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Dodo remains from an in situ context from Mare aux Songes, Mauritius

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Abstract Since 2005, excavations at Mare aux Songes, Mauritius, have revealed the presence of a very rich, ~4,200-year-old fossil bone bed including dodo (*Raphus cucullatus*) bones and bone fragments. The recently excavated dodo assemblage comprises at least 17 individuals and is characterised by the presence of small and fragile skeletal elements, a dominance of leg elements and an absence of juveniles. The hydrology of the area suggests that dodos, like many other species, were probably lured to Mare aux Songes by the presence of freshwater during times of drought. The most likely scenario for the origin of the fossil deposit is that animals became trapped in the sediment in repeated miring events, which would favour the conservation of hindlimbs. Such a scenario is fully in accordance with the taphonomic characteristics of the bone assemblage.

Keywords *Raphus cucullatus* · Insular ecosystem · Mare aux Songes · Mauritius · Taphonomy

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Introduction

Since its demise in the seventeenth century (Hume et al. 2004), the dodo (*Raphus cucullatus*) has become an icon of extinction. The small number of genuine but often contradictory and inadequate contemporary accounts and illustrations cause our knowledge of the dodo's morphology and ecology to be clouded by assumptions and misinterpretations (for instance, see the recent discussion on dodo body mass by Angst et al. (2011a, b) and Louchart and Mourer-Chauviré (2011)). Even though the recent history of human colonisation and impact on Mauritius is well documented (Cheke and Hume 2008), virtually no records of the prehuman ecosystem exist, making it difficult to assess the magnitude of the changes brought about by human settlement.

The first fossil remains of the dodo, together with those of most of the now-extinct vertebrates of the island, were discovered in 1865 by Harry Higginson and George Clark in a richly fossiliferous horizon in the Mare aux Songes (MAS) marsh (Fig. 1) (Clark 1866; Hume et al. 2009). Even though large amounts of dodo material were recovered by George Clark and subsequent excavators (Günther 1875; Carié
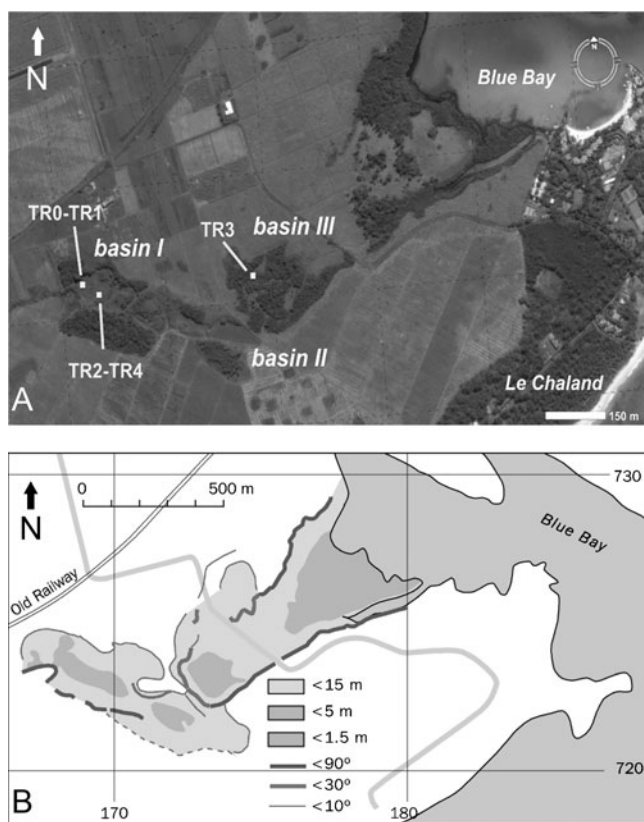
Fig. 1 **a** Google earth image of Mare aux Songes and position of sub-basins I, II and III and trenches (*TR*). The forested parts and scrub rich fields mark steep slopes and wet depressions. **b** Geomorphology of MAS, the *thickness of lines* indicates the steepness classes of the slopes. *Yellow* indicates a dirt road. Reprinted from Rijsdijk et al. (2009) with permission

1930; Hoffstetter 1945, 1946a, b; Newton and Gadow 1893; Hume et al. 2009), no contextual geological or paleoecological data were recorded at the time. Furthermore, the exact location where these bones were found within the MAS is still unknown, but Hume et al. (2009) suggest that the original locality was situated farther upslope from MAS basin I (Fig. 1). In an effort to eradicate malaria, the marsh was in-filled with dolerite blocks and gravels in the 1940s, after which, the site was neglected by the scientific community. By the 1980s, the Mare aux Songes marsh was erroneously believed to have been completely destroyed by the development of nearby Sir Seewoosagur Ramgoolam International Airport (Cowles 1987).

The re-examination in 2005 of the MAS area provided a unique opportunity to excavate the Mauritian vertebrate fauna in context. Excavations at MAS revealed the presence of a very rich fossil bed containing a diverse array of macro- and micro-flora and fauna, including the dodo, giant tortoises *Cylindraspis* spp., and vast numbers of seeds of the endemic Tambalacoque *Sideroxylon grandiflorum* and other tree species (Rijsdijk et al. 2009). Radiocarbon dating

suggests that accumulation of the vertebrate bones occurred within a narrow time window between 4235 and 4100 cal. year BP (Rijsdijk et al. 2011). However, geomorphological, taphonomic and botanical evidence (Rijsdijk et al. 2009) excludes a catastrophic event, such as a tsunami or volcanic eruption, as the cause for the accumulation.

Here, we describe the dodo assemblage from recent excavations at Mare aux Songes (2006–2008) within a taphonomic context. We aim to explore several death scenarios that are related to drought, including thirst, the drinking of poor quality/toxic water, and a scenario in which animals becoming trapped in the peat substrate (miring). All are examined here against the taphonomic characteristics of the dodo assemblage.
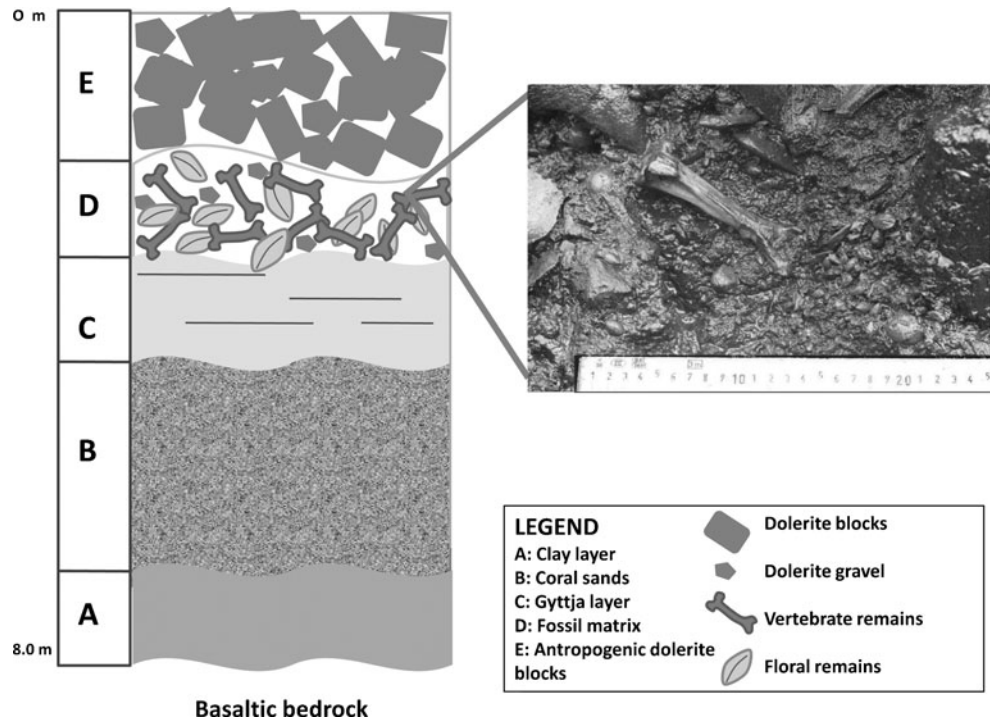
Material and methods

The geological setting of Mare aux Songes

The marsh area (20°26′51, 2″ S; 57°41′23, 5″ E) is situated at the south-eastern part of Mauritius within an isolated basaltic rock basin less than 1 km from the Indian Ocean (Fig. 1a). The basin was formed as a result of the collapse of a lava tunnel, which resulted in three separate basins (I, II and III), all situated at <0.5 m above mean sea level (Fig. 1b). Basins I and III contain vertebrate fossils, whereas basin II, filled in by a 1–2 m + accumulation of anthropogenic dolerite boulders, did not yield any vertebrate material. Within the basins, actual groundwater levels range from just below, and rise during heavy rainfalls to just above, the present surface (Rijsdijk et al. 2009). In 2005, a fossil bone bed was discovered in basin I. Several cores and excavation trenches (Fig. 1, Tr. 0–4) showed the bone bed to cover an area of 1.86 ha with a thickness between 0.25 and 1.5 m.

A detailed description of the sedimentology is given by Rijsdijk et al. (2009). In summary, the rock basin is filled with tropical clays that are overlain by eolian coral sands (Fig. 2, unit B). On top of these carbonate sands lies an approximately 40 cm thick discontinuous lenticular grey lake marl (Fig. 2, unit C), which is covered by fossil bed layer D. The top of layer D contains small basaltic (dolerite) gravels that increase in concentration as well as in grain size to the top of layer D. A layer of larger, anthropogenic dolerite gravels and blocks (layer E) caps layer D and has sealed MAS since the 1940s. At Tr. 0 and Tr. 1, the bone bed is on average 0.5 m thick and consists almost entirely of bones, seeds and wood (wood cross-section >1 cm) debris. Trenches 0–1 are located at the north-western edge of the basin. Here, bone and wood remains dominate and fine matrix material is nearly absent. Therefore, the fossil bed here is believed to represent a

Fig. 2 Generalised stratigraphic profile of basin I based on stratigraphic profiles of three trenches within basin I by Rijsdijk et al. (2009). Actual thicknesses of layers A–E vary depending upon location within the basin. Top of profile is located at −1 m below sea level. Detail of layer D depicts vertebrate remains, with tarsometatarsus of *R. cucullatus* in the middle within matrix of floral remains and debris

LEGEND
A: Clay layer
B: Coral sands
C: Gyttja layer
D: Fossil matrix
E: Antropogenic dolerite blocks

Dolerite blocks
Dolerite gravel
Vertebrate remains
Floral remains

Basaltic bedrock

shallow lake shore facies. Wind-driven currents at the lake shore led to reworking of the fossil layer and winnowing of the fine sediments, leading to a coarse bone-rich layer. Trenches 2 and 4 are located in the centre of basin I, where the fossil layer is thicker and the bones are dispersed in a chestnut brown organic matrix (gyttja). The bones are estimated to constitute 10–30% of the total weight of the fossil layer. The gyttja consists of fine organic debris indicating

Fig. 3 Proportions of cranial, wing, leg and axial skeletal elements within the MAS dodo assemblage (**a**), and in a non-bias setting (**b**), and for trenches 0 and 1 (**c**) and trenches 2 and 4 (**d**)

A MAS assemblage

B Unbiased setting

C Trenches 0 & 1

D Trenches 2 & 4

HEAD
WING
LEG
AXIAL
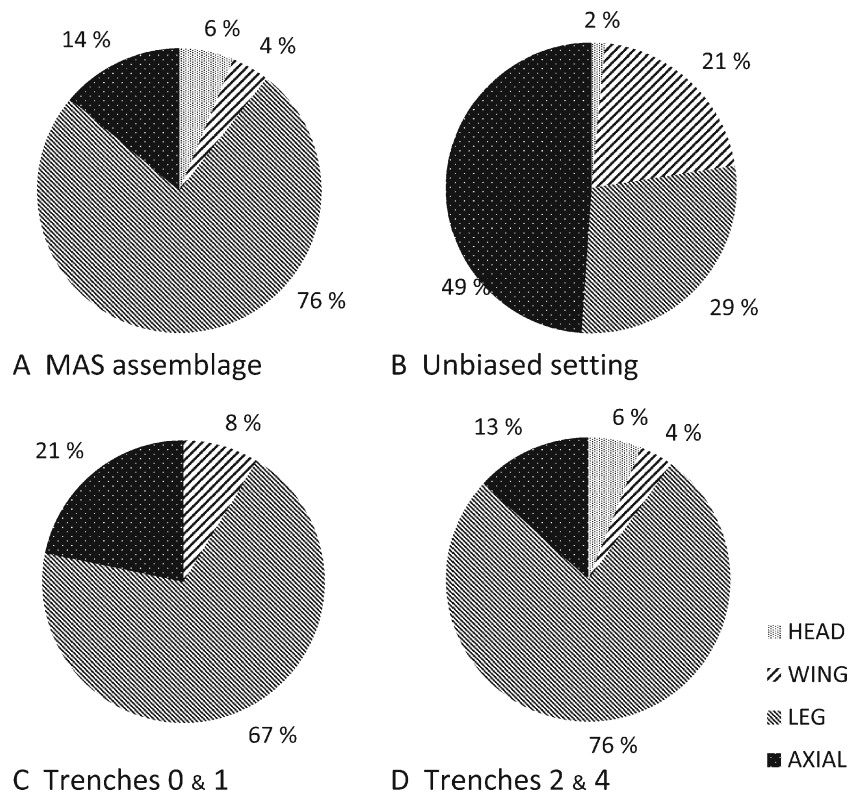
accumulation under low-energy conditions that prevailed in the deeper centre of the lake. These contrasting lake shore and centre depositional environments may have affected the taphonomy of the vertebrate assemblage.

Hydrological and geological data indicate that MAS formed ca. 5000 cal. year BP ago as a shallow freshwater lake in response to eustatic sea level rise (Rijsdijk et al. 2009). Radiocarbon dating of nine vertebrate bones yielded a weighted average ^{14}C age of 3850 ± 15 ^{14}C year BP, indicating that fossil deposition occurred over a very short period of time between 4235 and 4100 cal. year BP (Rijsdijk et al. 2009, 2011). The age of the MAS assemblage coincides with a period of regional aridification (Gasse 2000; Marchant and Hooghiemstra 2004; Rijsdijk et al. 2011). On volcanic islands, stagnant freshwater is rare due to the great permeability of the basaltic rocks, which cause rainwater to infiltrate easily into the soil. On Mauritius, however, groundwater flowed via aquifers towards the dry coastal regions where it emerged at depressions, such as MAS, forming freshwater lakes (Rijsdijk et al. 2011). Because MAS provided a rare source of freshwater within the dry coastal lowlands, it attracted a diverse fauna, especially during the dry season.

Excavation methods

All excavations and subsequent analyses were carried out with permission of the Mauritius National Heritage Fund and Omnicane. As a result of the coincidental discovery of the fossil bed in 2005, bones were handpicked from material that was brought above surface with a mechanical digger's scoop. In 2006, trenches were dug at basins 1 (Fig. 1, Tr. 1–2) and 3 (Fig. 1, Tr. 3) using a mechanical shovel scoop to penetrate the upper layer of gravel and boulders and expose the fossil layer. As a result of the rapid infilling of groundwater, it was not possible to excavate under dry conditions. Initially, a bulk sampling method was employed in which the relatively undisturbed sedimentary structures within the centre of the shovel scoop were used for sedimentological and stratigraphic analyses. However, association, articulation and orientation of skeletal material were not assessed systematically, as the in situ vertebrate material was disturbed during scooping and removal. The scooped bulk samples were sieved with a nested sieve system using 15, 10 and 4 mm meshes to retrieve macrofossil remains. Sieve residue subsamples were dried and microfossils were handpicked.

Taphonomic analyses

All bone material from the excavations at Mare aux Songes is stored at Omnicane, Mauritius, and all dodo bones have been numbered and categorised. We have focused our taphonomic analyses on a dataset that is limited to bone and

bone fragments from the excavations in basin 1 from 2006 to 2008 ($n=235$) (see ESM). Bones handpicked during the initial discovery in 2005 ($n=14$) have been excluded in order to reduce taphonomic bias relating to size sorting. From 2009, bones were excavated in an in situ situation, which differs from the excavation techniques employed previously. For the taphonomic analyses, the following parameters were scored: side of the bone (dexter or sinister), completeness (in case of bone fragment, proximal, middle or distal part), colour [six categories, ranging from 0.5 (light ochre) to 3 (dark brown)], bone weathering class following Behrensmeyer (1978), degree of erosion [eight classes ranging from 1 (no erosion) to 8 (severe erosion)], degree of fusion and the presence of pathologies and gnawing, cutting and/or burning marks. We assessed skeletal part survivorship as expressed as the percentages of anterior elements (%A) relative to the total number of (A) and posterior (P) elements following Ericson (1987), where A = ulna + carpometacarpus + humerus and P = femur + tibiotarsus + tarsometatarsus. The ratio of anterior and posterior limb elements provides evidence for taphonomic processes that affect paleoecological signals and values that deviate significantly from 50% indicate taphonomic overprinting.

Results

During the 2006–2008 field campaigns of the Dodo Research Programme, a total of 235 dodo bones and bone fragments were retrieved from the MAS (see ESM). The assemblage comprises cranial bone elements, including mandibula, nasal bar, palatine, premaxillary, pterygoid and jugal bones, sternal elements, vertebrae, humeri, scapulae, radii, carpometacarpi, pelves, femora, fibulae, tibiotarsi, tarsometatarsi and phalanges (Figs. 3a, 4 and 5). Only 26 fragments could not be assigned to a bone element. All bones are fully ossified and no bones of juvenile dodos were found. The retrieval of numerous small elements such as phalanges confirms that the dominance of larger elements in previously collected museum dodo material was due to sampling bias (Hume 2005). The total number of identifiable specimens is 209. The minimum number of individuals (MNI) is based on the most common element, which was the left tibiotarsus ($n=17$). Note that the 36 pelvic fragments (ESM) may not represent 36 individuals, as we cannot rule out that some may have come from the same individual pelvis.

Taphonomical characteristics

In situ articulation and association could not be assessed systematically within the scoop samples, but the presence of at least three partly associated pelvic bone constellations (i.e. bone clusters belonging to one individual) suggests that partial

Fig. 4 Selected dodo upper body remains from Mare aux Songes: **a** sternum (AG 94); **b** cervical vertebra (AG 83); **c** left scapula (AG 57); **d** left humerus (AG 112); **e** left radius (AG 16); **f** left carpometacarpus (AG 62). *Scale bar* notes 5 cm
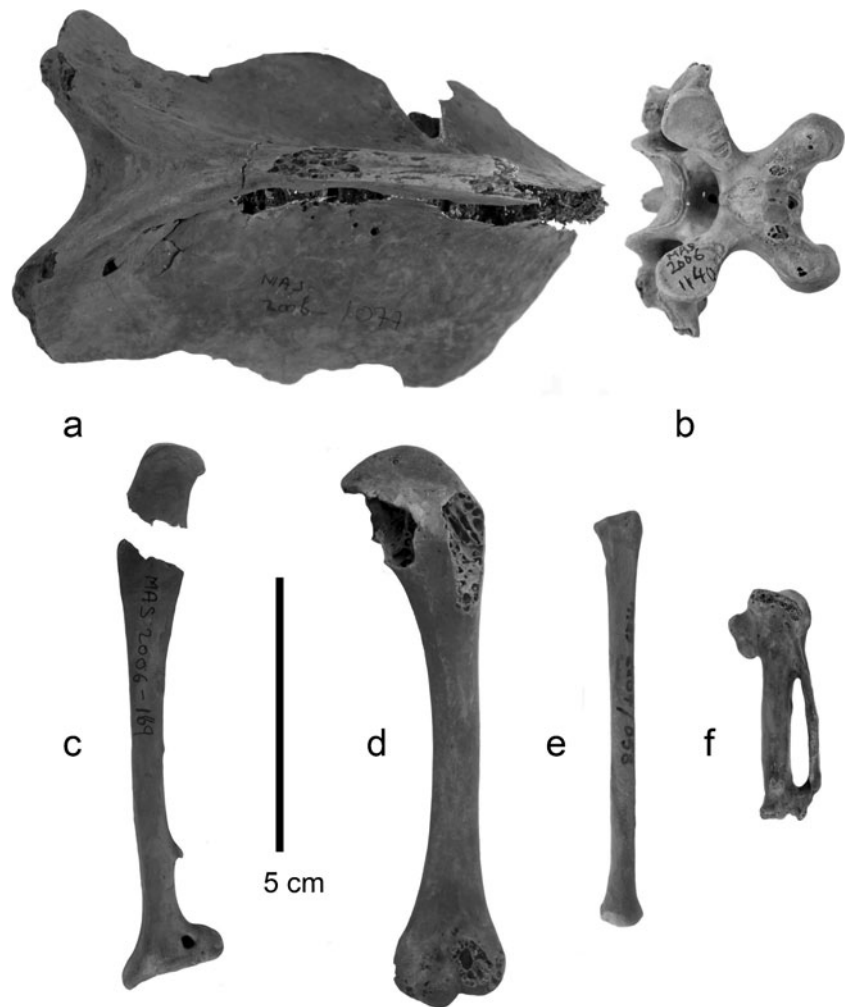
in situ association occurs (MAS-AG 171-173, 184-189 and 183-196-472). Throughout the dodo assemblage, bone preservation is good. The majority of the MAS dodo bones (>70%) shows a medium to dark brown colouration (colour classes 2.0–3.0), with lighter colours being less common.

There are no signs of subaerial weathering: the surface of the bones is very smooth and small bone structures are still present. The dodo bones were therefore all assigned to weathering stage 0 as defined by Behrensmeyer (1978), i.e. no signs of cracking and flaking. The majority of the bones show small, non-parallel scratches (Fig. 6) on the surface. They range in length from several millimetres to 10 mm in length and are generally similar in colour or darker than the bone. No gnawing, cutting or burning marks were found on the bones. Most of the bones show no to medium erosion (68%). Heavy and severe erosion is less common. Erosion is most evident on the proximal and distal articular surfaces of the bones due to the thinness of the cortical bone compared to the shaft. Increasing stages of erosion resulted in holes in the bones and sometimes even the removal of the articular surface. It was not clear if a fragmented bone resulted from friction (accumulated erosion) or actual breakage (quick break caused by the pressure of a large object on top of the bone). However, the bones show recent fractures that are thought to have been caused by the dumping of rocks and the sampling with a mechanical digger scoop. These 'new' fractures are generally oblique to the bone long axis, relatively sharp and generally lighter in colour than the undamaged bone surface.

Bias towards hind limb elements

The MAS dodo assemblage is dominated by leg elements, constituting 76% (n=158) (Fig. 3a). Elements from the axial skeleton (including the sternum) are, after the leg elements, far less common (14%; n=29). Cranial bones constitute only 6% (n=13) of the assemblage, whereas wing elements are scarcest with only 4% (n=9). The number of leg elements in MAS is almost twice as many as might be expected if there were no preservational bias (Fig. 3b), whereas wing elements and bones from the axial column are notably under-represented. When skeletal part survivorship is assessed, the %A in the MAS dodo assemblage is 5% suggesting a strong degree of taphonomic overprinting.

Fig. 5 Selected dodo pelvic girdle remains from Mare aux Songes: **a** pelvic fragment with the acetabular region (AG 128-130); **b** right femur (AG 125); **c** right tibiotarsus (AG 100); **d** right tarsometatarsus (AG 480); **e** phalanges (AG 39-40). *Scale bar* notes 5 cm

A difference in location, and thus depositional setting, between Tr. 0 and 1 (located near the north-western edge of the basin) and Tr. 2 and 4 (located more towards the middle) may account for an over-representation of leg elements in one of the two sites. However, a breakdown of the assemblage into trenches (Fig. 3c–d) shows a dominance of leg elements in both Tr. 0 and 1 ($n=26$, leg elements 67%, %$A=0$) and Tr. 2 and 4 ($n=209$, leg elements 76%, %$A=5$). Dominance of hind limb elements was also true of the original nineteenth century collections in which the most common element recovered was the tarsometatarsus (MNI=300) (Hume 2005; Rijsdijk et al. 2009).

Discussion

The recently excavated MAS assemblage and existing collections

The retrieval of small and fragile skeletal elements and the colouration of the recently excavated MAS bone material is in contrast to the material collected in the nineteenth and early twentieth century (Hume et al. 2009). The variation in colour observed in dodo bones in museum collections, ranging from dark brown to almost white, is greater than in the recently excavated assemblage. Also, despite the fact that Carié's collection included small specimens (i.e. Angst and Buffetaut 2010), museum collections appear to be biased towards large elements. These differences confirm the observations by Hume et al. (2009) that the dodo bones excavated in the nineteenth and early twentieth century are derived from another locality outside basin 1 at the eastern margin of the basin complex (Hume et al. 2009). There is no clear indication that sediments were fine sieved during these excavations, as Clark (1866) even described that his workers located fossils in the marshy sediments by using their bare feet. These practices lead to the assumption that there was a taphonomic bias towards larger elements. The recent

Fig. 6 Dodo left femur with polydirectional scratches (*inset*) interpreted as derived from bioturbation such as giant tortoise trampling and/or the anthropogenic deposition of boulders
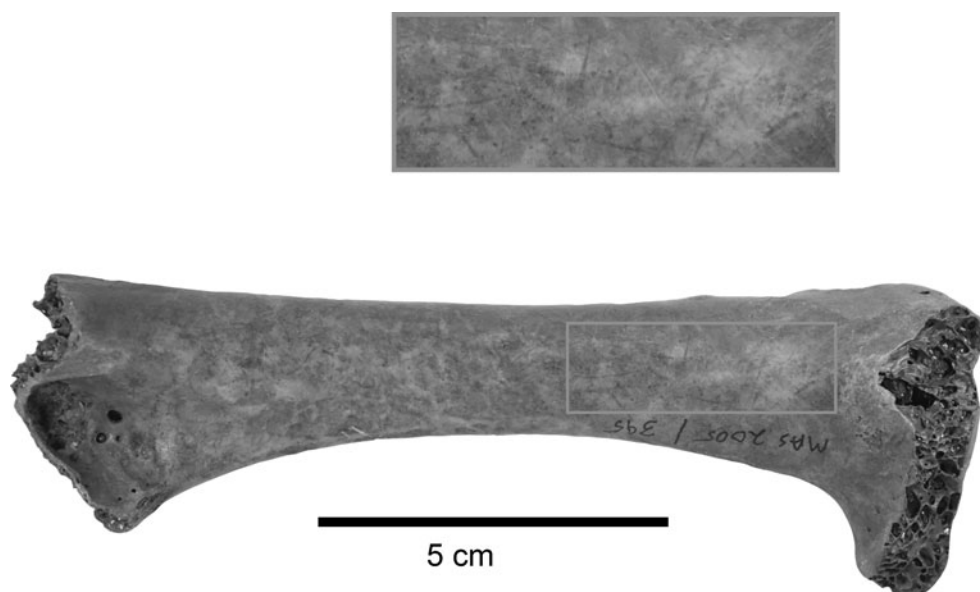
excavation of small elements at MAS confirms that the over-representation of larger elements in previously collected fossil material was at least partly due to sampling bias (Hume 2005).

Dodo death scenarios

Before exploring possible hypotheses for the deposit's formation during the megadrought event, it is important to note that there is very little evidence for post-depositional transport, indicating that the birds died at, or close to, the marsh. Partial observation was only observed incidentally. This is thought to result from in situ disturbances, such as the wallowing of giant tortoises (Hume 2005). Also, due to the insular nature of the fauna, predators as accumulating agents would have contributed little to dodo mortality. Hydrological evidence (Rijsdijk et al. 2009, 2011) indicates that MAS was a rare source of freshwater in a dry, lowland coastal setting which, certainly in times of a megadrought (4235–4100 cal. year BP, Rijsdijk et al. 2011), would have attracted a range of animals.

The simplest death scenario would entail animals dying of starvation and/or thirst, as animals are tied to the water and cannot range far enough to forage. In such a scenario, the bones of the deceased animals would have been exposed at the surface, resulting in weathering of the bone surface (Behrensmeyer 1978; Behrensmeyer et al. 2003). This is in contrast to the good preservation of the bones, indicating that exposure of the bones was limited and burial occurred rapidly after death. A drought scenario alone also does not account for the over-representation of leg bones, as the ratio of anterior and posterior elements (%A and %P) should have been more or less equal. Furthermore, the absence of juveniles, which as a vulnerable subset of the population would certainly have been severely affected, does not support drought-induced death.

Another possibility to explain such a dense assemblage of animals is that in times of drought, animals that gathered at MAS resorted to drinking low quality or even toxic water. As MAS is connected to the sea, brackish groundwater may have flowed into the lake during droughts when lake level dropped below ocean level due to high evaporation rates. Alternatively, toxic cyanobacteria may bloom in standing freshwater lakes during dry, warm periods. There is at least one fossil locality (Neumark Nord, Germany) at which toxic cyanophycean blooms are linked to mass death of vertebrates (Braun and Pfeiffer 2002). So far, there is no evidence to support the presence of toxic algae in MAS. Also, the Neumark Nord vertebrate assemblage was characterised by the presence of complete and articulated skeletons, which have not been found at MAS.

An alternative scenario for the formation of the fossil deposit is that the MAS functioned as a mire in which (heavy) animals became trapped. Mire is an ecological term broadly synonymous with peatland (Johnson and Gerbeaux 2004), and the term 'miring' refers to the trapping of animals in such sites. Miring can lead to well-preserved, associated remains as the sediments would protect the submerged lower parts of the animal's body from subaerial exposure and weathering. After the animal's death, the exposed parts of the carcass may have attracted scavengers, and any remaining exposed parts of the animal on the surface (vertebral column and cranial elements) would have been prone to erosion and scavenging. A miring scenario explains the overrepresentation of hind limb elements and the preservation of small phalanges, and repeated miring events at MAS, over perhaps long periods of time, may have led to the final accumulation.

A miring scenario has also been proposed for Pleistocene and Holocene assemblages of the large, flightless moa (Family Dinornithidae) from New Zealand (Holdaway and Worthy 1997; Worthy 1998; Wood et al. 2008). Particularly, the sites of Pyramid Valley (Holdaway and Worthy 1997) and Te Aute (Worthy 2000) are similar to Mare aux Songes in many respects. Both Pyramyid Valley and Te Aute are swamp deposits, Holocene of age, dominated by large, flightless birds, characterised by an over-representation of leg elements and dense accumulations of mostly disarticulated bones (Holdaway and Worthy 1997; Worthy 2000). For the Pyramid Valley, it is hypothesized that the mire operated seasonally and that mostly heavy, adult females were trapped in summer when water levels were low (Holdaway and Worthy 1997; Turvey and Holdaway 2005). A seasonally active mire at MAS could explain the absence of juvenile dodos in the MAS assemblage. Alternatively, the absence of juvenile dodos may also be indicative of a very low reproductive rate and rapid growth to adulthood, as appears to be the case in the endemic Hawaiian geese, the Moa-nalos (S. Olson, personal communication), or that the breeding grounds were elsewhere. However, it should be noted that the population structure of excavated samples does not necessarily reflect that of the surrounding population, as stratigraphic and taphonomic variation can preferentially affect the preservation of groups within populations (Turvey and Holdaway 2005).

Although the time window for MAS is much shorter than for the NZ sites, a miring scenario explains both the excellent preservation of the bones and the over-representation of posterior elements (%P). Ideally, miring would also lead to finding leg bones articulated and in vertical position. As yet, however, there is no evidence for this at Mare aux Songes. The presence of small polydirectional scratches on the bones (Fig. 6) indicates that there was significant bioturbation during and after deposition of the accumulation (Behrensmeyer et al. 1989). Animals becoming trapped and fighting to get out, as well as giant tortoises scavenging on the carcasses would have caused significant bioturbation at the time of deposition (Hume 2005). The anthropogenic deposition of boulders in the 1940s also might have caused disturbance of the sediments post-deposition.

Conclusions

Taphonomic characteristics of the Mare aux Songes dodo assemblages suggest that the animal remains are found close to the place they died. The hydrology of the area indicates that the presence of freshwater during times of drought drew the animals to the site. Of the various scenarios presented here that might explain the origin of the Mare aux Songes fossil bed, only a miring scenario agrees with the taphonomic evidence thus far. Miring would have specifically affected heavy and flightless animals such as adult dodos and giant tortoises, and repeated miring events at MAS led to the final accumulation.

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