First record of avian extinctions from the Late Pleistocene and Holocene of Timor Leste

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Abstract

Timor has yielded the earliest evidence for modern humans in Wallacea, but despite its long history of modern human occupation, there is little evidence for human-induced Late Pleistocene extinctions. Here, we report on Late Pleistocene and Holocene bird remains from Jerimalai B and Matja Kuru 1, sites that have yielded extensive archaeological sequences dating back to >40 ka. Avian remains are present throughout the sequence, and quails (Phasianidae), buttonquails (Turnicidae) and pigeons (Columbidae) are the most abundant groups. Taphonomic analyses suggest that the majority of bird remains, with the exception of large-bodied pigeons, were accumulated by avian predators, likely the Barn owl *Tyto* sp. All species represent extant taxa that are still present on Timor today, with the exception of a crane, *Grus* sp., from the Late Pleistocene of Jerimalai B, and a large buttonquail, *Turnix* sp., from Matja Kuru 1. The crane likely represents an extirpated population of cranes, which were much more widespread throughout the Indonesian archipelago during the Quaternary. The large buttonquail is present at Matja Kuru 1 alongside the extant *T. maculosus* until at least 1372–1300 cal BP. These two species represent the first records of avian extinctions on Timor. However, a causal relationship between the extinction of these two taxa and human impact cannot be demonstrated at this point.

**Keywords:** Quaternary, island biogeography, Wallacea, birds, extinction, megafauna
1. Introduction

The island of Timor, the largest in the Lesser Sunda island chain, has been the subject of ornithological exploration for more than two hundred years (Hellmayr, 1914; Mayr, 1944). The avifauna consists of 262 bird species, of which 169 are breeding species, 76 migrants and 17 vagrants (Trainor et al., 2008). The Timor Group (including associated islands) has the highest level of endemics (28) within the Lesser Sundas. Due to its relatively close position to Australia, the Timor avifauna contains the highest proportion of Australian elements within Indonesia, initially reported to be ~50% (Mayr, 1944; Monk et al., 1997), but is now believed to lie around 31% due to phylogenetic changes and wider sampling of taxa (Trainor et al., 2008). Despite this long tradition of ornithological research, little is known regarding past avian distributions and diversity. This is in line with the rest of Wallacea, as the fossil bird record for Island Southeast Asia is quite poor (Meijer, 2014).

Timor has yielded the earliest evidence for modern humans in Wallacea, and it may have been the final stepping stone for modern humans dispersing into Australia via the southern route (O’Connor, 2007). Archaeological sequences from Jerimalai Shelter, Lene Hara Cave, and Laili Cave in Timor Leste date back to 43–41 ka, ~42 ka and ~44 ka, respectively (Hawkins et al., 2017b; O’Connor, 2007; O’Connor et al., 2017). The evidence from Jerimalai and Lene Hara indicates that early modern humans on Timor were adept at exploiting marine resources (O’Connor, 2007; O’Connor et al., 2010, 2011). Nonetheless, data from Laili Cave suggest that Late Pleistocene modern humans targeted a wide range of different resources, including terrestrial vertebrates, depending on availability (Hawkins et al., 2017b).

The systematic exploitation of birds was once considered a behavior exclusive to modern humans (Klein 1989) but has now also been observed in Neanderthals (Blasco et al.,
2014; Finlayson et al., 2016) and may even extend back into the Middle Pleistocene (Blasco et al., 2012). Hunting birds for subsistence is currently widespread throughout the Indonesian archipelago, but there is as of yet no evidence for the systematic exploitation of birds by hominins in the region. On Flores, hominins have been present since the early Middle Pleistocene (van den Bergh et al., 2016), but evidence for the exploitation of birds as a food source at either Liang Bua or the So’a Basin is lacking (Meijer et al., 2013, 2015a). On Timor, bird remains are present throughout the sequence at Laili Cave (Hawkins et al., 2017a,b), as well as in Tron Bon Lei rock shelter on nearby Alor Island (Hawkins et al., 2017c). Taphonomic signatures suggests that the majority of bird remains at Laili and Tron Bon Lei were the result of Barn owl predation (Hawkins et al., 2017a,c). However, the presence of pigeons and ducks at Laili, taxa with a body size outside the preferred prey size of Barn owls, has been interpreted as evidence for humans occasionally foraging on birds (Hawkins et al., 2017a).

Despite recording the oldest modern human occupation site in Wallacea, the Laili sequence has not yielded any extinct avian taxa. This is in line with evidence from other Late Pleistocene modern human sites on Timor where fossils of extinct megafauna are absent. In the Pleistocene, Timor likely hosted two species of pygmy proboscidean, *Stegodon timorensis* and *Stegodon ‘trigonocephalus’*, a giant tortoise, and a large, possibly endemic species of *Varanus* (Hooijer, 1971, 1972; Verhoeven, 1964). The absence of these taxa in the earliest modern human sequences at Laili and other cave sites suggests that Timor’s Quaternary megafauna became extinct before the arrival of modern humans on the island (Louys et al., 2016).

Here, we report on bird remains excavated from deposits at Jerimalai Square B and Matja Kuru 1 Squares A and AA that cover the Holocene and Late Pleistocene. The avian assemblages from both sites significantly extend the Timor fossil bird record known from
Laili; they are the most diverse described from Timor so far, and contain a number of previously unrecorded species. In addition, these assemblages yield the first extinct avian taxa for Timor, thereby shedding light on past avian extinctions on the island as well as the island’s Quaternary megafauna.

2. Materials and Methods

2.1 Regional setting

Jerimalai (8°24.84’ S, 127°17.50’ E) is a small coralline limestone shelter located southeast of the village of Tutuala at the easternmost tip of Timor Leste (Figure 1). It currently sits 75 m above sea level and a kilometer from the current coastline. The site was located in 2004, and two test pits of 1m x 1m (Square A and B) were excavated at Jerimalai in 2005. Excavations were carried out in spits of 1–5 cm which followed stratigraphic boundaries where visible. Sediments were wet-screened through 1.5 mm mesh screens. Matja Kuru 1 (8°24.87’ S, 127°07.36’ E) is located in an uplifted limestone ridge northeast of the modern village of Poros, approximately 370 m above sea level and about 8 kilometers from the coast. Excavations at Matja Kuru 1 took place in 2001 and consisted of a 1 x 2 m test-pit (conjoined Squares A and AA), also sampled in approximately 5 cm spits. The geochronology and archaeological sequences of Jerimalai and Matja Kuru 1 have been described by O’Connor (2007) and Langley and O’Connor (2015) and we refer to those publications for more details.

2.2 Fossil analyses
Avian remains were identified by using the avian skeleton collection at the Smithsonian Institution's National Museum of Natural History (prefix NMNH) in Washington, DC (USA), and the Bergen University Museum (prefix B and BM) collections in Bergen, Norway. Comparative material examined (Appendix 1) included skeletons of resident and migrant bird species from Timor (following Eaton et al., 2016 and Trainor et al., 2008), Indonesia, and Australia (following Avibase). The systematic framework follows Howard and Moore's Checklist (Dickinson and Christides, 2014; Dickinson and Remsen, 2013), with the exception of Gruidae (cranes), as species formerly placed in Anthropoides (A. virgo and A. paradisea) and Antigone (A. canadensis, A. vipio A. antigone and A. rubicunda) are now placed within Grus (Yu et al., 2011), and Turnicidae, for which there is now strong support for placing them in Charadriiformes (Baker et al., 2007). Osteological terminology primarily follows Baumel and Witmer (1993) and Howard (1929). Juveniles were identified based on the porosity and texture of the bone surfaces. Measurements were taken with digital calipers to the nearest 0.01 mm. Specimens were examined for signs of bone surface modification, such as bite and cut marks and digestion, using a Leica MZ16 stereo microscope. Digestion patterns were scored in five categories following Andrews (1990), with 0 = no digestion, 1 = minimal, 2 = moderate, 3 = heavy, 4 = extreme. Ten specimens were coated with carbonate on the outer surface and no observations on surface modifications could be made for these specimens. AMS radiocarbon dating was performed at the ANU Radiocarbon Dating Centre (Fallon et al., 2010). Dates are calibrated in Oxcal 4.3 (Bronk Ramsey, 2009) using the ShCal 13 calibration curve (Hogg et al., 2013) to 95.4%.

3. Results
### 3.1 Bone distribution and taphonomy

A total of 416 avian bones and bone fragments were retrieved from excavations at Jerimalai B (n = 231) and Matja Kuru 1A and AA (n = 185). Of these, 269 specimens (65%) were too fragmentary to allow identification beyond Aves. The remaining 147 specimens could be identified to at least 29 avian taxa in 16 families (Table 1).

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<td>Small passerine sp. 2</td>
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Table 1. Species recovered from Jerimalai B and Matja Kuru 1.

The majority of the avian remains from Jerimalai B and Matja Kuru 1 show signs of digestion (Table 2). At Jerimalai B, 51.3% showed no signs of digestion, with 35.9% showing minimal digestion. At Matja Kuru 1A, 38.5% showed no digestion and 55.1% showed minimal digestion. At Matja Kuru 1AA, no digestion and minimal digestion are 27.4% and 66.7%, respectively. Although there is variation between the sites, the taphonomic signatures are consistent with predation by barn owls (Andrews, 1990).

Table 2. Digestion scores for avian assemblages from Jerimalai B, Matja Kuru 1A and 1AA.
Avian remains are present throughout the sequences in Jerimalai B and Matja Kuru 1A and AA, but there are distinct differences in abundance between localities. Quails and buttonquails are most abundant at Matja Kuru 1 (Table 1), in contrast to Jerimalai B, where quails and buttonquails are rare and pigeons are the most abundant taxon. In terms of abundance, avian bone remains (including those that cannot be assigned beyond Aves) in Jerimalai B are most abundant in spit 13 (NISP = 24, Figure 2). O’Connor et al. (2011) distinguish four distinct phases at Jerimalai B. During phases I–III (spits 69–21, 42,000–5,500 cal yr BP), the number of avian bone remains is low, ranging at around 1–3 specimens per spit, with a small peak in spit 58 (NISP = 9) (Table 2). Avian remains are most abundant in phase IV (spits 20–3) which ranges in age from 5,500 cal yr BP to the recent past. Archaeological and faunal evidence from Jerimalai B shows that already during the early occupation phase (I, 42–38,000 cal yr BP), modern humans were exploiting marine resources (O’Connor et al., 2011). Terrestrial fauna, including birds, may have only been opportunistically exploited. During the Last Glacial Maximum, the site was only infrequently occupied, but the early Holocene saw an increase in deposition that reflects more intense occupation. The peak in avian bone abundance observed in Jerimalai B’s Phase IV coincides with this increase in deposition. Avian bone abundance in Matja Kuru 1A and AA varies more than in Jerimalai B (Figure 2). In Matja Kuru 1A, avian bone abundance peaks in spit 34 (NISP = 19), whereas in Matja Kuru 1AA, avian bone abundance peaks in spit 23 (NISP = 14). The peak in bone abundance in Matja Kuru 1A occurs just before 5,600 cal yr BP and coincides roughly with phase IV at Jerimalai B. The peak in Matja Kuru 1AA appears to have occurred earlier, as it occurs below a date of ~ 16 ka cal BP from spit 21 (although as Langley and O’Connor (2016) note the lower MK1 deposits may have been disturbed post-
depositionally, as the 16,000 cal BP date is inverted, underlain by a date from spit 25 of ~ 11 ka cal BP).

### 3.2 Species accounts

#### 3.2.1 Anseriformes

##### 3.2.1.1 Anatidae (ducks, geese and swans)

1. **Aythya australis**

A distal left ulna from Matja Kuru 1AA’s spit 3 represents a medium-sized anatid larger than *Dendrocygna, Anas gibberifrons/gracilis* and *Nettapus pulchrellus*, and is in the size range of *Aythya australis* and *Tadorna radjah*. In both *Aythya* and tadornines, the distal half of the shaft is straighter than in *Anas* and *Dendrocygna* (Worthy, 2004; Worthy and Lee, 2008). Although the fossil specimen is incomplete, the preserved shaft appears to be straighter than in *Anas*. It further differs from *Anas* in having a shallower incisura tuberculum carpale and consequently a less pronounced tuberculum carpale (the incisura is deeper and the tuberculum more pointed in *Anas*). As such, the specimen mostly resembles *Tadorna* and *Aythya*. In distal view, the dorsal surface between the condylus ventralis ulnaris and the tuberculum carpale is bulging in *Tadorna*, whereas it is rather flat in *Aythya* and the fossil specimen. Although the specimen is somewhat more robust than the specimens of *Aythya* available for inspection, it is morphologically most similar to this genus. The Hardhead *Aythya australis* is a common visitor from Australia (Eaton et al., 2016; Trainor et al., 2008), and given the young age of the specimen (spit 3), it is referred to this species.

2. **Dendrocygna arcuata**

The Wandering Whistling-duck *Dendrocygna arcuata* is recognized based on a right coracoid from Matja Kuru 1AA, spit 16 (Fig. 3A). The specimen lacks a pneumatic foramen under the
acrocoracoid and bears a distinct broad depression on the ventral surface of the sternal blade. This depression is located just proximal of the sternal articular facet and extends laterally to the linea intermuscularis ventralis. This depression was not observed in any species of *Tadorna, Anas, Aythya, or Nettapus*, but was present in more than half of *Dendrocygna arcuata* and *D. bicolor* specimens. In size, it agrees best with *D. arcuata*, which is the only species of *Dendrocygna* known to occur on Timor today (Eaton et al., 2016; Trainor et al., 2008).

### 3.2.2 Galliformes

#### 3.2.2.1 Phasianidae (pheasants and allies)

Twenty-nine specimens can be assigned to quails (Phasianidae). Quails are morphologically close to buttonquails (Turnicidae) and rails (Rallidae), but can be distinguished from these groups based on a number of osteological features. In the quail humerus, the tuberculum ventrale is connected to the caput humeri by a distinct crista incisura capitis, which bisects the incisura capitis. In rails, the tuberculum ventrale is not connected to the caput humeri (and the incisura capitis is wide and not bisected), whereas in buttonquails, the incisura capitis is very short and limited to the ventral aspect of the bone. In the phasianid carpometacarpus, the processus intermetacarpalis is distinct and reaches the os metacarpale minor. The carpal trochlea is rounded in ventral aspect, but in dorsal aspect, the dorsal rim of the trochlea is only rounded proximally, and distally cuts away in a straight line towards the processus intermetacarpalis. In Turnicidae, the dorsal rim is fully rounded. Small phasianid tibiotarsi can be distinguished from *Turnix* and small rails by having a relatively narrower distal end, and a higher tendinal bridge that is oriented more obliquely than in Turnicidae (horizontal in Rallidae). In proximal view, the rim formed by the facies articularis medialis and fossa retropatellaris is smooth in phasianids whereas it is notched in *Turnix* (i.e. facies
articulare medialis projects more medially than the fossa retropatellaris). In the proximal
tarsometatarsus, the lateral and medial sides are caudally excavated in *Synoicus* (Phasianidae),
unlike in Rallidae and Turnicidae. Moreover, *Synoicus*, as other Phasianidae, has one canal
for the tendon of the musculus flexor digitorum longus (open sulcus in Rallidae), but a
plantarly open sulcus for the superficial flexor tendons of the muscles that flex the second toe
(Mayr, 2016), and the hypotarsus is located laterally. The hypotarsal ridges are
proximodistally equally long in *Synoicus*, but the lateral ones are shorter in *Turnix*. In
Rallidae, there is one long central ridge, and some shorter ones. In the distal tarsometatarsus,
the medial and lateral plantar ridges are distinct in *Synoicus*, and the fossa metatarsi I is most
prominent in *Synoicus*. All specimens agree in these features with Phasianids, particularly
*Synoicus*. Only three species of phasianid are present on Timor, one of which is the much
larger *Gallus gallus*. The other two are *Synoicus ypsilophorus* and *S. chinensis*, with the
former being larger than the latter (del Hoyo et al., 2017). Within the twenty-nine specimens,
two species can be distinguished based on size differences.

### 3.2.2.1.1 *Synoicus ypsilophorus*

Twenty-eight specimens (a fragment of a sternum, one coracoid, eleven humeri, two
carpometacarpi, one femur, five tarsometatarsi, and seven tibiotarsi; Jerimalai B, spits 42, 47,
and 62; Matja Kuru 1A, spits 11, 14, 15, 22, 31, 32 and 34; Matja Kuru 1AA, spits 17, 21, 22,
26, 24, 25, 35) are assigned to the Brown Quail *S. Ypsilophorus* (Fig. 3C, E). Although only
two specimens of extant *S. ypsilophorus* were available for measurements, the remains from
Matja Kuru 1 and Jerimalai B reported agree with *S. ypsilophorus* in size, and are consistently
larger in measurements of the humerus, tibiotarsus and tarsometatarsus than *S. chinensis*
(Figure 4).

### 3.2.2.1.2 *Synoicus chinensis*
The Blue-breasted Quail *S. chinensis* is represented by only a single fragmentary left distal tibiotarsus from Jerimalai B, spit 69. The specimen is incomplete, but what remains of the bone is similar in morphology to *S. ypsilophorus*, yet smaller. The only meaningful measurement, distal width (3.1 mm), is smaller than *S. ypsilophorus*, and in the size range of *Synoicus chinensis* (Figure 4B).

### 3.2.3 Podicipediformes

#### 3.2.3.1 Podicipedidae (grebes)

3.2.3.1.1. cf. *Tachybaptus*

Grebes are represented by a single specimen, a right proximal humerus, from Matja Kuru 1 AA, spit 23. This specimen represents only the proximal articulation and a section of the shaft. The crista deltapectoralis is mostly missing, but appears to have extended down the shaft for a significant length. The tuberculum dorsale is distinct and set off medially of the caput humeri. The fossa pneumotricipitalis ventralis is not pneumatized, the fossa pneumotricipitalis dorsalis is absent, and the margo caudalis is pronounced. In these features, the specimen agrees very well with the Podicipedidae. Two species of grebe are known from Timor, *Tachybaptus ruficollis* and *T. novaehollandiae* (Eaton et al., 2016; Trainor et al., 2008). In overall size, the specimen from Matja Kuru agrees with smaller grebes such as *Tachybaptus*, but is more gracile than *T. ruficollis* (width of the proximal articulation in fossil specimen: 8.27 mm, *T. ruficollis* 8.88 – 9.76 mm, n = 3). The fossil specimen may represent *T. novaehollandiae* instead, which is slightly smaller (del Hoyo et al., 2017), but no specimens of that species were available for comparisons. We therefore tentatively refer it to the genus *Tachybaptus* until more comparative material becomes available.
3.2.4 Columbiformes

3.2.4.1 Columbidae (pigeons and doves)

Pigeons are represented by at least 6 species, and include large-bodied and small pigeons.

3.2.4.1.1 Large pigeon cf. Ducula/Caloenas

A sternal fragment (Jerimalai B, spit 12), a distal right coracoid (Jerimalai B, spit 14) (Fig. 3H), and juvenile tarsometatarsus shaft (Matja Kuru 1AA, spit 9), represent a large-sized columbid more robust than Columba and in the size range of Ducula (Imperial pigeons) and Caloenas (Nicobar pigeon). Both genera are extant on Timor, but the fragmentary nature of the specimens does not allow for a generic identification.

3.2.4.1.2 Columba vitiensis

The Metallic Pigeon is represented by six specimens from Jerimalai B: a proximal right coracoid (spit 10) (Fig. 3L), a distal right coracoid (spit 11), a proximal and distal left coracoid (spit 16 and 17), a left humerus shaft (spit 11), and a distal tibiotarsus (spit 29); a distal right coracoid from Matja Kuru 1A (spit 15), and a sternal fragment (spit 6) and a distal right coracoid (spit 13) from Matja Kuru 1AA. The proximal coracoids lack a pneumatic foramen under the processus acrocoracoideus, which separates them from similarly sized species of Ptilinopus and Macropygia (Worthy and Wragg, 2008). Furthermore, the proximal coracoids have a relatively short processus acrocoracoideus, which distinguishes them from Ducula and Caloenas, which have a more elongated processus acrocoracoideus. In these aspects, the specimens agree best with Columba. The only native species of Columba known from Timor today is Columba vitiensis (C. livia is considered recently introduced, Eaton et al., 2016), and as the specimens agree well with this species, they are therefore assigned to this taxon.

3.2.4.1.3 cf. Treron
A green pigeon is tentatively reported based on a medium-sized left coracoid from Jerimalai B, spit 16. The coracoid also lacks a foramen under the processus acrocoracoideus, and therefore can be distinguished from *Ptilinopus* and *Macropygia*. The processus acrocoracoideus itself is more elongated than in *Streptopelia* and *Chalcophaps*. The specimen is more gracile than the *Columba vitiensis* coracoid from the same spit, and agrees well with species within the genus *Treron* in size and morphology. However, since a number of columbid species were unavailable for comparison, we only tentatively refer it to this genus.

### 3.2.4.1.4 Macropygia sp.

Cuckoo doves are reported based on three right coracoids, a left distal tarsometatarsus, and a proximal right scapula from Jerimalai B, spits 4, 10 (Fig. 3I), 11 and 14 and Matja Kuru 1AA, spit 12. The coracoids have a pneumatic foramen under the processus acrocoracoideus, in agreement with *Macropygia* and *Ptilinopus*. The specimens are more robust than *Ptilinopus* and agree in size with *Macropygia*. The scapula and tarsometatarsus are in the size range of *Macropygia* and are therefore tentatively referred to this genus as well.

### 3.2.4.1.5 Ptilinopus sp.

A right proximal coracoid and a left distal carpometacarpus from Jerimalai B’s spit 18 are referred to fruit doves; the coracoid is small with a large pneumatic foramen under the processus acrocoracoideus, and because of its small size, it is attributed to *Ptilinopus* rather than *Macropygia*. The distal carpometacarpus from the size spit is columbiform in shape and agrees in size with *Ptilinopus* as well. Two species of fruit dove are known from Timor, *P. cinctus* and *P. regina* (Trainor et al., 2008), with the latter being larger. The small size of the Jerimalai specimens may indicate that they belong to *P. cinctus*, but no specimens of this species were available for comparison.

### 3.2.4.1.6 Geopelia sp.
A small dove in the genus *Geopelia* is represented by a right proximal coracoid from Jerimalai B, spit 29. This coracoid lacks a foramen under the processus acrocoracoideus, is smaller in size than *Streptopelia* and *Chalcophaps*, and fits quite well with *Geopelia striata*. However, since this species is considered introduced (Eaton et al., 2016) and no comparative material of the second species of *Geopelia* on Timor, *G. maugeus* was available; more material is needed for this specimen to be assigned to species level.

3.2.4.1.7 Columbidae indet.

A right distal humerus from Jerimalai B, spit 39, represents a small species of columbid, but the specimen is too damaged for any meaningful comparisons.

3.2.5 Cuculiformes

3.2.5.1 Cuculidae (cuckoos and allies)

3.2.5.1.1 Cuculidae gen. et sp. indet

A cuckoo has been identified based on a proximal right coracoid from Jerimalai B, spit 50. The morphology of the proximal coracoid superficially resembles the passerine coracoid, with a processus acrocoracoideus that overhangs the ventral side of the bone (a “hooked” processus acrocoracid). However, the proximal articulation is more compressed and wider, the facies articularis clavicularis is straight, and the surface beneath it somewhat excavated. Compared to *Cuculus*, the specimen is more stout, and the scapular facet projects distinctly further dorsally from the shaft. The processus procoracoideus is broken and its shape and size cannot be ascertained. Therefore the specimen is assigned to Cuculidae gen. et sp. indet.

3.2.6 Gruiformes

3.2.6.1 Gruidae (cranes)

3.2.6.1.1 *Grus* sp.
Remains of a crane, *Grus* sp., were recovered from Jerimalai B, spit 59. The specimen is a stout and almost complete axis, with only the tip of the processus ventralis corporis missing (Fig. 3M–N). The specimen is slightly longer (20.2 mm) than high (18.1 mm), and differs in that respect from Accipitriformes (higher than long), Anseriformes (much longer than high), and Phoenicopteriformes (more elongated). The specimen is in the size range of *Ciconia*, but differs from that genus (and other Ciconiiformes) in having a longer vertebral body and a lower processus spinosus. In that respect, it agrees well with larger members of the Gruiformes, Gruidae (and differs from, for instance Rallidae in having a much broader dens and a blunter and rounded processus spinosus, more projecting in Rallidae). Cranes are absent from Timor today, but Australia and New Guinea are home to several species of crane, including the Sarus crane *Grus antigone* and the Brolga *G. rubicunda*. However, the Jerimalai specimen differs from the extant species of *Grus* examined here, including *G. antigone*, *G. rubicunda* and *G. grus*, in having a facies articularis caudalis that is oriented slightly more caudally, having a bulbous, relatively low and blunt processus spinosus, having a relatively wide and blunt dens, and in dorsal view the caudal zygapophyses join the shaft more abruptly (more gradual in *Grus*). No species of crane is known from Timor, and the specimen clearly represents a species of crane absent from the region today. We refrain from naming this taxon until more material becomes available.

3.2.6.2 Rallidae (rails and coots)

3.2.6.2.1 Large rail

The remains of a large rail were recovered from Matja Kuru 1A (a proximal coracoid, a partial quadrate, a distal left tibiotarsus and a proximal right humerus, spits 12, 19, 21, and 26) and Matja Kuru 1AA (a distal right tibiotarsus from spit 23). The remains represent a mixture of osteological characters and may represent more than one species, which is why we refrain
from assigning it to a genus at this point. The specimens are in the size range of the Purple
Swamphen *Porphyrio porphyrio* and larger than most *Fulica atra*. The coracoid displays a
processus procoracoideus which carries a facet for the scapula medially of the cup-shaped
scapular facet, similar to *P. porphyrio*, but differs from that species in having a relatively
shorter processus acrocoracoideus. In this aspect, the specimen is more similar to *Fulica atra*,
but differs from that species in that the facies articularis clavicularis is wider. Moreover, the
corpus coracoidei is wider and the processus procoracoideus is not distinctly set off from its
medial margin, unlike *Fulica*.

3.2.6.2.2. Medium rail 1 cf. *Rallus/Rallina/Amaurornis*

A medium rail is represented by two right distal tibiotarsi and a right coracoid from Matja
Kuru 1A (spit 14) and Matja Kuru 1AA (spits 15 and 19). In size, the specimens agree with
*Rallus, Rallina* and *Amaurornis*. The right coracoid has a rather long and pointed processus
acrocoracoideus, and is more gracile than the left one and agrees with the genera *Rallus,
Rallina*, and *Amaurornis*.

3.2.6.2.3 Medium rail 2

A second species of medium rail was retrieved from Matja Kuru 1AA, spit 20. The specimen,
a left proximal coracoid, differs from the right proximal coracoid retrieved from Matja Kuru
1AA (spit 19) in that the processus acrocoracoideus is shorter and more blunt, and the
specimen itself is more robust than *Rallus, Rallina* and *Amaurornis*.

3.2.6.2.4 Zapornia sp.

A proximal right humerus from Matja Kuru 1A (spit 8) represents a small rail in the genus
*Zapornia* (formerly *Porzana*). There are currently three species of *Zapornia* known from
Timor (Eaton et al., 2016; Trainor et al., 2008), but the specimen does not allow for a species
identification.
3.2.7 Charadriiformes

3.2.7.1 Scolopacidae (waders)

3.2.7.1.1 Calidris spp.

A right coracoid (Matja Kuru 1AA, spit 25), a left carpometacarpus (Matja Kuru 1A, spit 16) and two left distal humeri (Matja Kuru 1A, spits 4 and 6) are assigned to sandpipers of the genus *Calidris*. The coracoid is small and has the typical charadriiform shape (a broad, overhanging facies articularis clavicularis and a deep, circular scapular facet) and lacks the foramen n. supracoracoidei in the procoracoid. This foramen is absent in Scolopacidae but variable in Glaeolidae, Alcidae and Turnicidae (Mayr, 2011) but these have a derived morphology of the coracoid. Within Scolopacidae, it can be distinguished based on its small size and agrees well with *Calidris*. The two distal humeri display an elongated and proximally directed processus supracondylaris dorsalis (characteristic for Charadriiformes). They are assigned to Scolopacidae because of the relatively shorter and more rounded processus flexorius which projects from the shaft at a right angle (oriented more proximally in the similarly-sized *Charadrius*). In both humeri, the fossa brachialis is deep and proximally clearly bordered off from the rest of shaft, a feature that is more pronounced in the smaller scolopacids such as *Arenaria* and *Calidris*. The specimens are smaller than *Arenaria*, and agree very well with *Calidris*. Carpometacarpus morphology is rather uniform within Charadriiformes, with a very straight os metacarpale majus, a proximally projecting processus extensorius, and a trochlea carpalis with a rounded ventral rim and an elliptical dorsal one.

Given the small size of the specimen, it is referred here to *Calidris* as well. At least eight species of *Calidris* are known from Timor (Trainor et al., 2018), but because of the significant overlap in size, more material is needed to identify these remains to species level.
3.2.7.2 Laridae (gulls and terns)

3.2.7.2.1 Laridae indet.

A small species of Laridae is represented by a right coracoid from Matja Kuru 1A, spit 16. The specimen is broken in two and lacks the procoracoid, but has a wide and overhanging processus acrocoracoideus and a cup-shaped scapular facet, typical of Charadriiformes. The area under the processus acrocoracoideus is deeply excavated, much more so than in Charadriidae and Scolopacidae, and agrees most with the condition seen in Laridae. Distally, the medial sternal surface is excavated deeply as well, and in distal view, the extremitas sternalis is strongly curved, with the medial portion of facies articularis sternalis greatly dorsoventrally widened (Mayr, 2011). The specimen is small but larger than *Chroicocephalus ridibundus*, *Sternula albifrons* and *Chlidonias hybrida*, and is comparable in size with terns in the genus *Sterna*. Given that not all species were available for comparison, we refrain from assigning it to genus level.

3.2.7.3 Turnicidae (buttonquails)

Buttonquails are the most abundant taxon in the assemblages with a total of 38 specimens. The *Turnix* assemblage displays variation in size that is most pronounced in the humeri, coracoids and tarsometatarsi. The size variation surpasses that seen in specimens of extant taxa, and suggests that at least two species of buttonquail were present on Timor until quite recently.

3.2.7.3.1 Turnix maculosus

The smaller morphotype is reported from Jerimalai B (spits 48 and 49), Matja Kuru 1A (spits 12, 13, 23, 33, and 34) and Matja Kuru 1AA (spits 18, 19, 20, 22, 23, 25 and 35), and is referred to the Red-backed Buttonquail *T. maculosus*. The material consists of five distal tarsometatarsi, one distal right tibiotarsus, one proximal right carpometacarpus, two left
humeri, one proximal right humerus, a distal right humerus, four proximal right coracoids and
three proximal left coracoids (MNI = 18) (Fig. 3P–Q, V). The specimens are smaller than *T.
suscitator* in most measurements and partially overlap with *T. sylvaticus* (Fig. 5) for
dimensions of the coracoid, humerus and tarsometatarsus. The modern Timor avifauna
contains only *T. maculosus*, for which no skeletons were available for comparison for this
study. However, *T. maculosus* is described as small and its body measurements and body
weight (del Hoyo et al., 2017; Dunning, 2008) are smaller than for other species including *T.
suscitator*. Furthermore, Hawkins et al. (2017b) identified *T. cf. maculosus* from Late
Pleistocene deposits at Laili Cave, and it is therefore likely that the small morphotype group
from Jerimalai and Matja Kuru 1A and 1AA represents the extant *T. maculosus* as well.

3.2.7.3.2 Large *Turnix*†

A second, larger species of *Turnix* is reported from Matja Kuru 1A (spit 8, 13, 18, 20, 24, 25,
32 and 34) and Matja Kuru 1AA (spits 11, 14, 17, 20, 22, 23, 24 and 35), but not Jerimalai B.
It is represented by a left carpometacarpus, three proximal left coracoids and two proximal
right coracoids, one left humeri, four distal left humeri, one proximal right humerus, three
right tarsometatarsi, one distal right tarsometatarsus, one proximal left tarsometatarsus, two
distal left tibiotarsi and one distal right tibiotarsus (MNI = 20) (Fig. 3R, W, X). This larger
morphotype is larger than *T. sylvaticus*, and partially overlaps with *T. suscitator*, *T. tanki* and
*T. ocellatus*. However, the width and depth of shaft of the coracoid (Figure 5A) and the
proximal and distal dimensions of the tarsometatarsus (Figs. 5E-F) surpass those of *T.
suscitator*, *T. tanki* and *T. ocellatus*. This could indicate that this morphotype represents larger
individuals of one or more of these three extant taxa (in which case they would represent an
extirpated population, as none of these taxa occur on Timor today), albeit with slightly
different proportions. Alternatively, this morphotype represents an unknown species whose
dimensions only partially overlap with extant taxa. This indicates that a second, larger species
of *Turnix* was present on Timor in the Terminal Pleistocene and Holocene, and this species is now likely extinct. Radiocarbon dating of the latest occurrence of this morphotype, a proximal coracoid from Matja Kuru 1 A, spit 8 (Fig. 3X), indicates an age for this specimen of 1372–1300 cal BP (S-ANU# 55223, 1490 ± 24 BP).

3.2.7.4. Charadriiformes indet

A right distal humerus from Matja Kuru 1AA (spit 26) and a proximal left tibiotarsus from Jerimalai (spit 15) represent medium-sized charadriiforms, but the specimens do not allow for a generic assignment.

3.2.8. Accipitriformes

3.2.8.1 Accipitridae (diurnal birds of prey)

3.2.8.1.1 *Haliaeetus leucogaster*

A proximal left tarsometatarsus from Matja Kuru 1A, spit 24 (Fig. 3AA), and a distal right tarsometatarsus from Jerimalai B, spit 16 (Fig. 3AC), are referred to the White-bellied Sea Eagle *Haliaeetus leucogaster*. The proximal tarsometatarsus preserves the two articular cotyla and the hypotarsal region. The crista lateralis is short and blunt, unlike *Accipiter*, *Pernis*, *Elanus*, *Aviceda*, *Butastur*, *Circus* and *Aquila*, and is agrees with the condition seen in *Haliaeetus*. The sulcus hypotarsi is deep and proximally bordered by a ridge that separates it from the proximal articular surface. In this aspect, the specimen differs from the similarly sized *Circaetus* and *Aquila*, and agrees with *Haliaeetus leucogaster*. Cranially, the impressiones retinaculi extensorii are distinct and form two parallel lines of approximately 3 mm length, with the lateral one connecting to the cotyla. In *Aquila* and *Circaetus*, these impressions are less pronounced, whereas they are very distinct in *Haliaeetus leucogaster*.

The distal right tarsometatarsus preserves only the most distal part of the shaft and the
trochlea. It differs from *Aquila* and *Circaetus* in having a slightly shorter trochlea metatarsi II in distal view, and agrees in this aspect best with *H. leucogaster*.

3.2.9 Strigiformes

3.2.9.1 Tytonidae (barn owls)

3.2.9.1.1 cf. *Tyto*

A proximal left phalanx proximalis digiti majoris and a distal left humerus, recovered from Jerimalai B, spit 59, and Matja Kuru 1A, spit 33, are tentatively referred to barn owls. Only the proximal half remains of the phalanx, but it is assigned to Tytonidae rather than Strigidae in that the proximal part of the blade rises gradually, whereas in Strigidae, the blade rises more abruptly from the pila cranialis, and that the dorsal surface of the pila cranialis is rather flat (more concave in Strigidae) (also see Göhlich and Ballman, 2013). The distal humerus only preserves the articular end which hampers identification of the specimen. However, what remains of the fossa musculi brachialis is well defined and excavated, typical for Tytonidae (see Suárez and Olson, 2015), and therefore this specimen is referred to Tytonidae rather than Strigidae. The specimen differs from *Phodilus* in having a broader epicondylus ventralis and a less pronounced tuberculum supracondylare dorsale. However, in most of the *T. alba* and *T. longimembris* specimens examined, the tuberculum supracondylare dorsale protrudes more distinctively from the shaft in cranial view, and the fossa olecrani on the caudal surface is deeper. The size of these two fragmentary remains is consistent with both specimens belonging to one species which is larger in dimensions than extant *Tyto*; the proximal left phalanx proximalis digiti majoris measures 9.25 mm in length (6.88 mm in *T. alba*, n = 7), the distal width of the humerus measures 16.29 mm (13.28 mm in *T. alba*, n = 7; 17.2 mm in *T. longimembris*, n = 1) The specimens may represent an endemic species of extinct barn owl, but given their fragmentary state, this identification should be treated with caution.
3.2.9.2 Strigidae (typical owls)

3.2.9.2.1 cf. *Ninox*

A distal tibiotarsus from Jerimalai B, spit 61 represents a boobook owl. Similar to all Strigiformes, the specimen lacks a pons supratendineus, and its mediolateral dimensions are slightly wider than its antero-posterior ones, which distinguishes it from Tytonidae. In size, it agrees well with the boobook owls in the genus *Ninox*, and is much larger than *Otus*, the other genus of strigid owls on Timor and one which displays small body size. It is therefore tentatively referred to *Ninox*.

3.2.10 Falconiformes

3.2.10.1 Falconidae (falcons)

3.2.10.1.1 *Falco* sp.

Falcons are represented by a right coracoid from Matja Kuru 1AA (spit 24). The specimen lacks the acrocoracoid, but the procoracoid is elongated and triangular in shape, and what remains of the scapular facet indicates that it was shallow. These features are characteristic of Falconidae. The specimen lacks a foramen in the procoracoid, a feature characteristic for a few species within Falconidae, i.e. *Falco*, *Microhierax* and *Polihierax* (Suárez and Olson, 2001). The latter two are small species, and the Matja Kuru specimen agrees better with *Falco*. Four species of *Falco* have been recorded on Timor, *Falco moluccensis*, *F. subbuteo*, *F. longipennis* and *F. peregrinus*. There is significant overlap in size between these species, and without the complete bone, we refrain from assigning this specimen to species level.

3.2.11 Passeriformes

3.2.11.1 Motacillidae (wagtails and pipits)
3.2.11.1 Anthus/Motacilla

A left proximal humerus from Matja Kuru 1AA’s spit 22 represents a motacillid in the genera Anthus or Motacilla. This small proximal humerus displays a very deep fossa pneumotricipitalis dorsalis that is confluent with the fossa pneumotricipitalis ventralis.

Confluent fossae like this are present in only a few passerine groups, including Prunellidae, Aegithalidae, Remizidae, and Motacillidae (Jánossy, 1983). The crus dorsale fossae is absent and the floor of the fossa pneumotricipitalis (i.e., the bicipital shelf) is very thin. In these features the specimen agrees with Motacillidae. Seven species of Motacillidae in the genera Motacilla and Anthus are present on Timor, but the current incomplete specimen does not allow for a distinction between them.

3.2.11.2 Family indet.

3.2.11.2.1 Medium passerine

A right humerus from Matja Kuru 1AA (spit 34) represents a medium-sized passerine. The humerus lacks the most diagnostic part, the proximal articulation, but based on size belongs to a medium-sized passerine.

3.2.11.2.2 Small passerine sp. 1

A left proximal humerus from Matja Kuru 1AA (spit 20) represents a species of very small passerine. The humerus displays a deep fossa pneumotricipitalis dorsalis that is separated from the fossa pneumotricipitalis ventralis by the crus dorsale fossae. This specific humeral morphology is present in several groups of small passerines, including Rhipiduridae and Zosteropidae, and a family level identification cannot be ascertained at this point.

3.2.11.2.3 Small passerine sp. 2

A second species of small passerine is represented by two humeri from Matja Kuru 1A’s spits 24 and 34. They differ from the previous small passerine humerus in that the fossa...
pneumotricipitalis dorsalis is completely separated from the fossa pneumotricipitalis ventralis by the crus dorsale fossae, and thus represent a separate species.

Discussion

Bird remains from Timor were first described by Hawkins et al. (2017a,b), who reported six taxa from Late Pleistocene (44.6–11.2 ka) deposits at Laili Cave. The current study adds twenty-four new taxa to the avian fossil record of Timor, including rails, cuckoos, sandpipers, terns, sea-eagles, falcons, owls and wagtails. In addition, we identify two taxa that are currently not known from Timor, a large buttonquail \textit{Turnix} sp. and the crane \textit{Grus} sp., both likely representing extinct species. Fragmentary remains hint at a potentially extinct large barn owl, but the material currently available does not allow unambiguous identification.

Both Jerimalai B and Matja Kuru 1 preserve evidence for early human occupation, but no cut marks or other signs indicative of human subsistence were observed on any bird bones. This does not necessarily mean that birds were not eaten by early humans, since many birds are small enough to be eaten whole. The taphonomy of the Jerimalai B and Matja Kuru 1 assemblages (Table 2) suggests that avian predators, most likely barn owls, were the main accumulating agents for the majority of the assemblage. This is in agreement with the avian assemblage from Laili cave (Hawkins et al., 2017a,b). However, Hawkins et al. (2017a) suggested that pigeons may have been hunted by humans, as they fall outside the prey size spectrum for barn owls. At Jerimalai, the pigeon remains show a somewhat different taphonomic profile, with equal numbers showing no digestion and minimal digestion. Quails, buttonquails and songbirds show predominantly minimal digestion, and all three groups of
birds fall within the barn owl prey size (< 200 gr., Morris, 1979). Furthermore, pigeons are most abundant during phase IV (Figure 7), which saw the most intense human occupation. This could suggest that the pigeon remains were accumulated by a taphonomic agent other than barn owls. This is in line with the conclusions of Hawkins et al. (2017a) for Laili cave, who suggested that some pigeons may have been deposited by humans instead.

Despite the long presence of modern humans on Timor and adjacent islands, there is as of yet no evidence for an anthropogenic role in the extinction of Pleistocene (mega)fauna (Louys et al., 2016). The crane *Grus* sp. and the buttonquail *Turnix* sp. represent the first records of avian extinctions on Timor. Although our data as of yet do not allow for an explanation for their disappearance, the fact that they disappear at different points in time may point to different causal mechanisms.

The crane *Grus* sp. is represented by only a single specimen from spit 59 at the base of the Jerimalai B sequence. Radiometric dating of marine shells from Jerimalai B’s lower levels indicates an age of at least 42,000 cal BP (O’Connor et al., 2011; Langley and O’Connor, 2016: table 2) for the base of the sequence. Depositional mixing of the lower levels is believed to be very limited, and the *Grus* sp. specimen is therefore assumed to be Late Pleistocene in age as well. Cranes are generally absent from Island Southeast Asia, but two species of cranes are known from Southern Asia and Australia (del Hoyo et al., 2017). The Brolga (*Grus rubicunda*) occurs in northern Australia and small parts of New Guinea, whereas the Sarus Crane (*G. antigone*) is currently found in northwest India, Myanmar, Cambodia and northern Australia, but not in between (del Hoyo et al., 2017). Both birds are wetland species and non-migratory, rendering it unlikely that the Jerimalai specimen represents a seasonal migrant. Genetic work has retrieved the Brolga and Sarus Crane as sister taxa (Yu et al., 2011). In addition, the Sarus Crane likely originated in Southeast
Asia, dispersed northwards and southwards during times of low sea level, and subsequently became extinct in most of Island Southeast Asia (Das, 2010; Wood and Krajweski, 1996).

Although the axis from Jerimalai cannot be assigned to species level, it is indicative of a Late Pleistocene population of cranes on Timor that has since been extirpated. On the basis of the single occurrence of Grus sp. at the base of the Jerimalai sequence, Grus sp. clearly overlapped with modern humans at Jerimalai. However, as we know virtually nothing of its ecology, any interpretation of its likely cause of extinction would be speculative. Likewise, inferring timing of extinction based on one specimen is uncertain at best. It should be noted that Wetmore (1940) identified a humerus from Late Pleistocene deposits at Watoealang on Java as belonging to the Common Crane Grus grus. It is unclear if Wetmore compared the specimen to G. rubicunda and G. antigone, but this record strengthens the notion that cranes were more widespread in Island Southeast Asia in the Late Pleistocene. If that is indeed the case, the disappearance of Grus from Timor may have been in response to regional factors, beyond those specific to Timor.

The large buttonquail is absent from Jerimalai, but is present from spits 34–8 at Matja Kuru 1A, and from spits 35–11 at Matja Kuru 1AA. The deepest levels at Matja Kuru 1A and AA date to ~11 ka (Langley and O’Connor, 2016: tables 3–4). Mollusk shells from Matja Kuru 1A spit 8, which marks the larger Turnix morphotype’s highest stratigraphic occurrence, have been dated to 5,456–5,274 cal BP (Langley and O’Connor, 2016: tables 3). However, radiocarbon dates produced for this site suggest it has undergone considerable disturbance. Because of this, we elected to obtain a direct radiocarbon date from the larger Turnix morphotype from spit 8. This indicated a much younger age (of 1,372–1,300 cal BP, see above), suggesting that it disappeared more recently than expected from the site chronostratigraphic profile. Interestingly, this date is roughly coeval with the disappearance of
Timor’s giant rats (Aplin and Helgen, 2010; O’Connor and Aplin, 2007), such that these extinctions may have a common anthropogenic or environmental cause.

So far, this represents the first extinction of a bird species in the Holocene in Island Southeast Asia. However, as the fossil record for birds in this region remains poor (Meijer, 2014), more Holocene and Pleistocene extinctions will undoubtedly be recorded as new material continues to be excavated. An extirpated species of buttonquail, *Turnix novaecaledoniae* (previously considered a subspecies of the Australian *T. varius*, BirdLife International 2016), was also recovered from Holocene deposits on New Caledonia (Anderson et al., 2010; Balouet and Olson, 1989). This species has not been seen for over a century, but is abundant in pre-European cave deposits (Balouet and Olson, 1989) and may have survived until quite recently, as indicated by its presence in surface layers at Mé Auré (Boyer et al., 2010) and Pindai caves (Anderson et al., 2010). Interestingly, fossil specimens of *T. novaecaledoniae* are larger than their modern-day equivalent (Balouet and Olson, 1989), but Balouet and Olson do not give an explanation for this. Measurements of the coracoids and humeri of the larger Timor morphotype overlap with *T. novaecaledoniae*. Although this could be interpreted as the larger Timor buttonquail representing a Timorese population of *T. novaecaledoniae*, the sheer distance between Timor and New Caledonia renders this unlikely. The reasons for the disappearance of *T. novaecaledoniae* also remain unclear, but may include an anthropogenic increase in fire frequency, introduction of non-native predators and loss of habitat, specifically a reduction of dry forest (Boyer et al., 2010). While similar factors may have played a role in the extinction of the Timor buttonquail, more research is needed to ascertain the presence and last occurrence date of this taxon in other sites, and in relation to other extinctions in the late Holocene of Timor.
The absence of high numbers of extinct avian taxa from Late Pleistocene deposits at Jerimalai and Matja Kuru 1 is in line with evidence from other Late Pleistocene avian assemblages from the region, such as Flores (Meijer et al., 2015b) and Borneo (Stimpson, 2010). Although the fossil bird record for Island Southeast Asia remains rather poor, the emerging pattern suggests that Late Pleistocene avian extinctions in Wallacea were few, with extinctions limited to large-bodied taxa, and that avian lineages have been continuous across Southeast Asia since at least the Late Pleistocene. This is in contrast to other oceanic island archipelagoes, where the arrival of modern humans in the Holocene often resulted in dramatically reduced avian diversity (Cheke and Hume, 2008; James, 1995; James and Olson, 1991; Milberg and Tyrberg, 1993; Olson and James, 1991; Steadman, 2006; Wood et al., 2017; Worthy and Holdaway, 2002). The extinction of the crane *Grus* sp., a large-bodied bird on Timor would be in line with the extinction of other large avian taxa from Flores, such as the giant stork *Leptoptilos robustus* and the vulture *Trigonoceps* sp. (Meijer et al., 2015b), and indicates that Quaternary megafauna extinctions in Wallacea included avian taxa as well as proboscideans and reptiles.

**Acknowledgements**

We thank Chris Milensky (NMNH, USA) for access to comparative collections and Megan Spitzer (NMNH, USA) for discussions on taxonomic identifications. Stewart J. Fallon (ANU Radiocarbon Dating Centre) dated the *Turnix* bone.

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Figure 1. Location of Matja Kuru 1 and Jerimalai in Timor-Leste.
Figure 2. Abundance of avian number of identifiable specimens (NISP) throughout the sequence at Jerimalai B, Matja Kuru 1A and 1AA. X-axis indicates spit number.
Figure 3. Selected avian remains from Jerimalai B and Matja Kuru 1A and 1AA. Right coracoid in
ventral view of *Dendrocygna arcuata* from Matja Kuru 1AA, spit 16 (A) and extant *D. arcuata*, NMNH 344843 (B). Right tarsometatarsus in dorsal view of *Synoicus ypsilophorus* from Matja Kuru 1AA, spit 24 (C), and extant *S. ypsilophorus* NMNH 553359 (D). Right humerus in caudal view of *S. ypsilophorus* from Matja Kuru 1A, spit 14 (E) and extant *S. ypsilophorus*, NMNH 553359 (F). Right coracoid in dorsal view of extant *Ducula perspicillata*, NMNH 560802, (G) and partial right coracoid of cf. *Ducula/Caloenas* Jerimalai B, spit 14 (H). Right coracoid in dorsal view of cf. *Macropygia* from Jerimalai B, spit 10 (I), and extant *Macropygia unchall* NMNH 344626 (J), extant *Columba vitiensis* NMNH 560654, (K) and partial right coracoid of *Columba vitiensis* from Jerimalai B, spit 10 (L). Axis of *Grus* sp. from Jerimalai B, spit 59 in cranial (M), and lateral (N) view. Axis of extant *Grus grus* B 6898 in lateral view (O) Left humerus in caudal view of *Turnix maculosus* from Matja Kuru 1A, spit 33 (P), *Turnix maculosus* from Matja Kuru 1AA, spit 35 (Q), large *Turnix* morphotype from Matja Kuru 1A, spit 32 (R), extant *T. suscitator* NMNH 562149 (S), extant *T. sylvaticus* NMNH 429078 (U). Partial left coracoid in dorsal view of *Turnix maculosus* from Matja Kuru 1AA, spit 33 (V), large *Turnix* morphotype from Matja Kuru 1AA, spit 3 (W), and large *Turnix* morphotype Matja Kuru 1A, spit 8 (X). This specimen marks the last occurrence of this taxon. Left coracoid in dorsal view of extant *T. suscitator*, NMNH 562149 (Y), and extant *T. sylvaticus* NMNH 429078 (Z). Partial left tarsometatarsus in dorsal view of *Haliaeetus leucogaster* from Matja Kuru 1A, spit 24 (AA), and extant *H. leucogaster* NMNH 556992 (AB) Partial right tarsometatarsus in dorsal view of *Haliaeetus leucogaster* from Jerimalai B, spit 16 (AC), and extant *H. leucogaster* NMNH 556992 (AD). Scale bars denote 2 cm, except for M,N, O (*Grus*) and P–Z (*Turnix*) where they equal 1 cm.
Figure 4. Phasianidae. A. Measurements of the humerus (A), tibiotarsus (B) and tarsometatarsus (C) of fossil Phasianid remains from Matja Kuru 1 and Jerimalai B and extant *Synoicus ypsilophorus* and *S. chinensis*. The dotted line in (B) indicates the distal width of the single *S. chinensis* specimen from Jerimalai B.
Figure 5. Selected measurements of extant Turnicidae and fossil specimens from Matja Kuru 1 and Jerimalai B. A–B, coracoid; C–D, humerus, crosses indicate data range for T. varius and T. novaecaledoniae from Balouet and Olson (1989); E–F, tarsometatarsus.
**Figure 6.** Digestion scores for four of the major groups of birds at Jerimalai B and Matja Kuru 1A and 1AA.

**Figure 7.** Distribution of pigeons (Columbidae), quails (Phasianidae) and buttonquails (Turnicidae) over time in Matja Kuru 1A and 1AA, and Jerimalai B.