

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

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26 **Abstract**

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

44

45 **Keywords:** Quaternary, island biogeography, Wallacea, birds, extinction, megafauna

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## 51 **1. Introduction**

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53           The island of Timor, the largest in the Lesser Sunda island chain, has been the subject  
54 of ornithological exploration for more than two hundred years (Hellmayr, 1914; Mayr, 1944).  
55 The avifauna consists of 262 bird species, of which 169 are breeding species, 76 migrants and  
56 17 vagrants (Trainor et al., 2008). The Timor Group (including associated islands) has the  
57 highest level of endemics (28) within the Lesser Sundas. Due to its relatively close position to  
58 Australia, the Timor avifauna contains the highest proportion of Australian elements within  
59 Indonesia, initially reported to be ~50% (Mayr, 1944; Monk et al., 1997), but is now believed  
60 to lie around 31% due to phylogenetic changes and wider sampling of taxa (Trainor et al.,  
61 2008). Despite this long tradition of ornithological research, little is known regarding past  
62 avian distributions and diversity. This is in line with the rest of Wallacea, as the fossil bird  
63 record for Island Southeast Asia is quite poor (Meijer, 2014).

64           Timor has yielded the earliest evidence for modern humans in Wallacea, and it may  
65 have been the final stepping stone for modern humans dispersing into Australia via the  
66 southern route (O'Connor, 2007). Archaeological sequences from Jerimalai Shelter, Lene  
67 Hara Cave, and Laili Cave in Timor Leste date back to 43–41 ka, ~42 ka and ~44 ka,  
68 respectively (Hawkins et al., 2017b; O'Connor, 2007; O'Connor et al., 2017). The evidence  
69 from Jerimalai and Lene Hara indicates that early modern humans on Timor were adept at  
70 exploiting marine resources (O'Connor, 2007; O'Connor et al., 2010, 2011). Nonetheless,  
71 data from Laili Cave suggest that Late Pleistocene modern humans targeted a wide range of  
72 different resources, including terrestrial vertebrates, depending on availability (Hawkins et al.,  
73 2017b).

74           The systematic exploitation of birds was once considered a behavior exclusive to  
75 modern humans (Klein 1989) but has now also been observed in Neanderthals (Blasco et al.,

76 2014; Finlayson et al., 2016) and may even extend back into the Middle Pleistocene (Blasco  
77 et al., 2012). Hunting birds for subsistence is currently widespread throughout the Indonesian  
78 archipelago, but there is as of yet no evidence for the systematic exploitation of birds by  
79 hominins in the region. On Flores, hominins have been present since the early Middle  
80 Pleistocene (van den Bergh et al., 2016), but evidence for the exploitation of birds as a food  
81 source at either Liang Bua or the So'a Basin is lacking (Meijer et al., 2013, 2015a). On Timor,  
82 bird remains are present throughout the sequence at Laili Cave (Hawkins et al., 2017a,b), as  
83 well as in Tron Bon Lei rock shelter on nearby Alor Island (Hawkins et al., 2017c).  
84 Taphonomic signatures suggests that the majority of bird remains at Laili and Tron Bon Lei  
85 were the result of Barn owl predation (Hawkins et al., 2017a,c). However, the presence of  
86 pigeons and ducks at Laili, taxa with a body size outside the preferred prey size of Barn owls,  
87 has been interpreted as evidence for humans occasionally foraging on birds (Hawkins et al.,  
88 2017a).

89         Despite recording the oldest modern human occupation site in Wallacea, the Laili  
90 sequence has not yielded any extinct avian taxa. This is in line with evidence from other Late  
91 Pleistocene modern human sites on Timor where fossils of extinct megafauna are absent. In  
92 the Pleistocene, Timor likely hosted two species of pygmy proboscidean, *Stegodon timorensis*  
93 and *Stegodon 'trigonocephalus'*, a giant tortoise, and a large, possibly endemic species of  
94 *Varanus* (Hooijer, 1971, 1972; Verhoeven, 1964). The absence of these taxa in the earliest  
95 modern human sequences at Laili and other cave sites suggests that Timor's Quaternary  
96 megafauna became extinct before the arrival of modern humans on the island (Louys et al.,  
97 2016).

98         Here, we report on bird remains excavated from deposits at Jerimalai Square B and  
99 Matja Kuru 1 Squares A and AA that cover the Holocene and Late Pleistocene. The avian  
100 assemblages from both sites significantly extend the Timor fossil bird record known from

101 Laili; they are the most diverse described from Timor so far, and contain a number of  
102 previously unrecorded species. In addition, these assemblages yield the first extinct avian taxa  
103 for Timor, thereby shedding light on past avian extinctions on the island as well as the  
104 island's Quaternary megafauna.

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## 107 **2. Materials and Methods**

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### 109 **2.1 Regional setting**

110

111 Jerimalai (8°24.84' S, 127°17.50' E) is a small coralline limestone shelter located  
112 southeast of the village of Tutuala at the easternmost tip of Timor Leste (Figure 1). It  
113 currently sits 75 m above sea level and a kilometer from the current coastline. The site was  
114 located in 2004, and two test pits of 1m x 1m (Square A and B) were excavated at Jerimalai in  
115 2005. Excavations were carried out in spits of 1–5 cm which followed stratigraphic  
116 boundaries where visible. Sediments were wet-screened through 1.5 mm mesh screens. Matja  
117 Kuru 1 (8°24.87' S, 127°07.36' E) is located in an uplifted limestone ridge northeast of the  
118 modern village of Poros, approximately 370 m above sea level and about 8 kilometers from  
119 the coast. Excavations at Matja Kuru 1 took place in 2001 and consisted of a 1 x 2 m test-pit  
120 (conjoined Squares A and AA), also sampled in approximately 5 cm spits. The geochronology  
121 and archaeological sequences of Jerimalai and Matja Kuru 1 have been described by  
122 O'Connor (2007) and Langley and O'Connor (2015) and we refer to those publications for  
123 more details.

124

### 125 **2.2 Fossil analyses**

126

127 Avian remains were identified by using the avian skeleton collection at the  
128 Smithsonian Institution's National Museum of Natural History (prefix NMNH) in  
129 Washington, DC (USA), and the Bergen University Museum (prefix B and BM) collections in  
130 Bergen, Norway. Comparative material examined (Appendix 1) included skeletons of resident  
131 and migrant bird species from Timor (following Eaton et al., 2016 and Trainor et al., 2008),  
132 Indonesia, and Australia (following Avibase). The systematic framework follows Howard and  
133 Moore's Checklist (Dickinson and Christides, 2014; Dickinson and Remsen, 2013), with the  
134 exception of Gruidae (cranes), as species formerly placed in *Anthropoides* (*A. virgo* and *A.*  
135 *paradisea*) and *Antigone* (*A. canadensis*, *A. vipio*, *A. antigone* and *A. rubicunda*) are now  
136 placed within *Grus* (Yu et al., 2011), and Turnicidae, for which there is now strong support for  
137 placing them in Charadriiformes (Baker et al., 2007). Osteological terminology primarily  
138 follows Baumel and Witmer (1993) and Howard (1929). Juveniles were identified based on  
139 the porosity and texture of the bone surfaces. Measurements were taken with digital calipers  
140 to the nearest 0.01 mm. Specimens were examined for signs of bone surface modification,  
141 such as bite and cut marks and digestion, using a Leica MZ16 stereo microscope. Digestion  
142 patterns were scored in five categories following Andrews (1990), with 0 = no digestion, 1 =  
143 minimal, 2 = moderate, 3 = heavy, 4 = extreme. Ten specimens were coated with carbonate on  
144 the outer surface and no observations on surface modifications could be made for these  
145 specimens. AMS radiocarbon dating was performed at the ANU Radiocarbon Dating Centre  
146 (Fallon et al., 2010). Dates are calibrated in Oxcal 4.3 (Bronk Ramsey, 2009) using the ShCal  
147 13 calibration curve (Hogg et al., 2013) to 95.4%.

148

### 149 **3. Results**

150

151 **3.1 Bone distribution and taphonomy**

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

Order	Family	Taxon	JeriB	MK1A	MK1AA
Anseriformes	Anatidae	<i>Aythya australis</i>			1
		<i>Dendrocygna arcuata</i>			1
Galliformes	Phasianidae	<i>Synoicus ypsilophorus</i>	5	11	12
		<i>Synoicus chinensis</i>	1		
Podicipediformes	Podicipedidae	cf. <i>Tachybaptus</i>			1
Columbiformes	Columbidae	Large pigeon cf. <i>Ducula/Caloenas</i>	2		1
		<i>Columba vitiensis</i>	6	1	2
		cf. <i>Treron</i>	1		
		<i>Macropygia</i> sp.	4		1
		<i>Ptilinopus</i> sp.	2		
		<i>Geopelia</i> sp.	1		
		Columbidae indet.	1		
Cuculiformes	Cuculidae	gen. et sp. indet.	1		
Gruiformes	Gruidae	<i>Grus</i> sp.†	1		
	Rallidae	Large rail cf. <i>Fulica/Gallinula?</i>		4	1
		Medium rail 1		1	2
		Medium rail 2			1
		Small rail cf. <i>Zapornia</i>		1	
Charadriiformes	Scolopacidae	<i>Calidris</i> spp.		3	1
	Laridae	gen. et sp. indet.		1	

	Turnicidae	<i>Turnix large†</i>	9	11
		<i>Turnix maculosus</i>	2	5
		Charadriiformes indet.	1	1
Accipitriformes	Accipitridae	<i>Haliaeetus leucogaster</i>	1	1
Strigiformes	Tytonidae	cf. <i>Tyto</i>	1	1
	Strigidae	cf. <i>Ninox</i>	1	
Falconiformes	Falconidae	<i>Falco</i> sp.		1
Passeriformes	Motacillidae	<i>Anthus/Motacilla</i>		1
	Indet	Medium passerine	1	
		Small passerine sp. 1		1
		Small passerine sp. 2	2	

156

157 **Table 1.** Species recovered from Jerimalai B and Matja Kuru 1.

158

159 The majority of the avian remains from Jerimalai B and Matja Kuru 1 show signs of  
160 digestion (Table 2). At Jerimalai B, 51.3% showed no signs of digestion, with 35.9 %  
161 showing minimal digestion. At Matja Kuru 1A, 38.5 % showed no digestion and 55.1%  
162 showed minimal digestion. At Matja Kuru 1AA, no digestion and minimal digestion are  
163 27.4% and 66.7%, respectively. Although there is variation between the sites, the taphonomic  
164 signatures are consistent with predation by barn owls (Andrews, 1990).

165

	<b>D0</b>	<b>D1</b>	<b>D2</b>	<b>D3</b>	<b>D4</b>
<b>Jerimalai B</b>	51,3	35,9	8,5	4,3	0
<b>Matja Kuru 1A</b>	38,5	55,1	6,4	0	0
<b>Matja Kuru 1AA</b>	27,4	66,7	6,0	0	0

166

167 **Table 2.** Digestion scores for avian assemblages from Jerimalai B, Matja Kuru 1A and 1AA.



168

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

192 depositionally, as the 16,000 cal BP date is inverted, underlain by a date from spit 25 of ~ 11  
193 ka cal BP).

194

## 195 **3.2 Species accounts**

196

### 197 **3.2.1 Anseriformes**

#### 198 3.2.1.1 Anatidae (ducks, geese and swans)

##### 199 *3.2.1.1.1 Aythya australis*

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

##### 214 *3.2.1.1.2 Dendrocygna arcuata*

215 The Wandering Whistling-duck *Dendrocygna arcuata* is recognized based on a right coracoid  
216 from Matja Kuru 1AA, spit 16 (Fig. 3A). The specimen lacks a pneumatic foramen under the

217 acrocoracoid and bears a distinct broad depression on the ventral surface of the sternal blade.  
218 This depression is located just proximal of the sternal articular facet and extends laterally to  
219 the linea intermuscularis ventralis. This depression was not observed in any species of  
220 *Tadorna*, *Anas*, *Aythya*, or *Nettapus*, but was present in more than half of *Dendrocygna*  
221 *arcuata* and *D. bicolor* specimens. In size, it agrees best with *D. arcuata*, which is the only  
222 species of *Dendrocygna* known to occur on Timor today (Eaton et al., 2016; Trainor et al.,  
223 2008).

224

### 225 **3.2.2 Galliformes**

#### 226 3.2.2.1 Phasianidae (pheasants and allies)

227 Twenty-nine specimens can be assigned to quails (Phasianidae). Quails are  
228 morphologically close to buttonquails (Turnicidae) and rails (Rallidae), but can be  
229 distinguished from these groups based on a number of osteological features. In the quail  
230 humerus, the tuberculum ventrale is connected to the caput humeri by a distinct crista incisura  
231 capitis, which bisects the incisura capitis. In rails, the tuberculum ventrale is not connected to  
232 the caput humeri (and the incisura capitis is wide and not bisected), whereas in buttonquails,  
233 the incisura capitis is very short and limited to the ventral aspect of the bone. In the phasianid  
234 carpometacarpus, the processus intermetacarpalis is distinct and reaches the os metacarpale  
235 minor. The carpal trochlea is rounded in ventral aspect, but in dorsal aspect, the dorsal rim of  
236 the trochlea is only rounded proximally, and distally cuts away in a straight line towards the  
237 processus intermetacarpalis. In Turnicidae, the dorsal rim is fully rounded. Small phasianid  
238 tibiotarsi can be distinguished from *Turnix* and small rails by having a relatively narrower  
239 distal end, and a higher tendinal bridge that is oriented more obliquely than in Turnicidae  
240 (horizontal in Rallidae). In proximal view, the rim formed by the facies articularis medialis  
241 and fossa retropatellaris is smooth in phasianids whereas it is notched in *Turnix* (i.e. facies

242 articularis medialis projects more medially than the fossa retropatellaris). In the proximal  
243 tarsometatarsus, the lateral and medial sides are caudally excavated in *Synoicus* (Phasianidae),  
244 unlike in Rallidae and Turnicidae. Moreover, *Synoicus*, as other Phasianidae, has one canal  
245 for the tendon of the musculus flexor digitorum longus (open sulcus in Rallidae), but a  
246 plantarly open sulcus for the superficial flexor tendons of the muscles that flex the second toe  
247 (Mayr, 2016), and the hypotarsus is located laterally. The hypotarsal ridges are  
248 proximodistally equally long in *Synoicus*, but the lateral ones are shorter in *Turnix*. In  
249 Rallidae, there is one long central ridge, and some shorter ones. In the distal tarsometatarsus,  
250 the medial and lateral plantar ridges are distinct in *Synoicus*, and the fossa metatarsi I is most  
251 prominent in *Synoicus*. All specimens agree in these features with Phasianids, particularly  
252 *Synoicus*. Only three species of phasianid are present on Timor, one of which is the much  
253 larger *Gallus gallus*. The other two are *Synoicus ypsilophorus* and *S. chinensis*, with the  
254 former being larger than the latter (del Hoyo et al., 2017). Within the twenty-nine specimens,  
255 two species can be distinguished based on size differences.

256

#### 257 3.2.2.1.1 *Synoicus ypsilophorus*

258 Twenty-eight specimens (a fragment of a sternum, one coracoid, eleven humeri, two  
259 carpometacarpi, one femur, five tarsometatarsi, and seven tibiotarsi; Jerimalai B, spits 42, 47,  
260 and 62; Matja Kuru 1A, spits 11, 14, 15, 22, 31, 32 and 34; Matja Kuru 1AA, spits 17, 21, 22,  
261 26, 24, 25, 35 ) are assigned to the Brown Quail *S. Ypsilophorus* (Fig. 3C, E). Although only  
262 two specimens of extant *S. ypsilophorus* were available for measurements, the remains from  
263 Matja Kuru 1 and Jerimalai B reported agree with *S. ypsilophorus* in size, and are consistently  
264 larger in measurements of the humerus, tibiotarsus and tarsometatarsus than *S. chinensis*  
265 (Figure 4).

#### 266 3.2.2.1 .2 *Synoicus chinensis*

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

272

### 273 **3.2.3 Podicipediformes**

#### 274 3.2.3.1 Podicipedidae (grebes)

##### 275 3.2.3.1.1. cf. *Tachybaptus*

276 Grebes are represented by a single specimen, a right proximal humerus, from Matja Kuru 1  
277 AA, spit 23. This specimen represents only the proximal articulation and a section of the  
278 shaft. The crista deltapectoralis is mostly missing, but appears to have extended down the  
279 shaft for a significant length. The tuberculum dorsale is distinct and set off medially of the  
280 caput humeri. The fossa pneumotricipitalis ventralis is not pneumatized, the fossa  
281 pneumotricipitalis dorsalis is absent, and the margo caudalis is pronounced. In these features,  
282 the specimen agrees very well with the Podicipedidae. Two species of grebe are known from  
283 Timor, *Tachybaptus ruficollis* and *T. novaehollandiae* (Eaton et al., 2016; Trainor et al.,  
284 2008). In overall size, the specimen from Matja Kuru agrees with smaller grebes such as  
285 *Tachybaptus*, but is more gracile than *T. ruficollis* (width of the proximal articulation in fossil  
286 specimen: 8.27 mm, *T. ruficollis* 8.88 – 9.76 mm, n = 3). The fossil specimen may represent  
287 *T. novaehollandiae* instead, which is slightly smaller (del Hoyo et al., 2017), but no  
288 specimens of that species were available for comparisons. We therefore tentatively refer it to  
289 the genus *Tachybaptus* until more comparative material becomes available.

290

291 **3.2.4 Columbiformes**

292 3.2.4.1 Columbidae (pigeons and doves)

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

294 3.2.4.1.1 Large pigeon cf. *Ducula/Caloenas*

295 A sternal fragment (Jerimalai B, spit 12), a distal right coracoid (Jerimalai B, spit 14) (Fig.  
296 3H), and juvenile tarsometatarsus shaft (Matja Kuru 1AA, spit 9), represent a large-sized  
297 columbid more robust than *Columba* and in the size range of *Ducula* (Imperial pigeons) and  
298 *Caloenas* (Nicobar pigeon). Both genera are extant on Timor, but the fragmentary nature of  
299 the specimens does not allow for a generic identification.

300 3.2.4.1.2 *Columba vitiensis*

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

314 3.2.4.1.3 cf. *Treron*

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

#### 322 3.2.4.1.4 *Macropygia* sp.

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

#### 329 3.2.4.1.5 *Ptilinopus* sp.

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

#### 338 3.2.4.1.6 *Geopelia* sp.

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

#### 345 3.2.4.1.7 Columbidae indet.

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

348

### 349 3.2.5 Cuculiformes

#### 350 3.2.5.1 Cuculidae (cuckoos and allies)

##### 351 3.2.5.1.1 Cuculidae gen. et sp. indet

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

360

### 361 3.2.6 Gruiformes

#### 362 3.2.6.1 Gruidae (cranes)

##### 363 3.2.6.1.1 *Grus* sp.



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

382

### 383 3.2.6.2 Rallidae (rails and coots)

#### 384 3.2.6.2.1 Large rail

385 The remains of a large rail were recovered from Matja Kuru 1A (a proximal coracoid, a  
386 partial quadrate, a distal left tibiotarsus and a proximal right humerus, spits 12, 19, 21, and 26)  
387 and Matja Kuru 1AA (a distal right tibiotarsus from spit 23). The remains represent a mixture  
388 of osteological characters and may represent more than one species, which is why we refrain

389 from assigning it to a genus at this point. The specimens are in the size range of the Purple  
390 Swamphen *Porphyrio porphyrio* and larger than most *Fulica atra*. The coracoid displays a  
391 processus procoracoideus which carries a facet for the scapula medially of the cup-shaped  
392 scapular facet, similar to *P. porphyrio*, but differs from that species in having a relatively  
393 shorter processus acrocoracoideus. In this aspect, the specimen is more similar to *Fulica atra*,  
394 but differs from that species in that the facies articularis clavicularis is wider. Moreover, the  
395 corpus coracoidei is wider and the processus procoracoideus is not distinctly set off from its  
396 medial margin, unlike *Fulica*.

#### 397 3.2.6.2.2. Medium rail 1 cf. *Rallus/Rallina/Amaurornis*

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

#### 403 3.2.6.2.3 Medium rail 2

404 A second species of medium rail was retrieved from Matja Kuru 1AA, spit 20. The specimen,  
405 a left proximal coracoid, differs from the right proximal coracoid retrieved from Matja Kuru  
406 1AA (spit 19) in that the processus acrocoracoideus is shorter and more blunt, and the  
407 specimen itself is more robust than *Rallus*, *Rallina* and *Amaurornis*.

#### 408 3.2.6.2.4 *Zapornia* sp.

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

413

414

### 415 **3.2.7 Charadriiformes**

#### 416 3.2.7.1 Scolopacidae (waders)

##### 417 3.2.7.1.1 *Calidris* spp.

418 A right coracoid (Matja Kuru 1AA, spit 25), a left carpometacarpus (Matja Kuru 1A, spit 16)  
419 and two left distal humeri (Matja Kuru 1A, spits 4 and 6) are assigned to sandpipers of the  
420 genus *Calidris*. The coracoid is small and has the typical charadriiform shape (a broad,  
421 overhanging facies articularis clavicularis and a deep, circular scapular facet) and lacks the  
422 foramen n. supracoracoidei in the procoracoid. This foramen is absent in Scolopacidae but  
423 variable in Glareolidae, Alcidae and Turnicidae (Mayr, 2011) but these have a derived  
424 morphology of the coracoid. . Within Scolopacidae, it can be distinguished based on its small  
425 size and agrees well with *Calidris*. The two distal humeri display an elongated and proximally  
426 directed processus supracondylaris dorsalis (characteristic for Charadriiformes). They are  
427 assigned to Scolopacidae because of the relatively shorter and more rounded processus  
428 flexorius which projects from the shaft at a right angle (oriented more proximally in the  
429 similarly-sized *Charadrius*). In both humeri, the fossa brachialis is deep and proximally  
430 clearly bordered off from the rest of shaft, a feature that is more pronounced in the smaller  
431 scolopacids such as *Arenaria* and *Calidris*. The specimens are smaller than *Arenaria*, and  
432 agree very well with *Calidris*. Carpometacarpus morphology is rather uniform within  
433 Charadriiformes, with a very straight os metacarpale majus, a proximally projecting processus  
434 extensorius, and a trochlea carpalis with a rounded ventral rim and an elliptical dorsal one.  
435 Given the small size of the specimen, it is referred here to *Calidris* as well. At least eight  
436 species of *Calidris* are known from Timor (Trainor et al., 2018), but because of the significant  
437 overlap in size, more material is needed to identify these remains to species level.

438

439 3.2.7.2 Laridae (gulls and terns)

440 3.2.7.2.1 Laridae indet.

441 A small species of Laridae is represented by a right coracoid from Matja Kuru 1A, spit 16.

442 The specimen is broken in two and lacks the procoracoid, but has a wide and overhanging

443 processus acrocoracoideus and a cup-shaped scapular facet, typical of Charadriiformes. The

444 area under the processus acrocoracoideus is deeply excavated, much more so than in

445 Charadriidae and Scolopacidae, and agrees most with the condition seen in Laridae. Distally,

446 the medial sternal surface is excavated deeply as well, and in distal view, the extremitas

447 sternalis is strongly curved, with the medial portion of facies articularis sternalis greatly

448 dorsoventrally widened (Mayr, 2011). The specimen is small but larger than *Chroicocephalus*

449 *ridibundus*, *Sternula albifrons* and *Chlidonias hybrida*, and is comparable in size with terns in

450 the genus *Sterna*. Given that not all species were available for comparison, we refrain from

451 assigning it to genus level.

452

453 3.2.7.3 Turnicidae (buttonquails)

454 Buttonquails are the most abundant taxon in the assemblages with a total of 38

455 specimens. The *Turnix* assemblage displays variation in size that is most pronounced in the

456 humeri, coracoids and tarsometatarsi. The size variation surpasses that seen in specimens of

457 extant taxa, and suggests that at least two species of buttonquail were present on Timor until

458 quite recently.

459 3.2.7.3.1 *Turnix maculosus*

460 The smaller morphotype is reported from Jerimalai B (spits 48 and 49), Matja Kuru 1A (spits

461 12, 13, 23, 33, and 34) and Matja Kuru 1AA (spits 18, 19, 20, 22, 23, 25 and 35), and is

462 referred to the Red-backed Buttonquail *T. maculosus*. The material consists of five distal

463 tarsometatarsi, one distal right tibiotarsus, one proximal right carpometacarpus, two left

464 humeri, one proximal right humerus, a distal right humerus, four proximal right coracoids and  
465 three proximal left coracoids (MNI = 18) (Fig. 3P–Q, V). The specimens are smaller than *T.*  
466 *suscitator* in most measurements and partially overlap with *T. sylvaticus* (Fig. 5) for  
467 dimensions of the coracoid, humerus and tarsometatarsus. The modern Timor avifauna  
468 contains only *T. maculosus*, for which no skeletons were available for comparison for this  
469 study. However, *T. maculosus* is described as small and its body measurements and body  
470 weight (del Hoyo et al., 2017; Dunning, 2008) are smaller than for other species including *T.*  
471 *suscitator*. Furthermore, Hawkins et al. (2017b) identified *T. cf. maculosus* from Late  
472 Pleistocene deposits at Laili Cave, and it is therefore likely that the small morphotype group  
473 from Jerimalai and Matja Kuru 1A and 1AA represents the extant *T. maculosus* as well.

#### 474 3.2.7.3.2 Large *Turnix*†

475 A second, larger species of *Turnix* is reported from Matja Kuru 1A (spit 8, 13, 18, 20, 24, 25,  
476 32 and 34) and Matja Kuru 1AA (spits 11, 14, 17, 20, 22, 23, 24 and 35), but not Jerimalai B.  
477 It is represented by a left carpometacarpus, three proximal left coracoids and two proximal  
478 right coracoids, one left humeri, four distal left humeri, one proximal right humerus, three  
479 right tarsometatarsi, one distal right tarsometatarsus, one proximal left tarsometatarsus, two  
480 distal left tibiotarsi and one distal right tibiotarsus (MNI = 20) (Fig. 3R, W, X). This larger  
481 morphotype is larger than *T. sylvaticus*, and partially overlaps with *T. suscitator*, *T. tanki* and  
482 *T. ocellatus*. However, the width and depth of shaft of the coracoid (Figure 5A) and the  
483 proximal and distal dimensions of the tarsometatarsus (Figs. 5E-F) surpass those of *T.*  
484 *suscitator*, *T. tanki* and *T. ocellatus*. This could indicate that this morphotype represents larger  
485 individuals of one or more of these three extant taxa (in which case they would represent an  
486 extirpated population, as none of these taxa occur on Timor today), albeit with slightly  
487 different proportions. Alternatively, this morphotype represents an unknown species whose  
488 dimensions only partially overlap with extant taxa. This indicates that a second, larger species

489 of *Turnix* was present on Timor in the Terminal Pleistocene and Holocene, and this species is  
490 now likely extinct. Radiocarbon dating of the latest occurrence of this morphotype, a proximal  
491 coracoid from Matja Kuru 1 A, spit 8 (Fig. 3X), indicates an age for this specimen of 1372–  
492 1300 cal BP (S-ANU# 55223,  $1490 \pm 24$  BP).

493

#### 494 3.2.7.4. Charadriiformes indet

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

498

### 499 **3.2.8. Accipitriformes**

#### 500 3.2.8.1 Accipitridae (diurnal birds of prey)

##### 501 3.2.8.1.1 *Haliaeetus leucogaster*

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

514 trochlea. It differs from *Aquila* and *Circaetus* in having a slightly shorter trochlea metatarsi II  
515 in distal view, and agrees in this aspect best with *H. leucogaster*.

516

### 517 **3.2.9 Strigiformes**

#### 518 3.2.9.1 Tytonidae (barn owls)

##### 519 3.2.9.1.1 cf. *Tyto*

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

539

540 3.2.9.2 Strigidae (typical owls)

541 3.2.9.2.1 cf. *Ninox*

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

548

549 **3.2.10 Falconiformes**

550 3.2.10.1 Falconidae (falcons)

551 3.2.10.1.1 *Falco* sp.

552 Falcons are represented by a right coracoid from Matja Kuru 1AA (spit 24). The specimen  
553 lacks the acrocoracoid, but the procoracoid is elongated and triangular in shape, and what  
554 remains of the scapular facet indicates that it was shallow. These features are characteristic of  
555 Falconidae. The specimen lacks a foramen in the procoracoid, a feature characteristic for a  
556 few species within Falconidae, i.e. *Falco*, *Microhierax* and *Polihierax* (Suárez and Olson,  
557 2001). The latter two are small species, and the Matja Kuru specimen agrees better with  
558 *Falco*. Four species of *Falco* have been recorded on Timor, *Falco moluccensis*, *F. subbuteo*,  
559 *F. longipennis* and *F. peregrinus*. There is significant overlap in size between these species,  
560 and without the complete bone, we refrain from assigning this specimen to species level.

561

562 **3.2.11 Passeriformes**

563 3.2.11.1 Motacillidae (wagtails and pipits)



564           3.2.11.1.1 *Anthus/Motacilla*

565   A left proximal humerus from Matja Kuru 1AA's spit 22 represents a motacillid in the genera  
566   *Anthus* or *Motacilla*. This small proximal humerus displays a very deep fossa  
567   pneumotricipitalis dorsalis that is confluent with the fossa pneumotricipitalis ventralis.  
568   Confluent fossae like this are present in only a few passerine groups, including Prunellidae,  
569   Aegithalidae, Remizidae, and Motacillidae (Jánossy, 1983). The crus dorsale fossae is absent  
570   and the floor of the fossa pneumotricipitalis (i.e., the bicipital shelf) is very thin. In these  
571   features the specimen agrees with Motacillidae. Seven species of Motacillidae in the genera  
572   *Motacilla* and *Anthus* are present on Timor, but the current incomplete specimen does not  
573   allow for a distinction between them.

574

575   3.2.11.2 Family indet.

576           3.2.11.2.1 Medium passerine

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

580           3.2.11.2.2 Small passerine sp. 1

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

586           3.2.11.2.3 Small passerine sp. 2

587   A second species of small passerine is represented by two humeri from Matja Kuru 1A's spits  
588   24 and 34. They differ from the previous small passerine humerus in that the fossa

589 pneumotricipitalis dorsalis is completely separated from the fossa pneumotricipitalis ventralis  
590 by the crus dorsale fossae, and thus represent a separate species.

591

592

## 593 **Discussion**

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

602

603 Both Jerimalai B and Matja Kuru 1 preserve evidence for early human occupation, but  
604 no cut marks or other signs indicative of human subsistence were observed on any bird bones.  
605 This does not necessarily mean that birds were not eaten by early humans, since many birds  
606 are small enough to be eaten whole. The taphonomy of the Jerimalai B and Matja Kuru 1  
607 assemblages (Table 2) suggests that avian predators, most likely barn owls, were the main  
608 accumulating agents for the majority of the assemblage. This is in agreement with the avian  
609 assemblage from Laili cave (Hawkins et al., 2017a,b). However, Hawkins et al. (2017a)  
610 suggested that pigeons may have been hunted by humans, as they fall outside the prey size  
611 spectrum for barn owls. At Jerimalai, the pigeon remains show a somewhat different  
612 taphonomic profile, with equal numbers showing no digestion and minimal digestion. Quails,  
613 buttonquails and songbirds show predominantly minimal digestion, and all three groups of

614 birds fall within the barn owl prey size (< 200 gr., Morris, 1979). Furthermore, pigeons are  
615 most abundant during phase IV (Figure 7), which saw the most intense human occupation.  
616 This could suggest that the pigeon remains were accumulated by a taphonomic agent other  
617 than barn owls. This is in line with the conclusions of Hawkins et al. (2017a) for Laili cave,  
618 who suggested that some pigeons may have been deposited by humans instead.

619

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

626         The crane *Grus* sp. is represented by only a single specimen from spit 59 at the base of  
627 the Jerimalai B sequence. Radiometric dating of marine shells from Jerimalai B's lower levels  
628 indicates an age of at least 42,000 cal BP (O'Connor et al., 2011; Langley and O'Connor,  
629 2016: table 2) for the base of the sequence. Depositional mixing of the lower levels is  
630 believed to be very limited, and the *Grus* sp. specimen is therefore assumed to be Late  
631 Pleistocene in age as well. Cranes are generally absent from Island Southeast Asia, but two  
632 species of cranes are known from Southern Asia and Australia (del Hoyo et al., 2017). The  
633 Brolga (*Grus rubicunda*) occurs in northern Australia and small parts of New Guinea,  
634 whereas the Sarus Crane (*G. antigone*) is currently found in northwest India, Myanmar,  
635 Cambodia and northern Australia, but not in between (del Hoyo et al., 2017). Both birds are  
636 wetland species and non-migratory, rendering it unlikely that the Jerimalai specimen  
637 represents a seasonal migrant. Genetic work has retrieved the Brolga and Sarus Crane as sister  
638 taxa (Yu et al., 2011). In addition, the Sarus Crane likely originated in Southeast

639 Asia,dispersed northwards and southwards during times of low sea level, and subsequently  
640 became extinct in most of Island Southeast Asia (Das, 2010; Wood and Krajweski, 1996).  
641 Although the axis from Jerimalai cannot be assigned to species level, it is indicative of a Late  
642 Pleistocene population of cranes on Timor that has since been extirpated. On the basis of the  
643 single occurrence of *Grus* sp. at the base of the Jerimalai sequence, *Grus* sp. clearly  
644 overlapped with modern humans at Jerimalai. However, as we know virtually nothing of its  
645 ecology, any interpretation of its likely cause of extinction would be speculative. Likewise,  
646 inferring timing of extinction based on one specimen is uncertain at best. It should be noted  
647 that Wetmore (1940) identified a humerus from Late Pleistocene deposits at Watoealang on  
648 Java as belonging to the Common Crane *Grus grus*. It is unclear if Wetmore compared the  
649 specimen to *G. rubicunda* and *G. antigone*, but this record strengthens the notion that cranes  
650 were more widespread in Island Southeast Asia in the Late Pleistocene. If that is indeed the  
651 case, the disappearance of *Grus* from Timor may have been in response to regional factors,  
652 beyond those specific to Timor.

653

654         The large buttonquail is absent from Jerimalai, but is present from spits 34–8 at Matja  
655 Kuru 1A, and from spits 35–11 at Matja Kuru 1AA. The deepest levels at Matja Kuru 1A and  
656 AA date to ~11 ka (Langley and O’Connor, 2016: tables 3–4). Mollusk shells from Matja  
657 Kuru 1A spit 8, which marks the larger *Turnix* morphotype’s highest stratigraphic occurrence,  
658 have been dated to 5,456–5,274 cal BP (Langley and O’Connor, 2016: tables 3). However,  
659 radiocarbon dates produced for this site suggest it has undergone considerable disturbance.

660         Because of this, we elected to obtain a direct radiocarbon date from the larger *Turnix*  
661 morphotype from spit 8. This indicated a much younger age (of 1,372–1,300 cal BP, see  
662 above), suggesting that it disappeared more recently than expected from the site  
663 chronostratigraphic profile. Interestingly, this date is roughly coeval with the disappearance of

664 Timor's giant rats (Aplin and Helgen, 2010; O'Connor and Aplin, 2007), such that these  
665 extinctions may have a common anthropogenic or environmental cause.

666         So far, this represents the first extinction of a bird species in the Holocene in Island  
667 Southeast Asia. However, as the fossil record for birds in this region remains poor (Meijer,  
668 2014), more Holocene and Pleistocene extinctions will undoubtedly be recorded as new  
669 material continues to be excavated. An extirpated species of buttonquail, *Turnix*  
670 *novaecaledoniae* (previously considered a subspecies of the Australian *T. varius*, BirdLife  
671 International 2016), was also recovered from Holocene deposits on New Caledonia (Anderson  
672 et al., 2010; Balouet and Olson, 1989). This species has not been seen for over a century, but  
673 is abundant in pre-European cave deposits (Balouet and Olson, 1989) and may have survived  
674 until quite recently, as indicated by its presence in surface layers at Mé Auré (Boyer et al.,  
675 2010) and Pindai caves (Anderson et al., 2010). Interestingly, fossil specimens of *T.*  
676 *novaecaledoniae* are larger than their modern-day equivalent (Balouet and Olson, 1989), but  
677 Balouet and Olson do not give an explanation for this. Measurements of the coracoids and  
678 humeri of the larger Timor morphotype overlap with *T. novaecaledoniae*. Although this could  
679 be interpreted as the larger Timor buttonquail representing a Timorese population of *T.*  
680 *novaecaledoniae*, the sheer distance between Timor and New Caledonia renders this unlikely.  
681 The reasons for the disappearance of *T. novaecaledoniae* also remain unclear, but may include  
682 an anthropogenic increase in fire frequency, introduction of non-native predators and loss of  
683 habitat, specifically a reduction of dry forest (Boyer et al., 2010). While similar factors may  
684 have played a role in the extinction of the Timor buttonquail, more research is needed to  
685 ascertain the presence and last occurrence date of this taxon in other sites, and in relation to  
686 other extinctions in the late Holocene of Timor.

687

688           The absence of high numbers of extinct avian taxa from Late Pleistocene deposits at  
689 Jerimalai and Matja Kuru 1 is in line with evidence from other Late Pleistocene avian  
690 assemblages from the region, such as Flores (Meijer et al., 2015b) and Borneo (Stimpson,  
691 2010). Although the fossil bird record for Island Southeast Asia remains rather poor, the  
692 emerging pattern suggests that Late Pleistocene avian extinctions in Wallacea were few, with  
693 extinctions limited to large-bodied taxa, and that avian lineages have been continuous across  
694 Southeast Asia since at least the Late Pleistocene. This is in contrast to other oceanic island  
695 archipelagoes, where the arrival of modern humans in the Holocene often resulted in  
696 dramatically reduced avian diversity (Cheke and Hume, 2008; James, 1995; James and Olson,  
697 1991; Milberg and Tyrberg, 1993; Olson and James, 1991; Steadman, 2006; Wood et al.,  
698 2017; Worthy and Holdaway, 2002). The extinction of the crane *Grus* sp., a large-bodied bird  
699 on Timor would be in line with the extinction of other large avian taxa from Flores, such as  
700 the giant stork *Leptoptilos robustus* and the vulture *Trigonoceps* sp. (Meijer et al., 2015b), and  
701 indicates that Quaternary megafauna extinctions in Wallacea included avian taxa as well as  
702 proboscideans and reptiles.

703

704

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709

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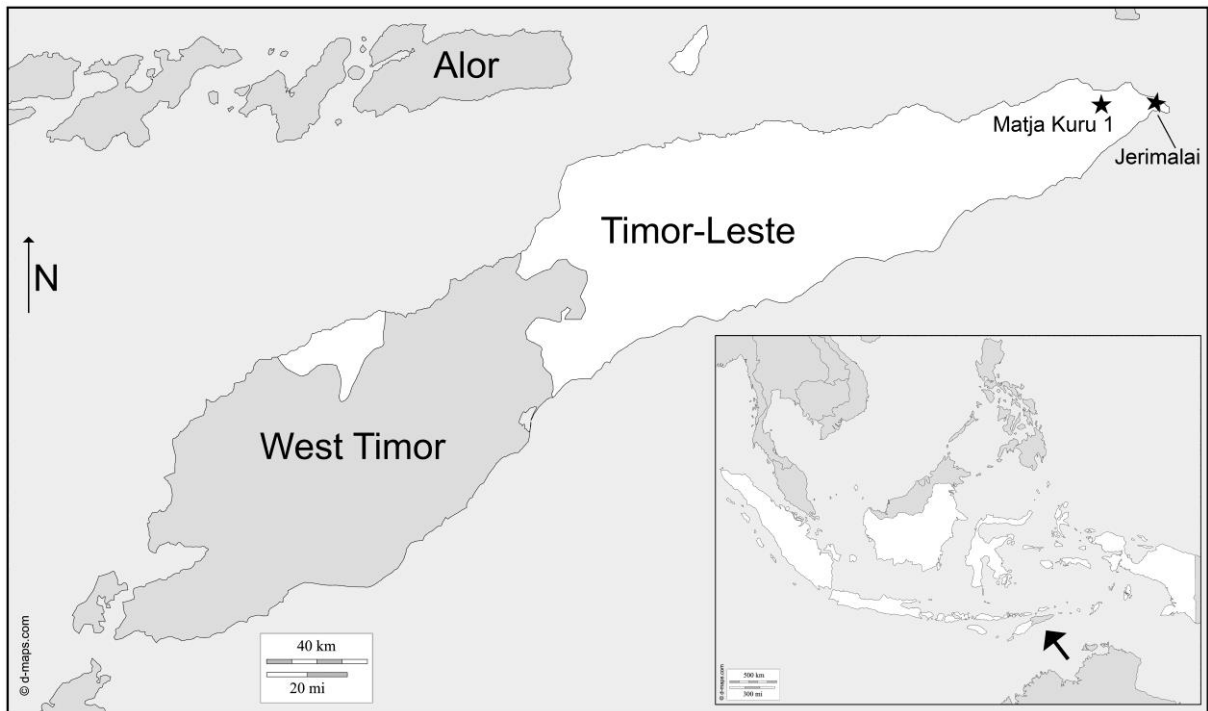
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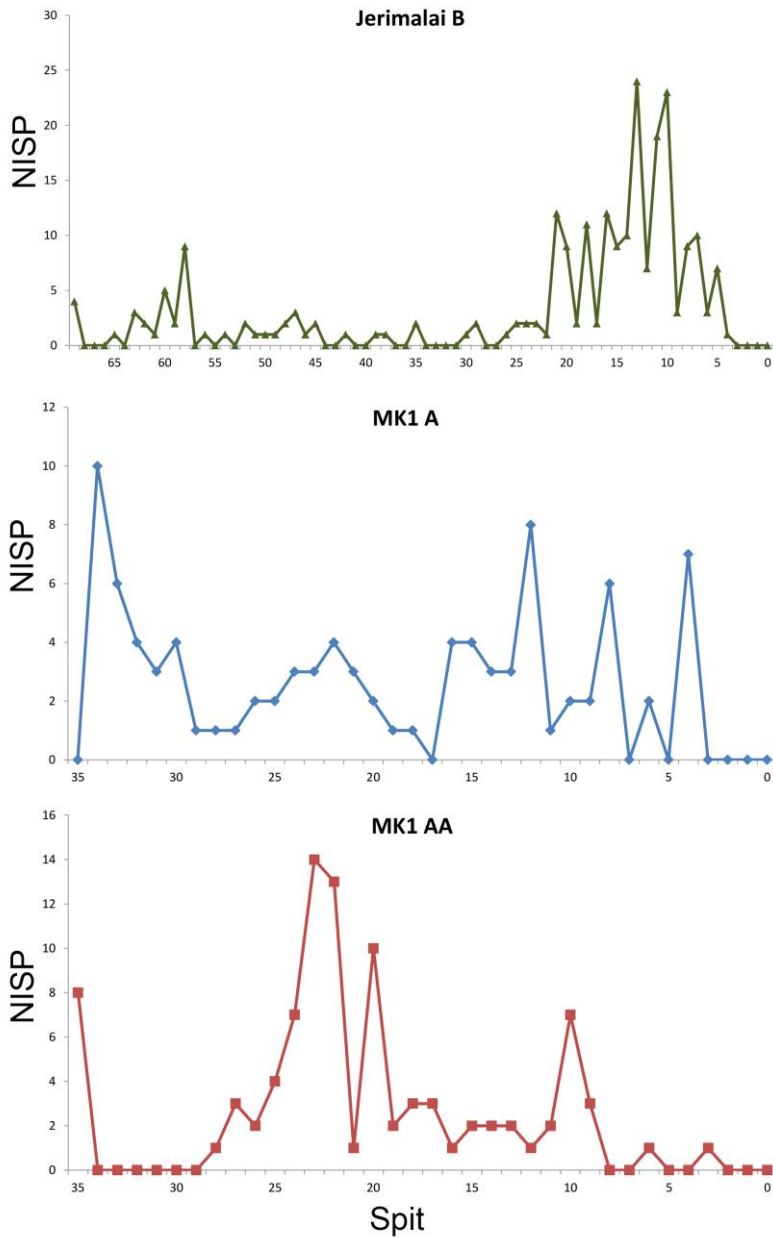
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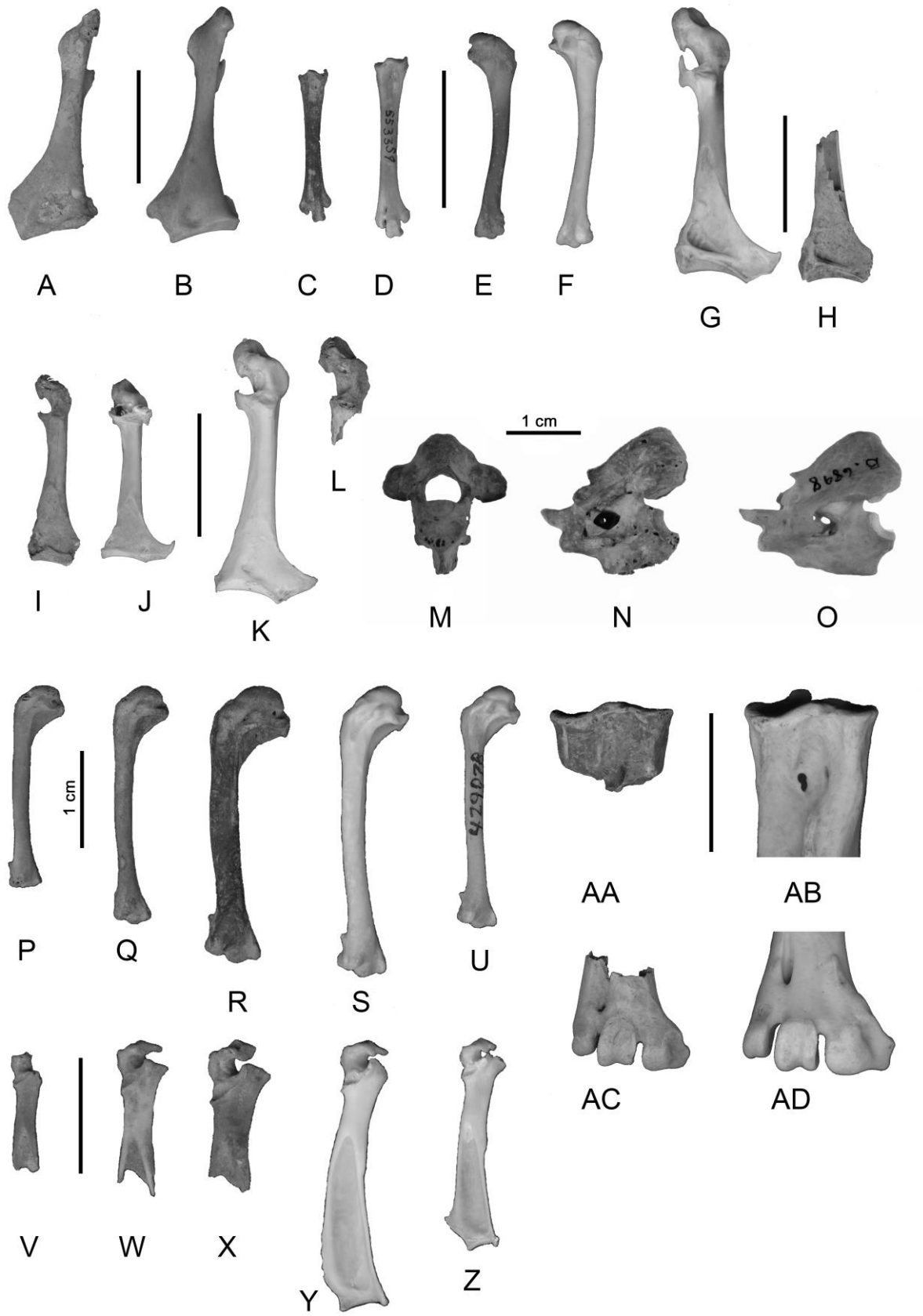
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**Figure 1.** Location of Matja Kuru 1 and Jerimalai in Timor-Leste.



**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.

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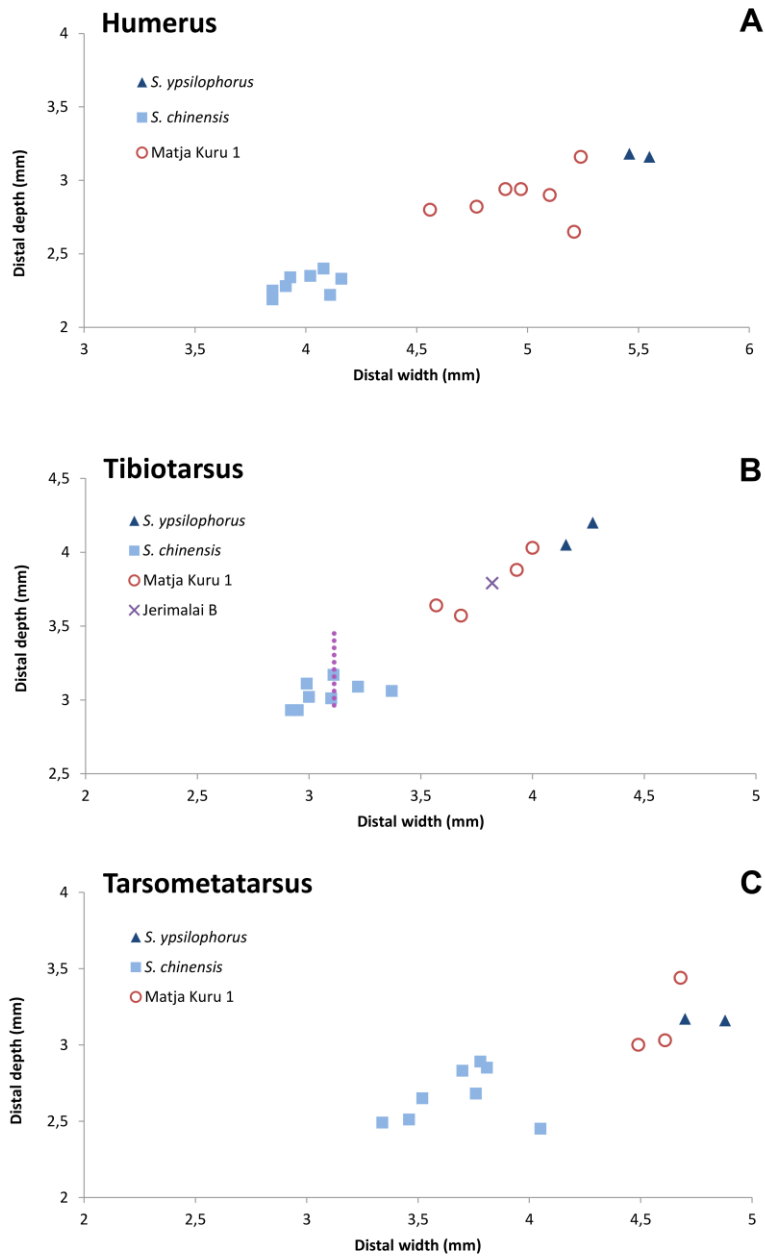
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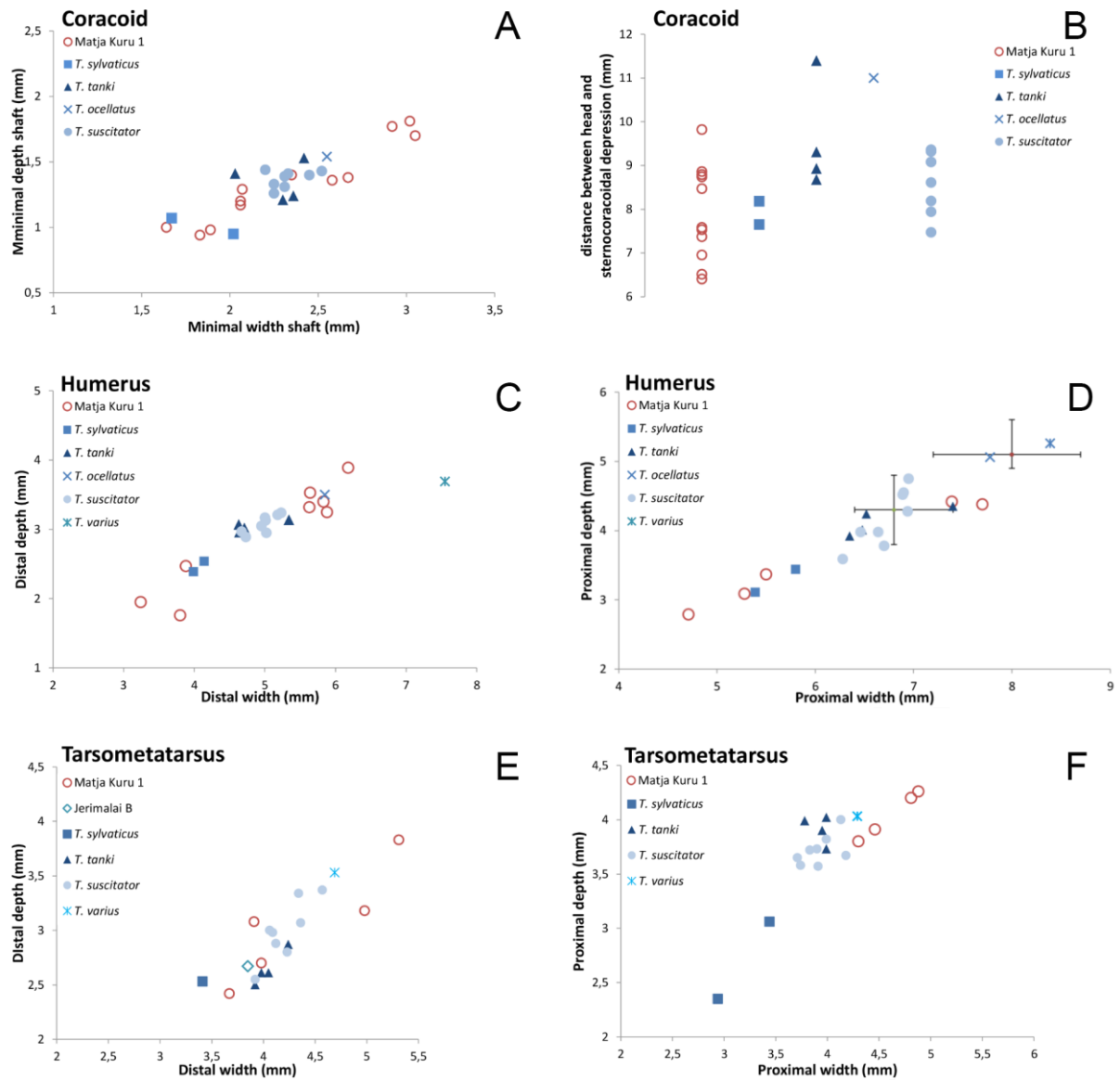
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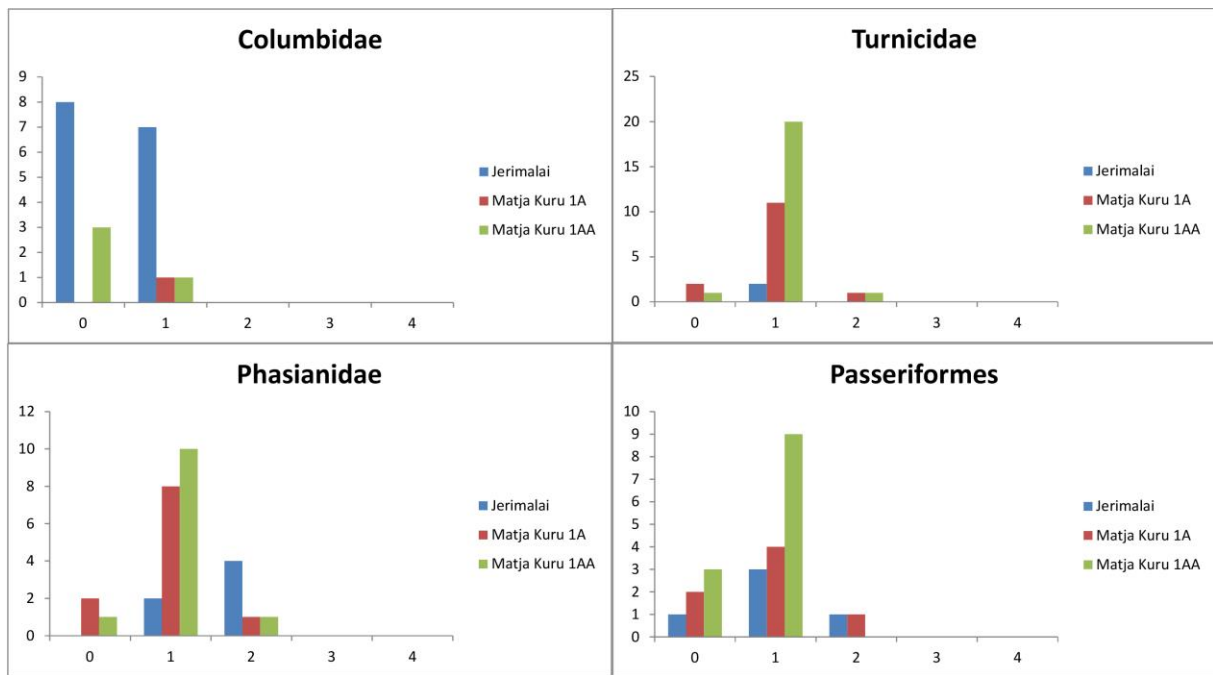




**Figure 4.** Phasianidae. A. Measurements of the humerus (A), tibiotarsus (B) and tarsometatarsus (C) of fossil Phasianid remains from Matja Kuru 1 and Jerimalai B and extant *Synoicus ypsilophorus* and *S. chinensis*. The dotted line in (B) indicates the distal width of the single *S. chinensis* specimen from Jerimalai B.

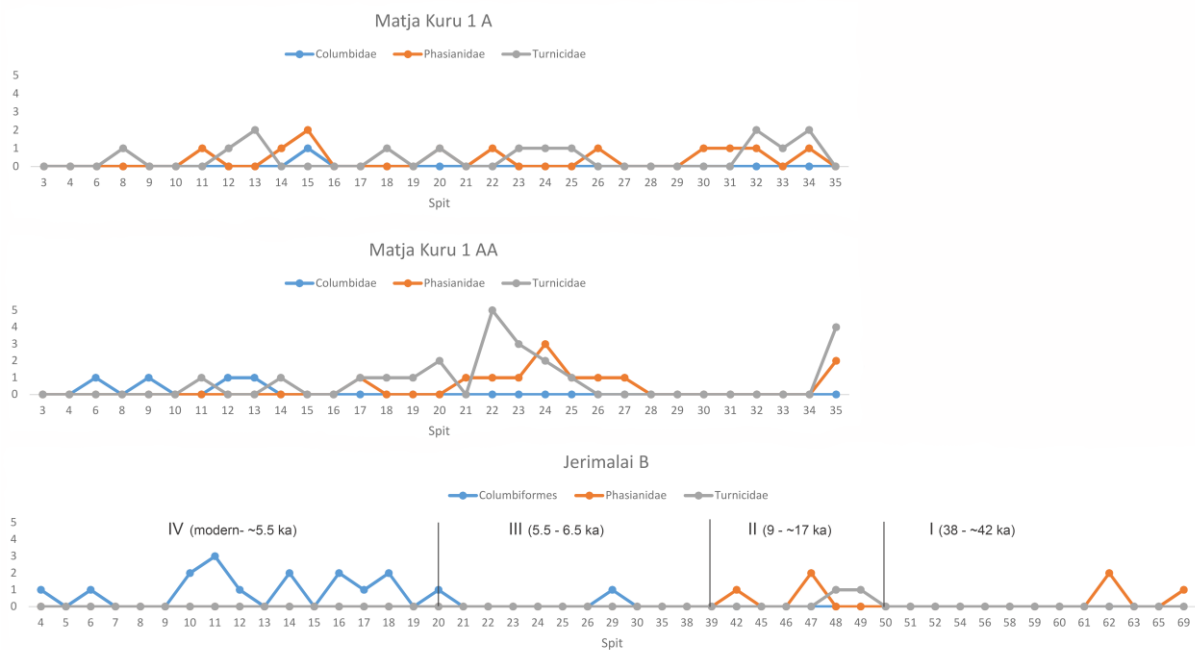


**Figure 5.** Selected measurements of extant Turnicidae and fossil specimens from Matja Kuru 1 and Jerimalai B. A–B, coracoid; C–D, humerus, crosses indicate data range for *T. varius* and *T. novaecaledoniae* from Balouet and Olson (1989); E–F, tarsometatarsus.



**Figure 6.** Digestion scores for four of the major groups of birds at Jerimalai B and Matja Kuru 1A and 1AA.

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

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