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Lapita colonisation and avian extinctions in Oceania

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Abstract

Birds perform important functions for the maintenance of island ecosystems, and historically have been highly valued as food and for providing materials for the manufacture of items that display power and status. When Lapita migrants first arrived in Oceania they encountered a much more diverse avifauna than exists today. Naïve endemic fauna, having evolved in isolation, were vulnerable to invasive human socioeconomic systems and introduced invasive mammals. Rapid reduction in avian biodiversity in Remote Oceania and likely impacts on ecosystem functionality occurred. While the evidence for bird extinctions and extirpations in Polynesia is well established, it is not the case for Lapita–bird interactions in the Melanesian and western Polynesian region. Here we review the evidence for Lapita bird exploitation and extinctions in the South-West Pacific region of Oceania. We use the incomplete Lapita, immediately Post-Lapita and pre-Neolithic archaeological record in Oceania to critically evaluate the evidence for the causes of avian extinctions, considering bird characteristics, human activities and biased sampling issues. Our data indicate that bird hunting in Oceania originated in the Pleistocene and was extensive throughout the Lapita distribution, resulting in widespread extinctions and extirpations of land and sea birds. This pattern probably represents a conservative estimate, the full extent of prehuman avifauna diversity and early human impacts are likely obscured by limited sampling of archaeological and palaeontological sites.

Introduction

Recent studies indicate that birds have played a significant part in Pacific Island cultures and continue to do so today. In these insular communities, birds have been traditionally hunted for food and/or materials to make feathered cloaks and headdresses as displays of chiefly power (Best 1979; Hartnup et al. 2011; Harwood 2011; Kirch 1997; Speiser 1996). Indeed, human–bird interactions like these have roots deep in hominin prehistory with the development of more complex cognition associated with the advent of specialised technologies and methods to capture these often small and elusive prey (Blasco and Peris 2009; Finlayson et al. 2012). At some stage, this highly developed hunting behaviour spread to the tropical Asia-Pacific region during the late Pleistocene (Hawkins et al. 2017; Stimpson 2016; Wickler 2001). This complex human behaviour continued into the late Holocene when horticulturalist human colonisation had a profound effect on avifaunal diversity in the Pacific Islands and was likely associated with ecosystem degradation (Steadman 2006a; Worthy et al. 2015).

Oceanic islands are laboratories that have proven deleterious prehistoric human impacts on avifauna (Steadman 1995, 2006a) compared to continental landmasses, which typically have fewer recorded avian extinctions (Hull et al. 2015; Meijer 2014; Meijer et al. 2015). Many reasons have been proposed for the greater susceptibility of birds to extinction on more isolated tropical islands during human colonisation, including island size, degree of isolation from sources of faunal immigration, bird characteristics and, most importantly, complex human behavioural developments (Duncan et al. 2013; Hull et al. 2015; Karels et al. 2008; Meijer et al. 2015; Steadman 2006a; Steadman and Martin 2003).

In some cases, the model of ‘overkill’ or ‘blitzkrieg’—that is, intensive human hunting and rapid depletion of populations—has been implied as the main mechanism for bird extinctions (Bedford 2006). However, any level of hunting that was unsustainable for the taxon in question can be considered as ‘overkill’. It is important to note that this overkill rate will vary between taxa depending on the individual biological attributes of those taxa, such as longevity, fecundity, etc. Further, the development of more complex sociopolitical horticultural economies during the late Holocene, which saw the introduction of invasive mammals, and more intensive habitat fragmentation (forest clearance for crops), were also likely important factors that combined to exacerbate the situation (Blackburn et al. 2004; Hawkins et al. 2017; Pimm and Askins 1995; Prebble and Wilmshurst 2009; Steadman 2006a). These models, however, have rarely been tested in the prehistoric record (Duncan et al. 2002; Nagaoka 2012), probably because they are difficult to evaluate rigorously as fossil and archaeological records are mostly missing and patchy at best (Duncan et al. 2013; Hull et al. 2015).

Nonetheless, the most dramatic examples of avian extinctions are revealed in the archaeological records of the Pacific, particularly those settled in the eastern Polynesian region by horticultural societies (Steadman 1995, 2006a; Steadman et al. 2002b), c. 1000 BP (Wilmshurst et al. 2011). It is estimated that about 50–90 per cent of endemic species, especially flightless rails and megapodes, disappeared on several island groups in this region (Cook Islands, Easter Island, Hawai‘i, Henderson Island, Marquesas, New Zealand, Society Islands) sometime after initial human arrival (Steadman 1995, 2006a). Replacements of the lost taxa, estimated to be upwards of 1000 species in total, by new arrivals, has yet to occur and extinction occurred at a considerably greater rate than generally seen in the fossil record (Duncan et al. 2013).

Bird extinctions revealed by avifauna associated with earlier horticultural arrival in Oceania, whether Lapita or immediately Post-Lapita settlements, are also documented (Hawkins 2015; Steadman 2006a). The emergence of Lapita, a maritime Neolithic pottery-making mixed economic culture originating in East Asia and rapidly arriving in the Bismarck Archipelago c. 3300 BP (Skoglund et al. 2016), has been linked to a dramatic rise in human impacts on island environments and biota in Oceania (Blackburn et al. 2004; Prebble and Wilmshurst 2009; Steadman 2006a; Stevenson 1999; Summerhayes et al. 2009). Lapita voyagers became the first humans to cross a 350-km water gap at the end of the main Solomon Islands chain (Sheppard 2011) and colonised the previously uninhabited South-West Pacific Remote Oceanic Islands of eastern Melanesia and western Polynesia by c. 2850 cal. BP (Burley et al. 2015; Reith et al. 2008). They introduced invasive mammals (rats, pigs) to the region that are likely to have had a great impact on prehistoric naïve fauna lacking behavioural defences (Blackburn et al. 2004; Hawkins 2015). The archaeological record within this region of Lapita expansion has provided a few examples of extinctions of not just birds, but also of endemic large-bodied terrestrial reptiles such as turtles, crocodylians and iguanas (Hawkins 2015; Hawkins et al. 2016; Irwin et al. 2011; Mead et al. 2002; Pregill and Steadman 2004; Pregill and Worthy 2003; White et al. 2010).

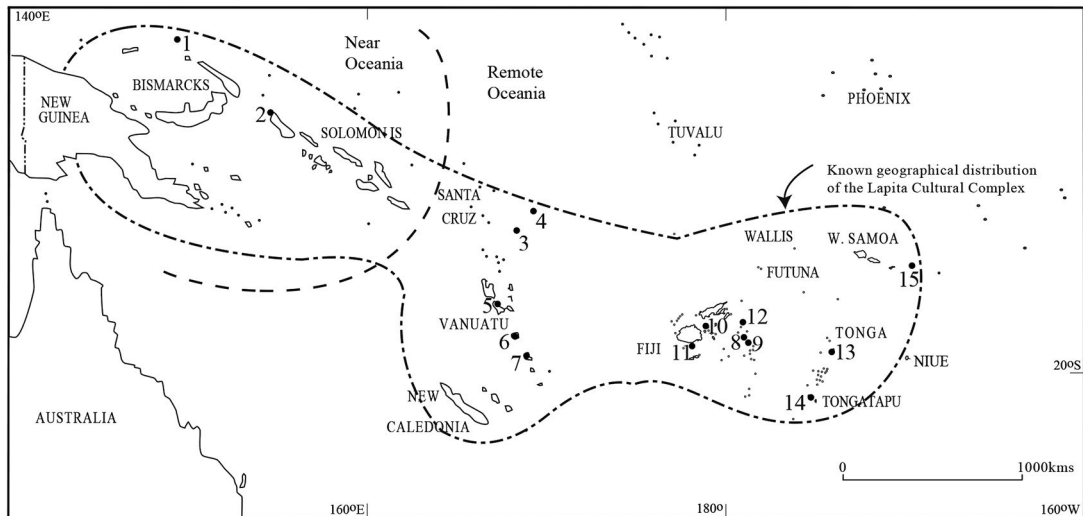


Figure 21.1. Map of the South-West Pacific (Near and Remote Oceania) and locations of one Pre-Lapita and 32 Lapita and immediately Post-Lapita age archaeological sites with evidence of human hunting and avian extinctions.

1: Mussau Island (Sites ECA, ECB, EKQ), 2: Kilu Cave, Buka Island, 3: Tikopia (Sites TK-4, TK-1, TK-32, TK-36), 4: Anuta (Site AN-6), 5: Malakula Island (Sites Yalo south, Navaprah, Malua Bay, Woplamlam), 6: Efate (Sites Teouma, Arapus, Mangaasi), 7: Erromango (Sites Ponamla, Ifo), 8: Lakeba (Sites Qaranipuqa rock shelter, Wakea), 9: Aiwa Levu and Aiwa Lailai (Sites Cave 1, Cave 2, Aiwa 1, Dau RS), 10: Naigani, 11: Beqa, 12: Mago (Sites Votua, Sovanibeka), 13: Ha'apai (Sites Tongoleleka, Holopeka, Faleloa, Toumu'a), 14: Tongatapu (Site Ha'ateiho), 15: Ofu Island (Site To'aga).

Source: Illustration by the authors.

However, detailing human–bird interactions from Lapita times has been problematic, as most Lapita sites in Oceania have typically yielded small vertebrate assemblages from mostly small-scale excavations (Hawkins 2015) or their descriptions have lagged far behind that of material culture and dating of sequences. The use of coarse recovery methods in many excavations has also occasionally limited vertebrate sample sizes, while preservation issues have been prevalent at other sites (Hawkins 2015). These factors have severely hampered our understanding of Lapita interactions with birds and the associated impacts on avifaunal diversity on Near and Remote Oceanic Islands. As such, early Neolithic archaeological avifaunal records are sparsely distributed in the Bismarck Archipelago in Near Oceania (Steadman and Kirch 1998). They increase steadily where Lapita people dispersed via the gateway to Remote Oceania; in Tikopia, Anuta (Steadman 2006a; Steadman et al. 1990) and Vanuatu (Bedford 2006; Hawkins 2015; Steadman 2006a, 2006b; Worthy et al. 2015); and onwards to Fiji (Irwin et al. 2011; Worthy and Clark 2009), Tonga (Steadman 1993a, 2006a; Steadman et al. 2002b) and Samoa (Steadman 1993b).

These problems in establishing the true scale of human impacts on avifauna by Lapita in Oceania are compounded by the restriction of palaeontological records, critical to reconstructing prehuman ecologies, within the region of Lapita expansion to New Caledonia, Fiji and Tonga (Anderson et al. 2010; Balouet 1991; Balouet and Buffetaut 1987; Balouet and Olson 1989; Koopman and Steadman 1995; Molnar et al. 2002; Poplin 1980; Worthy 2000, 2001, 2004; Worthy et al. 1999; Worthy et al. 2016).

In this summary, we review the current published data on Lapita bird exploitation, primarily for the period c. 3300–2800 BP, and document the subsequent extinctions in Near Oceania and Remote Oceania in the South-West Pacific (Figure 21.1). This we hope will improve our understanding of human–bird interaction and its consequences during this remarkable period of long-distance human dispersal and colonisation of the far-flung regions of Oceania. We identify issues with current models discussed above and advances in zooarchaeology that

have been made recently at the Teouma Lapita site (Worthy et al. 2015). We also include one archaeological site (Kilu Cave, Buka Island) in the northern Solomons that is substantially older and hints at possible Pre-Lapita extinctions in this archipelago during the late Pleistocene (28.7–20.1 ka BP) (Wickler 2001). We exclude analyses of the avifauna from the Pindai Caves, New Caledonia, reported by Balouet and Olson (1989) and Anderson et al. (2010), because these are primarily non-archaeological assemblages accumulated by pitfall and owl predation with age ranges that extended well into the Pre-Lapita period. There is some mixing of early Post-Lapita archaeological materials into these natural faunas, but it is impossible to separate archaeological versus natural components of the total accumulation, with the exception of some burnt bones that include *Sylviornis*.

We assess factors that may have contributed to the extinction of birds, including their inherent characteristics such as flight capability and habitat preference, within the context of the period of occupation (radiocarbon age and ceramic sequence), site type (open beach or cave), area excavated (m²) and faunal recovery methods used. To assess models of human hunting we present the number of extinct or extirpated taxa present, and the number of extinct/extirpated bird bones relative to total number of bones of terrestrial animals in early archaeological sites.

Methods

A few avian assemblages from early archaeological sites in the Mussau Islands, Solomons, Vanuatu, Fiji, Tonga and Samoa have been published in detail (see Tables 21.1–21.3). These were assessed for period of settlement based on calibrated radiocarbon dates and ceramic sequences, site type, areal excavation size (m²), number of extinct species identified, quantity of extinct bird bones relative to total terrestrial vertebrate remains and recovery methods employed. Dates, when available, were calibrated in Oxcal 4.2, using ShCal 13 (Hogg et al. 2013) and Marine13 (Reimer et al. 2013) to 95.4 per cent. Ceramic sequences follow those identified in regional studies (e.g. Bedford 2006; Best 1984; Clark 2009; Kirch and Yen 1982). Extinct avian taxa were quantified based on published identifications (Table 21.1) relative to extant taxa in the region (Bregulla 1992; Doughty et al. 1999; Dutson 2012), and their remains tallied by the number of identified specimens present (NISP) for each site. Total non-fish fauna including total bird NISP were included to estimate the proportion of birds exploited during Early Lapita colonisation when these data were available, although this was not always the case, as some sites lacked total bone counts from all faunal classes. Recovery methods, particularly the sieving protocols used, were also considered important to understanding the zooarchaeological record in the region, and so we list mesh size in millimetres and whether wet or dry sieving was used, given these factors can have a dramatic impact on the quantity and size of bones recovered (Hawkins 2015).

Each identified avian taxon was assessed for certain characteristics including general habitat preference and flight capability (Tables 21.2 and 21.3). Habitat preferences were estimated for each taxon based on where they spend most of their time foraging or nesting in the case of sea birds into four general habitats (coastal, wetlands, forest, open woodlands).

Table 21.1. List of archaeological sites under review by country, island, age, ceramic period, site type, island size, distance to nearest island, area excavated, number of extinct taxa, number of extinct bird bones, total non-fish fauna (NISP), and recovery methods used. Sites must have radiocarbon ages that overlap with Lapita settlement and/or presence of Lapita ceramics, and must have extinct or extirpated avifauna remains.

Region/ Island site	Site	Date range cal. BP (2 σ)	Ceramics	Site type	Area excavated area m ²	Extinct/ extirpated taxa	Extinct/ extirpated bird NISP	Extinct NISP/m ²	Total non- fish NISP	Recovery method	Referenced data
Papua New Guinea											
Mussau	ECA, ECB, EKQ	3636-2161	L to P-L	OB	41	4	10	0.24	1165	5 mm dry	Steadman and Kirch 1998; Kirch 1987; Kirch et al. 1991
Solomon Islands											
Buka	Kilu Cave	29 000-5000	P-C	C	3	8	49	16.3	6606	3.2 mm wet	Wickler 2001; Steadman 2006a
Tikopia	TK-4, Sinapupu, TK-1, TK-32 and TK-36	2990-500	K to S	OB	83	6	30	0.36	6537	6.4 mm dry	Kirch and Yen 1982; Steadman et al. 1990
Anuta	AN-6	3156-1002	I and P	OB	27	4	125	4.62	4383.5	6.4 mm dry	Kirch and Rosendahl 1973; Steadman et al. 1990
Vanuatu											
Erromango	Ponaamla	3076-1320	L-PL	OB	29	3	4	0.14	775	1-2 mm wet, 5 mm dry	Bedford 2006; Steadman 2006a
Erromango	Ifo	3062-2489	L to P-L	OB	33	1	2	0.06	153	1-2 mm wet, 5 mm dry	Bedford 2006; Steadman 2006a
Efate	Arapus	2900-2500	A to E	OB	70	2	5	0.07	3252	1-2 mm wet, 5 mm dry	Bedford 2006; Steadman 2006a; Bedford and Spriggs 2000
Efate	Mangaasi	2704-153	Late E to M	OB	18	2	2	0.11	1412	1-2 mm wet, 5 mm dry	Bedford 2006; Steadman 2006a
Efate	Teouma	3000-2500	L to E	OB	473	8	220	0.47	49207	1-2 mm wet, 5 mm dry	Worthy et al. 2015; Hawkins 2015
Malakula	Malua Bay School	2758-740	Late L to P-L	OB	14	1	2	0.14	66	1-2 mm wet, 5 mm dry	Bedford 2006; Steadman 2006b
Malakula	Woplampam	283-0	I and P	C	2	2	4	2	829	1-2 mm wet, 5 mm dry	Bedford 2006; Steadman 2006a
Malakula	Navaprah	2731-335	P-L	C	6	2	13	2.17	1935	1-2 mm wet, 5 mm dry	Bedford 2006; Steadman 2006a
Malakula	Yalo South	2700-2500	P-L	C	1.5	2	5	3.33	1186	1-2 mm wet, 5 mm dry	Bedford 2006; Steadman 2006a
Fiji											
Lakeba	Qaraniyuqa rock shelter and Wakea	3130-160	L to P-L	C	2	3	141	70.5	302*	2.5, 5 mm dry	Best 1984; Steadman 2006a; Worthy and Clark 2009
Aiwa Levu	Cave 2	2490-0	P-L	C	3	1	1	0.33	374	1.5, 3, 6.4, 12.7 mm dry	Steadman 2006a; Jones et al 2007
Aiwa Levu	Aiwa 1	2290-0	P-L	C	6	4	8	1.33	3092	1.5, 3, 6, 12.mm dry	Steadman 2006a; Jones et al 2007

Region/ Island site	Site	Date range cal. BP (2σ)	Ceramics	Site type	Area excavated area m ²	Extinct/ extirpated taxa	Extinct/ extirpated bird NSIP	Extinct NSIP/m ²	Total non- fish NSIP	Recovery method	Referenced data
Aiwa Lailai	Dau RS			C							
Naigani	Matanamuani VL 21/5	3211-2614	L to P-L	OB	120	2	10	0.08	n/a	2.5, 3.5, 7.1 mm dry	Irwin et al. 2011
Beqa	Kulu Bay 1	2380-0	L to P-L	OB	3	1	1	0.33	125	2, 4 mm wet	Worthy and Clark 2009
Mago	Votua	2930-1990	L to P-L	OB	4	3	7	1.75	18	3 mm wet	Worthy and Clark 2009
Mago	Sovanibeka	2720-2360	P-L	C	0.5	0	0	0	>218	n/a	Worthy and Clark 2009
Tonga											
Ha'apai	(5 sites) Pukotala, Tongoleleka, Faleloa, Vaipuna, Mele Havea	2950-2750	L to P-L	OB	9-12	11	519	n/a	2774	n/a	Steadman 2006a; Steadman et al. 2002b; Pregill and Steadman 2004
Tongatapu	Ha'ateiho	2923-2380	L to P-L	OB	12.3	6	n/a	n/a	437	n/a	Burley et al 2001; Steadman 2006
Samoa											
Ofu	To'aga	3400-640	I and P	OB	30	6	46	1.53	687	5 mm dry	Steadman 1993a; Kirch and Hunt 1993

Ceramics: L=Lapita; P-L=Post-Lapita; I=incised; P=plainware; A=Atapus; E=Eureti; M=Mangaasi; P-C=pre-ceramic; K=Kiki; S=Sinapupu. Site Type: OB=open beach; C=cave.
Source: See references in table.

Results

To date, the bones (total bird NISP=5741; 55 per cent of which come from Teouma and five Ha'apai sites) of 33 families (excluding Passeriformes) representing at least 131 distinct species have been identified from 29 Lapita and immediately Post-Lapita sites and one Pre-Lapita site (Kilu Cave). These sites geographically span from the Mussau Islands in the Bismarcks to as far as Samoa in Remote Oceania (Tables 21.1 and 21.3), a distance of some 4500 km. Diversity was clearly much higher in the basal layers of the Early Lapita sites. Extinctions are classed as either locally extinct, where a taxon is no longer found on a given island, or globally extinct. Fifty-eight species (including eight from the small sample from Kilu Cave on Buka), representing 16 families and 27 genera, are identified as being extinct (27 extinct globally) or extirpated from their island groups or regions in the Pacific Island nations of Papua New Guinea, the Solomons, Vanuatu, Fiji, Tonga and Samoa, from the combined sample (total extinct bird NISP=639; Tables 21.1 and 21.3).

Most taxa that have disappeared from the record are like known extant tropical forest-dwelling species, while others represent wetland rails and crakes, and some are migratory sea birds. Thirteen (39.4 per cent) of these taxa are the ground-dwelling megapodes, rails and one ground dove, whose terrestrial habits contributed to their greater vulnerability. These are likely to have disappeared very soon after initial human settlement, although some are present—probably secondarily mixed—in Post-Lapita cave contexts, which are notorious for complex depositional histories (O'Connor et al. 2011). Others were from small isolated islands such as Tikopia and Anuta, which may have initially been settled in very late or Post-Lapita times.

Most of the archaeological sites reported here were open settlements behind beaches (n=22) with midden deposits, although a number of archaeological cave and rock shelter sites (n=8) were also represented and contained extinct species; for example, on Buka in the Solomons (Wickler 2001), on the north-west coast of Malakula in Vanuatu (Bedford 2006) and in the Lau group in Fiji (Jones et al. 2007; Worthy and Clark 2009). Many of the excavations were quite small, c. <10 m², but four sites (Arapus, Naigani, Teouma and Tikopia) stand out as being relatively much larger. The recovery methods employed during these excavations were generally suited to recovery of avifaunal material. Dry sieving was extensively employed at most of the sites reviewed. A variety of mesh sizes was used, ranging from rather coarse at 12.7 mm, only employed in some layers at Aiwa Levu (Jones et al. 2007), to 1.5 mm, although 5 mm to 6.4 mm was more commonly employed. A number of the sites in Vanuatu (Bedford 2006; Hawkins 2015), at Kilu Cave (Wickler 2001) and one in Fiji (Worthy and Clark 2009) also saw extensive wet sieving of basal deposits. Despite these recovery methods, sample sizes of bird bones relative to total terrestrial vertebrate counts are quite low, except for Lakeba and Votua in Fiji (both small sample sizes) and possibly Anuta, which had relatively abundant bird bones (NISP=299; Steadman et al. 1990, Table 11) but did not have total bone count data available, only weight in grams (Kirch and Rosendahl 1973).

Eleven of the sites are exclusively Post-Lapita in age and/or ceramic style and a large proportion of extinct/extirpated taxa in the region are associated exclusively with these Post-Lapita deposits, with 17 out of the 58 extinct or extirpated taxa (29.3 per cent). The best evidence for Lapita impact on regional avifauna during early colonisation of Remote Oceania is from Vanuatu and Tonga. In Vanuatu there are nine extinct/extirpated taxa listed in Table 21.2, from the Early Lapita site at Teouma (Worthy et al. 2015) and in Tonga there are 10 extinct or extirpated species recorded from sites in Ha'apai and Tongatapu (Steadman 2006a).

Table 21.2. Taxonomic list of extinct/extirpated taxa by family, species, common name, archaeological distribution, period, habitat and flight.

Family	Species	Common name	Distribution of extirpations/extinctions	Ceramic period recorded	Habitat	Flight
Megapodiidae	<i>Megapodius freycinet</i> (= <i>layardi</i> or <i>eremita</i>)*	Common megapode	Tikopia	Post-Lapita	F	no
	<i>Megapodius</i> sp. C†	Scrubfowl	Arapus	immediately Post-Lapita	F	no
	<i>Mwalau walterlini†</i>	Lini's megapode	Teouma	Lapita	F	no
	<i>Megapodius pritchardi*</i>	Tongan megapode	Há'apai	Lapita to Post-Lapita	F	no
	<i>Megapodius alimentum†</i>	Extinct scrubfowl	Votua, Qaraniupu, Aiwa Levu rock shelter 1, Há'apai, Há'ateiho	Lapita to Post-Lapita	F	no
	<i>Megapodius magn. molistructor†</i>	n. sp. size of <i>M. molistructor</i> of New Caledonia	Há'apai, Há'ateiho	Lapita	F	no
	<i>Megapodius</i> n. sp. B†	indet. megapode size of molistructor	Kilu Cave	Pre-Lapita	F	no
	<i>Megapodius</i> cf. <i>amissus</i> / <i>molistructor†</i>	indet. megapode (? <i>amissus</i> / <i>molistructor</i>)	Naigani, Aiwa Levu rock shelter 1, Há'ateiho	Lapita to Post-Lapita	F	no
	<i>Megavitiornis altirostris†</i>	Noble megapode	Naigani	Lapita	F	no
	<i>Hypotaenidia philippensis*</i>	Buff-banded rail	Tikopia, Votua	Post-Lapita	W	no
	<i>Hypotaenidia (Gallirallus)</i> n. sp. †	Rail	Aiwa Levu rock shelter 1	Post-Lapita	W	no
	<i>Hypotaenidia (Gallirallus)</i> n. sp. B†	Rail	Kilu Cave	Pre-Lapita	W	no
	<i>Hypotaenidia (Gallirallus)</i> n. sp. E†	Rail	Há'apai	Lapita	W	no
	<i>Hypotaenidia (Gallirallus)</i> n. sp. F†	Rail	Há'apai	Lapita	W	no
	<i>Hypotaenidia (Gallirallus)</i> n. sp. G†	Rail	Há'ateiho	Lapita	W	no
	<i>Porphyrion</i> n. sp. B†	Giant flightless sp. cf. New Ireland bird	Kilu Cave	Pre-Lapita	W	no
<i>Porzana large</i> sp. A†	Crake	Navaprah, Yalo South	Post-Lapita	W	no	
<i>Porzana</i> n. sp. †	Crake	Aiwa Levu rock shelter 1	Post-Lapita	W	no	
<i>Porzana tabuensis*</i>	Spotless crake	Woplamlam, Navaprah, Yalo South	Post-Lapita	W	no	
Rallid n. sp. †	Large flightless rail	Teouma	Lapita	W	no	
<i>Pareudias n. sp. †</i>	cf. Makira moorhen, <i>P. silvestris</i>	Kilu Cave	Pre-Lapita	W	no	

Family	Species	Common name	Distribution of extirpations/extinctions	Ceramic period recorded	Habitat	Flight
Procellariiformes	<i>Puffinus lherminieri</i> *	Audubon's shearwater	Tikopia, Anuta, To'aga	Post-Lapita	C	yes
	<i>Puffinus pacificus</i> *	Wedge-tailed shearwater	Anuta, Ponomla, To'aga	Post-Lapita	C	yes
	<i>Puffinus cf. gavia</i> *	Fluttering shearwater	Woplamlam	Post-Lapita	C	yes
	<i>Puffinus griseus</i> *	Sooty shearwater	To'aga	immediately Post-Lapita	C	yes
	<i>Pseudobulweria rostrata</i> *	Tahiti petrel	To'aga, Teouma	Lapita?	C	yes
	<i>Pterodroma</i> sp.*	Petrel	Mussau, To'aga	Lapita	C	yes
	<i>Papasa abboti</i> *	Abbott's booby	Tikopia, Mangaasi	Post-Lapita	C	yes
	<i>Sula sula</i> *	Red-footed booby	Tikopia, Anuta, To'aga	Post-Lapita	C	yes
	<i>Sula leucogaster</i> *	Brown booby	Mussau	Lapita	C	yes
	<i>Sterna fuscata</i> *	Sooty tern	Tikopia, Anuta	Post-Lapita	C	yes
Sturnidae	<i>Aplonis</i> sp.*	Starling	Ponomla	Post-Lapita	F	yes
	<i>Aplonis tabuensis</i> *	Polynesian starling	Votua	Lapita	F	yes
Halcyonidae	<i>Halcyon farquhari</i> *	Vanuatu kingfisher	Ponomla, Mangaasi	Post-Lapita	F	yes
	<i>Nycticorax</i> sp. A†	n. sp. Night heron	Kilu Cave	Pre-Lapita	W	yes
Ardeidae	<i>Nycticorax</i> n. sp. B†	n. sp. Night heron	Ha'apai	Lapita	W	yes
	<i>Ducula large</i> sp.†	Imperial pigeon	Ifo	Lapita	F	yes
Columbidae	<i>Alopecoenas</i> sp.*	Ground dove	Teouma	Lapita	F	no
	<i>Alopecoenas</i> (= <i>Gallicolumba</i>) <i>stairii</i> *	Friendly ground dove	Lakeba, Aiwa Cave 2, Aiwa rock shelter 1	Lapita to Post-Lapita	F	no
	Columbid gen. et n. sp. A†	Pigeon/dove	Kilu Cave	Pre-Lapita	F	?
	Columbid gen. et n. sp. B†	Pigeon/dove	Kilu Cave	Pre-Lapita	F	?
	Columbid gen. et n. sp. C†	Pigeon/dove	Ha'apai, Ha'ateiho	Lapita	F	?
	<i>Caloenas canacorum</i> *	New Caledonian pigeon	Ha'apai	Lapita	F	yes
	<i>Caloenas nicobarica</i> *	Nicobar pigeon	Mussau, Kilu Cave	Pre-Lapita	F	yes
	<i>Didunculus strigirostris</i> *	Tooth-billed pigeon	Lakeba	Lapita	F	yes
	<i>Didunculus plapopedetest</i>	Tongan tooth-billed pigeon	Teouma, Ha'apai, Ha'ateiho	Lapita	F	yes
	<i>Ducula goliathi</i> *	New Caledonian imperial pigeon	Teouma	Lapita	F	yes
	<i>Ducula lakebat</i>	Lakeba imperial pigeon	Kulu Bay, Qaranipuqa, Naigani, Aiwa Levu 2	Lapita to Post-Lapita	F	yes
	<i>Caloenas</i> or <i>Ducula</i> sp.	Large pigeon	Mussau	Lapita	F	yes
<i>Ducula</i> n. sp.†	Imperial pigeon	Ha'apai	Lapita	F	yes	

Family	Species	Common name	Distribution of extirpations/extinctions	Ceramic period recorded	Habitat	Flight
Accipitridae	<i>Accipiter fasciatus</i> [*]	Brown goshawk	Arapus, Teouma	Lapita to Post-Lapita	F/O	yes
Psittaculidae	<i>Ecdectus n. sp.</i> †	Parrot	Malua Bay School	Post-Lapita	F	yes
	<i>Ecdectus infectus</i> †	Tongan eclectus	Ha'apai	Lapita	F	yes
	<i>Ecdectus sp. cf. E. infectus</i> †	Eclectus sp.	Teouma	Lapita	F	yes
Bucerotidae	<i>Pyrrhulopsis (=Prosopcia) sp. indet.</i> [*]	indet. sp. Shining (=Musk) parrot	Lakeba	Lapita	F	yes
	<i>Rhyticeros cf. R. plicatus</i> [*]	cf. Papuan hornbill	Teouma	Lapita	F	yes
Cuculidae	<i>Centropus sp.</i> [*]	Coucal sp.	Teouma	Lapita	F	yes
Meliphagidae	<i>Gymnomyza viridis</i> [*]	Giant forest honeyeater	Votua	Lapita	F	yes
	<i>Tyto cf. alba</i> [*]	Barn owl	Mussau	Lapita to Post-Lapita	O	yes

† indicates extinct taxa; * indicates extirpated taxa.

Habitats: C=coastal, W=wetlands, F=forest, O=open woodlands.

Source: Compiled by authors.

Early Lapita bird exploitation strategies in the Pacific

The full details of the nature of Lapita utilisation of wild birds is not clear, with only one study focusing on bird bone taphonomy in Tonga (Steadman et al. 2002a). However, our findings indicate a variety of Pacific Island bird exploitation strategies. First, introduced domestic chickens (*Gallus gallus*) are present in 19 of the Lapita and Post-Lapita sites (Table 21.3) corroborating their extensive introduction early in horticultural Pacific prehistory (Storey et al. 2008) and the establishment of human commensal subsistence strategies. Second, hunting of small- to medium-bodied native volant and ground-dwelling birds from coastal, forested and wetland habitats is apparent throughout the Lapita distribution in the Pacific and since Lapita times in Near Oceania (Table 21.3). These were likely hunted using a sophisticated array of technology and methods such as ranged weapons, snares, traps and striking weapons (see Best 1979 for a treatise on Māori bird-hunting techniques). All archaeological sites targeted in this study have relatively (to other faunal components) small quantities of non-commensal bird bones representing wild taxa (including extinct taxa) (Tables 21.2–21.3), suggesting that Lapita and Post-Lapita bird hunting was extensively practised but was not as important as the exploitation of marine resources, fruit bats and large-bodied reptiles (Hawkins 2015; Hawkins et al. 2016; Pregill and Steadman 2004).

Birds may have had other uses during Pacific prehistory that go beyond mere meat and egg consumption and reflect more sociocultural values. The capture of birds of prey for ornamental feathers appears to have originated with the Neanderthals potentially using simple bait and hand capture techniques, at least since the late Pleistocene in Europe (Finlayson et al. 2012; Finlayson and Finlayson 2016). This appears to extend to modern human use of raptors at Niah cave in Borneo, by 45 ka BP (Piper and Rabett 2014). Birds of prey and owls are also common in Roman and Medieval sites in Europe where they were used for falconry in demonstrations of social status by the landed aristocracy (Bochenski et al. 2016; Dobney and Jaques 2002; Wallis 2014; Zeiler 2010). The earliest convincing evidence for falconry in the archaeological record appears to precede Lapita culture by one or two millennia during the Bronze Age in Syria (Wallis 2014). The many raptor species, not known as food items, present in 13 early Neolithic archaeological sites in the Pacific, from the Mussau Islands to Tonga (Tables 21.2–21.3), may reflect these otherwise unknown aspects of Lapita and immediately Post-Lapita culture. These include four species of birds of prey (brown goshawk, osprey, Brahminy kite, Sanford's sea eagle) and two species of owl (fearful owl, barn owl). Indeed, birds appear to have played a significant role in Lapita symbology as evidenced by pottery decorations. Three-dimensional birds have been found at the Reefs-Santa Cruz site RF-6 (Green 1979) and on pot rims at Teouma in Vanuatu (Bedford and Spriggs 2007), while there is a suggestion by Noury (2017) that elaborate and distinctive Lapita pottery face motifs distributed from the Bismarcks to Fiji could in fact be symbolic depictions of birds. However, there is little direct archaeological evidence that Lapita elites practised falconry or were wearing feathered garments (although see Hawkins 2015 for an exception on the possible use of feathers at Teouma).

Lapita impact on avifauna diversity in Oceania

Prehistoric human–bird interactions clearly had an impact on bird diversity and populations, although the quantity and diversity of extinct bird bones in most Lapita sites is also small, relative to excavation size and total NISP from most sites (Table 21.1). However, we argue that the unexpectedly small samples of extinct bird bones in Lapita sites are likely an artefact of excavation size and disparate preservation conditions. The diversity of avifauna, including both extant and extinct species, increases with sample size. For instance, the large areas of excavations at Teouma have revealed nine extinct taxa and account for a significant proportion of such taxa recorded in our review. In addition, a few sites including Qaranipuqa 197 rock shelter on Lakeba in Fiji, and Tikopia (NISP=468 from several sites combined) in the south-east Solomon Islands, and

the Ha'apai and Tongatapu sites, have revealed significant diversity and quantity of extinct taxa from small-sized excavations, sharply revealing human impacts and disparate excavation spatial sampling issues at the intra- and inter-site level.

Other effects of early human colonisation such as forest clearance and introduction of invasive mammals (rats and pigs) are also evident. This is reflected by the attributes of birds that went extinct versus those that are still extant. The families most impacted by extinction are the megapodes, columbids and rallids. Large, flightless (or weakly flying) and forest-dependent taxa are over-represented. Although some of the megapodes were not flightless, such as *Megapodius alimentum*, egg harvesting by humans, rats and pigs was likely a fatal contributing factor to their extinction. In the Indo-Pacific region, hunting had a big impact on some island bird species, particularly those of large size such as the dodo (Cheke and Hume 2008). The South Pacific flightless birds in our study could not be considered large-bodied and thereby at increased risk of extinction by human hunting, as were moas in New Zealand (Duncan et al. 2002). Potential exceptions revealed in the fossil record could have been the giant galliforms *Sylviornis neocaledoniae* from New Caledonia (Worthy et al. 2016) and *Megavitiornis altirostris* from Fiji (Worthy 2000) as well as the giant flightless pigeon *Natunaornis gigoura* reported by Worthy (2001), also from Fiji. However, direct evidence for humans hunting the giant galliform species in Oceania is generally tenuous (Anderson et al. 2010; Irwin et al. 2011) and absent for the giant pigeon. Large browsing ground-dwelling herbivorous birds, such as the moa-nalos of Hawai'i (Sorenson et al. 1999) and moa (Dinornithiformes) of New Zealand (Worthy and Scofield 2012), apart from *Natunaornis*, are absent in the archaeological and fossil record of the Melanesian region and may have never formed significant radiations there. This may be due to the presence of large-bodied land turtles (Hawkins et al. 2016), which may have taken the ground-level browsing/grazing niche for Vanuatu and Viti Levu, as they did/do on the Mascarenes and Galapagos Islands (Cheke and Hume 2008; van Denburgh 1914).

Being naïve and lacking behavioural defences, however, did make medium-sized birds that disappeared in the South Pacific more vulnerable to invasive introduced mammals and to the more destructive Lapita economic systems. Localised habitat change may also have been significant in the disappearance of these taxa in the archaeological record. At Teouma, the forest bird taxa declined significantly relative to wetland bird taxa, which has been argued was the result of forest habitat disturbance and the creation of swamp lands due to horticultural expansion after Lapita arrival, and possibly also due to an explosion in the rat and pig population (Hawkins 2015). Numerous species from many sites, which may have had more favourable longevity attributes, survived the initial Lapita onslaught in the South Pacific, only to succumb to the cumulative effects of ecological degradation from encroaching settlement and agricultural expansion sometime later.

An explanation for the discrepancy between the smaller number of extinctions that are recorded in Near Oceania compared to Remote Oceania is required. For example, there are few extinct birds recorded from Lapita sites in the Bismarcks where Lapita culture first appears c. 3300 BP at Talepakemalai in the Mussau Islands (Steadman and Kirch 1998). Several reasons can be advocated to explain this. The Bismarcks had already been settled by people for at least 40 000 years (Leavesley 2004) and had exposure to terrestrial mammals (rodents) for a much longer period. This makes it probable that birds had long since lost some of their naïvety to predatory mammals. Also, the proximity of the islands to the diverse Papuan avifauna possibly allowed supplantation of the Bismarck Island bird populations. Similar factors have been noted for Island Southeast Asia and Australia, where over long periods birds coevolved with mammals in the Sunda and Sahul regions. Here, closely spaced islands could result in rapid repopulation from continental sources, making extirpations much less likely. This is reflected in the Pleistocene fossil and archaeological record of Island Southeast Asia where few extinctions have been recorded

(Meijer et al. 2015). On the other hand, some bird species, the most vulnerable to human impacts, may have become extinct much earlier, long before Neolithic cultures developed in Island Southeast Asia.

The limited fossil record hints that the avifauna was more diverse during the Pleistocene as Steadman et al. (1999) identified 12 extinct bird species on New Ireland, where it has been estimated that only fewer than 20 per cent of bird species disappeared from the fossil and archaeological record (Steadman 2006a). At Kilu Cave on Buka Island in the Solomon Islands, where human occupation ranged between 29 000 and 5000 BP, with a later horticultural component (Wickler 2001), eight extinct and previously unknown species were present in Pre-Lapita deposits (Steadman 2006a). No extinct taxa were identified in any of the later deposits (Steadman 2006a; Wickler 2001), leaving open the possibility that Pleistocene and early Holocene human hunting, and not the more invasive Lapita and Post-Lapita agricultural complex, may have been responsible for extinctions in the Solomons. Additionally, the limited fossil record for the prehuman period is a severely limiting factor in interpreting human impact. The few detailed records that are available indicate how inadequate archaeological sampling from small-scale excavations combined with variable bone preservation has been. There is as yet no prehuman fossil record in Vanuatu and Samoa, but in New Caledonia, Fiji and Tonga, fossil records indicate a more diverse prehuman avifauna with many species not appearing in the archaeological record (Anderson et al. 2010; Koopman and Steadman 1995; Worthy et al. 1999).

Degree of isolation and island size appears to have greatly influenced the extirpation of sea birds (Steadman 2006a) with extinctions of shearwater, booby and tern species on the small isolated islands of Tikopia, Anuta and Ofu appearing quite early in the archaeological record (Tables 21.2–21.3). This targeting of colony-nesting resident seabirds was clearly a successful hunting strategy, given the concentration of easily harvested fauna providing optimal foraging conditions. Seabird colonies have been proven to be quite vulnerable to human disturbances and invasive mammals during the modern period (Petry and Fonseca 2002), and this is also likely to have been the case during the initial period following prehistoric human arrival on these islands. While single shearwater species, each present at Ponamla and Woplamlam, also disappeared from the larger and inter-visible islands of Erromango and Malakula in the Vanuatu archipelago, small quantities of sea birds were present at Teouma on Efate. The identified species still visit Efate today; Efate is large and positioned close to other islands for possible repopulation after initial declines. The island is also more central to urban settlement and ornithological observations in Vanuatu, and other islands may require more detailed studies to record more accurate data on extant seabird populations before we can understand whether they fluctuated in the region in response to changing patterns in human settlement intensity.

Some insight into the likely causes of extinctions may be found not so much in what species went extinct after Lapita settlement, but rather by identifying those that were exploited by Lapita people and are still extant today. Table 21.3 shows 73 distinct taxa from 26 families represented in these same archaeological sites that are still extant on their respective islands today. The large number of extinct or extirpated taxa present in Post-Lapita deposits indicates many species survived the initial human settlement, either because of biological attributes facilitating longer extinction trajectories (e.g. larger populations, mean longer life expectancy, and greater fecundity), or that they succumbed to cumulative changes in ecology from human activities. Most of these are forest/woodland taxa, including many small passerine species recorded from cave sites on the north-west coast of Malakula. Wetland and coastal bird species are represented, but in fewer numbers. Nearly all these species are volant, with just one, the chicken, not capable of sustained flight. The Vanuatu scrubfowl, buff-banded rail and spotless crane might not choose to fly often, but they are all adept fliers, as attested to by their widespread distribution. These extant taxa are all small to medium-sized birds, the largest of which are migrant seabirds or successful open forest predators such as the barn owl.

Table 21.3. Taxonomic list of extant taxa by family, species, common name, archaeological distribution, period of disappearance, habitat, flight capability and residential status.

Family	Species	Common name	Mussau Islands	Kilu Cave, Buka	Arapus	Mangassi	Teuma	Woplamlam	Yalo	Navaprah	Malua Bay	Ponamla	Ito	Tikopia (Steadman et al. 1990)	Anuta	Kulu Bay, Bega I	Lakeba + Wakea	Volua, Mago I	Sovanibeka, Mago I	Naigani	Cave 1, Aiwa Levu	Cave 2, Aiwa Levu	Aiwa1, Aiwa Levu	Dau RS, Aiwa Lalai	Ha'apai (5 sites)	Tongatapu Ha'ateiho	To'aga	Habitat
Anatidae	<i>Anas superciliosa</i>	Pacific black duck	-	1	-	1	14	-	-	-	-	-	2	-	-	-	2	-	-	-	-	1	-	11	-	-	W	
Megapodiidae	<i>Megapodius freycinet</i> (= <i>layardi</i> or <i>eremita</i>)	Common megapode	-	-	-	1	169	3	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Megapodius</i> sp. C	Scrubfowl	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Megapodius alimentum</i>	Extinct scrubfowl	-	-	-	-	-	-	-	-	-	-	-	-	-	-	49	5	-	-	-	3	-	369	X	-	F	
	<i>Mwalalu walterlinii</i>	Lini's megapode	-	-	-	-	45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Megapodius pritchardii</i>	Tongan megapode	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	F	
	<i>Megapodius magn. mollistructor</i>	n. sp. size of <i>M. mollistructor</i> of New Caledonia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	29	X	-	F	
	<i>Megapodius</i> n. sp. B	indet. megapode size of <i>mollistructor</i>	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Megapodius</i> sp.	indet. megapode (? <i>amissus</i> / <i>mollistructor</i>)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	X	2	F	
Phasianidae	<i>Megavitiornis altirostris</i>	Noble megapode	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Gallus gallus</i>	Chicken	12	-	13	23	339	-	-	2	2	33	23	75	19	3	4	1	4	1	4	1	7	8	3	-	16	Cm
Indet. galliform		indet. sp. galliform	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	?	
Columbidae	<i>Columba vitiensis</i>	White-throated pigeon	-	-	1	2	70	-	1	-	-	20	1	-	-	-	8	-	-	-	1	5	-	-	-	-	F	
	<i>Macropygia mackinlayi</i>	Mackinlay's cuckoo-dove	-	-	-	-	9	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Chalcophaps indica</i>	Emerald dove	-	-	-	-	49	-	4	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Ducula goliath</i>	New Caledonian imperial pigeon	-	-	-	-	55	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Ducula lakeba</i>	Lakeba pigeon	-	-	-	-	-	-	-	-	-	-	-	-	-	1	92	-	-	8	-	-	-	-	-	-	F	
	<i>Ducula pacifica</i>	Pacific imperial pigeon	-	-	3	-	200	-	1	-	1	15	17	5	-	6	-	-	-	-	-	10	14	60	X	-	F	
	<i>Ducula latrans</i>	Barking imperial pigeon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	1	60	X	-	F	

Family	Species	Common name	Mussau Islands	Kilu Cave, Buka	Arapus	Mangassi	Teuma	Woplamlam	Yalo	Navaprah	Malua Bay	Ponamia	Ifo	Tikopia (Steadman et al. 1990)	Anuta	Kulu Bay, Bega I	Lakeba + Wakea	Votua, Mago I	Sovanibeka, Mago I	Naigani	Cave 1, Aiwa Levu	Cave 2, Aiwa Levu	Aiwa1, Aiwa Levu	Dau RS, Aiwa Lailai	Ha'apai (5 sites)	Tongatapu Ha'ateiho	To'aga	Habitat
	<i>Ducula rubricera</i>	Red-knobbed imperial pigeon	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Ducula pistrinaria</i>	Island imperial pigeon	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Ducula</i> n. sp. (= <i>D. Steadman</i> et al 2002)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25	-	-	-	F
	<i>Ducula</i> sp. indet.	Imperial pigeon	1	1	-	102	1	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	Columbid gen. et n. sp. A		-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	Columbid gen. et n. sp. B		-	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	35	X	-	F
	Columbid gen. et n. sp. C		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	-	-	F
	<i>Caloenas canacorum</i>	New Caledonian pigeon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Caloenas nicobarica</i>	Nicobar pigeon	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Didunculus strigirostris</i>	Tooth-billed pigeon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-	-	F
	<i>Didunculus placopedetes</i>	Tongan tooth-billed pigeon	-	-	-	72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	X	-	F
	<i>Alopecoenas</i> sp.	Ground dove	-	-	-	12	-	-	-	-	-	-	-	-	-	-	-	-	1 (not 5)	-	-	-	-	-	-	-	-	F
	<i>Alopecoenas</i> (= <i>Galliolumba</i>) <i>stairii</i>	Friendly ground dove	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	3	-	2	65	X	3	F	
	<i>Galliolumba rufigula</i>	Cinnamon ground dove	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Ptilinopus</i> cf. <i>tannensis</i>	Tanna fruit dove	-	-	-	0	2	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Ptilinopus greyii</i>	Red-bellied fruit dove	-	-	-	2	17	2	1	6	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Ptilinopus porphyraceus</i>	Crimson-crowned fruit dove	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13	-	-	-	-	-	-	-	28	X	-	F
	<i>Ptilinopus perousii</i>	Many-colored fruit dove	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	24	X	-	F
	<i>Ptilinopus</i> sp. indet.	indet. Fruit dove	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	F
	<i>Columbidae</i> sp.	indet. Pigeon	-	1	4	1	72	1	1	-	-	12	-	-	-	-	20	-	1	-	-	-	-	-	-	-	-	F
	<i>Cuculus optatus</i>	Oriental cuckoo	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Chrysocoryx lucidus</i>	Shining bronze cuckoo	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Eudynamis taitensis</i>	Pacific long-tailed cuckoo	-	-	-	1	-	-	-	1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	F

Family	Species	Common name	Mussau Islands	Kilu Cave, Buka	Arapus	Mangasii	Teouma	Woplampam	Yalo	Navaprah	Malua Bay	Ponamia	Ifo	Tikopia (Steadman et al. 1990)	Anuta	Kulu Bay, Beqa I	Lakeba + Wakea	Votua, Mago I	Sovanibeka, Mago I	Naligan!	Cave 1, Aiwa Levu	Cave 2, Aiwa Levu	Aiwa1, Aiwa Levu	Dau RS, Aiwa Lailai	Ha'apai (5 sites)	Tongatapu Ha'ateiho	To'aga	Habitat
	<i>Centropus</i> sp.	Coucal sp.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Cacomantis</i> cf. <i>flabelliformis</i>	Fan-tailed cuckoo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	X	-	-	F	
Rallidae	<i>Hypotaenidia philippensis</i> *	Buff-banded rail	-	-	1	17	64	2	8	1	2	20	-	5	-	-	9	3	-	-	10	1	7	165	X	-	W	
	<i>Hypotaenidia</i> (<i>Gallirallus</i>) n. sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	W	
	<i>Hypotaenidia woodfordi tertius</i>	Woodford's rail	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	W	
	<i>Hypotaenidia</i> (<i>Gallirallus</i>) n. sp. B	flightless sp.	-	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	W	
	<i>Hypotaenidia</i> (<i>Gallirallus</i>) n. sp. E		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	W	
	<i>Hypotaenidia</i> (<i>Gallirallus</i>) n. sp. F		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	W	
	<i>Hypotaenidia</i> (<i>Gallirallus</i>) n. sp. G		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	W	
	<i>Porphyrion melanotus</i>	Pacific swamphen	-	-	11	81	244	-	4	1	5	65	8	31	-	-	41	-	4	-	1	3	1	-	180	X	-	W
	<i>Porphyrion</i> n. sp. B	Giant flightless sp. cf. New Ireland bird	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	W
	<i>Porzana tabuensis</i> *	Spotless crane	-	-	0	3	5	3	3	12	-	1	-	-	-	-	1	-	5	-	-	-	-	-	28	X	-	W
<i>Porzana</i> n. sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	W	
Rallid n. sp.		-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	W	
Phaethontidae	<i>Pareudiasia</i> n. sp.	cf. Makira moorhen, <i>P. silvestris</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	W
	<i>Phaethon lepturus</i>	White tropicbird	-	-	-	-	-	-	-	-	-	-	15	1	-	9	-	-	-	-	-	-	1	-	X	-	W	
	<i>Phaethon rubricauda</i>	Red-tailed tropicbird	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	X	-	-	W	

Family	Species	Common name	Mussau Islands	Kilu Cave, Buka	Arapus	Mangassi	Teouma	Woplamlam	Yalo	Navaprah	Malua Bay	Ponamia	Ifo	Tikopia (Steadman et al. 1990)	Anuta	Kulu Bay, Bega I	Lakeba + Wakea	Votua, Mago I	Sovanibeka, Mago I	Naigani	Cave 1, Aiwa Levu	Cave 2, Aiwa Levu	Aiwa1, Aiwa Levu	Dau RS, Aiwa Lalai	Ha'apai (5 sites)	Tongatapu Ha'ateiho	To'aga	Habitat	
Procellariidae	<i>?Pseudobulweria rostrata</i>	Tahiti petrel	-	-	-	-	1	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	C
	<i>?Puffinus cf. bailloni</i>	Tropical shearwater	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C
	<i>Puffinus lherminieri</i>	Audubon's shearwater	-	-	-	-	-	-	-	-	-	-	1	35	-	-	-	-	-	-	-	-	-	-	x	-	-	2	C
	<i>?Puffinus pacificus</i>	Wedge-tailed Shearwater	-	-	-	-	1	-	-	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-	x	-	-	11	C
	<i>Puffinus bulleri</i>	Buller's shearwater	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	C
	<i>Puffinus griseus</i>	Sooty shearwater	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	C
	<i>Pterodroma nigripennis</i>	Black-winged petrel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	C
	<i>Pterodroma sp. medium</i>	medium <i>pterodroma</i> , sp. indet.	2	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	x	-	-	2	C
	<i>Nesofregata fuliginosa</i>	Tropical storm petrel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	C
	<i>Pachyptila sp.</i>	indet. prion	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	C
Charadriidae	Procellariid sp. indet.	indet. <i>procellariid</i>	-	-	-	-	-	-	-	-	-	-	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	9	C
	<i>Pluvialis fulva</i>	Pacific golden plover	-	-	-	-	-	-	-	-	-	-	-	4	3	-	1	-	-	-	-	-	-	-	-	-	-	-	C
	<i>Pluvialis dominica</i>	American golden plover	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C
Scolopaciidae	<i>Limosa lapponica</i>	Bar-tailed godwit	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	C
	<i>Numenius tahitiensis</i>	Bristle-thighed curlew	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	C
	<i>Numenius sp.</i>	Curlew	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C
	<i>Heteroscelus incanus</i>	Wandering tattler	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C
	<i>Arenia interpres</i>	Ruddy turnstone	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	C
	<i>Sterna sumatrana</i>	Black-naped tern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	C
	<i>Onychoprion (=Sterna) lunatus</i>	Grey-backed tern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	C
	<i>Onychoprion (=Sterna) anaethetus</i>	Bridled tern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	C
	<i>Sterna fuscata</i>	Sooty tern	3	-	-	-	-	-	-	-	-	-	-	2	4	-	-	-	-	-	-	-	-	-	x	-	-	-	C

Family	Species	Common name	Mussau Islands	Kilu Cave, Buka	Arapus	Mangasasi	Teuma	Woplamlam	Yalo	Navaprah	Malua Bay	Ponamla	Ifo	Tikopia (Steadman et al. 1990)	Anuta	Kulu Bay, Bega I	Lakeba + Wakea	Votua, Mago I	Sovanibeka, Mago I	Naligan!	Cave 1, Aiwa Levu	Cave 2, Aiwa Levu	Aiwa1, Aiwa Levu	Dau RS, Aiwa Lailai	Ha'apai (5 sites)	Tongatapu Hatheho	To'aga	Habitat		
Alcedinidae	<i>Sterna hirundo</i>	Common tern	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C
	<i>Anous stolidus</i>	Brown noddy	10	4	-	-	-	-	-	-	-	-	135	44	-	-	-	-	-	-	-	-	6	3	X	-	-	-	C	
	<i>Anous minutus</i>	Black noddy	6	-	-	-	-	-	-	-	-	-	35	10	-	-	-	-	-	-	-	-	7	1	X	-	-	-	C	
	<i>Gygis alba candida</i>	White tern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	X	-	-	-	C	
	<i>Gygis alba microhyncha</i>	White tern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	C	
	<i>Sternidae</i> sp. indet.	indet. tern	1	-	-	-	-	-	-	-	-	-	-	20	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C
	<i>Ardea alba</i>	White heron	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C
	<i>Egretta sacra</i>	Pacific reef heron	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	C
	<i>Butorides striatus</i>	Mangrove heron	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	W
	<i>Nycticorax</i> n. sp. A	Night heron n. sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	W
<i>Nycticorax</i> n. sp. B	Night heron n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	W	
<i>Threskiornithidae</i>	<i>Threskiornis</i> cf. <i>molucca</i>	Australian white ibis	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	W	
Fregatidae	<i>Fregata ariel</i>	Lesser frigatebird	-	-	-	-	-	-	-	-	-	-	3	7	-	1	-	-	-	-	-	-	-	-	X	-	-	-	C	
	<i>Fregata minor</i>	Great frigatebird	-	-	-	-	-	-	-	-	-	-	9	12	-	-	-	-	-	-	-	-	-	-	X	-	-	-	C	
	<i>Fregata</i> sp.	Indet. frigatebird	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	2	-	C	
Sulidae	<i>Sula leucogaster</i>	Brown booby	7	-	-	-	8	-	-	-	-	-	2	5	-	-	-	-	-	-	-	-	-	-	X	-	-	-	C	
	<i>Sula dactylatra</i>	Masked booby	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	C	
	<i>Sula sula</i>	Red-footed booby	-	-	-	-	-	-	-	-	-	-	44	85	-	-	-	-	-	-	-	-	-	-	X	-	1	-	C	
	<i>Sula</i> sp.	Booby	-	-	-	-	-	-	-	-	-	-	27	51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	
	<i>Papasula abbotti</i>	Abbott's booby	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C
Accipitridae	<i>Accipiter fasciatus</i>	Brown goshawk	-	1	-	-	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Pandion haliaetus</i>	Osprey	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	X	-	-	C	
	<i>Haliaeetus indus</i>	Brahminy kite	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	W	
	<i>Haliaeetus sanfordi</i>	Sanford's sea eagle	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C

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Strigidae	<i>Nesasio solomonensis</i>	Fearful owl	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
Tytonidae	<i>Tyto alba</i> (=delicatula)	Barn owl	1	-	2	14	2	6	35	-	6	1	-	-	-	-	4	-	-	-	1	-	-	3	-	-	-	0	
Bucerotidae	<i>Rhyticeros</i> cf. <i>R. plicatus</i>	cf. Papuan hornbill	-	-	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
Alcedinidae	<i>Todiramphus</i> cf. <i>chloris</i>	Collared kingfisher	-	-	2	6	6	-	-	-	1	-	-	-	-	-	2	1	2	2	2	3	-	111	-	-	-	W	
Apodidae	<i>Collocalia esculenta</i>	Glossy swiftlet	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Aerodramus</i> (= <i>Collocalia</i>)	White-rumped swiftlet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	>60	-	4	1	-	-	-	-	-	F	
	<i>Spodopygia</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Collocalia</i> sp.	Swiftlet, ?Glossy swiftlet	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
Psittaculidae	<i>Ecluctus infectus</i>	Tongan eclectus	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	F	
	<i>Ecluctus</i> n. sp.		-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Ecluctus</i> sp. cf. <i>E. infectus</i>	Eclectus sp.	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Pyrrhuloxia</i> (= <i>Prosopelia</i>) sp. indet.	indet sp. Shining (=Musk) parrot	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	F	
	cf. <i>Charmosyna palmarum</i>	Palm lorikeet	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	? <i>Charmosyna amabilis</i>	?Red-throated lorikeet	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Phigys</i> (<i>Vim</i>) <i>solitarius</i>	Collared lory	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-	3	-	-	-	F	
	<i>Chalcopsitta cardinalis</i>	Cardinal lory	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Trichoglossus haematodus</i>	Rainbow lorikeet	-	-	-	3	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
Turdidae	<i>Turdus poliocephalus</i>	Island thrush	-	-	-	-	1	10	5	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	X	-	-	F	
Zosteropidae	<i>Zosterops lateralis</i>	Silvereye	-	-	-	-	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Zosterops flavifrons</i>	Vanuatu white-eye	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
Sturnidae	<i>Aplonis</i> sp.	Starling	-	-	-	-	3	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Aplonis tabuensis</i>	Polynesian starling	-	-	-	-	-	-	-	-	-	-	2	-	-	5	1	10	-	-	-	-	-	-	132	X	-	F	
	<i>Aplonis metallica</i>	Metallic starling	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	

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Estrildidae	<i>Erythrura sp.</i>	Parrotfinch	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
Campephagidae	<i>Concina caledonica</i>	South Melanesian cuckooshrike	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
	<i>Lalage maculosa</i>	Polynesian triller	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	X	-	-	F	
	<i>Lalage sp.</i>	Triller	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	F		
Acanthizidae	<i>Gerygone flavolateralis</i>	Fan-tailed gerygone	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
Petroicidae	<i>Petroica multicolor</i>	Norfolk Robin	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	F	
Pachycephalidae	<i>Pachycephala pectoralis</i>	Australian golden whistler	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Pachycephala jacquinoti</i>	Tongan whistler	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	F	
Rhipiduridae	<i>Rhipidura sp.</i>	Fantail	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
Monarchidae	<i>Myiagra/Neolalage</i>	Bradbills/Buf-bellied monarch	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Clytorhynchus vitiensis</i>	Fiji shrikebill	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	F	
Meliphagidae	<i>Lichmera incana</i>	Grey-eared honeyeater	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Myzomela cardinalis</i>	Cardinal myzomela	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	F	
	<i>Phylidomyris notabilis</i>	White-bellied honeyeater	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	
	<i>Foulehaio carunculata</i>	Wattled honeyeater	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	X	-	-	F	
	<i>Gymnomyza viridis</i>	Giant forest honeyeater	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	F	
Passeriformes	Passerines indet.		-	-	2	94	2	5	7	-	-	-	-	-	-	-	-	-	-	5	2	58	1	-	-	-	-	F	
		Total	55	76	35	141	1714	22	63	98	12	184	51	468	299	5	302	12	26	18	22	20	127	27	1453	437	74	5741	
																													excludes seabirds

*=extirpated taxa, X=present.

Habitat: W=wetlands; F=forest; C=coastal; Cm=commensal; O=open.

Source: Aiwa Levu and Aiwa Lailai data from Steadman 2006a (Tables 6-8); Ha'apai fauna data is from Steadman 2006a (Tables 6-19) (land birds only).

Limitations in the data

Insufficient Early Lapita deposits have been sampled in the region to capture the real former avian diversity. The archaeological record does not support an inference that there was intensive bird hunting, in that there are no dense bone middens of species such as for moa in New Zealand, or for the flightless sea ducks *Chendytes* spp. from islands off California (Livezey 1993), but this could be a reflection of archaeological sampling limitations (small excavation size, few excavations) and also taphonomic effects (e.g. post-deposition bone destruction by scavenging mammals, bioturbation, agricultural disturbance and weathering), which limit the preservation of complete vertebrate assemblages.

While the sieving protocols employed at the sites varied, generally they all were effective at recovering a reasonable sample, although at some sites such as Teouma and Votua, the recovery of bones was exceptional. The lack of sieving during excavations at some sites in the region, which did not make this list (because of the lack of bird bones), may have further contributed to the loss of key data (see Hawkins 2015) on the extent of bird extinctions during Lapita settlement of Remote Oceania. However, preservation characteristics are clearly an issue in some island regions. For instance, in Fiji the deposits recovered from early sites to date are very fragmented and eroded (Worthy and Clark 2009) due to post-depositional processes.

Disparate sampling and recording of avian vertebrate deposits from archaeological sites have resulted in some regions being more under-represented than others. In some cases, such as the St Maurice-Vatcha Lapita site of New Caledonia, abundant animal bone (rats, fruit bats, fish, marine turtles) from basal Lapita levels are noted (Leach et al. 1997; Sand 1999). There is no mention of bird bones, but a complete record of the fauna has yet to be published in any detail. The lack of detailed studies of vertebrate deposits in New Caledonia is the single greatest contributing factor for this region being the most under-represented island group in this study.

Palaeontological records in New Caledonia and Fiji indicate that the archaeofauna underestimates the extinctions in the region (Anderson et al. 2010; Worthy et al. 1999). For example, on Fiji, the palaeontological record has revealed the following terrestrial birds with no extant populations: *Megavitiornis altirostris*, the weakly flying *Megapodius amissus*, an indeterminate teal *Anas* sp., a giant flightless pigeon *Natunaornis gigoura*, a large *Ducula* species, a snipe *Coenocorypha miratropica*, and three rails, the flightless *Vitirallus watlingi*, weakly flying *Hypotaenidia poeciloptera*, and a *Pareudiastes* species of moorhen. None of these have been found in archaeological sites on Viti Levu, although two have been recovered from Lapita sites on nearby islands, *Megavitiornis* on Naigani and possibly the large *Ducula* on Beqa (Worthy and Clark 2009).

These issues are important considering conservative estimates indicating that half the fossil record does not get recovered (Hull et al. 2015). We therefore predict that once more fossil and Lapita sites with abundant vertebrate remains are uncovered and expertly identified, an increase in the range of known species and the number of novel species will be revealed, presenting a far more dramatic story of avifaunal decline and ecological fragmentation during the Lapita settlement of Remote Oceania, and possibly Near Oceania too, than previously revealed. Even some of the extinctions associated with Lapita deposits may not have been the result of Lapita settlement, because without a fossil record to establish the natural fauna pre- and post-human arrival to the region we cannot rule out that some of these extinctions may have happened only recently.

Conclusions

We have reviewed the data for prehistoric bird hunting and subsequent extinctions during Lapita colonisation of Oceania c. 3300–2800 BP. Our findings indicate that birds were extensively hunted across the region, but not necessarily intensively enough to support an overkill model in isolation. Many bird extinctions and extirpations followed initial human settlement in Remote Oceania, through a combination of hunting pressure, forest clearance and the effects of invasive mammal species. However, human hunting of birds has a greater antiquity in Near Oceania, and bird extinctions may have occurred long before Lapita colonists arrived in that region. Domesticated chickens were exploited in the Bismarck Archipelago to Samoa region during initial Lapita colonisation. Birds may also have been exploited for feathers or used in falconry, as evidenced by raptor bones in many Early Lapita sites.

More importantly, this study indicates that a research gap exists during this critical period of human migration where few Lapita sites with preserved vertebrate remains exist, especially in New Caledonia, Fiji, Samoa and the Near Oceanic region of the Bismarck Archipelago. This is likely a result of archaeological sampling and variability in preservation of vertebrate remains. Most of the evidence for avian extinctions derives from Teouma in Vanuatu and sites in the Ha'apai Group, Tonga, but we argue this reflects an incomplete record across the region.

We predict that the discovery of more Lapita sites and the recovery of more abundant vertebrate assemblages will result in a much broader story of colonising impacts during early human settlement in the south-west Pacific. Most of these extinctions were terrestrial taxa, either ground-dwelling or possessing weak flight in the families Megapodiidae, Columbidae and Rallidae, and/or birds dependent on forest habitats. Nesting seabirds on more isolated small islands such as Tikopia, Anuta and Ofu were also dramatically impacted, with nesting colonies eliminated soon after human arrival. These taxa, which had developed few behavioural defences in isolation, were quite vulnerable to the sudden introduction of invasive mammals, and human agriculture-related forest clearance. Many extinctions occurred later than initial settlement in the region, as evidenced by many taxa that disappeared sometime during Post-Lapita periods. However, the majority of these were forest bird species that may have disappeared during more recent times after the introduction of more intensive European agricultural practices and further predators.

Archaeological and fossil records are the keys to elucidating the profound implications of long-term human–bird interactions on Oceanic islands. Understanding long-term patterns of avian extinctions is important when considering human actions going forward and what this means for the future of biodiversity and ecological sustainability. Birds are vital to maintaining ecosystems around the world, with their functions in ecosystems only now becoming clearer (Wenny et al. 2011). Yet today, increasing human activity is threatening many species and it is estimated that, while conservation has been effective in slowing down the rate of avian extinctions, their decline in numbers and increasing geographical restriction are resulting in the cessation of their key ecological functions (Butchart et al. 2006; Pimm et al. 2006; Şekercioğlu et al. 2004). It is predicted that in the twenty-first century, global extinctions will dramatically increase with the rising intensity of habitat destruction (Hull et al. 2015). This is a process likely happening in the Pacific with historic accounts in the region of bird hunting and agricultural restrictions of natural ranges (Bregulla 1992; Speiser 1996). However, there are few effective studies measuring the rate of decline in fauna, and critical debate has ensued due to limitations in datasets and assigning extinction labels to rare taxa in both extant and fossil populations.

This study only serves to highlight this issue. The rate of extinction since Lapita times is likely to have been so rapid that time-averaged archaeological deposits, few of which are stratified, combined with a lack of fossil records in the region, means that attributing extinctions to

Lapita settlement is problematic as these may have happened at any point in time after first settlement. More work needs to be carried out to estimate prehistoric avian diversity. The large-scale excavation of additional well-preserved Lapita deposits using fine-grained recovery methods as well as the discovery and detailed examination of more palaeontological prehuman fossils will most likely illuminate an increasing picture of declining avian diversity soon after Lapita arrival in Oceania.

Acknowledgements

The concept for this chapter was first suggested to the authors by Stuart Bedford during the Eighth Lapita Conference in Port Vila, Vanuatu, 5–10 July 2015. Stuart Hawkins was supported by Australian Research Council Laureate Project FL120100156 and Trevor H. Worthy by Australian Research Council Discovery Early Career Researcher Award DE130101133 and a Flinders University Vice-Chancellor's Postdoctoral Research Fellowship. The figure and tables were produced by the authors.

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This text is taken from *Debating Lapita: Distribution, Chronology, Society and Subsistence*,
edited by Stuart Bedford and Matthew Spriggs, published 2019 by ANU Press,
The Australian National University, Canberra, Australia.

doi.org/10.22459/TA52.2019.21