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Biogeography of Tongan birds before and after human impact

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ABSTRACT **Bones deposited in caves show that, before the arrival of humans, at least 27 species of land birds lived on the Tongan island of 'Eua, where 13 indigenous species live today. Six of these 13 species were recorded from pre-human strata; three others probably occurred on 'Eua in pre-human times but were not in the fossil sample; and four others probably colonized 'Eua since the arrival of humans ≈3000 years ago. Of the 23 species of extinct or extirpated land birds recorded from 'Eua, the nearest geographic occurrences of conspecifics or most closely related congeners are from the Solomon Islands (1 species), New Caledonia (2 species), Fiji and/or Samoa (9 species), elsewhere in Tonga (8 species), or unknown (3 species). The avifauna of West Polynesia (Fiji–Tonga–Samoa) is more closely related to that of Melanesia than that of East Polynesia. There was little pre-human turnover in Tongan land birds. The arrival of humans has influenced the Tongan avifauna more than any climatic, tectonic, or biological event of the past ≈100,000 years.**

Traditional biogeographic studies of Pacific birds are based on species records of the past 200 years. Wherever there is an ample prehistoric record of birds, however, the modern avifaunas of Pacific islands are found to be remnants of the much richer species assemblages that existed at human arrival (1, 2). Thus we should calibrate biogeographic concepts and theories (3) with data that describe the avifaunas before human impact.

Assemblages of bones from archaeological sites reveal these new biogeographic paradigms about land birds from East Polynesia (Marquesas, Society, Tuamotu, Pitcairn, Austral, and Cook islands; refs. 2, 4–10): (*i*) ranges of most living species are smaller today than at first human contact; (*ii*) few if any volant species are truly endemic to only one or two islands; (*iii*) many species have become extinct in the past 2000 years; (*iv*) prehistorically, most islands probably supported two or more endemic species of flightless rails (*Gallirallus* spp., *Porzana* spp.); (*v*) numerous congeneric species pairs once inhabited individual islands, while only two such pairs survived to this century (11); (*vi*) at least four formerly widespread genera (*Gallirallus, Porphyrio, Macropygia, Myiagra*) now are absent from East Polynesia; and (*vii*) because these reductions in distribution, diversity, and richness are due to human impact, the modern avifaunas do not reflect natural biogeographic patterns. For West Polynesia, paradigms *i–iii* and *vii* apply as stated, whereas *iv–vi* apply in concept but differ in taxonomy.

Mainly because of the absence of native cave-dwelling predators such as barn owls (*Tyto alba*), I have found no East Polynesian bone assemblages that pre-date human arrival. Thus I am not certain that any of the East Polynesian sites, even those that represent the first few centuries of human occupation, have sampled all of the birds that existed at first human contact. In the West Polynesian island group of Tonga, bones deposited in caves by non-human predators provide an opportunity to describe the prehuman avifauna of a Polynesian island.

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Tonga: Geography and Geology

As one moves west from East Polynesia toward New Guinea, the islands average larger, less isolated, and geologically older. The Kingdom of Tonga lies close to Fiji and Samoa and midway between East Polynesia and the large island groups of Melanesia. Tonga consists of three clusters of uplifted limestone islands (Tongatapu, Ha'apai, Vava'u), with volcanic outliers in the north, south, and west (Fig. 1). The islands lie at the eastern margin of the Australia–India plate, beneath which the westward-moving Pacific plate subducts into the Tonga–Kermadec trench (12–16). Tonga is oceanic in origin, with no prior continental connections. The basement rocks and the oldest exposed rocks are Early or Middle Eocene (17). Each island is capped with Miocene or younger limestones or volcanic rocks. The carbonate rocks permit excellent bone preservation in caves and calcareous beach sands. The geology of 'Eua is relatively well studied, particularly the limestones and caves (18–20).

Prehistoric Birds from 'Eua

For 10 weeks in 1987–1989, colleagues and I excavated 15 bone deposits in caves and rock shelters on 'Eua. Most of the deposits represent the prey of barn owls and postdate human arrival on 'Eua, as indicated by the presence of *Rattus* bones. An exception is 'Anatú ("Ground-Dove Cave"), near the southern tip of 'Eua in "Quaternary reefal limestone of the '400 feet' terrace" (19). We excavated 'Anatú for 4 weeks in 1989, sieving all sediment through screens of 0.32-cm or 0.16-cm mesh.

Stratum I of 'Anatú is 40–60 cm of stratified, organic, dark brown sediment containing bones deposited by humans and barn owls. Stratum I, unlike the underlying strata II and III, contains cultural features, artifacts, ash, charcoal, and bones of non-native species (chicken, rat, pig, and dog). Four concordant ^{14}C dates from stratum I range from 570 ± 70 to 2710 ± 70 years B.P. Strata II and III are a combined 100–140 cm of poorly stratified, calcareous, yellowish-orange sediment. Strata II and III resemble each other lithologically but are separated by a 2- to 5-cm-thick bed of calcite flowstone with three uranium series dates that range from 60.0 ± 3.0 to 78.8 ± 2.7 kiloyears (kyr) B.P.

The pre-human bone assemblages portray the avifauna of 'Eua in the absence of human influence. This is prerequisite to understanding the magnitude of the losses caused by humans. The primary data in this paper are the chronostratigraphic summaries of land birds from 'Anatú (Table 1) and from all of 'Eua (Table 2), upon which the pre-human avifauna is summarized (Table 3). From these data I will outline the major features of avian distribution, turnover, and species richness. Separate papers on the systematics and community ecology of 'Eua's landbirds and seabirds will be presented elsewhere. The lizard (27) and bat bones from 'Anatú also include extinct or extirpated species.

Abbreviation: kyr, 1000 years.

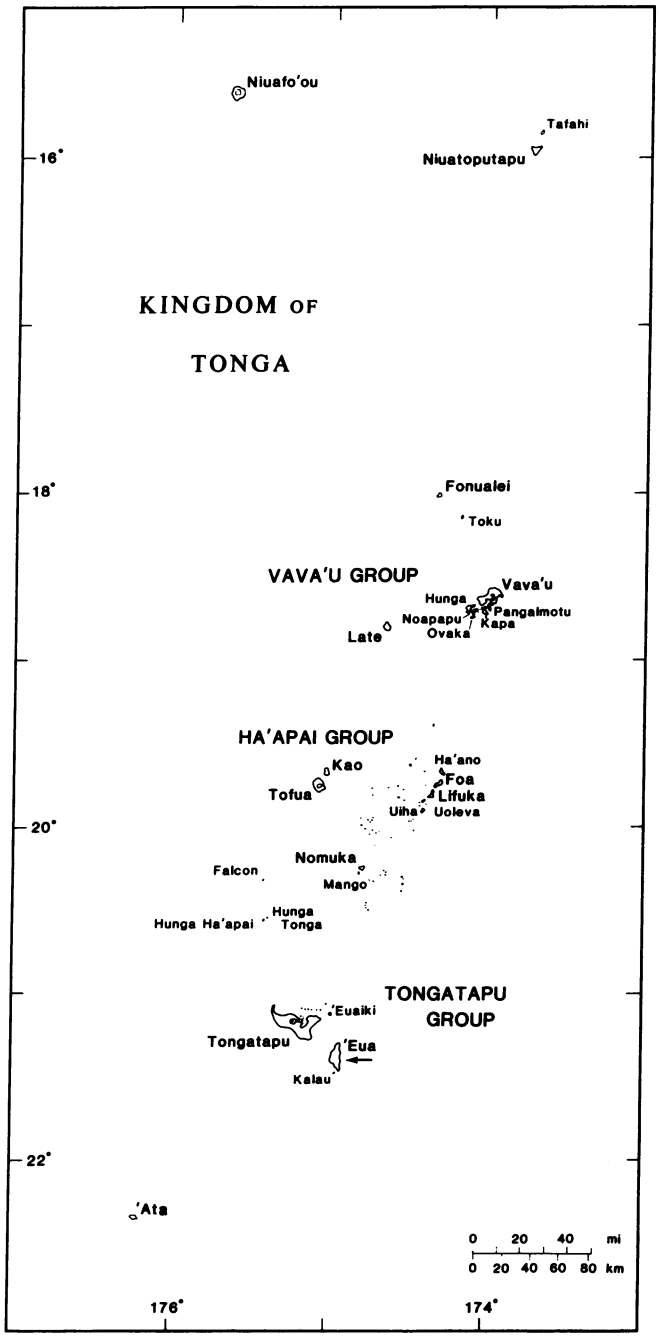

FIG. 1. Kingdom of Tonga.

Elsewhere in Tonga, bird bones have been recovered from archeological sites on Tongatapu (unstudied; ref. 28), Niuatoputapu (only seabirds; ref. 29; unpublished observations), and Lifuka. From the Tongoleleka Site on Lifuka (Ha'apai Group), cultural strata that span much of Tonga's prehistory (*ca.* 3000–1000 years B.P.; refs. 30 and 31) produced bones of the megapodes *Megapodius* cf. *molistructor* and *M. alimentum*, the pigeons *Caloenas* cf. *canacorum*, *Ducula* cf. *david*, *Ducula* new sp., and *D. pacifica*, and starling *Aplonis tabuensis* (32). Only the last two species survive anywhere today. All except *M.* cf. *molistructor* and *C.* cf. *canacorum* have been recovered at 'Anatú. These two extinct species are otherwise known only from New Caledonia (33).

Distribution

Of Tonga's terrestrial plant communities (34), the five categories of coastal and lowland rain forest, well represented on

Table 1. Stratigraphic analysis of bones of land birds from 'Anatú, 'Eua, Tonga

Species	Stratum III	II/III	II	I	NISP
Herons					
Nycticorax new sp.*	—	—	3	—	3
Hawks					
Accipiter cf. *rufitorques*†	2	1	—	—	3
Megapodes					
*Megapodius alimentum**	9	14	20	—	43
Megapodius pritchardii†	1	—	—	—	1
Megapodius new sp.*	2	—	1	1	4
Chickens					
Gallus gallus (i)	—	—	—	25	25
Rails					
Gallirallus new sp.*	30	19	39	—	88
Gallirallus philippensis	—	—	—	18	18
Porzana tabuensis†	—	—	—	85	85
Gallinula new sp.*	1	—	1	—	2
Porphyrio porphyrio	—	—	—	38	38
Pigeons and doves					
Gallicolumba stairi†	18	10	27	—	55
Didunculus new sp.*	6	5	11	3	25
Ptilinopus porphyraceus	2	—	3	—	5
Ptilinopus perousii	—	—	3	3	6
*Ducula david**	4	3	5	—	12
Ducula new. sp.*	2	2	5	—	9
Ducula pacifica	—	—	—	10	10
Parrots					
Vini solitarius†	—	1	—	—	1
Vini australis†	1	—	1	1	3
Eclectus new sp.*	6	—	2	2	10
Swifts					
Collocalia spodiopygia	—	—	—	2	2
Kingfishers					
Halcyon chloris	3	1	5	18	27
Trillers					
Lalage maculosa	1	1	1	5	8
Whistlers, robins					
Eopsaltria sp.*†	—	1	2	—	3
Monarchs					
Clytorhynchus vitiensis†	—	2	3	25	30
Myiagra sp.†	3	—	5	—	8
Warblers					
Cettia sp.*†	1	—	1	—	2
Thrushes					
Turdus poliocephalus†	15	5	20	4	44
Starlings					
Aplonis tabuensis	5	9	29	36	79
Honeyeaters					
Myzomela cardinalis†	1	—	12	1	14
Foulehaio carunculata	4	2	10	77	93
White-eyes					
Zosteropidae new sp.*	—	—	1	—	1
Totals					
No. of bones (all species)	117	76	210	329	732
No. of bones*†	102	63	159	122	446
% bones*†	87	83	76	37	61
No. of species	21	15	24	17	32
No. of *† species	16	11	18	8	22
% *† species	76	73	75	47	69

Stratum III is >60–80 kyr B.P. Stratum II/III is mixed pre-human sediment from slumped lower walls of the excavation. Stratum II is <60–80 but >2.7 kyr B.P. Stratum I postdates the arrival of humans (<2.7 kyr B.P.). NISP, number of identified specimens. i, Introduced by humans; not included in totals.

*Extinct species.

†Extirpated species (extant elsewhere, but no longer occurs on 'Eua).

Table 2. Preliminary chronology of all resident land birds from 'Eua, Tonga

Species	Pre-human record	Archeological record	Historic record	Extant in 1988
Herons				
Egretta sacra	—	X	X	X
Nycticorax new sp.*	X	—	—	—
Ducks				
Anas superciliosa	—	—	X	X
Hawks				
Accipiter cf. *rufitorques*†	X	—	—	—
Megapodes				
*Megapodius alimentum**	X	X	—	—
Megapodius pritchardii†	X	—	—	—
Megapodius new sp.*	X	X	—	—
Chickens				
Gallus gallus (i)	—	X	X	X
Rails				
Gallirallus new sp.*	X	—	—	—
Gallirallus philippensis	—	X	—	X
Porzana tabuensis†	—	X	X	—
Gallinula new sp.*	X	—	—	—
Porphyrio porphyrio	—	X	X	X
Pigeons and doves				
Gallicolumba stairi†	X	X	—	—
Didunculus new sp.*	X	X	—	—
Ptilinopus porphyraceus	X	X	X	X
Ptilinopus perousii	X	X	—	X
*Ducula david**	X	X	—	—
Ducula new sp.*	X	X	—	—
Ducula pacifica	—	X	X	X
Parrots				
Vini solitarius†	X	—	—	—
Vini australis†	X	X	X	—
Prosopeia tabuensis (i)	—	X	X	X
Eclectus new sp.*	X	X	—	—
Barn owls				
Tyto alba	—	X	X	X
Swifts				
Collocalia spodiopygia	—	X	X	X
Kingfishers				
Halcyon chloris	X	X	X	X
Trillers				
Lalage maculosa	X	X	X	X
cf. *Lalage* sp.*†	—	X	—	—
Whistlers, robins				
Eopsaltria sp.*†	X	—	—	—
Monarchs				
Clytorhynchus vitiensis†	X	X	X	—
Myiagra sp.†	X	X	—	—
Warblers				
Cettia sp.*†	X	—	—	—
Thrushes				
Turdus poliocephalus†	X	X	—	—
Starlings				
Aplonis tabuensis	X	X	X	X
Sturnus vulgaris (i)	—	—	—	X
Acridotheres fuscus (i)	—	—	—	X
Honeyeaters				
Myzomela cardinalis†	X	X	—	—
Foulehaio carunculata	X	X	X	X
White-eyes				
Zosteropidae new sp.*	X	—	—	—
Total species	27	26	14	13
Total *† species	21	14	3	0
No. of sites/no. of bird bones	1/401	14/888	—	—

Pre-human record = >3000 years B.P. (= strata II and III of 'Anatú). Archaeological record = 3000–200 years B.P. (15 different sites). Data for "Historic Record" (= 19th century specimen) are from refs. 21–24. Data for "Extant in 1988" are from refs. 21, 25, and 26 and personal observations from 1988 and 1989. i, Introduced by humans; not included in totals.
*Extinct species.
†Extirpated species.

'Eua, are the most important for land birds. The modern range of virtually every extant Tongan land bird has gaps that lack an obvious geographical or ecological basis. As in East Polynesia (see above), I regard most or all of these geographic hiatuses as the result of human activity, exemplified by these eight species from 'Anatú that had not been recorded previously on 'Eua but survive elsewhere in Fiji–Tonga–Samoa: *Accipiter rufitorques*, a goshawk now only in Fiji; *Megapodius pritchardii*, a megapode surviving only on the northern Tongan island of Niuafo'ou; *Gallicolumba stairi*, a ground-dove widespread but very local and declining in the region; *Vini solitarius*, a parrot confined today to Fiji; *Myiagra* sp., a flycatcher closely related to or conspecific with *M. vanikorensis* or *M. azureocapilla* of Fiji or *M. albiventris* of Western Samoa; *Cettia* sp., a warbler closely related or conspecific with *C. (Vitia) ruficapilla* of Fiji; *Turdus poliocephalus*, a thrush from large islands of Fiji and Western Samoa; and *Myzomela cardinalis*, a honeyeater confined in the region to Samoa, with the closely related *M. jugularis* in Fiji.

Three other extirpated species, all widespread but local and declining in Fiji–Tonga–Samoa, survived on 'Eua into historic times (21): *Porzana tabuensis*, a rail last recorded in 1889; *Vini australis*, a parrot last seen about 50 years ago; and *Clytorhynchus vitiensis*, a shrikebill recorded in 1876 and surviving in low numbers on 'Eua's offshore islet of Kalau.

Of biogeographic and systematic interest are 11 extinct species from 'Anatú: *Nycticorax* new sp., a genus of night heron unknown in Oceania east of New Caledonia; *Megapodius alimentum*, a megapode larger than any extant congeners (32); *Megapodius* new sp., the world's smallest megapode; *Gallirallus* new sp., a flightless rail probably endemic to 'Eua; *Gallinula* new sp., a flightless gallinule also probably endemic; *Didunculus* new sp., a tooth-billed pigeon (the only congener, *D. strigirostris*, had been regarded as a species through subfamily endemic to Western Samoa); *Ducula david*, a pigeon also known from Uvea (Wallis Island), north of Fiji (35) and Lifuka, Tonga (32); *Ducula* new sp., a pigeon nearly the size of New Guinea crested pigeons (*Goura* spp.), known also from Lifuka (32); *Eclectus* new sp., a parrot with congeners no closer than the Solomon Islands; *Eopsaltria* new sp., an "Australian robin" with no congeners east of New Caledonia; and Zosteropidae new sp. (genus unknown, larger than *Zosterops*), a white-eye without congeners in Polynesia, perhaps related to *Rukia* or *Megazosterops* of Micronesia or *Woodfordia* of the Solomon Islands.

Species Richness

The increase in species number with increasing island area may be "one of community ecology's few genuine laws" (36). Nevertheless, the best ornithological examples of this relationship, such as the Solomon Islands avifauna (37), have not been calibrated by data on human impact. In East Polynesia, when anthropogenic losses are considered, the

Table 3. Resident land birds from pre-human contexts on 'Eua, Tonga

Species	Status
Nycticorax new sp.	E
Accipiter cf. *rufitorques*	X
Megapodius alimentum	e
Megapodius pritchardii	X
Megapodius new sp.	E
Gallirallus new sp.	E
Gallinula new sp.	E
Gallicolumba stairi	X
Didunculus new sp.	E
Ptilinopus porphyraceus	L
Ptilinopus perousii	L
Ducula david	e
Ducula new sp.	e
Vini solitarius	X
Vini australis	x
Eclectus new sp.	E
Halcyon chloris	L
Lalage maculosa	L
Eopsaltria sp.	E
Clytorhynchus vitiensis	x
Myiagra sp.	E/X
Cettia sp.	E/X
Turdus poliocephalus	X
Aplonis tabuensis	L
Myzomela cardinalis	X
Foulehaio carunculata	L
Zosteropidae new sp.	E
Totals: E = 8–10, e = 3, X = 6–8, x = 2, L = 6.	

From data in Tables 1 and 2. E, extinct species, unknown elsewhere; e, extinct species, recorded on other island(s); L, lives today on 'Eua; X, extirpated species, not recorded historically on 'Eua; x, extirpated species, recorded historically on 'Eua.

relationship between island area and species richness is uncertain (2). A primary reason why large Polynesian islands support relatively rich avifaunas may be simply because it has been more difficult for humans to extinguish species on large, mountainous islands than on small, low islands.

Today 13 species of indigenous land birds live on 'Eua. Twenty-seven species are known from a pre-human context. Twenty-seven is a minimum because the pre-human record almost certainly is incomplete. Of the 9 indigenous species not recorded in pre-human strata (Table 2), four (*Egretta sacra, Tyto alba, Collocalia spodiopygia*, cf. *Lalage* sp.) probably were present before human arrival but their bones were not found in 'Anatú. The heron *E. sacra* lives mainly along the coast, not in forests such as those surrounding 'Anatú. Bones of predatory birds, such as the barn owl *T. alba*, usually are rare in cave sites on islands (38). The swiftlet *C. spodiopygia* may be more common now that much of 'Eua's forest has been disturbed or removed, providing better conditions for aerial foraging. The small triller cf. *Lalage* sp. is known only from two bones found at That Cave; its absence from 'Anatú may be a sampling artifact.

Five other indigenous species absent from pre-human strata (Table 2) may not have lived on 'Eua before human arrival. The duck *Anas superciliosa* needs wetlands or pyrophytic fernlands, not forests, and may have arrived in Polynesia after humans (39). The rails *Porzana tabuensis, Gallirallus philippensis*, and *Porphyrio porphyrio* live in disturbed habitats, not forests, and thus either were rare or absent from 'Eua in pre-human times. As on New Zealand (40) and New Caledonia (33), there is no stratigraphic (and therefore temporal) overlap on 'Eua between the extant and extinct species of rails. *Ducula pacifica*, unlike other forest birds on 'Eua, is a "supertramp" species that regularly flies between islands (41).

Four species have been introduced to 'Eua by humans. The chicken *Gallus gallus* and the parrot *Prosopeia tabuensis* arrived prehistorically (22, 42). The starling *Sturnus vulgaris*, native to Eurasia, was first seen in the 1980s (21). I saw the myna *Acridotheres fuscus*, native to Southeast Asia, for the first time in December 1988, foraging among cattle.

Except for isolated 'Ata (43), 'Eua is the southernmost island in Tonga, relatively remote from faunal source areas in Fiji and Samoa. The evidence from 'Eua suggests that about 30 species of land birds would be found on a typical major Tongan island in pre-human times. The minimum island area needed to support such a species assemblage will remain unknown until pre-human avifaunas are discovered on smaller Tongan islands.

Faunal Turnover

The only previous evidence for turnover in Pacific island birds on an evolutionary time scale was that inferred from frequency of extant endemic forms (44). This method presumes that high levels of endemism indicate low turnover rates. This presumption has been validated for the highly endemic avifauna on the Hawaiian Islands, where 17 of the 18 species of land and freshwater birds from a site on Oahu dated at >120 kyr B.P. also occurred on Oahu in late Holocene sites (45), suggesting a very low turnover rate under natural conditions.

The avifauna of Tonga has a much lower level of endemism than that of Hawaii. Therefore, theory would predict turnover rates to be greater in Tonga than in Hawaii. This can be tested at 'Anatú by comparing the avifaunas of stratum III (>60–80 kyr B.P.), stratum II (<60–80 but >2.7 kyr B.P.), and stratum I (<2.7 kyr B.P.). Only 6 of the 27 species recorded from strata II and III still occur on 'Eua, compared to 9 of 18 species from stratum I (Table 1). Of the 21 extinct or extirpated species from strata II and III, 7 are recorded from stratum I as well, demonstrating their survival into the human period. Five others (*Megapodius alimentum, M. pritchardii, Gallicolumba stairi, Ducula david*, and *Ducula* new sp.) survived into human times elsewhere in Tonga (2, 6, 46) and thus may have done so on 'Eua as well.

Twenty-seven species of land birds are known from strata II and III of 'Anatú. Nineteen of these occur in both strata. The 8 species not shared by strata II and III probably represent sampling artifacts rather than natural colonizations or extinctions (i.e., turnover). These 8 species are represented by only 1–5 bones each ($\bar{X} = 2.5$), compared to 2–88 bones ($\bar{X} = 20.2$) for each of the other 19 species. Furthermore, 9 of the 14 extinct/extirpated species from strata II or III that have not been recorded from stratum I are known from only 1–5 bones. A larger bone sample would help to learn which of these species survived into human times. More bones also would increase pre-human species richness. That 10 of 'Eua's 23 extinct/extirpated species are represented by ≤5 bones suggests that more such species await discovery. Another way to improve the turnover data would be to refine the age ranges of strata II and III by additional uranium series dating of speleothems and radiocarbon dating of bones (47) of extinct or extirpated species from stratum II. Stratum III presumably is too old to be dated by radiocarbon.

Although estimates of modern turnover or extinction rates for island birds are related to the length of time between surveys (44, 48–50), these studies are based upon continental islands (off Great Britain and California or within Sweden) that are close to biotically rich source areas. In at least the first two cases, the islands are dominated by human-modified habitats (ref. 51; unpublished observations). Many of the birds that come and go on these islands today are migratory

species that may not have resided there under natural conditions. Even if only nonmigratory land birds are considered, the short-term (= decades rather than centuries or millennia) rates of "colonization" and "extinction" are greater on temperate continental islands than on oceanic islands of the tropical Pacific. On Karkar Island, only 16 km from New Guinea (a rich faunal source area that is "continental" compared to Polynesia), surveys in 1914 and 1969 showed significant turnover in land birds (52). Each of the five apparent extinctions on Karkar was either a rail, pigeon, or parrot, the same three families in which the greatest prehistoric losses have occurred in Polynesia (2). The apparent turnover on Karkar and temperate continental islands is of unknown importance on an evolutionary time scale.

Although short-term variation in species composition of continental islands is interesting in its own right, it may have little bearing on natural turnover rates in Polynesian land birds. Much like species of continental tropical land birds that seldom if ever cross water gaps or clearings between forest patches (53–55), most Polynesian forest birds rarely stray between islands, an exception being the supertramp *Ducula pacifica*. Unlike in Melanesia (52, 56), I have found no cases of an extirpated Polynesian forest bird recolonizing the same island under its own power. Nor are indigenous forest birds known today to colonize non-intervisible islands. The current reluctance to disperse in most modern Polynesian forest birds, especially understory species, may be of limited value, however, in understanding the long-term residency of species. We now know that at least 21 species were established on 'Eua ≥60–80 thousand years ago. This time scale is orders of magnitude greater than the typical days, weeks, months, or even years of observation by ornithologists.

The long-term residency of most Polynesian land birds is exemplified further by the fact that most have differentiated into recognizable subspecies on individual islands or on clusters of nearby islands. Many Polynesian islands underwent only minor increases in land area and reductions in interisland distances during periods of glacially lowered sea levels. Each of the three main clusters of Tongan islands, however, experienced a major increase in land area accompanied by coalescence of what today are individual islands. Thus it is logical to assume that colonization of Tongan islands by forest birds occurred more during glacial than interglacial times.

Conclusions

The faunal assemblages from 'Eua span the two major late Quaternary events that influenced ecosystems worldwide: the glacial–interglacial transition (≈11 kyr B.P.) and the first arrival or technological advance of humans (≈3 kyr B.P. in the case of 'Eua). Until human disruption, perhaps the land bird fauna of 'Eua (and, presumably, elsewhere in Polynesia) had been increasing in species with time, had undergone little natural extinction, and therefore had not yet reached "equilibrium." If equilibrium is a valid concept for Polynesian birds, the species numbers are much higher than indicated by 19th or 20th century surveys. Furthermore, the loss of land birds has had impacts of great ecological and biogeographic importance to the coevolved plant and animal communities that once inhabited Polynesia.

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