The avian fossil record in Insular Southeast Asia and its implications for avian biogeography and palaeoecology

Excavations and studies of existing collections during the last decades have significantly increased the abundance as well as the diversity of the avian fossil record for Insular Southeast Asia. The avian fossil record covers the Eocene through the Holocene, with the majority of bird fossils Pleistocene in age. Fossil bird skeletal remains represent at least 61 species in 53 genera and 27 families, and two ichnospecies are represented by fossil footprints. Birds of prey, owls and swiftlets are common elements. Extinctions seem to have been few, suggesting continuity of avian lineages since at least the Late Pleistocene, although some shifts in species ranges have occurred in response to climatic change. Similarities between the Late Pleistocene avifaunas of Flores and Java suggest a dispersal route across southern Sundaland. Late Pleistocene assemblages of Niah Cave (Borneo) and Liang Bua (Flores) support the rainforest refugium hypothesis in Southeast Asia as they indicate the persistence of forest cover, at least locally, throughout the Late Pleistocene and Holocene.

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INTRODUCTION

7

8   Ever since the seminal observations of Alfred Russel Wallace (1863, 1869), a plethora of

9 studies has highlighted the avian species richness, high levels of endemism, and unique

10 biogeographical patterns, as well as the conservation threats across Insular Southeast Asia (i.e.

11 Mayr, 1944; Huxley, 1868; Butchart et al., 1996: Brooks, Pimm & Collar, 1997, 1999:

12 Stattersfield et al., 1998; Myers et al., 2000; Trainor & Lesmana, 2000; Birdlife International,

13 2001; Jones et al., 2001; Jones, Marsden & Linsley, 2003; Ding et al., 2006; Jønsson et al., 2008,

14 2010; Holt et al., 2013). However, very little is known regarding the evolutionary history of birds

15 in this region. Evidence for extinction events and faunal turnovers in Insular Southeast Asia

16 comes mainly from the mammalian fossil record, particularly proboscideans and primates (i.e.

17 van den Bergh, 1999; van der Geer et al., 2010; Louys & Meijaard, 2010; Meijaard, 2003; de Vos,

18 van den Hoek Ostende & van den Bergh, 2007). How past events have shaped current patterns of

19 avian distributions remains unexplored. Here, I provide a synthesis of the current fossil record of

20 birds in Insular Southeast Asia and its implications for avian biogeography.

Localities with avian remains in Insular Southeast Asia

21

22   Although Australia and Asia have both yielded extraordinary fossil bird remains (for an

23 overview, see Murray and Vickers-Rich (2004) and Chiappe (2007)), some of them dating back

24 well into the Cretaceous and including some of the world's earliest birds (Vickers-Rich, 1991;

25 Chiappe, 2007; Martin et al., 2013), fossil bird remains from the island archipelagos in between

26 these continental landmasses are rare. There are no Mesozoic bird remains, which can be

27 attributed to the fact that the majority of islands didn't constitute dry land until the Cenozoic

28 (Hall, 2002).

29 *Sumatra*

30   The oldest bird remains from Insular Southeast Asia are represented by an almost

31 complete skeleton of the pelecaniform *Protoplotus beauforti* (Lambrecht, 1931) from Sibang in

32 the Sangkarewang Formation, West Sumatra (Fig. 1). The age of the sediments has been disputed,

33 but they are thought to be at least of Eocene age (van Tets, Rich & Marino-Haiwardoyo, 1966).

34 Avian footprints have been described from the Oligocene Sawahlunto Formation near Kandi in

35 West Sumatra. These footprints are attributed to two distinct ichnospecies of *Aquatilavipes, A.*

36 *wallacei* and *Aquatilavipes* sp. A (Zaim et al., 2011, Zonneveld et al., 2011, 2012), and are most

37 similar to tracks produced by small shorebirds such as sandpipers, rails and plovers (Zonneveld et

38 al., 2011).

39 *Java*

40   Alexander Wetmore (1940) described bird bones from bone-bearing terraces near

41 Watualang, situated near the Solo River in central Java (Fig. 1). These terraces are considered to

42 be Late Pleistocene of age and identical with the Ngandong terraces. The bones represented two

43 fossil bird species: a crane, *Grus grus* and a new species of giant stork, *Leptoptilos titan*.

44 Wetmore (1940) also tentatively mentions remains of an extinct vulture of the subfamily

45 Aegypinae, but the whereabouts of these fossils is unknown.

46   Weesie (1982) described avian remains collected from the Middle Pleistocene site of

47 Trinil HaubtKnochen (HK), the type locality for *Homo erectus,* and from Sumber Kepuh, a

48 locality that is considered to be contemporaneous with *H. erectus* (Storm, 2012). Weesie (1982)

49 ascribes the fossils from Trinil HK to the stork *Leptoptilos* cf. *dubius*, Black-necked Stork

50 *Ephippiorhynchus* cf. *asiaticus*, the red-breasted Goose *Branta* cf. *ruficollis*, and the Australian

51 Shelduck *Tadorna tadornoides* and the single fossil from Sumber Kepuh to the Green Peafowl

52   *Pavo m. muticus* (Supplementary table 1).

53   *Philippines*

54   Reis & Garong (2001) reported on an Early Holocene terrestrial vertebrate assemblage

55   excavated in four caves in Quezon Municipality on Palawan. Thirty-five bones were identified as

56   avian, and could be assigned to twelve avian taxa (Supplementary table 1); a species of scops

57   owl, *Otus* sp., three species of swiftlets in the genus *Collocalia,* and eight species of Passerine

58   birds.

59   *Borneo*

60   Stimpson (2009, 2010, 2013) described fossil bird assemblages associated with human

61   settlements from the Late Pleistocene and Holocene sediments of Great Cave of Niah in Sarawak,

62   North-western Borneo. He identified 28 taxa (Supplementary table 1) in 8 families, including

63   raptors and owls, hornbills, and swiftlets.

64   *Flores*

65   Late Pleistocene and Holocene bird remains from Liang Bua, a limestone cave on the

66   western part of the island, were described by Meijer & Due (2010) and Meijer et al. (2013). The

67   Liang Bua fossil bird assemblage is diverse and contains at least 25 non-passerine taxa in 14

68   families (Supplementary table 1), including a giant marabou stork *Leptoptilos robustus*, a vulture

69   *Trigonoceps* sp., and swiftlets.

70   *Other sites*

71   Bird remains have been documented for Madai Cave on Sabah (Harrison, 1998) but these

72   remains have not been identified yet.

The fossil bird record in Insular Southeast Asia

73

74　　　　To date, sixty-one species of fossil birds have been identified in Insular Southeast Asia,

75　representing at least 53 genera and 27 families (Supplementary table 1). Two taxa are

76　represented by fossil footprints only. While the avian fossil record covers the Eocene through to

77　the Holocene, the majority of fossil avians come from Quaternary sediments. Accipitridae,

78　Strigidae and Apodidae owls are present and abundant in all cave sites excavated, and are

79　ubiquitous elements in the modern Southeast Asian avifauna. The current fossil record for birds

80　forms a significant extension of the last overview of Southeast Asian fossil birds (Rich et al.,

81　1986), which only listed the record for Java. The recent expansion reflects both renewed interest

82　in existing collections (Borneo) as well as new excavation efforts on Sumatra, Flores and

83　Palawan.

84　　　　It is important to note the differences in taphonomy between some of the sites. Both Javan

85　sites, i.e. Watualang and Trinil, are open-air sites in fluvial deposits, whereas the sites on Borneo,

86　Palawan and Flores are cave sites that are more favourable for the preservation of smaller bones.

87　Bone accumulations in caves may result from fluvial transport, pitfalls, burrow deaths,

88　hibernation/aestivation and predation (Andrews, 1990). For Niah Caves, deposition of swiftlets

89　likely resulted from natural death, as the caves have sustained populations of swiftlets for at least

90　48,000 years (Stimpson, 2013). At Liang Bua (Flores), signs of digestions on the bone surfaces

91　suggest that birds of prey, most likely a species of barn owl (*Tyto* sp.), are responsible for the

92　accumulation of the majority of non-predatory birds (Meijer et al., 2013). Although most of the

93　bird bones have been found in association with hominid or modern human remains, no cut marks

94　or other signs indicative of human hunting have been reported for any bird bones, in contrast to

95 the remains of the pygmy elephant *Stegodon florensis insularis* (Van den Bergh et al., 2009).

96 **DISCUSSION**

97 **Avian biogeography**

98   Avian dispersal patterns in Insular Southeast Asia are complex (Jønsson et al., 2008,

99 2010; Carstensen & Olesen, 2009; Michaux, 2010), as the geological history of the region is

100 complicated (Hall, 2002) and the avifauna contains elements of both Indo-Malayan and

101 Australasian origin (Mayr, 1944; Michaux, 2010). Especially for the Philippines (minus Palawan)

102 and Wallacea, the use of land bridges to explain inter-island faunal similarities is limited as these

103 archipelagos were never connected to mainland Asia or Australia. The deep sea straits between

104 islands formed a dispersal barrier for terrestrial animals, and although birds are generally less

105 hindered by such barriers, the extent to which sea straits affected avian dispersal and

106 diversification in Insular Southeast Asia is poorly understood (Hosner, Nyári & Moyle, 2013).

107 Molecular studies suggest complex patterns of mainland-island interchange and diversification

108 for passerines (Cumings Outlaw & Voelker, 2008; Jønsson et al., 2010, 2011), but little work has

109 been done for non-passerine birds (Birks & Edwards, 2002). Fossil occurrences can provide

110 calibration points for dispersal models based on molecular data. Especially the occurrence of

111 extinct taxa may reveal successful colonization events, and thus past dispersal routes, while

112 diminishing the (artificial) importance of other lineages.

113 With the exception of the extinct giant storks from Flores and Java (Supplementary table 1),

114 species recorded in fossil assemblages are extant species, suggesting continuity of avian lineages

115 across Southeast Asia since at least the Late Pleistocene. A contraction in species range does

116 seem to have occurred for a number of species. On Java, the Middle Pleistocene *L.* cf. *dubius* and

117 *B. ruficollis* are currently restricted to more northern regions. *Tadorna tadornoides* and *E.* cf.

118 *asiaticus* are nowadays occasional visitors, and Weesie (1982) considers their presence in Middle

119 Pleistocene Java as indicative of cooler climatic conditions. Whereas the Middle Pleistocene

120 mammal fauna from Java went extinct at the transition to the Late Pleistocene (de Vos, van den

121 Hoek Ostende & van den Bergh, 2007; van der Geer et al., 2010), birds might have responded by

122 a range shift rather than extinction. On Palawan, *Zosterops montanus* now occurs at higher

123 elevations and seems to have undergone a recent range contraction (Reis & Garong, 2001). The

124 presence of vultures in Late Pleistocene Insular Southeast Asia is significant, as they are

125 conspicuously absent from the modern avifauna (Thiollay, 1998). Remains of the white-headed

126 vulture *Trigonoceps* sp. were recovered from Late Pleistocene sediments at Liang Bua (Flores)

127 (Meijer et al., 2013). Wetmore (1940) reported on two bones from Late Pleistocene sediments at

128 Watualang (Java) "being from a species about the size of *Pseudogyps bengalensis*. These are

129 typical in form of birds of this group and apparently represent an extinct species." Unfortunately,

130 the whereabouts of these bones remains unclear and their vulturine nature cannot be confirmed at

131 present. The presence of vultures on Flores, and possibly on Java, indicates that the ranges of

132 extant genera of vultures, even those with current distributions limited to Africa, may have been

133 much larger in the past, a conclusion also supported by the presence of two African vulture

134 genera in the middle Pleistocene of China (Zhang et al., 2012). According to Thiollay (1998), the

135 lack of vultures in the modern avifauna results from the lack of mammalian carcasses on islands.

136 Additionally, species impoverishment along the continent-island gradient results from nestedness,

137 in which the abundant, generalist and forest species make up the poorer, island species subset.

138 Avifaunas within Southeast Asia indeed show a high level of nestedness (Carstensen & Olesen,

139 2009), but nestedness alone cannot explain the modern absence of vultures. The disappearance of

140 *Trigonoceps* sp. from the Liang Bua sequence at the end of the Late Pleistocene seems to be tied

141 to the disappearance of *Homo floresiensis* and *Stegodon florensis insularis* (Meijer et al., 2013),

142 which left the island devoid of large mammals. Also, both the extant as well as the fossil Javan

143   fauna contains a number of large mammals, including large bovids and deer (and until recently,

144   proboscideans and rhinos as well), which could have provided potential food resources for

145   vultures. The current absence of vultures in insular Southeast Asia seems to be an effect of Late

146   Pleistocene extinction events rather than nestedness.

147   **Avian dispersal routes**

148   For the Lesser Sunda Islands, different dispersal scenarios have been proposed.

149   Stresemann (1939) suggested that certain terrestrial birds colonized the Sunda Islands from the

150   north (Sulawesi), but others have argued for a route via Southeastern Sundaland based on the

151   similarities between the extant avifaunas of Flores, Java and Bali (Mayr, 1944; Mees, 2006).

152   Such a route agrees with the presence of giant storks in the Late Pleistocene of both Java and

153   Flores, as their large size might represent an adaptation to a more terrestrial life style (though it

154   should be noted here that *L. robustus* from Flores displays wing morphology similar to modern *L.*

155   *dubius,* Meijer and Due, 2010). Both the Javan and Flores giant stork may represent late

156   offshoots of the lineage that also contains *L. falconeri* from the Siwalik Hills in India (Louchart et

157   al., 2005). Living Ciconidae display significant sexual dimorphism (Louchart et al., 2005), but

158   Weesie (1892) does not consider the possibility that the stork remains from the Middle

159   Pleistocene of Java (which he attributed to the modern *Ephippiorhynchus* cf. *asiaticus* and *L.* cf.

160   *dubius*) might, in fact, be smaller (female) specimens of *L. titan.*

161   Although most of the Sunda Shelf was dry land at some point during the Pleistocene

162   (Hall, 2002), there is no unambiguous geological evidence that Palawan was once connected to

163   Sundaland (see discussion in Reis & Garong, 2001). Fossil and modern faunal data suggest that

164   Palawan might have been a stepping stone between Borneo and the Philippines. In that light, the

165   fossil presence of the mossy-nest swiftlet *Aerodramus salanganus* in the very early Holocene is

166 interesting, since it is absent on Palawan, but present in the Greater Sundas as well as in the

167 Philippines. Its presence in the early Holocene could indicate that Palawan served as a stepping-

168 stone for the dispersal of *A. salanganus* from the Greater Sundas into the Philippines.

169 **Palaeoecological implications**

170   The climatic and ecological conditions of Pleistocene Sundaland have been subject of

171 much debate. Heaney (1991) proposed the presence of a continuous savannah corridor during

172 glacial maxima, which stretched from the Malaysian Peninsula through central Sundaland all the

173 way to the Lesser Sunda Islands. This savannah corridor presumably facilitated the dispersal of

174 hominins and other terrestrial megafauna across Sundaland, and acted as a dispersal barrier for

175 forest-dependent taxa between Sumatra and Borneo. Although geomorphological,

176 biogeographical, and palynological evidence, as well as vegetation modelling indicate that drier

177 conditions prevailed over Insular Southeast Asia during the Last Glacial Period (for a review, see

178 Bird, Taylor & Hunt, 2005), there is only very limited support for a continuous savannah corridor

179 at the scale proposed by Heaney (1991). The savannah corridor hypothesis is based on the

180 climatic conditions that occurred during glacial maxima, a situation that existed only for short

181 periods of time during the Pleistocene (Voris, 2000). Furthermore, Slik et al. (2011) argue that the

182 biogeographic difference between Sumatra and the Malay Peninsula, and Borneo can also be

183 explained by exposed sandy sea-bed soils that acted as a dispersal barrier. Instead of savannah

184 vegetation, swamps and heath forest dominated central Sundaland.

185   Birds are closely associated with vegetation, and their abundance and diversity in fossil

186 assemblages adds valuable palaeoecological insights. The habitat spectrum inferred from Liang

187 Bua's avifauna (Meijer et al., 2013) shows that, during the Late Pleistocene, forest habitats, as

188 well as wetland and open grassland habitats dominated around Liang Bua, and provided ample

189 resources for hominins. Studies of the fossil bird assemblage from Niah Cave on Borneo

190 (Stimpson, 2010, 2013) showed that swiftlets, obligate insectivores, had been persistently present

191 from well into the Late Pleistocene until today (Stimpson, 2013). Their continuous ==indicates== that

192 habitats within the feeding range of these birds supported a sufficient base of aerial arthropods to

193 support swiftlet populations. Despite ample evidence for drier conditions based on

194 geomorphological, palynological, biogeographical data and climate modelling (see references in

195 i.e. Bird, Taylor & Hunt, 2005; Westaway et al 2009), and the concomitant contraction of forests,

196 Late Pleistocene fossil bird assemblages from both Flores and Borneo suggest that forests

197 persisted at least locally. These findings are consistent with other studies (Cannon, Morley &

198 Bush, 2009; Wurster et al., 2010) that suggest that forest refugia were maintained across Insular

199 Southeast Asia throughout the Late Pleistocene and Holocene.

200 **CONCLUSION**

201   The avian fossil record in Insular Southeast Asian has significantly increased in

202 abundance and diversity over the last decades, and now consists of at least 61 species,

203 representing 53 genera in 27 families, and 2 ichnospecies. Fossil bird remains span the last 50

204 million years, from the Eocene to the Holocene, but most remains have been found in Quaternary

205 sediments. Swiftlets, birds of prey and owls are present and abundant in all cave sites excavated,

206 and are ubiquitous elements in the modern Southeast Asian avifauna.

207   Extinctions seem to have been few, as the majority of the species in the fossil record are

208 extant taxa. Range shifts are observed for species that are currently restricted to cooler regions.

209 Similarities between the Late Pleistocene avifaunas of Flores and Java suggest a dispersal route

210 across southern Sundaland. The mossy-nest swiftlet *A. salanganus* might have dispersed into the

211 Philippines via Palawan. The Late Pleistocene record of forest birds, particularly swiftlets,

212 suggest that the structural diversity of forest habitats was maintained, at least locally, throughout

213 the Late Pleistocene and into the present.

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390   **FIGURE CAPTIONS**

391   **Figure 1.** Map of Insular Southeast Asia indicating the location of localities with fossil bird

392   remains.

393   **Supplementary Table 1**. Fossil bird species from Insular Southeast Asia. † indicates an extinct

394   species; (†) indicates a possibly extinct species; * indicates a species that is no longer

395   present in Insular Southeast Asia.

Figure 1

Map of Insular Southeast Asia indicating the location of localities with fossil bird remains.