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Extinction and Biogeography of Bats on 'Eua, Kingdom of Tonga

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ABSTRACT

Prehistoric bones from caves on the island of 'Eua, Kingdom of Tonga, document the former presence of the megachiropterans *Pteropus tonganus*, *Pteropus samoensis*, and *Notopteris macdonaldi* and the microchiropterans *Emballonura semicaudata* and *Chaerephon jobensis*. Of these five species of bats, only *Pteropus tonganus* and *Emballonura semicaudata* still occur on 'Eua or

anywhere else in Tonga. Bones of all five species occur in sediments that predate the arrival of humans on 'Eua (i.e., those more than 3500–3000 years old) as well as in younger deposits. The extinction of bat species on 'Eua, as with the two species of lizards and 23 species of land birds, is probably related to human impact.

INTRODUCTION

Traditional biogeographic studies on Pacific island vertebrates have been based on species recorded during the past 200 years, especially the past century (Mayr, 1945; MacArthur and Wilson, 1967; Stoddart, 1993).

Wherever prehistoric remains of vertebrates have been discovered, however, the modern faunas of tropical Pacific islands have been found to be only remnants of richer species assemblages that existed when the first hu-

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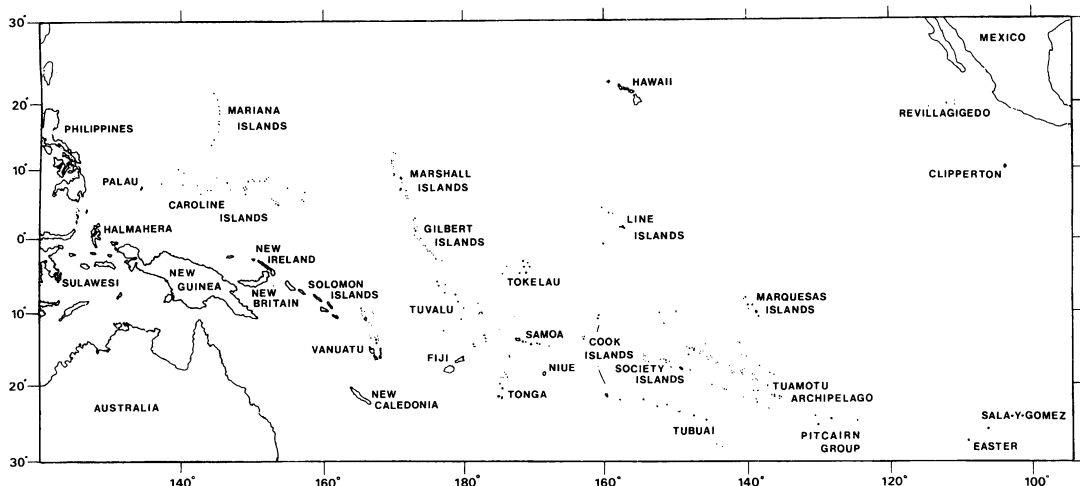


Fig. 1. The tropical Pacific, showing island groups mentioned in the text.

mans arrived (James and Olson, 1991; Olson and James, 1991; Steadman, 1989a, 1993a; Kirch et al., in press). Biogeographic concepts and theories about Pacific island vertebrates thus require calibration with data that reflect the faunal composition before human impact.

A single species of fruit bat (*Pteropus tonganus*) and two species of skink (*Emoia trosula* and *E. cyanura*) in the southern Cook Islands may mark the eastern limit of endemic and certainly indigenous nonmarine reptiles and mammals in Oceania (Wodzicki and Felten, 1980; Crombie and Steadman, 1987). Indigenous bats and lizards seem to be absent from the rest of East Polynesia (Marquesas, Society, Tuamotu, Pitcairn, Easter, and Austral islands; fig. 1), though nonendemic (but supposedly indigenous) species of *Emoia* (e.g., *cyanura*) do occur (see Brown, 1991). By necessity, therefore, research on East Polynesian archaeological assemblages of nonmarine vertebrates has focused on birds. In the West Polynesian island group of Tonga, where individual islands tend to be less isolated and geologically older than those of East Polynesia, there are indigenous species of nonmarine reptiles (lizards) and mammals (bats) as well as birds. This paper will describe the prehistoric record of bats (the only native land mammals) from the Tongan island of 'Eua.

The Kingdom of Tonga lies between Fiji, Samoa, and Niue, to the west of East Poly-

nesia and east of Melanesia. Tonga consists of three groups of uplifted limestone islands (Tongatapu, Ha'apai, Vava'u), with outlying volcanic islands in the north, south, and west (fig. 2). Tonga lies at the eastern margin of the Australia-India plate, beneath which the westward moving Pacific plate is being subducted into the Tonga-Kermadec trench (Bloomer and Fisher, 1987; Hamilton, 1988). Tonga is oceanic in origin, without any past continental connections. While the basement rocks and the oldest exposed rocks date to the Early or Middle Eocene (Duncan et al., 1985), each island is capped with Miocene or younger limestones or volcanic rocks. The carbonate rocks of Tonga, as elsewhere in the South Pacific, create an excellent geochemical environment for bone preservation in caves and rockshelters (Steadman, 1993a; Pregill, 1993) and in calcareous beach sands with cultural deposits (Pregill and Dye, 1989; Steadman, 1989b; Dye, 1990; Dickinson et al., 1994).

The limestones and caves of 'Eua have been described by Taylor and Bloom (1977), Cunningham and Anscombe (1985), and Lowe and Gunn (1986). For ten weeks in 1987–89, Steadman and colleagues (see Acknowledgments) excavated bone deposits in 15 different caves and rockshelters on 'Eua (Steadman, 1989a, 1993a; Pregill, 1993). Most of the bone deposits represent the prey of barn owls (*Tyto alba lulu*) and postdate the arrival

of humans on 'Eua, as indicated by the presence of 'Anatú, Tupou Cave, That Cave, Bat Cave, Midden Cave, and Anokula Cave 1, which are dry (perched above the present water table), shallow (less than 30 m of passage), and have horizontal (walk-in) entrances on the seaward-facing cliffs that separate the various uplifted coralline limestone terraces. Another type of cave on 'Eua, represented herein only by Collapse Cave, is longer (usually hundreds of meters), wetter (with pools or streams), has variable (horizontal to vertical) entrances, and is developed inland, away from the late Pleistocene marine terraces.

The most important bone locality discovered thus far on 'Eua is 'Anatú (Ground-Dove Cave), which opens on an escarpment near the island's southern tip, in the "Quaternary reefall limestone of the 400 feet terrace" of Cunningham and Anscombe (1985). The bone deposit at 'Anatú was excavated for four weeks in 1989. At 'Anatú, as at all other sites, all sediment was sieved through screens of $\frac{1}{2}$, $\frac{1}{4}$, and $\frac{1}{8}$ or $\frac{1}{16}$ in. mesh.

Stratum I of 'Anatú is the upper 40–60 cm of stratified, organic, dark brown sediment containing bones deposited by both humans and barn owls. Stratum I, unlike the underlying strata II and III, contains cultural features, artifacts, ash, charcoal, and bones of nonnative species that arrived with early human colonists (the chicken *Gallus gallus*, Pacific rat *Rattus exulans*, pig *Sus scrofa*, and dog *Canis familiaris*). Four temporally concordant ^{14}C dates from stratum I range from 570 ± 70 to 2710 ± 70 yr BP (radiocarbon years before present). Strata II and III are a combined 100–140 cm of poorly stratified, calcareous, yellowish orange pebbly to bouldery silt. Strata II and III resemble each other lithologically but are separated by a 2 to 5 cm bed of calcite flowstone. Three uranium-series dates from this flowstone range in age from 60.0 ± 3.0 to 78.8 ± 2.7 ka (thousands of years before present; Steadman, 1993a).

The prehuman bone assemblages from 'Anatú represent the vertebrate fauna of 'Eua before the period of human influence. These data help to calibrate the magnitude of the losses caused by humans. In this paper we present chronostratigraphic summaries of the bat bones from 'Anatú (table 1) and all excavated deposits on 'Eua (tables 2, 3). We use

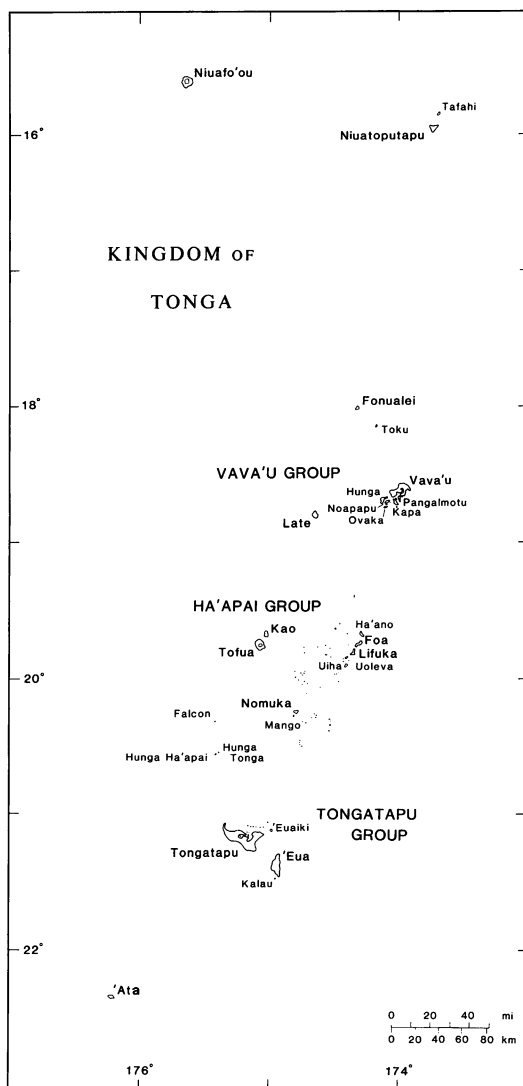


Fig. 2. The Kingdom of Tonga.

these data to review the major features of the biogeography and extinction of Tongan bats.

MATERIALS AND METHODS

Field methodology is reviewed above and in Steadman (1993a). Skeletal terminology follows Vaughan (1970). Identifications of bat bones typically are based on skull elements for two reasons: (1) the skulls of bats, as in most mammals, tend to be rich in distinctive characters; and, (2) unfortunately, most bat specimens in museum collections consist only

TABLE 1
Stratigraphic Analysis of Prehistoric Bat Bones
from 'Anatú, 'Eua, Tonga
Figures represent the number of identified speci-
mens (NISP).

Species	Stratum				To- tal
	III	II/ III	II	I	
<i>Pteropus tonganus</i>	—	1	—	2	3
<i>Pteropus samoensis</i>	—	—	2	1	3
<i>Pteropus</i> sp.	3	—	3	10	16
<i>Notopteris macdonaldi</i>	—	—	2	4	6
<i>Emballonura semicaudata</i>	14	1	9	8	32
<i>Chaerephon jobensis</i>	2	6	27	2	37
Total	19	8	43	27	97

of skins and skulls, or fluid-preserved specimens from which skulls have been extracted. Few collectors have prepared complete skeletons.

By far the most useful postcranial bones are the humerus and radius, although distinctive characters are found as well in the femur, tibia, and proximal ends of the long metacarpals. Other postcranial elements are less useful. Aside from skulls, we have had available complete skeletons of both species still living in Tonga (*Pteropus tonganus*, AMNH 249992 from American Samoa; *Emballonura semicaudata*, UWM 35539, 35540 from 'Eua, Tonga), as well as of *Notopteris macdonaldi* (USNM 260072 from Viti Levu, Fiji). The only postcranial bones available for *Pteropus samoensis* were from a partial skeleton from Upolu, Western Samoa (W. E. Rainey, unnumbered). Because only partial skeletons were available for *Cha-*

erephon jobensis (AMNH 197154, 197170 from Mt. Anderson and Darby, Western Australia, respectively), we used a smaller congeneric species (*C. plicatus*) to identify most of the limb bones.

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ACCOUNTS OF SPECIES

ORDER CHIROPTERA

SUBORDER MEGACHIROPTERA

FAMILY PTEROPODIDAE

Pteropus tonganus Quoy and Gaimard, 1830.

MATERIAL: 17 specimens (mandible, lower incisor, 3 radii, 3 metacarpals, 7 manal phalanges, femur, tibia) from three sites (table 2).

TABLE 2
Prehistoric Bat Bones from Seven Caves on 'Eua, Tonga
Figures represent number of identified specimens (NISP).

Species	'Anatú	Tupou Cave	That Cave	Collapse Cave	Bat Cave	Midden Cave	Anokula Cave 1	Total
<i>Pteropus tonganus</i>	3	—	—	—	1	13	—	17
<i>Pteropus samoensis</i>	3	—	—	—	—	—	—	3
<i>Pteropus</i> sp.	16	—	—	—	—	—	1	17
<i>Notopteris macdonaldi</i>	6	—	—	9	—	1	—	16
<i>Emballonura semicaudata</i>	32	5	8	1	8	—	—	54
<i>Chaerephon jobensis</i>	37	—	—	12	—	—	—	49
Total NISP	97	5	8	22	9	14	1	156
Total species	5	1	1	3	2	2	1	5

REMARKS: The skull and mandible of *Pteropus tonganus* (from Vanuatu) are illustrated and measured in Felten (1964b).

Pteropus samoensis Peale, 1848.

MATERIAL: 3 specimens (mandible + lower canine, 2 radii) from one site (table 2).

REMARKS: Identification of the mandible (from stratum II of 'Anatú) is based on direct comparison with modern specimens. The two radii are referred to *P. samoensis* because they are more robust than in *P. tonganus*, which corresponds to cranial differences between the two species. This is the first record of *P. samoensis* from Tonga.

Pteropus sp.

MATERIAL: 17 specimens (3 humeri, radius, 5 metacarpals, 6 manal phalanges, sacrum, tibia) from two sites (table 2).

REMARKS: These mostly fragmentary specimens may represent either *Pteropus tonganus* or *P. samoensis*.

Notopteris macdonaldi Trouessart, 1908.

MATERIAL: 16 specimens (dentary, clavicle, 3 scapulae, 3 humeri, 2 radii, 3 metacarpals, 2 manal phalanges, femur) from three sites (table 2).

REMARKS: The reduced dentition of *Notopteris macdonaldi*, especially the virtually acusate premolars and molars, distinguishes this monospecific genus from *Pteropus* and the other pteropodid genus most likely once to have lived in Tonga, *Pteralopex*. The sharply cusped cheek teeth of *Pteralopex* (Andersen, 1909; Fijian specimen illustrated in Hill and Beckon, 1978) are especially different from those of *Notopteris*. Although the single mandible from 'Eua is edentulous, it is much more gracile and with a much less steeply ascending vertical ramus than in *Pteralopex*. *Notopteris macdonaldi* is also a much smaller bat than *Pteralopex acrodonta* (forearm length 65–69 mm versus 116–120 mm). This is the first record of *N. macdonaldi* from Tonga.

SUBORDER MICROCHIROPTERA

FAMILY EMBALLONURIDAE

Emballonura semicaudata (Peale, 1848).

MATERIAL: 54 specimens (7 dentaries, 29

TABLE 3

Prehistoric Bat Bones from 'Eua, Tonga: Comparison of Prehuman (Strata III, III/II, II of 'Anatú) Versus Posthuman Assemblages (Stratum I of 'Anatú + all other cave deposits). Only specimens identified to species are included. Based on data in tables 1 and 2. The first figure represents the number of identified specimens (NISP); the figure in parentheses is the percent of vertical total.

Species	Pre-human	Post-human ('Anatú only)	Post-human (all sites)
<i>Pteropus tonganus</i>	1 (2)	2 (12)	16 (21)
<i>Pteropus samoensis</i>	2 (3)	1 (6)	1 (1)
<i>Notopteris macdonaldi</i>	2 (3)	4 (24)	14 (19)
<i>Emballonura semi-caudata</i>	24 (38)	8 (47)	30 (40)
<i>Chaerephon jobensis</i>	35 (55)	2 (12)	14 (19)
Total NISP	64	17	75

humeri, 13 radii, 3 metacarpals, 2 femora) from five sites (table 2).

REMARKS: Skulls of *Emballonura semicaudata* (from Palau, Pohnpei, and Fiji) are illustrated in Tate and Archbold (1939) and Sanborn (1947).

FAMILY MOLOSSIDAE

Chaerephon jobensis (Miller, 1902).

MATERIAL: 49 specimens (4 dentaries, manubrium, 2 clavicles, 22 humeri, 12 radii, 3 metacarpals, 4 femora, tibia) from two sites (table 2).

REMARKS: A skull of *Chaerephon jobensis* (from Vanuatu) is illustrated in Felten (1964a). This is the first record of *C. jobensis* from Tonga.

DISCUSSION

TAPHONOMY

The relative abundance of each species in the bone deposits is summarized in table 3. Bat bones have accumulated in the 'Euan caves because of predators and the natural mortality of cave-roosting bats. Among the five species, *Notopteris macdonaldi*, *Emballonura semicaudata*, and *Chaerephon jobensis* roost in caves, whereas both species of *Pteropus* roost in trees. In prehuman times,

TABLE 4

Comparison of Skeletal Element Representation in Megachiropterans

(*Pteropus tonganus*, *P. samoensis*, *Pteropus* sp., *Notopterus macdonaldi*) Versus Microchiropterans (*Emballonura semicaudata*, *Chaerephon jobensis*) in all eight prehistoric sites on 'Eua, Tonga. Values are NISP, followed in parentheses by percentages.

	Mega-chiropterans	Micro-chiropterans
Mandible	3 (6)	11 (11)
Isolated tooth	1 (2)	0 (—)
Manubrium	0 (—)	1 (1)
Clavicle	1 (2)	2 (2)
Scapula	3 (6)	0 (—)
Humerus	6 (12)	51 (50)
Radius	8 (16)	25 (24)
Metacarpal	11 (22)	6 (6)
Manal phalanx	14 (28)	0 (—)
Sacrum	1 (2)	0 (—)
Femur	2 (4)	6 (6)
Tibia	2 (4)	1 (1)
Total	52 (100)	103 (100)

the predators of bats on 'Eua were some still to be determined set of diurnal and/or nocturnal birds, perhaps including night herons, hawks, falcons, or owls (see Steadman, 1993a). The high frequency (96% of all bat bones) of cave-roosting species in the prehuman deposits suggests that natural mortality was more important than avian predators in depositing bat bones in the caves. Nevertheless, after the arrival of people, all avian predators except barn owls were extirpated on 'Eua, leaving people, barn owls, and natural mortality as the sources for bat bones in caves. Based on modern food preferences of people throughout Oceania, it seems fairly safe to assume that all three species of pteropodids were consumed by prehistoric peoples, while the two microchiropterans were not.

Pteropus tonganus tends to be crepuscular, nocturnal, colonial, and a fast, rather maneuverable flyer, while *P. samoensis* is a more diurnal, solitary species that flies rather slowly on broad wings (W. E. Rainey, personal commun.). Such differences could have implications regarding to what extent humans or raptorial birds might have preyed upon

these two pteropodids. For example, *P. samoensis* in Fiji, where a resident population of the Peregrine Falcon *Falco peregrinus* exists, is apparently less prone to fly above the canopy than in Samoa, where no falcons reside (W. E. Rainey, personal commun.).

The two species that occur more frequently in posthuman than in earlier deposits are the pteropodids *Pteropus tonganus* and *Notopterus macdonaldi* (table 3). At 'Anatú, overall pteropodid bones increase from 8 to 42% in prehuman versus posthuman deposits. These circumstances may be related to human predation. At least in part, human food preferences may also account for the relative scarcity of *Chaerephon jobensis* in posthuman deposits, although they would not explain the roughly similar abundances of *Emballonura semicaudata* before and after the arrival of people.

Pteropodids and microchiropterans differ in the relative abundances of certain wing elements (table 4). In microchiropteran samples the humerus is overrepresented (50%, versus only 12% in pteropodids), whereas the metacarpals and manal phalanges are underrepresented (6 and 0% versus only 22 and 28% in pteropodids). These biases in microchiropteran bone frequencies are due to the relatively large and sturdy humerus that withstands postmortem processes better, and is more likely to be recovered in screens, than the smaller, more fragile distal wing elements. Of course, the humerus is also large and sturdy in Megachiroptera, but so are the metacarpals and some of the manal phalanges.

BIOGEOGRAPHY

We must qualify this section at the outset by saying that the modern range of each of the five species is imperfectly known. Additional fieldwork is sure to refine our knowledge of the current distribution and abundance of all South Pacific bats.

The modern range of *Pteropus tonganus* extends from the Schouten Islands (off northern Papua New Guinea; Rainey and Pierson, 1992) and Karkar Island (off northeastern Papua New Guinea; Koopman, 1979) eastward to the southern Cook Islands, and includes the intervening Solomon Islands, Vanuatu,

New Caledonia, Wallis and Futuna, Fiji, Tonga, Samoa, and Niue (Wodzicki and Felten, 1975; Nowak and Paradiso, 1983; Rainey and Pierson, 1992). While this range is the largest of any pteropodid in Oceania, the occurrence of *P. tonganus* on the individual islands is discontinuous, especially in Melanesia. In the Solomon Islands, for example, we have found no published records of *P. tonganus* other than from the outlying islands of Rennell (Phillips, 1968; Koopman, 1979) and at least five islands in the Santa Cruz group, including Tikopia (Kirch and Yen, 1982; Flannery et al., 1988). The small populations of *P. tonganus* on Rarotonga and Mangaia (Cook Islands) represent the easternmost limit of any species of megachiropteran (Wodzicki and Felten, 1980; Tiraa, 1992). The zooarchaeological record from Mangaia shows that *P. tonganus* has been hunted and consumed there since at least as early as 1000 yr BP (Steadman and Kirch, 1990). Such predation, along with forest clearance, is a likely factor in the extirpation of *P. tonganus* from Aitutaki (Steadman, 1991) and Ma'u'ke (Walter, 1990), two other islands in the Cook Group.

Within Tonga, the current distribution of *P. tonganus* is not completely documented by published records. It is known to occur on Tongatapu (Wiles and Payne, 1986; Gill, 1987; Steadman, personal obs., 1988, 1989; USNM specimens taken in 1899, L. K. Gordon, personal commun.), 'Eua (Gill, 1987; Steadman, personal obs., 1988, 1989), Nomuka (four specimens, USNM 142472–142475, taken on 2 December 1899; L. K. Gordon, personal commun.), Foa and Lofanga in Ha'apai (Gill, 1990), Late (Rinke, 1991), Vava'u (Steadman, personal obs., 1985; Gill, 1990), and Niuafu'ou (Rinke, 1991; USNM specimens taken in 1930; L. K. Gordon, personal commun.). It seems to be absent from Tonga's southernmost island of 'Ata (Rinke, 1991). *Pteropus tonganus* is widespread today in Samoa (Upolu, Savai'i, Tutuila, 'Aunu'u, Ofu, Olosega, Ta'u; Wilson and Engbring, 1992) and Fiji (Namena, Nirai, and Yasawa, fide Sanborn 1931; Viti Levu, Vanua Levu, Taveuni, Ovalau, Moala, Totoya, and "probably . . . many more" islands, fide Wilson and Engbring, 1992: 82).

The current range of *Pteropus samoensis* is

confined to Fiji and Samoa (Wodzicki and Felten, 1975; Rainey and Pierson, 1992). Within Samoa, *P. s. samoensis* is known from Upolu, Savai'i, Tutuila, Ofu, Olosega, and Ta'u (Wilson and Engbring, 1992). Within Fiji, *P. s. nawaiensis* is known from Viti Levu, Vanua Levu, Taveuni, Ovalau, Nauai, and probably many more islands (Sanborn, 1931; Wilson and Engbring, 1992: 81).

Reliable modern records of *Notopteris macdonaldi* are confined to Vanuatu, New Caledonia, and Fiji (Hill and Beckon, 1978; Nowak and Paradiso, 1983; Rainey, 1992). The supposed 19th century record of *N. macdonaldi* from Pohnpei (Caroline Islands) has never been reconfirmed and probably is a labeling error (W. E. Rainey, personal commun.). Within Vanuatu and Fiji, the individual island distribution is poorly documented. USNM specimen records of *N. macdonaldi* include no material from Vanuatu; Fijian specimens are either from Viti Levu or lack individual island localities (Sanborn and Nicholson, 1950; L. K. Gordon, personal commun.).

The current range of *Emballonura semicaudata* (tentatively including *E. palauensis* of Palau and *E. sulcata* of the Marianas and Carolines) consists of Palau, Mariana Islands, Caroline Islands, Vanuatu, Fiji (including Rotuma), Tonga, and Samoa (Miller, 1911; Thomas, 1915; Tate and Archbold, 1939; Sanborn, 1947, 1949; Bruner and Pratt, 1979; Nowak and Paradiso, 1983; Lemke, 1986). Within most of these archipelagos, the individual island distribution is poorly documented. The record from the Marshall Islands in Tate and Archbold (1939; repeated by Nowak and Paradiso, 1983) is erroneous (Sanborn, 1953; Lemke, 1986). Within Tonga, the current distribution of *E. semicaudata* is not well known. It has been recorded on 'Eua (ca. 25 individuals in one cave in 1989, Steadman, personal obs.) and Niuafu'ou (Rinke, 1991). It seems to be absent from 'Ata and probably from Late (Rinke, 1991).

The current range of *Chaerephon jobensis* comprises Jobi (= Japen) Island (off Irian Jaya), mainland Papua New Guinea (Flannery, 1990), northern Australia, Solomon Islands, Vanuatu, and Fiji (Felten, 1964a; Nowak and Paradiso, 1983). As with the other species considered herein, the individual is-

land distribution of *C. jobensis* is not well documented.

To summarize the biogeographic implications thus far, only two species of bats have been recorded in Tonga during modern times (the past two centuries): the flying fox *Pteropus tonganus* and the sheath-tailed bat *Emballonura semicaudata*. Both of these species are widespread in the Fiji-Tonga-Samoa region. While the island-by-island distribution of these two species within Tonga is imperfectly known, both species were still living on 'Eua in 1988 and 1989, although *E. semicaudata* was rare. Of the three extirpated species of bats from the 'Euan cave deposits, the modern records nearest to 'Eua are in Fiji and Samoa for the flying fox *Pteropus samoensis*, and in Fiji and Vanuatu for the long-tailed fruit bat *Notopteris macdonaldi* and the free-tailed bat *Chaerephon jobensis*.

Thus all three extirpated species from 'Eua (and both extant species) are still found in Fiji. Six species of bats are known from Fiji in modern times, these being the five that we have recorded from 'Eua as well as the distinctive pteropodid *Pteralopex acrodonta* (MacDonald, 1857; Hill and Beckon, 1978; L. K. Gordon, personal commun.). All except *Pteralopex acrodonta* either occur or have congeneric species in Vanuatu, which hosts a richer assemblage of four megachiropterans and eight microchiropterans (Bani, 1992). The three other species of *Pteralopex* are confined to the Solomon Islands where they tend to be montane species (Hill and Beckon, 1978; Flannery, 1991). We predict, however, that *Pteralopex* is likely to occur in bone deposits in Vanuatu, if such deposits were excavated and studied. Also, if more scientific attention were given the living bats of Vanuatu, a species of *Pteralopex* might be found still to live there.

The modern bat fauna of Samoa consists of *Pteropus tonganus*, *P. samoensis*, *Emballonura semicaudata*, and perhaps a second species of microchiropteran. A vespertilionid, *Myotis insularum*, was described by Dobson (1878: 313). The holotype and only specimen of *M. insularum* was collected supposedly in the "Navigator's Islands" (= Samoa, exact island unknown) by a Mr. Schmeltz before 1878. Without additional information, this record is difficult to eval-

uate. The holotype of *M. insularum* is in the British Museum (Natural History), where it was studied by Findley (1972), who considered it most like the Palearctic species *M. mystacinus*. The zooarchaeological record of terrestrial vertebrates is not nearly as rich in Samoa as in Tonga (Nagaoka, 1993; Steadman, 1993b). The only prehistoric record of a bat from Samoa is that of *Pteropus* sp. from the Falemoa site on Upolu (Nagaoka, 1993). Given the results from 'Eua, it would not surprise us if a more comprehensive record of prehistoric bats from Samoa would include *Notopteris macdonaldi* and/or *Chaerephon jobensis*.

East of Tonga, the only bat on Niue is *Pteropus tonganus* (Wodzicki and Felten, 1975). As already stated, the eastern limit of *Pteropus tonganus* is in the Cook Islands, which lie to the east of Niue. No microchiropterans are known to occur on Niue or any other islands east of Tonga or Samoa and west of Hawaii.

The overall biogeographic implications of the fossil bats from 'Eua resemble those of birds from the same sites. Before the arrival of humans, at least 27 species of land birds lived on 'Eua, where 13 indigenous species live today (Steadman, 1993a). 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). This indicates that the avifauna of West Polynesia (Fiji-Tonga-Samoa) is more closely related to that of Melanesia than that of East Polynesia.

Pregill (1993) reported nine species of lizards from the cave deposits on 'Eua, two of which no longer occur there. These are a gecko (*Perochirus* sp.) and Scincidae sp. (perhaps *Eugongylus* or *Emoia*, although not *Emoia trossula*). No species of *Perochirus* live in Polynesia today; the nearest species are in Vanuatu and various Micronesian islands (Zug, 1991). While species-level relationships of the larger Tongan forms of *Emoia* are not entirely resolved (Crombie and Steadman, 1987; Zug, 1991), the large species of *Emoia* that still lives on 'Eua does not resemble *E. tros-*

sula from Fiji or Rarotonga (Pregill, 1993; but see Brown, 1991). The other large skink (perhaps *Emoia* or *Eugonglyus*) reported by Pregill (1993), while no longer occurring on 'Eua, is too poorly known to suggest biogeographic affinities, although the only other large scincids of similar size are to the west of Tonga. The very large iguana (*Brachylophus* sp.) from archaeological deposits on Lifuka, Tonga (Pregill and Dye, 1989) represents a genus confined to Fiji and Tonga.

EXTINCTION

The late Quaternary fossil record of Pacific island bats, while limited, has documented the prehistoric or historic losses of species on several islands outside Tonga. Among pteropodids, bones from archaeological sites reveal the extirpation of *Pteropus tonganus* from Aitutaki (Steadman, 1991) and Ma'uake (Walter, 1990) in the Cook Islands. Among extirpated microchiropterans are *Emballonura semicaudata* from Rota, Mariana Islands (Steadman, 1992), *Nyctophilus howensis* from Lord Howe Island (McKean, 1975), *Mystacina robusta* from South Island, New Zealand (Hill and Daniel, 1985; Flannery, 1987), and *Lasiurus borealis* from Floreana Island, Galápagos (Steadman, 1986). In light of these records, as well as those reported herein, values for Quaternary species richness in bats from any island group are suspect if lacking prehistoric data.

The arrival of humans has influenced the terrestrial vertebrate fauna of Tonga more than any climatic, tectonic, or biological event of the past ~100,000 years (Steadman, 1993a). The most dramatic human influence has been the extirpation of many forest-dwelling species of reptiles, birds, and bats. These losses are due to various combinations of predation and/or pathogens from introduced species (Pacific rat, dog, pig, and chicken), direct human predation, and deforestation. The prehistoric vegetation of 'Eua has not been studied, although the two small lakes in the highlands of the island seem to be well suited for palynological and sedimentological research. A forest history for 'Eua, much like that done by Kirch et al. (1992) and Ellison (1994) for Mangaia, Cook Islands, would allow a much more detailed interpretation of

the role of anthropogenic habitat change in the prehistoric loss of vertebrates on 'Eua.

Although *Pteropus tonganus* is widespread in Tonga (see Biogeography section), its current population status is poorly documented (Wiles, 1992; Wilson and Engbring, 1992). No population estimate is available for 'Eua, where Gill (1987) reported "a few flying after dark" at 'Ufilei Beach, and "several" roosting in the forest below Femaeaki Lookout, in October 1986. In November 1988, Steadman noted two roosts of *P. tonganus* (minimally 400 and 2000 individuals) in primary forest near the central eastern coast of 'Eua. On Tongatapu, the protected roost at Kolovai (see photograph in Ditmars, 1935) was estimated to consist of 5200 individuals in 1981 (Wiles and Payne, 1986) and still comprised thousands of individuals in 1988 and 1989 (Steadman, personal obs.).

Hunting and consumption of *Pteropus tonganus* within Tonga are controlled to some extent, especially at the Kolovai roost on Tongatapu (Wiles and Payne, 1986), by the Royal Family and other Tongan nobility. Nevertheless, a total of 5080 individuals of *P. tonganus* were exported to Guam from Tonga between 1975 and 1989 (3050 in 1983, and 2030 in 1984; Wiles and Payne, 1986; Wiles, 1992). Hunting and consumption of *P. samoensis*, especially in Samoa, have been reviewed by Cox (1983), Pierson et al. (1992a), and Craig et al. (1994a, 1994b). In American Samoa, populations of both *P. tonganus* and *P. samoensis* have declined 80–90% during the past five years (Craig et al., 1994b).

Cave-roosting habits concentrate populations of bats and make them particularly vulnerable to human disturbance. *Notopteris*, being a cave-rooster as well as a palatable frugivore, might have been easy and desirable prey for early Tongans. While insectivorous bats are less likely to be killed by people for food, *Emballonura semicaudata* is rather easy to kill (regardless of the reason) because, like other emballonurids (Jolly, 1990), it tends to roost in subdued light near entrances rather than in total darkness deep within caves. In spite of visiting more than 50 caves on 'Eua during 1988 and 1989, Steadman found only a single colony of *E. semicaudata*. Pesticides, especially those associated with mosquito

control, could be another cause of decline in both insectivorous species. *E. semicaudata* may now be extirpated on the Samoan islands of Tutuila and Savai'i (W. E. Rainey, personal commun.).

As with granivorous, frugivorous, and nectarivorous birds (Franklin and Steadman, 1991; Steadman, 1993a), the loss of bats (especially pteropodids) on Pacific islands undoubtedly has had long-term impacts on the composition of forest communities. Flying foxes (*Pteropus* spp.) are important pollinators and seed dispersers within and between Pacific island forests (Cox et al., 1992a, 1992b;

Elmqvist et al., 1992; Fujita and Tuttle, 1991; Pierson and Rainey, 1992; Pierson et al., 1992a, 1992b; Wiles and Fujita, 1992; Fleming, 1993). Although poorly known, *Notopteris macdonaldi* is believed to be largely nectarivorous (Medway and Marshall, 1975), a feeding mode that is compatible with its elongate and papillated tongue, reduced dentition, and elongate, rather weak rostrum and mandible. A knowledge of which species of bats and birds once occurred on a given island may be important for plant ecologists who are interested in learning how these forests functioned under natural conditions.

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