subfossils deposits at Belo-sur-Mer and Manombo, based on a tarsometatarsus and tibiotarsus (Milne-Edwards & Grandidier, 1895; Goodman & Rakotozafy, 1997). *Coua berthae* was named from subfossil remains recovered from Anjohibe Cave on the basis of its large pelvis, as well as a tarsometatarsus collected at Ampasambazimba (Goodman & Ravoavy, 1993). The wing bones of these extinct couas resemble those of living members of the genus in being proportionately reduced in size, suggesting that the extinct species were similarly largely incapable of long-distance sustained flight. Both of these extinct coua species are presumed to have been forest-dwelling, presumably mostly or completely terrestrial.

Vanellus madagascariensis Malagasy Lapwing

Vanellus madagascariensis was previously known from two other subfossil sites in the southwest, Ampoza near Ankazoabo Atsimo (from where it was described) and Lamboharana (Goodman, 1996). As members of the genus across its New and Old World ranges are aquatic and terrestrial, it is presumed that the extinct Madagascar species had a similar life history.

Extant species no longer occurring at Tsimanampesotse

Ardea humbloti Humblot's Heron

Ardea humbloti is a waterbird distributed in Madagascar and neighboring islands of the Comoros. Their preferred habitat includes coastal habitats and freshwater lakes. This species is known in the west and southwest of Madagascar, with records north of Toliara (Safford and Hawkins, 2013). *Ardea humbloti* is considered Endangered on the IUCN Red List.

Threskiornis bernieri Malagasy Sacred Ibis

Threskiornis bernieri is well represented in certain deposits of the southwest, such as Beloha Anavoha, Beavoha, Lamboharana, Manombo-Toliara, and Tsiandroina (Goodman & Rakotozafy, 1997). The modern population of this species usually occurs in areas with shallow freshwater, as well as mangrove swamps (Safford and Hawkins, 2013), and occurs only on Madagascar and Aldabra. It has a broad geographic range on the western side of Madagascar, but is unknown to occur in the Tsimanampesotse protected area (Goodman *et al*., 2018). It is considered Endangered on the IUCN Red List.

Haliaeetus vociferoides Madagascar Fish-eagle

Haliaeetus vociferoides is endemic to Madagascar and is considered Critically Endangered on the IUCN Red List. Unlike other resident raptors on the island which are mostly forest-dwelling, this species is piscivorous and occurs in wetlands. Its modern range includes the western side of the island, from the far north to the southern Menabe Region (Safford & Hawkins, 2013), several hundred kilometers north of Tsimanampesotse.

Habitat reconstruction

Among the 35 bird species identified from the remains, 11 are forest-dwelling, five are not dependent on forest habitat, nine frequent both forest and open habitat, and 10 are aquatic (Table 1). Based on the natural history of the extant and extinct species, it can be inferred that, during the Late Holocene, the study site was dominated by forest and more open habitats associated with wooded grassland and had significant freshwater areas, which based on the presence of certain animals, such as hippopotami, were permanent. Goodman & Jungers (2013) suggested that the former wooded grassland habitat of the area may have been an ecological parallel to the modern Miombo woodlands of southern Africa. Few radiocarbon dates from bones of extinct species collected at Tsimanampesotse are available, but all of them over 2000 years old (MacPhee, 1986; Faina *et al*., 2021; Godfrey *et al*., 2021). At that time, Tsimanampesotse was dominated by C_3 plants and the vegetation cover may have been similar to that of other coastal sites, such as near Asafora Cave (Faina *et al*., 2021) or Andolonomby (Virah-Sawmy *et al*., 2016). *Pachylemur* and *Mesopropithecus*, the only extinct primates identified thus far at Vintany Cave, as well as *Megaladapis*, whose remains have been found at several other Tsimanampesotse caves, are known to have relied on C_3 plants (Godfrey *et al*., 2012).

Environmental change through time

There is clear evidence that, over the past several millennia, environmental change occurred in the natural ecosystems of Madagascar. Two triggers for these changes have been debated (Burney *et al*., 2003, 2004): 1) the ecosystem changes were anthropogenic in origin (Burns *et al*., 2016; Godfrey *et al*., 2019), and 2) the ecosystem changes resulted from natural aridification (Mahé & Sourdat, 1972; Goodman & Rakotozafy, 1997; Virah-Sawmy *et al*., 2010). These two explanations are not mutually exclusive.

The human side

The timing of the first human colonization of Madagascar has been debated for decades. Within the past few years, paleontological evidence of human presence earlier than previously assumed, previously around 2000 year BP (MacPhee and Burney, 1991), has been found in the form of butchery marks on two subfossil leg bones of an *Aepyornis maximus* in the central southwest of the island (Hansford *et al*., 2018). The site called Christmas River is located in the region of the Isalo Massif. Bones from the stratigraphic layer in which the butchered *Aepyornis* was found, including this specimen itself, were all dated at ~10,500 Cal yr BP (Muldoon *et al*., 2012; Hansford *et al*., 2018).

Dated material of butchered bones from Christmas River are thousands of years earlier than expected based on current archaeological evidence; they are outliers in the radiocarbon database for butchered subfossils. The existence of only two butchered bones (belonging to a single individual) older than 10,000 years may signal that the human population on Madagascar 10,000 years ago was very small; indeed, such early human populations may have died out before new immigrants arrived. Alternatively, some researchers believe that the evidence for early butchery is faulty (Mitchell, 2019), but Hansford *et al*. (2020) confirmed that the traces observed on the two bones are associated with human butchering. By analyzing and evaluating ^{14}C data on large-bodied animals and other features from subfossil and archaeological sites, Douglass *et al*. (2019) concluded that, even if these outliers are rejected by some authors, other evidence suggests that Madagascar was settled long before the large-bodied animals became extinct, certainly by 2000 years ago or earlier. Thus, the endemic extinct fauna, particularly large-bodied creatures, coexisted with humans for at least 1000 years before these animals disappeared.

The dearth of early evidence of human impacts on large-bodied animals does not mean that humans were not the primary triggers for their extinction, because changes in human activities could have negatively impacted the large-bodied fauna. Recent studies have attributed the extinction of these animals to the shift in subsistence from hunting and foraging to herding and farming (Godfrey *et al*., 2019). This would not have occurred until after Madagascar was settled by immigrant groups that brought with them cultivated plants and domesticated animals. Relatively rapidly thereafter, a new socio-ecological context resulted in geographical expansion of settlements and accelerated human population growth (Dewar, 2014; Pierron *et al*., 2017, Godfrey *et al*., 2019). Also, there is evidence of direct human impacts on large-bodied animals in the southwest in the form of butchering traces on subfossil bones and, without any doubt, these animals were hunted. Butchered bones of large-bodied animals have been found at several subfossil sites in the southwest including Ambolisatra, Lamboharana, Taolambiby, and Tsirave (Perez *et al.*, 2003, 2005; Godfrey *et al.*, 2019, unpublished data).

Climatic change

Another explanation for the loss of biodiversity during the Late Holocene is climatic change. The notion that aridification was the primary trigger for the loss of large-bodied animals was first championed by Mahé & Sourdat (1972). They argued that an intense and progressive drought occurred across Madagascar beginning several thousand years ago. In the early 1970s when they published this article, the general consensus was that humans only arrived on Madagascar around 1000 years ago. Thus, they believed that temporal overlap between large-bodied animals and humans would have been short, and thus humans could not have been responsible for the extinctions. Instead, they suggested, based primarily on radiocarbon dates then available for subfossils from the southwest, that the extinctions began around 3000 yr BP, with waves at 2200 and 1200 yr BP.

Other authors have also supported the notion that aridification negatively impacted the large-bodied fauna independently of humans (Burney, 1993; Goodman & Rakotozafy, 1993; Virah-Sawmy *et al.*, 2009, 2010), although Virah-Sawmy *et al.* (2009, 2010) believed that the extinctions happened well *after* (and not before) humans arrived. Indeed, on the basis of many more subfossil dates and with greater precision than were available to Mahé & Sourdat (1972), Virah-Sawmy *et al.* (2010) noted that the extinctions occurred after 1000 years ago. However, they also believed based on evidence from southeastern Madagascar that the extinctions coincided with a drought peak about 950 years ago.

The hypothesis that there was a drought across the island that peaked slightly less than 1000 years ago was contradicted by stable nitrogen isotope analysis of radiocarbon-dated subfossil remains, which showed that there was no island-wide drought (Crowley *et al.*, 2017). Indeed, Crowley *et al.* (2017) found a Late Holocene long-term trend toward decreasing moisture only at Andolonomby (=Ambolisatra), a subfossil site on the southwestern coast. Other regions experienced no change in moisture and indeed some showed a Late Holocene trend toward increasing moisture. These authors did not preclude significant drought on the southwest coast, but they argued against drought being the trigger for large-bodied animal extinction across Madagascar.

In northwestern Madagascar, Burns *et al.* (2016) and Godfrey *et al.* (2019) demonstrated that climate change played little or no role in triggering large-bodied animal decline. In this area, during the last two millennia, there were minor fluctuations in moisture, but no pronounced drought (Scroxton *et al.*, 2017). The rapid decline of large-bodied animals did occur with habitat transformation from dominant C_3 plants to dominant C_4 plants, or grasses, but that transformation was the result of human habitat modifications and not by aridification.

In contrast, in southwestern Madagascar, new evidence of Late Holocene severe drought has been accumulating both from the analysis of sediment cores and stalagmites. Faina *et al.* (2021) showed that aridification began slowly between ~3000 and 2000 years ago but it accelerated beginning 1680 Cal yr BP, and reached full drought conditions at ~1560 Cal yr BP. This drought was prolonged, lasting for centuries, from 1560 Cal yr BP until 880 Cal yr BP and coincided with a rapid decline in large-bodied animal populations in this portion of the island. Nevertheless, some of the now-extinct species survived the drought and only disappeared after pastoralists entered the region. These authors therefore hypothesized that, in the southwest, as in the northwest, agropastoralism played a critical role in the ultimate extinction of the regional large-bodied fauna.

What happened to the water birds at Tsimanampesotse?

Thus far we have determined that both aridification and human activities likely impacted the fauna of southwestern Madagascar. This by itself does not address the issue of which of the two was more important for the decline and disappearance of the water birds at Tsimanampesotse.

Two points are important to mention here. The first is that the present aquatic habitat of Tsimanampesotse based on the water chemistry could not support certain of the water bird species that once inhabited this region. The second is that there is no evidence of extensive human activity in the form of habitat modification at Tsimanampesotse prior to or during the drought. It is therefore tempting to infer that the prolonged drought was the trigger for the loss of water birds at Tsimanampesotse. This hypothesis is consistent with the data collected to date. Lake Tsimanampesotse was once a large freshwater lake but is now hypersaline. Whereas we do not know the chronology of salinization of Lake Tsimanampesotse, we do know the chronology of salinization for another hypersaline lake in the southwest, Lake Ihotry (Vallet-Coulomb *et al*., 2006), about 230 km to the north. There is evidence that Lake Ihotry did become hypersaline during the drought and there is independent evidence that the plant communities of the coastal southwest were directly affected by the drought (Faina *et al*., 2021).

None of the bones referred to extinct bird species recovered at Vintany Cave have been dated with radiocarbon techniques. Bones that have been under water for long periods of time generally lack collagen, which radiometric dating employs. However, all submerged bones of other non-avian extinct species from Vintany Cave that yielded radiometric dates lived before the drought. All C_{14} dates for submerged bones that postdate the drought belong to extant species. This may be evidence that the recovered extinct species did not survive the drought at this location. Many bird species have the capacity as local conditions change to move to areas with suitable ecological conditions. Isotope work by members of our team is underway to determine if the ecological preferences of specimens found at Tsimanampesotse are similar to populations recovered elsewhere.

At a broader regional level, it is possible that certain now extinct species survived for a longer period than at Tsimanampesotse. Further, the role of human pressures in the form of hunting may have contributed to local population declines, but at Vintany Cave we have no evidence of butchering or cut marks on the subfossils. A presumed non-native bird species, *Numida meleagris*, has been identified from the subfossil remains of Aven Cave. This species was assumed to be introduced to Madagascar (Benson, 1960) until Goodman *et al*. (2013) found some specimens at Ankilitelo Cave dating to over 11,000 years BP, long predating what was assumed to be the first human evidence on Madagascar at that time. A recent finding (Hansford *et al*., 2018, 2020) of butchering marks on bones from Christmas River dating to ~10,500 years ago has renewed interest in the possibility that *Numida* was introduced by the first human colonizers of the island. The species may have rapidly become widespread and acclimated to Madagascar's varied habitats (forest, grassland, bushland, etc.) (Safford & Hawkins, 2013).

Around 800 years ago, another introduced animal, the cat (*Felis catus* or *F. silvestris*), was present; radiocarbon-dated bones of this species have been found at Andranohilova Cave in close proximity to Vintany (Douglass *et al*., 2019; Godfrey et al., 2021). This suggests at least at a regional level that that people were present around 800 years ago. Nevertheless, human modification on the natural ecosystem during that period was not substantial, and extensive largely intact forest is still present on the western slope of the Mahafaly Plateau and on the plateau itself (Goodman *et al*., 2018). Goodman & Jungers (2013) have argued that human-induced disturbance of the local forests occurred only recently. They concluded that human-generated forest loss could not explain the local extirpation of the water birds.

Remains of freshwater aquatic birds at Vintany Cave indicate that wetter and non-saline habitats were once present in the immediate vicinity. As reported by Faina *et al*. (2021), more mesic conditions were known in the southwest prior to the onset of the drought around 1560 cal BP. At the local level, the extirpation of bird species that are now extinct may be related to this drought that is known to have resulted in salinization of other lakes in the southwest, although there is the possibility that for a certain period these species found refuge elsewhere in the region. The temporal sequence of habitat modifications associated with the drought at a regional level and its impacts on freshwater versus brackish aquatic birds will need to be assessed based on a series of radiocarbon dates of recovered bird subfossils and ecological inference based on isotope and other chemical analyses.

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