

# The biogeography and extinction of megapodes in Oceania

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The arrival of prehistoric peoples in Oceania over the past several millennia resulted in the extinction of many species and populations of megapodes. Before these anthropogenic losses, species of megapodes ranged across Melanesia, Western Polynesia, and much of Micronesia. Island groups that lack megapodes today but were inhabited by them in the past include New Caledonia, Fiji, the Ha`apai Group and `Eua (Tonga), Samoa, Niue, and Pohnpei. The extinct megapodes varied in size from a tiny, quail-like species of *Megapodius* in Tonga to the large, flightless *Sylviornis* of New Caledonia. Remote Tongan islands as small as 13 km<sup>2</sup> were able to sustain three species of *Megapodius* before human impact, thus calling into question the validity of using modern species assemblages to understand the function of natural communities.

## Introduction

The current distribution of species in the family Megapodiidae is centered in Indonesia, New Guinea, and Australia, with outlying species of the genus *Megapodius* Gaimard, 1823, locally distributed on continental islands to the west, and on oceanic islands to the north and east (Clark, 1964; Jones et al., 1995; fig. 1). Attempts to explain the western (continental) limit of the modern distribution of megapodes have focused on the theories of competition with species of Phasianidae (Olson, 1980) versus relative freedom from predation by placental carnivores (Dekker, 1989; Jones et al., 1995: 25).

In this paper I will demonstrate that the natural distribution and diversity of megapodes have been, in fact, very poorly understood at the family's eastern limit in Oceania, a region free of both phasianids and placental carnivores. Human-caused extinctions have obliterated most populations and species of megapodes in Oceania. Needless to say, study of the comparative biology of this fascinating family of galliforms has been damaged irreparably by these losses, which include both the largest and smallest species of megapodes ever discovered. The extinction of megapodes in Oceania is part of the massive loss of birdlife that has taken place during the past several thousand years of human occupation (Steadman, 1995). While far from complete, the prehistoric record of megapodes in Oceania fills in many puzzling gaps in the modern distribution of taxa and provides a glimpse of the formerly much richer taxonomic diversity of megapodes.

The early Tertiary (Paleocene-Eocene-Oligocene) fossil record of megapode-like birds begins in Europe, where two species (*Quercymegapodius depereti* (Gaillard, 1908), *Q. brodkorbi* Mourer-Chauviré, 1992) have been described from late Eocene deposits in France (Mourer-Chauviré, 1982; 1992; 1995). Although *Quercymegapodius* and modern megapodes clearly share characters in the coracoid, humerus, carpometacarpus, tibiotarsus, and tarsometatarsus, Mourer-Chauviré (1992) prefers to recognize the distinct but related family Quercymegapodiidae for the late Eocene fossils. The genus *Quercymegapodius* Mourer-Chauviré, 1992, is the only purely continental representation of megapode-like birds in the Northern Hemisphere.



True megapodes lived in the Australian region by the close of the early Tertiary, as evidenced by a single small species in an extinct genus from the late Oligocene of Australia, being described by Boles & Ivison (in press). No late Tertiary (Miocene-Pliocene) fossils of megapodes are known. Miocene avifaunas from mainland Asia include a variety of phasianids but no megapodes (Cheneval et al., 1991), suggesting that megapodes were confined to the Indonesia-Papua-Australia-Oceania region at that time.

The Quaternary fossil record of megapodes outside of Oceania is limited to Australia. *Progura gallinacea* De Vis, 1889, is known from late Pleistocene sites in Queensland and New South Wales (De Vis, 1889; Van Tets, 1974; Olson, 1985; Rich & Van Tets, 1985). With an estimated body weight of 5-7 kg (male) and 4-5 kg (female), *P. gallinacea* was two to three times heavier than the largest living species of megapode. A second species currently classified in the genus *Progura* De Vis, 1889, is *P. naracoortensis* Van Tets, 1974, from late Pleistocene cave deposits in South Australia (Van Tets, 1974). *Progura naracoortensis* was only slightly smaller than *P. gallinacea*, and has been suggested by Rich & Van Tets (1985) to be the female of that species. Olson (1985), on the other hand, has suggested that the two forms may not even be congeneric. They are illustrated by Baird (1991: 824, 826, 828, 869) and Rich (1991: 758-759).

As the Quaternary record improves in Indonesia, New Guinea, and Australia, I predict that, as in Oceania, it will be shown that humans have affected the distribution and diversity of megapodes for many millennia. The loss in Australia of both species of *Progura*, for example, may be related to prehistoric human predation and habitat alteration. Furthermore, an improved picture of the Quaternary distribution of megapodes in the Greater Sundas, Lesser Sundas, Moluccas, and Philippines may influence the debate between phasianid competition versus placental carnivore predation as the primary determinant of where megapodes now occur.

### **Prehistoric megapodes of Oceania: a brief geographic review**

For the past 60 years, all living forms of the genus *Megapodius* Gaimard, 1823, except the small, geographic outliers *M. laperouse* Gaimard, 1823, and *M. pritchardii* G.R. Gray, 1864, have been regarded as subspecies of *M. freycinet* Gaimard, 1823 (Mayr, 1938; Amadon, 1942). With improved knowledge of the biology of megapodes, the tendency in the past decade has been to recognize sets of the many allopatric populations of *M. freycinet* s.l. as distinct species (Roselaar, 1994; Jones et al., 1995). I will follow Jones et al. (1995) for nomenclature of living taxa, although aware that whether to recognize the various forms of *M. freycinet* s.l. at the subspecies versus species level can be a rather subjective decision.

The text that follows corresponds to the geographic sequence in table 1. References listed in table 1 are not repeated in the text except where they are needed for clarification. Coverage will move from west to east irregularly through Oceania (fig. 1).

Species-level identification of prehistoric megapode bones requires careful comparisons with skeletons of living species. Many bones from archaeological (cultural) and paleontological (non-cultural) sites are, of course, too fragmentary to identify precisely. The methodology for my osteological comparisons and descriptions is presented in Steadman (1989b).

Table 1. Prehistoric records of megapodes from Oceania. All records represent extinct populations or species except *Megapodius laperouse* on Ulong and Aguiguan, *M. cf. eremita* on New Ireland, and *M. layardi* on Malakula and Efate. † = extinct species.

Island group / island	Species	Reference
Palau		
Ulong	<i>Megapodius laperouse</i>	this paper
Mariana Islands		
Guam	<i>Megapodius laperouse</i>	this paper
Rota	<i>Megapodius laperouse</i>	Steadman, 1992; in press
Aguiguan	<i>Megapodius laperouse</i>	Steadman, in press
Tinian	<i>Megapodius laperouse</i>	Steadman, in press
Caroline Islands		
Pohnpei	<i>Megapodius laperouse</i>	this paper
Bismarck Archipelago		
New Ireland	<i>Megapodius cf. eremita</i> † <i>Megapodius</i> new species 1	Steadman et al., MS Steadman et al., MS
Solomon Islands		
Tikopia	<i>Megapodius cf. layardi / eremita</i>	Kirch & Yen, 1982; Steadman et al., 1990
Reef Islands	<i>Megapodius cf. layardi / eremita</i>	Green, 1976; Balouet & Olson, 1989; Steadman et al., 1990; this paper
Vanuatu		
Malakula	<i>Megapodius cf. layardi</i>	this paper
Efate	<i>Megapodius cf. layardi</i>	this paper
New Caledonia		
New Caledonia	† <i>Megapodius molistructor</i> † <i>Sylviornis cf. neocaledoniae</i>	Balouet & Olson, 1989 Balouet, 1984; 1987; Balouet & Olson, 1989
Isle of Pines	† <i>Sylviornis neocaledoniae</i>	Poplin, 1980; Poplin et al., 1983; Poplin & Mourer-Chauviré, 1985; Balouet & Olson, 1989
Fiji		
Lakeba	† <i>Megapodius cf. alimentum</i>	Best, 1984; Gibbons & Clunie, 1986; Steadman, 1989a; 1989b
Naigani	† <i>Megapodius cf. alimentum</i>	Best, 1984
Tonga		
Ha`ano	† <i>Megapodius molistructor</i>	this paper
Foa	<i>Megapodius pritchardii</i> † <i>Megapodius alimentum</i> † <i>Megapodius molistructor</i>	Steadman et al., in press
Lifuka	† <i>Megapodius alimentum</i> † <i>Megapodius cf. molistructor</i>	Steadman, 1989b; Steadman et al., in press Steadman, 1989b; Steadman et al., in press
`Uiha	† <i>Megapodius alimentum</i>	this paper
Ha`afeva	† <i>Megapodius alimentum</i>	this paper

Eua	† <i>Megapodius</i> new species 2 <i>Megapodius pritchardii</i> † <i>Megapodius alimentum</i>	Steadman, 1993; 1995 Steadman, 1993; 1995 Steadman, 1989b; 1993; 1995
American Samoa		
Ofu	(?†) <i>Megapodius</i> sp.	Steadman, 1991; 1994
Niue		
Niue	(?†) <i>Megapodius</i> sp.	T. Worthy & Steadman, pers. obs.

## Palau

The extant *Megapodius laperouse senex* Hartlaub, 1867, is the single species of megapode known from Palau. It has been recorded (tibiotarsus, three pedal phalanges) from a small, undated bone deposit in a rockshelter (ULON-1) on Ulong Island excavated by G. K. Pregill and myself on 16 January 1995. Megapodes are still common on Ulong in spite of an amazingly high concentration of non-native black rats (*Rattus rattus* (L.)), which may be important predators of megapode chicks and/or eggs. During a three-hour period on the evening of 16 January 1995, I kill-trapped 29 individuals of *R. rattus* within a 15 m radius of my tent on the same beach occupied by megapodes. The reproductive success of this megapode population is unknown.

## Mariana Islands

Bones of the extant *Megapodius l. laperouse* occur rarely to commonly in prehistoric sites (both cultural and non-cultural) in caves, rockshelters, and calcareous sand deposits on Guam, Rota, Aguiguan, and Tinian. The species no longer occurs on Guam or Rota, probably is gone from Tinian, and still is common on uninhabited Aguiguan. The evidence on Guam consists of an ulna from Coconut Cave (Andersen Air Force Base), collected by H. Hirsh and myself on 31 January 1997. From Rota, various bones of *M. laperouse* have been found at Payapai Cave, As Matmos Cave, and the Mochong Site, in both cultural and non-cultural contexts. Nine bones of *M. laperouse* have been recovered from the cultural bone midden at Pisonia Rockshelter on Aguiguan. From Tinian, bones of *M. laperouse* occur sparingly at two cultural sites, Railhunter Rockshelter and Unai Chulu.

## Caroline Islands

A single but very diagnostic tarsometatarsus of *Megapodius laperouse* s.l. was recovered by W. S. Ayres from the Nan Madol archaeological site on Pohnpei. This coastal site is as old as A.D. 500 (Ayres, 1990). This is the first record of *M. laperouse* outside of Palau or the Mariana Islands. It is likely that this small species, or a very closely related congeneric species, once lived through much of Micronesia, including Yap, Chuuk (Truk), Pohnpei, Kosrae, and many of the atolls as well.

## Bismarck Archipelago

Two species of megapodes occur in the rich bone deposits from late Pleistocene cultural sites on New Ireland. The first is *Megapodius* cf. *eremita* Hartlaub, 1867, the

local extant form of the *freycinet* species-group (see Mayr, 1938:12-15). The second is a very large, extinct, undescribed species (*Megapodius* new species 1) in the approximate size range of (but larger than) the extinct *M. molistructor* Balouet & Olson, 1989, of New Caledonia and Tonga. *Megapodius* new species 1 is known from only two fragmentary bones, a scapula from Panakiwuk Cave and a tarsometatarsus from the Balof 2 Rockshelter. Both bones are associated with the late Pleistocene cultural deposits described by Allen et al. (1988, 1989), Marshall & Allen (1991), and White et al. (1991).

#### Solomon Islands

From the very small, isolated island of Tikopia are 10 bones of a medium-sized species of *Megapodius*, most likely in the *freycinet* species-group and therefore probably referable (based purely on geography) to the extant *M. layardi* Tristram, 1879, or *M. eremita*. Eight of the 10 megapode bones from Tikopia are from the island's oldest cultural context (ca. 3000 years old). More poorly documented are bones of *Megapodius* from a roughly contemporaneous archaeological site in the Reef Islands, north of Santa Cruz (Nendo). This unknown number of bones, which I examined briefly in 1982, also can be tentatively referred to *M. layardi* or *M. eremita*. The Reef Islands lie closer to the modern range of *M. eremita* than Tikopia. It should be noted that the relationships are poorly understood between the two modern populations of megapodes nearest to Tikopia and the Reef Islands, namely *M. eremita* at its current eastern limit in San Cristobal (Solomon Islands) and *M. layardi* at its northern limit in the Banks Islands, Vanuatu (Roselaar, 1994: 33).

#### Vanuatu

The only prehistoric records of megapodes in Vanuatu are based on bones I have identified from two archaeological sites (ca. 2500 to 2000 years old) excavated over the past three years by S. H. Bedford and M. Spriggs of the Australian National University. In both cases the fragmentary bones probably belong to *Megapodius layardi*, the endemic and only species of megapode living in Vanuatu today. At the Woplampam site on Malakula Island are three juvenile bones (humerus, femur, tibiotarsus) of *M. cf. layardi*. From the Mangaas site on Efate Island is a badly charred adult tibiotarsus of *M. cf. layardi*.

#### New Caledonia

Megapodes are one of the most conspicuous components of the rich Holocene avifauna of New Caledonia and nearby Isle of Pines. Both species of megapodes discovered thus far are extinct and are recorded from cultural sites, thus showing that they survived until the arrival of humans ca. 3000 years ago. The endemic *Sylviornis neocaledoniae* Poplin, 1980, was originally described as a "ratite" based on two fragmentary bones from Isle of Pines (Poplin, 1980). Much better material from Isle of Pines allowed Poplin et al. (1983) to determine that *Sylviornis* Poplin, 1980, was a megapode rather than a paleognathous bird (Poplin et al., 1983; Poplin & Mourer-Chauviré, 1985). More bones from Isle of Pines, as well as abundant bones of *Sylviornis* from four caves on New Caledonia proper, were mentioned briefly by Balouet (1984, 1987) and Balouet & Olson (1989). A single, eroded distal tibiotarsus recently

excavated from the Lapita archaeological site on New Caledonia is referable to *Sylviornis* (DWS, pers. obs.). Species-level systematics of *Sylviornis* on Isle of Pines versus New Caledonia are unresolved. *Sylviornis* was the world's largest megapode and the only one that certainly was flightless. It probably stood ca. 1.2-1.6 m tall and weighed ca. 40 kg. *Sylviornis* was likely responsible for constructing the soil mounds (diameter 10-50 m, height 0.8-5 m) in New Caledonia known as "tumuli" (Green & Mitchell, 1983; Mourer-Chauviré & Poplin, 1985; Green, 1988).

*Megapodius molistructor* is the smallest megapode known thus far from New Caledonia yet is much larger than any living species of *Megapodius*. This volant species also has been recorded from Tonga (see below) and thus might be expected to have occurred as well in Fiji, Vanuatu, and perhaps Samoa.

## Fiji

The only record thus far of megapodes from Fiji is based on bones from archaeological sites up to 3000 years old on Naigani (off Viti Levu) and Lakeba (Lau Group). I tentatively refer these bones to *Megapodius alimentum* Steadman, 1989, a rather large extinct species that occurs commonly in prehistoric sites in Tonga (see below). Virtually all islands in Fiji probably once sustained megapodes. A reasonable working hypothesis would be that the Fijian megapodes included forms that were conspecific with or closely related to the four species of *Megapodius* known from Tonga.

## Tonga (fig. 2)

The prehistory of megapodes is documented better in Tonga than elsewhere. In modern times (since European contact), the only certain record of any extant population of megapode from Tonga (or elsewhere in Polynesia; Steadman, 1991) is that of *Megapodius pritchardii* from the volcanic island of Niuafu'ou. The life history of this species of megapode is relatively well studied (Weir, 1973; Todd, 1983; Rinke, 1986; 1991; Göth & Vogel, 1995; 1997). Long regarded as endemic to Niuafu'ou, bones of *M. pritchardii* now are known from an archaeological site on Foa in the Ha'apai Group of Tonga and from a pre-cultural context on 'Eua. Rather than being truly endemic to Niuafu'ou, *M. pritchardii* merely has been able to survive on this one island. Before the arrival of people in Tonga ca. 3000-2800 years ago (Burley et al., 1995), *M. pritchardii* probably occurred across the island group. Thus it is likely that tens, perhaps as many as 100, individual island populations of *M. pritchardii* have been lost.

The extinct *Megapodius* new species 2, the smallest megapode known, is also represented in both cultural and non-cultural contexts on 'Eua. Its bones average 10% smaller in linear dimensions than those of the sympatric *M. pritchardii*. Adults of this quail-sized bird would have weighed only ca. 180-270 grams (compared to 295 - 454 grams in adults of *M. pritchardii*; Jones et al., 1995: 148).

The extinct *Megapodius alimentum* is the most commonly occurring megapode in prehistoric sites on 'Eua as well as on five islands in the Ha'apai Group (Ha'ano, Foa, Lifuka, 'Uiha, and Ha'afeva). Like *M. pritchardii* and *M. new species 2*, it is likely that *M. alimentum* used to occur virtually throughout Tonga. If the bones from Naigani and Lakeba (see above) represent *M. alimentum*, then this species also lived at least as far west as western Fiji. Most bones of *M. alimentum* are fairly similar qualitatively to those of the living members of the *M. freycinet* species-group, although averaging

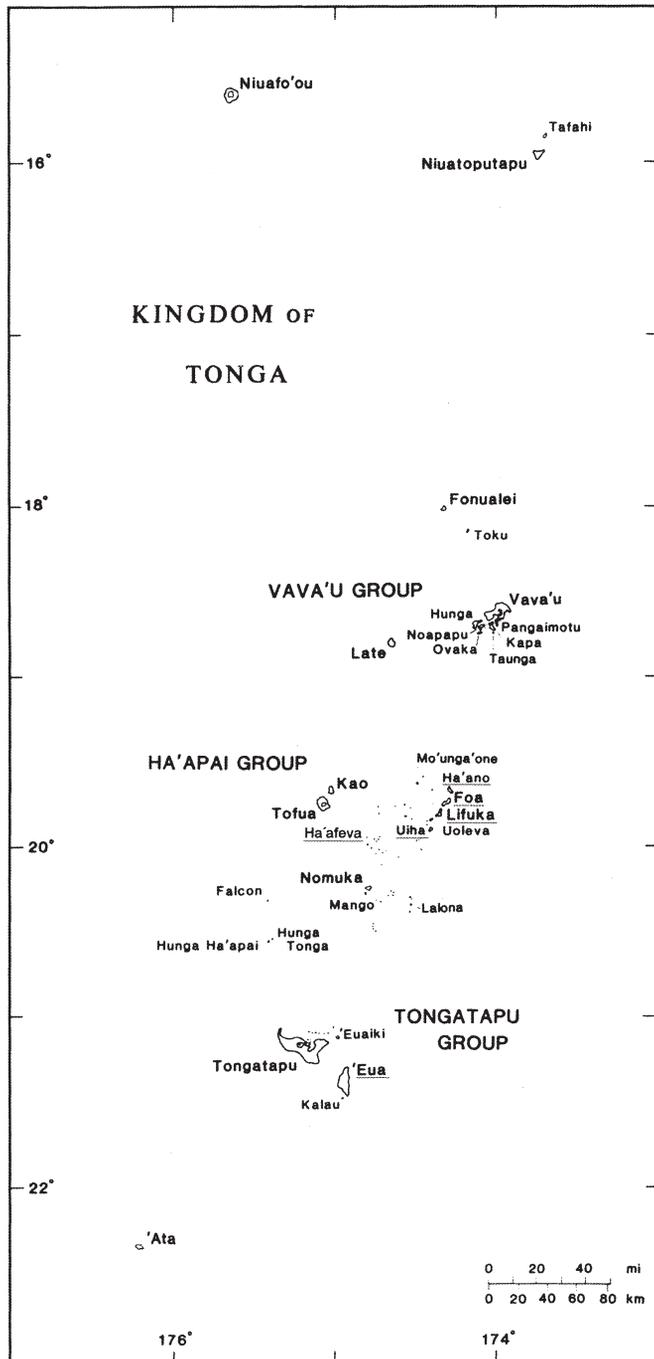


Fig. 2. The Kingdom of Tonga. The names of islands with prehistoric bones of megapodes are underlined.

larger. *Megapodius alimentum* may be the Tongan-Fijian representative of the *M. freycinet* species-group. If so, it is the largest known species in this "superspecies". The much smaller *M. pritchardii* was in fact broadly sympatric with *M. alimentum* in Tonga and therefore these two species cannot be allopatric representatives of a single lineage.

The last species of megapode from Tonga is the very large, extinct *Megapodius* cf. *molistructor*, represented thus far by single distinctive coracoids from the Pukotala site (Ha`ano), Faleloa site (Foa), and Tongoleleka site (Lifuka), as well as a scapula from Faleloa. Described originally from New Caledonia (see above), *M. molistructor* probably occurred prehistorically in Vanuatu and Fiji as well. The relative scarcity of bones of *M. molistructor* in Tonga, relative to those of *M. alimentum*, might reflect a lower population density that led to its more rapid extinction following human arrival. Being Tonga's largest ground-dwelling bird, *M. molistructor* may have been a highly favoured prey item to the early colonists of Tonga. While certain marine resources, such as sea turtles, large fish, and large shellfish, certainly were among the preferred prey for early Tongans, the most desirable terrestrial resources included seabirds (petrels, shearwaters) and the largest landbirds (megapodes, rails, pigeons).

#### American Samoa

A mere two bones of a medium-sized but undetermined species of *Megapodius* have been reported from the Toaga archaeological site on Ofu Island, Manu`a Group. This ulna and femur seem to represent a member of the *M. freycinet* species-group. Being at the small end of the size range in modern *M. freycinet* (Steadman, 1994: table 14.2), these bones certainly do not represent *M. alimentum*. That no bones of megapodes have been found in Western Samoa simply reflects that no prehistoric birds are known on these large volcanic islands.

#### Niue

From a pre-cultural cave site on Niue are various bones of a species of *Megapodius* that is intermediate in size between the smaller *M. pritchardii* and larger *M. alimentum* of Tonga. It seems to be a representative of the *M. freycinet* species-group and perhaps is conspecific with the megapode from American Samoa. Niue and American Samoa establish the eastern limit of the prehistoric distribution of megapodes.

### Discussion and Conclusions

#### Extinction

Megapodes are one component of the major loss of birdlife associated with the prehistoric human colonization of Oceania (Steadman, 1995). There is very little evidence for extinction of birds in Oceania before human arrival. From 3500 to 3000 years ago, people of the Lapita Cultural Complex moved rapidly from an undetermined part of Island Southeast Asia into Remote Oceania, settling by 3000 to 2800 years ago on islands as far east as Tonga and Samoa (Irwin, 1992; Burley et al., 1995; Kirch, 1995). ("Remote Oceania" refers to Pacific islands east of the Solomons and north of the Bismarcks, i.e., all of Polynesia and Micronesia as well as Vanuatu, New Caledonia, and Fiji; see Green, 1991). The Lapita peoples were agriculturalists as well

as hunters and fishers who exploited a wide range of marine and terrestrial animals (Nagaoka, 1988; Kirch, 1989; Dye & Steadman, 1990). The rapid movement of Lapita peoples to islands spread across thousands of kilometers of ocean is the sort of colonization event one might expect to be associated with a catastrophic extinction. The radiocarbon and faunal data from Lapita archaeological sites in the Ha`apai Group of Tonga suggest that the loss of most species of birds, including all four species of megapodes, occurred on these islands within no more than a few centuries.

Bones from cultural sites on many islands indicate that megapodes were killed and eaten prehistorically. Much of megapode exploitation today, as well as in the past, has focused on eggs, the harvesting of which is potentially sustainable only if strictly controlled and if natural habitats remain relatively intact (Broome et al., 1984; Lepofsky, 1989; Steadman, 1991; Jones et al., 1995).

At least five extinct species of megapodes are known now from Oceania. Considering these and the two species of *Progura* from Australia, and realizing how incomplete the late Quaternary fossil record is in most parts of Island Southeast Asia, Indonesia, Philippines, Papua New Guinea, Australia, and Oceania, I estimate that at least as many species of megapodes have gone extinct as still exist today. Thus, if not for people, the figure of 22 living species of megapodes (Jones et al., 1995) would increase to 45-55 species.

#### Biogeography and community ecology

The very rich fossil record of birds in East Polynesia has yielded no evidence of megapodes (Steadman, 1995). American Samoa and Niue appear to be the true eastern limit of the family. Moving north and west from American Samoa, no megapodes are known from the very scattered and incomplete prehistoric bone records from the remote atolls in Tokelau, Tuvalu, Kiribati, and the Marshall Islands. Living forms of *Megapodius* do live on atolls in spite of the currently depauperate floras and often limited forest structure on these low islands. Examples include *M. laperouse* on Kayangel, Palau, and *M. eremita* on Ontong Java and Sikaiana, Solomon Islands (Bayliss-Smith, 1972; Engbring, 1988; Jones et al., 1995). Among the high islands of eastern Micronesia, there is no bone record from Kosrae or Nauru which, given the former occurrence of *M. laperouse* on Pohnpei, may once have been inhabited by megapodes. Moving farther west to Chuuk (Truk) and Yap, it is virtually certain that megapodes once inhabited these high Micronesian islands because they lie between Palau, Marianas, and Pohnpei.

The prehistoric bone record demonstrates that the puzzling modern absence of megapodes throughout Fiji, Tonga (except *M. pritchardii* on Niuafo`ou), and Samoa is not because people were moving megapodes between islands, as suggested by Lister (1911). Nor is it the result of megapodes having "overshot Efate [Vanuatu] by at least 1600 km" (Diamond & Marshall, 1977:719). Rather, this absence is an artifact of human-caused extinction. Similarly suspect are the modern absences of megapodes on individual islands within the well-defined range of an extant species. For example, there are no ecological reasons other than human impact to account for the absence of *M. cumingii* Dillwyn, 1853, on Panay (Philippines), or *M. eremita* on Vangunu, Nggatukai, and Florida (Solomon Islands).

Megapodes incubate their eggs by using some blend of solar radiation, geother-

mal activity, and/or organic decomposition (Frith, 1956; Clark, 1964; Jones, 1989). The choice of methods is dictated largely by available substrates. On Ambrym Island in Vanuatu, *M. layardi* uses all three methods (Bowen, 1996). The nesting methods within various species of megapodes vary between islands as well. *Megapodius laperouse*, for example, nests today on atolls, limestone islands, old volcanic islands, and active volcanic islands in Palau and the Mariana Islands. These different geological types of islands must require different incubation strategies. The only surviving population of *M. pritchardii* nests in burrows in volcanically warmed soil on Niuafo`ou (Weir, 1973; Todd, 1983; Göth & Vogel, 1995; 1997). On the limestone islands of `Eua and Foa, where it formerly occurred, *M. pritchardii* must have used organic decomposition and perhaps solar radiation to incubate its eggs.

Although island size is regarded as one of the most fundamental influences on faunal composition on oceanic islands, it probably had little effect on distributions of megapodes in pre-cultural times. In Tonga, for example, *M. alimentum* occurred on islands as small and low as Ha`afeva (1.8 km<sup>2</sup>, elev. 10 m) and at least as large and high as `Eua (87 km<sup>2</sup>, elev. 325 m). An even greater range of island sizes is inhabited by some individual species of megapodes today, with the most extreme being among the many islands occupied by *M. eremita* in the Bismarcks and Solomons, *M. decollatus* Oustalet, 1878, in northern New Guinea and offshore islands, and *M. reinwardt* Dumont, 1823, on southern New Guinea, northern Australia, Lesser Sundas, and intervening islands (see range maps in Jones et al., 1995).

“Species packing” is another issue enlightened by the prehistoric record of megapodes. The large, high island of Misol (also called Misool) off western Irian Jaya is famous in megapode lore for sustaining three, perhaps four sympatric species, more than anywhere else (Ripley, 1960; 1964). These species are *M. freycinet freycinet*, *Eulipoa wallacei* (G.R. Gray, 1860) (breeding on Misol not yet proven for *E. wallacei*; R.W.R.J. Dekker, pers. comm.), *Aepyodius arfakianus misoliensis* Ripley, 1957, and *Talegalla cuvieri cuvieri* Lesson, 1828, the first two being relatively small and the last two large. Even in the rich, diverse forests of the Lesser Sundas, Moluccas, or mainland New Guinea, it is rare that as many as three species of megapodes occur sympatrically and when so, none is congeneric. Furthermore, in the most widespread genus (*Megapodius*) there is no evidence of congeneric species existing sympatrically today without interbreeding (Mayr, 1938).

The prehistoric record now demonstrates that, before human arrival and unlike today, multiple species of megapodes occurred on individual oceanic islands at least as far east as the small, remote islands of Tonga. The Tongan island of Foa (13.3 km<sup>2</sup>, elev. 20 m), for example, sustained three species of *Megapodius* until they were decimated by humans (table 1). The larger island of `Eua (87 km<sup>2</sup>, 325 m elev.) also was inhabited by three species of *Megapodius*, two of them the same as on Foa. As the prehistoric bone record becomes more complete, the past occurrence of multiple sympatric species of *Megapodius* likely will be shown to have been the rule rather than the exception throughout Melanesia and Western Polynesia.

Defining “assembly rules” (*sensu* Diamond, 1975) to explain such high levels of sympatry, especially congeneric sympatry, cannot be done by evaluating modern distributions, which are merely the residues left behind by millennia of human impact. How did three species of *Megapodius* co-exist until 2800 years ago on a small, flat

island like Foa? The three species differed from each other in overall size and therefore most likely in bill size (the bill of *M. molistructor* is not known), leading to a presumption of somewhat different food habits. I would speculate, however, that the food consumed by *M. pritchardii*, *M. alimentum*, and *M. molistructor* overlapped considerably. Perhaps their nesting methods were somewhat different, with one or two species preferring coastal sands and one or two others preferring interior forest soils. I question, however, whether directional natural selection away from potential competition needs to be invoked to account for this sympatry. Maybe two or three of the species laid their eggs in the same mounds, a sort of brood parasitism recorded for *Megapodius reinwardt* and *Talegalla jobiensis* A.B. Meyer, 1874, in the Southern Highlands Province of Papua New Guinea (Dwyer, 1981). How wonderfully informative it would be if we could go back in time to observe the bird communities on remote Pacific islands before they were torn apart by people.

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