

# The rat and the octopus: initial human colonization and the prehistoric introduction of domestic animals to Remote Oceania

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Received: 5 August 2007 / Accepted: 24 September 2008 / Published online: 9 December 2008  
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**Abstract** Remote Oceania was colonized initially in three migratory phases: the western archipelagos of Micronesia plus eastern Melanesia out to west Polynesia in the period 3500–2800 cal BP (all dates hereafter are cal BP), central and eastern Micronesia 2200–2000 BP and east and south Polynesia 1100–700 BP. The early and late migration phases are best-known archaeologically. During these phases a number of plants and animals were introduced. Of the latter, the pig (*Sus scrofa*), dog (*Canis familiaris*), fowl or chicken (*Gallus gallus*) and rats (*Rattus* spp., especially *R. exulans*) were most deliberately associated with human settlement. The pattern of introductions appears to be only partly in agreement with an implication of widespread early distribution derived from the orthodox colonisation model of ‘transported landscape’ coupled with sophisticated seafaring. Within the two main migrations the pattern of introductions is similar. Excepting in the movement to West Micronesia, all four taxa were transported into the islands nearest their proximate sources at, or soon after, the beginning of migration, but their introduction to more remote islands was partial and patchy. Evaluation of invasibility, invasiveness and transportability characteristics amongst

the four taxa suggest that island size and complexity, propagule pressure and seafaring capability were important factors in differential distribution and survival. Seafaring capability was especially important because it determined the extent of accessibility to islands near and far and the degree of propagule or introduction pressure that was exerted. Framing the archaeological data within a model of invasion biology offers a richer and more systematic approach to the complexities of introduction than adopting a culture-historical perspective.

**Keywords** Prehistoric colonization · Pacific islands · Faunal introduction · Invasion biology · Seafaring · Pig · Dog · Rat · Chicken

## Introduction

In a Pacific folktale, the rat refuses to share food with the land crab and when they go sailing the land crab chews a hole in the boat and walks off along the sea floor, leaving the rat to drown. But the rat prevails upon an octopus to carry him ashore on its head. As it does so, the rat chews the hair off the octopus’s head and then skips ashore, jeers at his bald benefactor, and arranges to have him killed and eaten. This widespread story acknowledges, in sly self-awareness by Pacific islanders, the consequences of human arrival in the islands of Remote Oceania. That region

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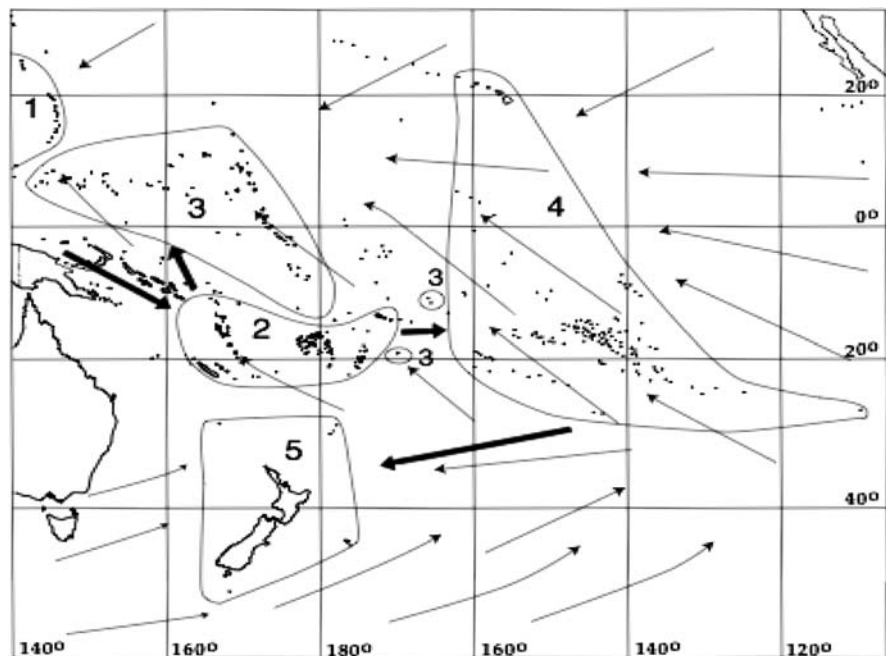
of the Pacific consists of Polynesia, Micronesia and eastern Melanesia, and human colonisation occurred across it, in several phases, between 3,500 and 700 years ago (Fig. 1).

The impact of prehistoric human colonisation in Remote Oceania has been taken up repeatedly over the last 50 years from broad historical (McNeill 1994) and other perspectives, such as ecosystemic change (Fosberg 1963; Kirch 1983; Kirch and Hunt 1997), sedimentary and vegetation change (Kirch and Ellison 1994; Anderson 1995; McGlone and Wilms-hurst 1999; Athens et al. 2002; Burney and Burney 2003), and faunal extinction (Olson and James 1992; Worthy and Holdaway 2002; Steadman 2006). Patterns of landscape change reveal an east–west difference. In the western archipelagos vegetation patterns derived from pollen frequencies disclose the initial entry of people, c. 3000 BP, but substantial deforestation in coastal areas and movement into the interior is often not apparent until 2,000 years ago; it may be tracking a late expansion of agriculture and population growth (Hope et al. 1999). In east and south Polynesia, massive landscape change generally began at the point of initial colonisation, 1,000–700 years ago, perhaps reflecting the influence of relatively more dense human populations on smaller, steeper islands east of the Andesite line, the faster

depletion of native resources and possibly increased climatic variability in the second millennium AD (Anderson 2002).

Late Holocene loss of native animals in Remote Oceania has been called ‘first contact extinction’ (Martin and Steadman 1999, p. 18), because it is strongly correlated with the first arrival of people and their biological and technological baggage. For example, in the Ha’apai islands of Tonga 34 landbirds are recorded from Lapita sites dating 2900–2700 BP. Of these at least 21 did not survive beyond the Lapita period and in the succeeding 2,500 years of prehistory, only one additional species disappeared (Steadman et al. 2002). Much the same pattern occurs on the very large islands. In New Zealand, all 14 landbird species over 12 kg body-weight, including nine moas, plus most of the smallest landbirds, went extinct within 200 years of the advent of human occupation (Tennyson and Martinson 2006). Similar data can be found for many Remote Oceanic islands and they show that the long-known, highly visible and taxonomically devastating losses in east and south Polynesia (Steadman 2006) are gradually being matched by evidence from west Polynesia, Fiji and Vanuatu where lists of first-contact extinction have recently added many new species of large land birds and reptiles (e.g. Steadman

**Fig. 1** The dispersal of initial human and animal colonisation in Remote Oceania, showing prevailing wind directions (*thin arrows*), major migrations (*broad arrows*) and areas colonized, as follows: 1 West Micronesia; 2 Lapita migration; 3 central Micronesia plus areas marginal to west Polynesia; 4 east Polynesia; 5 south Polynesia



1993; Worthy et al. 1999; Molnar et al. 2002). The faunal extinctions as a whole, therefore seem, in a sense, density-independent. They did not increase with predator-population density but were concentrated in colonisation eras when devastation depended upon the shock of novel predation and habitation destruction.

Integral to the overall synanthropic impact was the introduction of useful plants and animals, notably taro (*Colocasia esculenta*), yams (*Dioscorea* spp.), sweet potato (*Ipomoea batatas*), breadfruit (*Artocarpus altilis*) and banana (*Eumusa* spp.), and the pig (*Sus scrofa*), dog (*Canis familiaris*), Pacific rat (*Rattus exulans*) and domestic fowl (*Gallus gallus*). These were important in several respects. The introduced animals had direct impacts on native species, of which the predation of rats upon small birds is best documented (e.g. Atkinson and Towns 2005) and their impact on forest histories hypothesized (Athens et al. 2002; Hunt 2006). Many of the introduced taxa sustained agricultural productivity which, in turn, depended upon continuous deforestation and created a cascade of ecological effects including changes in forest structure and composition, changes in native animal habitats and populations, and erosion and sedimentation with consequences for freshwater and lagoonal habitats. Agriculture was closely related to population increase, especially of people, but also of agricultural commensals, notably the pig, which created additional and increasing pressure on native forest and animals and, through lowered terrestrial productivity, also upon inshore fisheries (Allen 2003; Anderson 2008).

Prehistoric introduction of plants and animals has been conceived as the ‘transported landscape’ (Anderson 1952; Kirch 1982), referring in Remote Oceania to the notion of serial replication of agriculturally oriented island landscapes (c.f. the ‘portmanteau biota’ of Crosby 1986, p. 89). In recent exegesis, the validation of the transported landscape model has been assigned primarily to linguistic reconstruction of lexical items for plant and animal domesticates, and only secondarily to archaeological evidence (Kirch and Green 2001, pp. 120–129). Two implications of the transported landscape can be derived for understanding biotic introductions. The first is that there were clusters of taxa interrelated within an economic system—root crops complemented by tree crops and

associated domestic scavengers able to convert agricultural waste into protein. The second is that the mode of transport facilitated frequent inter-island contact. That is argued to have consisted of strategic voyaging involving navigated passages in any direction by large, fast, windward-capable sailing vessels that maintained exchange and other interactive relationships (Finney 1979, 1994; Irwin 1992; Weisler 1997). Transported landscapes and strategic voyaging thus underwrote migration success through food production and created colonies perceived as similar and often connected, as in the classical metapopulation model of island or patch ecology (Lindenmayer and Fisher 2006, p. 57).

One way of evaluating the validity of this model of systematic colonisation is to consider the prehistoric distribution of introduced biota in relation to the pattern of initial colonisation; here, meaning the first colonisation of an island by people. If there is no substantial correspondence of introduced biota with early settlement then the hypothesis is falsified.

Deficiencies and uncertainties in archaeological databases eliminate most of the introduced biota from consideration in this exercise. Plants are especially problematic. In some cases it is not certain at which point they were translocated; for example the cultivated *Cordyline fruticosa* may have had a natural distribution as far east as west Polynesia (Hinkle 2007). In addition, few records of introduced food plants have resulted from numerous analyses of pollen and macrofossils, yet a very high rate of success is reported by one analyst who has identified archaeological starches and associated materials from sites across the region. Considering the potential variety of indigenous starches and other plant tissues that must exist in Remote Oceania, it is disconcerting to note that the comparative collections used in this work are stated as having been drawn exclusively from cultivated plants (Horrocks and Bedford 2005; Horrocks and Weisler 2006); the results, therefore, must be viewed with reserve. There are also few data concerning the extent to which undomesticated animals, such as landsnails (Cowie 2001), and lizards (Allison 1996), were introduced during colonisation, although many were widespread by the nineteenth century.

In fact, it is only possible to pursue this investigation, and then only in a preliminary fashion, in relation to introduced domestic animals (including

here, for convenience, the commensal *Rattus* spp.). These existed about 3,000 years ago in the Bismarck archipelago (Papua New Guinea) and were, in some manner that is the topic of this paper, introduced across Remote Oceania. I outline the pattern of initial human colonisation of Remote Oceania, and the archaeological data of introduced animal distribution in time and space, and then consider some hypotheses for understanding the process of introductions within a framework based on invasion biology.

### Initial colonisation sequence

Remote Oceania remained undiscovered until the late Holocene, despite the assumed existence nearby of populations with some offshore maritime capability. People had crossed sea-gaps more than 100 km wide in the Australia–New Guinea region since at least 40,000 BP, and were living on Buka Island, at the north of the Solomons, by 29,000 BP. Since the main Solomon Islands constituted a nearly continuous landmass during the last glacial maximum, it is reasonable to suppose that people were living on the southern tip (now Makira Island) for more than 20,000 years. The subsequent delay in movement to Remote Oceania has been explained in several ways; that the advent of agriculture was essential to support outward migration, or that mid-Holocene change in sailing technology or conditions enabled eastward movement (Kirch and Green 2001, p. 121; Irwin 1992). But it is also possible that the chronological gap was much smaller. Research on the Solomons has emphasized that the oldest sites still date to only 6,000 BP (Sheppard and Walter 2006), leaving open the possibility that people were not well-established at the southern end of the main chain much earlier than the onset of Remote Oceanic migration.

The one point that is clear is that when people first crossed into Remote Oceania they had significant ancestral connections with Southeast Asia, yet also substantial older Melanesian lines of descent (Friedlaender et al. 2007). The first colonists reached western Micronesia about 3,500 BP (Clark et al. 2006 on Palau and see references therein to Marianas), although there is enigmatic evidence possibly referring to an earlier migration (Athens et al. 2004). A second, and related cultural assemblage, called Lapita, then appeared in the northern offshore islands of

New Guinea by about 3,300 BP and spread into the western Pacific about 3,000 BP or slightly earlier (Specht and Gosden 1997).

Lapita settlement spread to the Reefs/Santa Cruz islands (Southeast Solomons), Vanuatu, New Caledonia and Fiji about 3,000–3,100 BP, according to current radiocarbon dates (Sand 2000; Nunn et al. 2004, p. 142; Bedford et al. 2006, p. 818). In Tonga and Samoa, at the eastern end of the Lapita range, the oldest dates are about 2,950 BP (Burley and Dickinsson 2001) and 2,800 BP (Petchey 2001), respectively. The matter of whether some plainware sites might be slightly older (Clark and Michlovich 1996; Galipaud 2006) remains unresolved, but it is unlikely to affect the chronology significantly.

Settlement began across eastern Micronesia and in various islands on the margins of west Polynesia, e.g. Rotuma, Tokelau, Pukapuka, Niue and 'Ata, at 2,200–2,000 BP (Walter and Anderson 2002; Intoh 1997), and initial colonisation of tropical east Polynesia was, until recently, thought to have begun about the same time, according to some archaeological and sedimentary radiocarbon dates (e.g. Flenley and King 1984; Kirch 1986; Kirch et al. 1991). It was also claimed that *Rattus exulans* was introduced to New Zealand 2,000 years ago (Holdaway 1996). Subsequently, re-dating of key archaeological sites across east Polynesia which had provided early radiocarbon dates showed, without exception, that the sites were significantly younger, indeed none older than about 1,000 BP (Rolett and Conte 1995; Anderson and Sinoto 2002). Recent sedimentary coring has fallen similarly into line with an estimate of 1,100–900 BP as the period of east Polynesian colonisation (e.g. Athens et al. 2002; Burney and Burney 2003; Kennett et al. 2006) and the early dates for rat introduction have been discredited (Anderson 2000a; Wilmshurst and Higham 2004). Colonisation of south Polynesia, and of other islands below the Tropic of Capricorn such as Rapa, Pitcairn and Easter, occurred around 700 years ago, several 100 years after colonisation of tropical east Polynesia (Anderson 1991, 2000b, 2003, 2005; Kennett et al. 2006; Hunt and Lipo 2006).

In summary, there were two main phases of migration in Remote Oceania, one early (3,500–2,800 BP) and western, and another late (1,100–700 BP) and eastern. Between them occurred another phase of migration around 2,000 BP which is less well-known but of some importance (below).

## Translocation of animals and plants

During these various migrations, animals and plants were moved on watercraft between islands, accidentally or deliberately. They are sometimes called “ethnotramps” and the process “translocation” or “ethnophoresy” (Heinsohn 2003). Deliberate movement of animals between Pacific islands has a long antiquity. Leaving aside the movement of the most pervasive and influential species, *Homo sapiens*, across Wallacea into the western Pacific about 45,000 years ago, the earliest reported example is the movement of the cuscus possum *Phalanger orientalis* from New Britain to New Ireland about 20,000 years ago. The chronology is robust (Leavesley and Allen 1998) but as people had been crossing to New Ireland since 38,000 BP and possum introduction coincides broadly with the period of lowest sea level, the possibility of an accidental event should not be discounted (Heinsohn 2003). Evidence of animal translocation in the western Pacific begins otherwise in the terminal Pleistocene, ca. 13,000 BP. This movement of *Phalanger* spp. and species of wallaby and bandicoot (Flannery and White 1991; Heinsohn 2003; White 2004; Anderson 2004), began at a time when movement and manipulation of plants and animals in various ways was becoming noticeable elsewhere in the Old World as well.

For Remote Oceania, the advent age of introduced plants and animals has been argued largely from historical observation, historical linguistics and archaeology. The first is broadly useful for establishing the immediately pre-European distribution of introduced taxa (e.g. Baldwin 1990), but there are frequent contradictions and uncertainties in the reports. Linguistic reconstruction is too imprecise for most purposes because it depends upon establishing sequences of language changes that can be matched to migration episodes. Unfortunately, many introduced taxa retained the same or very similar names over long periods that encompassed multiple migrations. For instance, the modern names, taro, the coconut or niu, and kava, are reconstructed for pre-Lapita languages (proto-Oceanic) as almost the same: \*talo, \*niuR and \*kava, and much the same is true of \*puaka (pig), \*kulii (dog) and \*moa (chicken), according to Kirch and Green (2001, p. 123, 129).

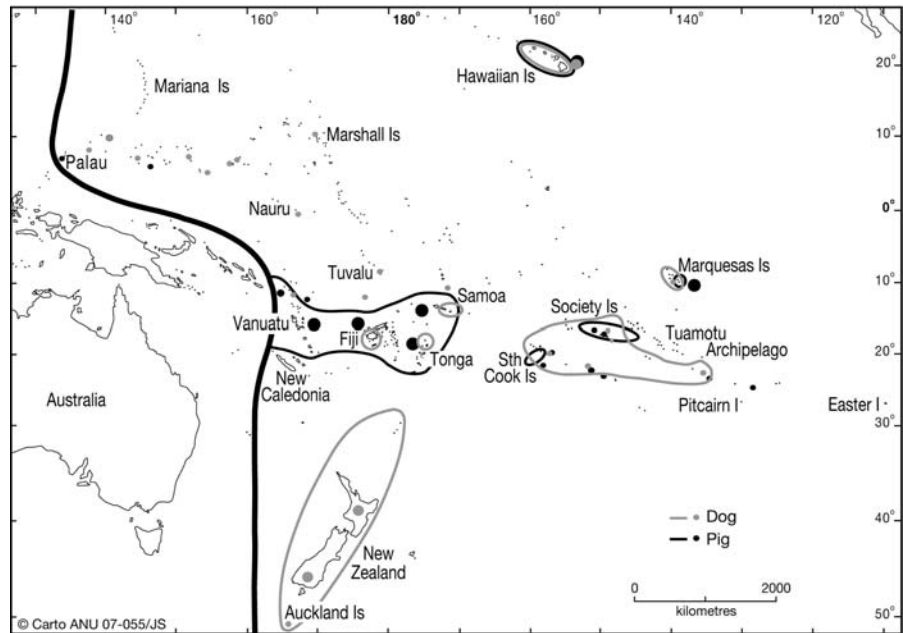
Apparent stratigraphic superimposition and association with items of known archaeological age span

are also problematical as temporal indices because many tropical sites have been severely disturbed by storm surges, bioturbation, or redistribution by building, burying and gardening on the same localities. So, for example, the scarce occurrence of pig and chicken bone through the stratigraphy of many Remote Oceanic sites that, on radiocarbon ages and by ceramic assemblage, extend to the Lapita period, is not in itself a reliable indication that these taxa were introduced with the first settlers. Nevertheless, given a general scarcity of direct radiocarbon dating of introduced items—something much to be desired—and leaving aside the technical problems often associated with bone dating, the stratigraphic and associational data are all that we have to go on. As the evidence is often uncertain, I have taken a conservative view of the distributional data. For example, I have accepted data indicating pig remains in prehistoric contexts in Palau and Fais, but not in Lamotrek, Yap, and Chuuk where the pig bone provenances are probably post-European (Intoh 1986). Figures 2 and 3 show the archaeologically recorded distribution of the domestic species in Remote Oceania by outline with larger dots for major clusters of evidence (details below). Rat distribution by species is still not widely disentangled archaeologically, although *Rattus exulans* seems to have been the only species in Polynesia. It was very widespread historically (Ponsonnet 1995; Sherley 2000) and, considering the vulnerability of *R. exulans* to competition from the larger species introduced historically, its historical distribution, as shown in Fig. 3, is probably a reasonable reflection of prehistoric distribution. Archaeological instances of *Rattus praetor* and *R. rattus* or *tanezumi*, plus islands colonized prehistorically but lacking evidence of rats are also shown (Fig. 3).

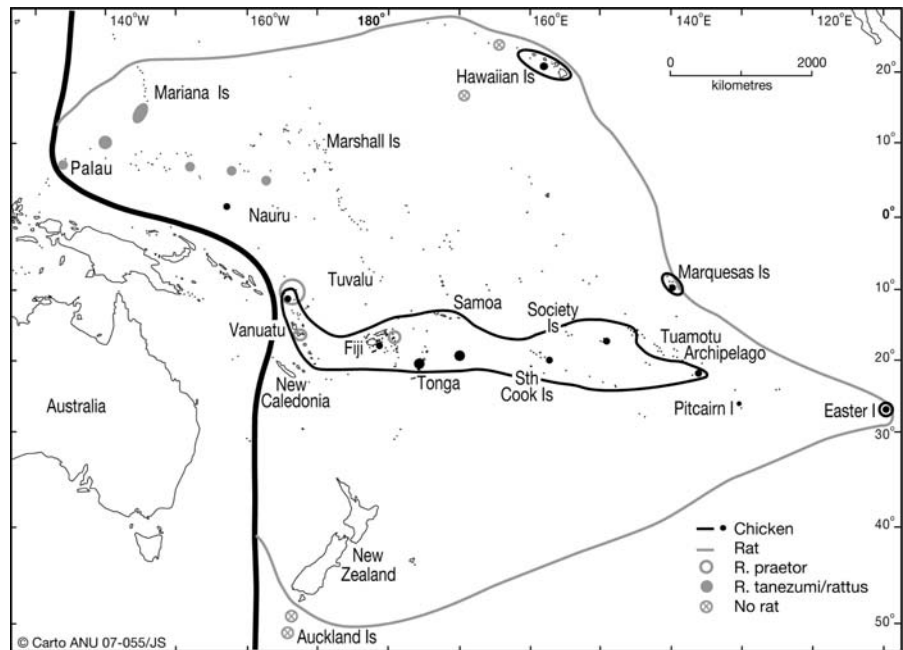
### Pig (*Sus scrofa*)

The pig occurs in the Bismarcks by 3200 BP (although only in small quantities at Mussau, Kirch 1987) and it was widely dispersed in the Pacific at European contact (Lynch 1991), but whether it was available in the early Holocene has been the subject of a long and unresolved debate (Blust 2002; Hide 2003). Evidence from mitochondrial DNA suggests that *Sus scrofa* originated in mainland Southeast Asia and that all Melanesian and Polynesian pigs form a

**Fig. 2** Archaeological distribution of *pig* and *dog* remains in Remote Oceania (western border shown as heavy line)



**Fig. 3** Archaeological distribution of *rat* and *chicken* remains in Remote Oceania



monophyletic clade which dispersed into Remote Oceania with Lapita migration. In western Micronesia, however, the original pigs were probably from east Asian sources, dispersed through Taiwan and the Philippines (Larson et al. 2007; Lum et al. 2006).

In Santa Cruz, a few pig bones were found in Lapita sites, but as there were also modern rat bones the stratigraphic security is uncertain (Green 1976).

Pig is reported from Lapita contexts in Tikopia (Kirch and Yen 1982). In Vanuatu, pig was recorded from upper levels of Lapita sites on Malo Island, but no pig or dog bone is reported from the earliest levels (3000–2800 BP) of the Arapus site (Bedford and Spriggs 2000), in which there was a suite of extinct fauna. At the sites of Ifo, Ponamla (Erromango) and Malua Bay (Malakula) small quantities of pig bone

were found in levels radiocarbon dated to between 2900 and 2500 BP (Bedford 2006). Bedford (pers. comm. 29.5.2007) has found pig in secure stratigraphic association with early (c. 2800–2900 BP) settlement at Vao Island (Malakula), indicating that whether or not pig arrived with the first colonists, it was at least within the early migration stream.

There was no pig prehistorically in New Caledonia (Sand 2000). In Fiji, pig bone from the Lapita site at Yanuca (Hunt 1981), has been re-identified as turtle (Clark and Anderson 2000). Pig (and dog and chicken) bone occurs in a site with Lapita ceramics at Naitabale, but the stratigraphy was recorded only diagrammatically and the radiocarbon dates cluster in the period 2800–2300 BP (Nunn et al. 2007). As many of the dates are reversed for depth, considerable disturbance is indicated. In other recently investigated Lapita sites like Votua in Lau and Natunuku on Viti Levu no early pig bone has been found, while on Lakeba in the Lau Group, Best (1984) shows pig appearing at about 1000 BP. In Tonga, pig bone was reported in early eastern Lapita contexts at Lolokoka site on Niautoputau (Kirch 1978), and pig (and dog and chicken) bone occurs in the upper levels of the Tongoleleka site on Lifuka Island which date to 2750–2850 BP, but the associated ceramics are post-Lapita (Polynesian plainware) in type (Steadman et al. 2002). It is difficult to be sure about the chronology, but it is possible that Polynesian plainware began in the period 2800–2500 BP, which overlaps at the earlier end with late Lapita (Burley et al. 1995). A recent analysis of stratigraphic and radiocarbon dating associations of pig bone in Tonga and Samoa (Smith 1999, p. 270–288) concluded, however, that the age of introduction was probably after 2500 BP.

Prehistoric pig remains in Micronesia are late. In Palau they occur after about 1250 BP and on Fais 1500–1700 BP (Intoh 1997; Intoh and Shigehara 2004; Masse et al. 2006). In east Polynesia, pigs were present widely during the colonisation era, but only on tropical islands; they were absent from south Polynesia.

#### Dog (*Canis familiaris*)

No dog bone has been recovered archaeologically in early sites of Santa Cruz or Vanuatu (Bedford 2006, p. 262) or in New Caledonia at all (Sand 2000, p. 30),

and it seems to be late, after 2000 BP, in New Guinea sites. In Fiji, no dog bone occurred at Votua or Natunuku, and possible dog bone at Yanuca in Lapita levels (Hunt 1981), should be re-analysed. Dog bone at Naitabale is subject to the same chronological uncertainty as the pig remains (above). At Naigani a piece of apparent dog bone in early Lapita context, unidentified to element, was recorded from the lower levels of the site (Kay 1984), but subsequent excavation and analysis indicates that there was no dog bone in Lapita layers at Naigani (Best pers. comm. 26.6.02). The earliest dog bone in stratigraphic sequence seems to be from Lakeba at about 1000 BP (Best 1984). Dog bone is very scarce and may be quite recent (Smith 1999).

In Tonga, dog bone occurred in the upper levels at Tongoleleka, where the age is uncertain (above). Burley (1998, p. 355; Burley et al. 2001), emphasizes the importance of wild maritime and terrestrial foods during the Lapita era and does not report dog or pig as present during the initial colonization phase in Tonga. In eastern Micronesia, dog remains are reported quite frequently from archaeological sites. They occur in deposits dated 650 BP on Ngulu Atoll, and 1500–1700 BP on Fais and in other early sites on Pohnpei, Chuuk, Kosrae, and after 1800 BP at Utrok Atoll in the Marshalls. They date to 1600 BP in Kiribati and 1300 BP on Nukuoro. In Pukapuka, dog dates to about 2300 BP on radiocarbon dates that remain enigmatic and are possibly too old (Chikamori and Yoshida 1988). In east Polynesia, dogs are widely spread, and constitute the only domesticated in south Polynesia. Genetic data show that Pacific dogs stem from several lineages that probably represent multiple introductions (Matisoo-Smith 2007).

#### Rats (*Rattus* spp.)

Recent genetic data for *Rattus exulans* suggest at least two introductions to Remote Oceania; one with Lapita migration and the other through Micronesia, about 1000 BP (Matisoo-Smith 2007). *Rattus exulans* bone occurs throughout the Lapita range and beyond (Bedford 2006, p. 227). It was once thought that *Rattus exulans* occurred everywhere that there had been prehistoric human settlement in Remote Oceania, but while that remains largely true, there are exceptions appearing (Fig. 3) in some of the more remote islands (e.g. Anderson 2005 on Auckland

islands and Snares). Further, while *Rattus exulans* certainly accompanied Lapita migrations, either or both as a stowaway or because it was a useful emergency food, there is a growing list of cases where it seems to arrive later. In a 3,000 year long sequence from Palau, no bone of *Rattus exulans* is apparent (Clark 2005), but it occurs about 1000 BP in an 1,800 year long sequence at Utrok Atoll, in the Marshall Islands (Weisler 2001). *Rattus exulans* also arrived quite late in the Marianas, about 1,200–1,000 years ago (Steadman 1999) and, near the other end of Remote Oceania, it first appears about 200 years after initial occupation around 900 BP in Mangareva (Conte and Kirch 2004, p. 104). Consequently, while the general patterns of Remote Oceanic colonisation established by archaeology are largely shadowed by the distribution of genetic variation in modern *Rattus exulans* populations (Matisoo-Smith et al. 1998), it does not follow that rats arrived invariably at particular destinations in the earliest migrations.

A second species, *Rattus praetor*, occurs in eastern Melanesia, earliest in Lapita deposits dated to about 3000 BP on Santa Cruz. It appeared at about 2300 BP on Tikopia, and from about 2600 BP on Malekula (Vanuatu). On Fiji it was found in Lapita sites dated to about 2700 BP on Mago Island and in post-Lapita levels at 2200 BP on Lakeba (White et al. 2000). A third species, *Rattus tanezumi*, has an exclusively north Pacific distribution in Micronesia. Probable *Rattus tanezumi* appears at about 1000 BP in Palau (Clark 2005; Masse et al. 2006). As it is difficult to distinguish osteologically from *Rattus rattus*, some uncertainty exists about whether identifications of the latter at 1700 BP on Fais in Micronesia, or on Nukuoro, might actually be *R. tanezumi*, or indeed whether all of these finds need closer consideration.

#### Domestic fowl (*Gallus gallus*)

The domestic fowl or chicken occurs throughout Lapita levels in Vanuatu (Bedford 2003, p. 154, 2006), where it is, for example, the only domesticate recorded in the early Lapita levels at Arapus. It is absent from New Caledonia. In Fiji, chicken bone occurs in Lapita levels at Lakeba, but it is very scarce. In Samoa, there is an AMS (Accelerator Mass Spectrometry) radiocarbon date on chicken bone of 1400 BP and in Tonga, where chicken is common in

Lapita sites, mean calibrated ages on chicken bones at the Tongoleleka site in the Ha'apai group indicate on that it arrived about 2750 BP, some 50–100 years after the loss of *Megapodius alimentum* and an undescribed iguana (*Brachylophus* sp.), probably from earlier human intervention (Steadman et al. 2002). In Niue, chicken was the only domesticate and extraordinarily abundant. It dates back to the origins of colonisation about 2000 BP (Walter and Anderson 2002).

In Micronesia, chicken occurs on Guam where it is dated to about 2000 BP (Storey et al. 2008). Other instances, in the Polynesian outliers, are uncertainly prehistoric. In east Polynesia the distribution of the chicken is more or less that of the pig, with the notable exception of Easter Island where it was the only domesticate and correspondingly abundant. There is no evidence to show that the chicken reached South Polynesia.

#### Patterns of introduction

The data of faunal introductions disclose some interesting patterns. First, evidence referring to the two earliest human migrations into Remote Oceania is scarce. The West Micronesian migration, probably 3500 BP, appears to have brought no domestic animals, and possibly no rats. When those did arrive, the pig was probably from an east Asian source, and *Rattus tanezumi*, which did not disperse beyond Micronesia, may have had a similar origin. *Rattus exulans*, dog, chicken, and pig, seem to have arrived around or after 2000 BP. The distribution of these species was patchy and indicative of relatively few attempts at translocation, judging, in particular, how readily most of them were taken up upon being introduced later by Europeans.

Second, although the Lapita migration is regarded as having translocated an integrated complex of domestic animals and commensals, support for that proposition is scarce. There is no compelling evidence that the pig reached Remote Oceania beyond Vanuatu at the beginning of the Lapita era, and the dog does not seem to have arrived in the Lapita expansion at all, at least not in viable populations. Other than occasional dog-teeth, possibly transported as part of garments or ornaments, dog bone is essentially absent from Lapita sites in Remote



Oceania, and the current data suggest that it may have been introduced, perhaps in populations of slightly different genetic character, after about 2000 BP (Matisoo-Smith 2007). Consequently, it seems that only rats and chickens can be demonstrated to have dispersed in the earliest migrations beyond Vanuatu, and chicken possibly slightly later than rat, with pig arriving at an indeterminate point in the Lapita period, judging by chronology/ceramic uncertainties in Tonga and Fiji (above), and dog populations possibly no earlier than 2000 BP.

Third, the distribution of domestic animals in east and south Polynesia is varied. In the high tropical islands of central east Polynesia and Hawaii, they are all documented in early sites, but the distribution is partial on remote low islands, such as Christmas Island, where only the rat is documented archaeologically (Anderson et al. 2002). In the cooler subtropics and temperate regions only one or two are found; pig and rat on Henderson, chicken and rat in Easter Island, dog and rat in Rapa Island, the Kermadecs and New Zealand, rat alone in the Chatham and Norfolk Islands and dog alone in the Subantarctic islands. It is interesting to note that only rats and chickens reached the most remote islands in both west and east Polynesia, Niue and Easter Island, respectively. Chicken of Polynesian origin has also been dated to about 600 BP in south-central Chile (Storey et al. 2007) and research has begun on rodent bone from the same and similar sites to check for the presence of *Rattus exulans*.

Fourth, amongst the introduced animals, body size covaries inversely with dispersal. This probably reflects some aspects of relative difficulty in long-distance transport (below). Even so, the anomalous situation of New Caledonia, where no pigs, dogs or chickens seem to have been translocated prehistorically, despite proximity to Vanuatu, indicates that some other factors, possibly including societal or ritual prohibition, also operated influentially.

Fifth, domestic animals introduced in prehistory to Remote Oceania quite often failed to survive into the European era, especially in remote islands where re-supply would seem to have been problematical which, by the same logic, might suggest that failure was quite common everywhere but masked by re-introduction in areas of relatively high island propinquity. In Micronesia, dogs, introduced 1300 BP to Nukuoro had disappeared by 500 BP; and those

introduced to Makin island in Kiribati at 1600 BP were gone by European contact, seemingly also on Chuuk (Rainbird 1994). Pig had disappeared from Yap and Palau by European contact (Intoh 1986). Pigs disappeared in prehistory from Mangaia and Tikopia (Kirch 2000), dogs from the Marquesas and Pukapuka, and dogs, pigs and chickens from Mangareva. The pig disappeared with people from Henderson and Pitcairn and the dog similarly from the Kermadec and Auckland islands (Anderson 2006).

Interesting as these patterns are, it would be as well to note that sample sizes of faunal data are often very small and dubiously representative, especially on islands where only one or two sites of colonization may have been investigated, as on Mangareva and the Auckland Islands. Substantial future research is almost certain to revise the current patterns of distribution throughout Remote Oceania. Whether this will have the effect of filling in the gaps to produce a more even distribution in time and space or, as at present, add new records but delete older records and thereby maintain an overall patchy distribution, remains to be seen.

### Introduction biology and seafaring

In evaluating the evidence of animal introductions to Remote Oceania, invasion or introduction biology provides a useful framework. ‘Invasion’ is a general term for movement of a species to an area where it is biologically foreign (Heger and Trepl 2003, p. 314), and it usually connotes a negative impact on resident biota (Alpert 2006, p. 1523), while ‘introduction’ denotes human agency and intentionality in the movement. The basic components of advantage or disadvantage in introduction are ‘invasiveness’ which is the ability of an invader or introduced species to reach and thrive in a new destination, and ‘invasibility’ which is the receptivity of a new destination to invasion (Colautti et al. 2006). Because long-range, sea-borne, introductions involve not just human assistance in a general sense, but also a critical component of seafaring technology, I have added ‘transportability’ which is the facility with which a species can be moved by people. These are considered in reference to the relative advantages possessed by the four introduced species discussed here. My

initial evaluation of these (Table 1), is simply whether one species was probably advantaged (+), or disadvantaged (−) relative to the others, or no difference is assumed (o). Most of the propositions against which the taxa are evaluated are from (Alpert 2006, p. 1524; Table 1), and at this stage there is insufficient evidence to discriminate amongst taxa in relation to many of them. The model used here is similar to that, for evaluating extinction, devised by Steadman and Martin (2003).

### Invasibility

There has been no systematic study of the relative invasibility of islands in Remote Oceania, but some general components determining the critical factor of relative resource abundance (Barlow and Kean 2004) can be suggested. Climatic variation, especially in precipitation regimes, strongly affected the invasibility of islands. Dry islands, which were also generally low coral islands, were less invisable, *ceteris paribus*, than humid, and generally high, islands and the scarcity of freshwater and other resources was often aggravated on low islands by forest comprised of only a few taxa, notably the guanophyte, *Pisonia grandis* (Fosberg 1991). Archipelagos, with the possibility of re-introduction amongst islands, were potentially more resilient than isolated islands. A full forest cover on high islands was differentially attractive, as rats and chickens had abundant access to forest seeds, fruit, invertebrates and bird eggs and chicks, but pigs were better suited to either sedimentary instability, as on the steep east Polynesian volcanic islands, or to later-established mosaic vegetation and agricultural resources. An exception might have been upon islands with abundant tree ferns bearing edible pith.

West to east in the Remote Oceanic tropics there is a substantial decline in biotic diversity, partly because of island size and lithological simplification which restricted the habitat array, and also because of increasing distance from continental centres of speciation, (Keast 1996). For introduced animals, the choice of potential resources by diversity and biomass decreased west to east. New Zealand exhibited high biotic diversity based on size, Gondwanan origins and wind dispersal from Australia, but it was reached late and its potential resources were unlike those with which the introduced taxa were familiar.

**Table 1** Comparative introduction advantage amongst taxa with respect to factors of introduction: +, relative advantage; o, no relative advantage; −, relative disadvantage

	Pig	Dog	Rat	Fowl
<i>Invasibility</i>				
Climatic catastrophe	−	−	+	o
Closed forest	−	−	+	+
Biotic diversity	o	o	o	o
Land area	−	o	+	o
<i>Invasiveness</i>				
Global competition	o	o	o	o
Unlike invader	o	o	o	−
Introduction pressure	o	o	+	o
Intentional filter	o	o	o	o
Unintentional filter	o	o	+	o
Enemy escape	o	o	o	−
Novel weapons	o	o	o	+
Missed mutualisms	o	o	o	o
Biotic resistance	o	o	o	−
Local adaptations	o	o	o	o
Population growth rate	o	o	+	o
<i>Transportability</i>				
Availability	o	−	o	o
Intended transport	o	o	o	o
Unintended transport	o	o	+	o
Free-water need	−	−	+	o
Food volume need	−	−	+	+
Weather resistance	o	+	+	o
Economic value	+	o	−	o
Companionship	o	+	o	o
Symbolic significance	o	+	o	+
Totals +/o/−	1/19/5	3/17/5	9/15/1	3/19/3

This was no disadvantage for the rat, and probably the dog, but competition from numerous cursorial birds, notably rails, was potentially disadvantageous to the chicken, while the general scarcity of native or introduced tubers and of large or oil-rich fruits and berries in the closed forest was potentially an initial disadvantage for the pig.

Island size was important. The size of tropical islands in Remote Oceania declines broadly west to east (e.g. New Caledonia 18,750 km<sup>2</sup>, Samoa 3,039 km<sup>2</sup>, Tahiti 1,045 km<sup>2</sup>, Rapa 22 km<sup>2</sup>, with the exception of Hawaii (29,311 km<sup>2</sup>), and whereas islands of almost any size could support viable rat populations, larger-bodied domesticates were

constrained by habitat. *Rattus exulans* in New Zealand has range sizes of about 66–1,000 m<sup>2</sup> (Atkinson and Towns 2005), whereas feral pigs have range sizes of 1.5 to over 40 km<sup>2</sup>, a minimum of 1,500 times as large. Pigs were unable to survive more than a few decades on islands of up to 100 km<sup>2</sup> in New Zealand (McIlroy 2005), inhabited or not, although they survived for about 130 years on subtropical Raoul Island (29 km<sup>2</sup>). Giovas (2006) showed that across the tropical Pacific pig survival co-varied with island area and was unsustainable below about 11 km<sup>2</sup>. Another proposition, which invokes island size by proxy, is that in trophic competition for plant food between people and pigs, it was pigs that had to go (Kirch 2000). I would enter the caveat, however, that as pigs converted unwanted garden rubbish, household scraps, carrion, and soil invertebrates to lipids in environments where nutritional fat for people was scarce and highly sought-after, this relationship was probably more complicated than it seems.

### Invasiveness

Alpert (2006) divides hypotheses about introduction into three groups. Arrival of a large number of species ('global competition') or of species dissimilar to natives ('unlike invader') is largely unaffected by any advantage or disadvantage of invasiveness because sheer numbers, diversity or difference are likely to bypass or overwhelm native species. Introduction of all four species at once probably represented global competition in Remote Oceania, emphasized by three being terrestrial mammals that were otherwise absent.

Mechanisms of advantage include: large colonising propagule or repeated transport ('introduction pressure') which differentially favoured the rat (below); selection for characteristics advantageous to colonisation such as fast breeding and growth, ('intentional filter'), which was probably true for the domesticates, and unintentional screening which coincidentally favoured a characteristic in an unforeseen destination ('unintentional filter'). For example, resistance to cold may have favoured the dog and rat, and resistance to drought, the rat which can survive many weeks without free water. In escape from predators, pathogens, competitors etc. ('enemy escape'), which were not found in the new

destination, the chicken was at a disadvantage because of native cursorial birds; but in introduction with a new species of a disadvantage to resident taxa, e.g. of a disease to which the latter had less resistance ('novel weapons'), the chicken was probably at a differential advantage in regard to introduction of bird diseases.

Propositions of disadvantage to invasiveness include susceptibility to extremes of environmental change ('reckless invader'), 'missed mutualisms' and other aspects of an initial inability to match 'local adaptation', and resistance to invasion by native biota ('biotic resistance'). In these, probably the pig and dog were at some disadvantage through the impact of catastrophic events such as hurricanes and tsunami which could devastate forest and agriculture on small islands (Table 1).

In a quantitative review of invasibility and invasiveness characteristics, Colautti et al. (2006) found that in the former case, human activity, disturbance and resource availability or quality were statistically significant and, in the latter case, reproductive output and an absence of habitat or niche separation between introduced and native species. Reproductive success in island destinations was a critical variable leading to differential survival amongst the four species. It is probable that rats were particularly advantaged by propagule size and behavioural flexibility. The current evidence of extinctions amongst small vertebrates, and hypotheses of rodentigenic change in forest patterns, plus emerging evidence of massive invertebrate extinctions (Porch pers. comm. 28.5.2007) in Remote Oceania, suggests that conjecture about a 'grey tide' of rats sweeping through hitherto pristine island environments (e.g. Anderson and McGlone 1991) may not be too far from the mark. Only in New Zealand do dogs seem to have attained large early population sizes, and only in Niue the chicken. Judging by archaeological data, pig populations reached substantial size during the colonisation phase only in Vanuatu (Bedford pers. comm. 29.5.2007). In these and similar cases it can be assumed that cultural encouragement of breeding, including supplementary feeding, was an important factor in post-migration success.

One characteristic of invasion biology stands out above others. It is the 'propagule pressure effect' (c.f. introduction pressure) that is exerted by either, or both, the number of individuals introduced or the

number of introduction attempts. Colautti et al. (2006) propose that because it is consistently associated with invasion success and is a simple, probabilistic measure, propagule pressure could stand as a null hypothesis. That is, it would be necessary to exclude it before invoking alternative propositions to account for relative invasion success. The null hypothesis in the current context is that if there was similar propagule pressure for each species then they should have been distributed sufficiently equally in space and time to produce archaeological remains of each species in the early prehistory of most islands.

In fact, it is noticeable that, in both the main migration phases, all the available taxa were introduced at or near the beginning of the phase, in other words closer to their proximate sources, but arrived later or less completely near the end of the phase (three species to Vanuatu by 2900 BP, but only two initially to Fiji–west Polynesia, and none to New Caledonia; four species to early sites in central east Polynesia and Hawaii, but only one or two later to the subtropical and temperate islands). These distributions are consistent with distribution of obsidian and other lithic resources which show that in the proximate areas of each main migration there were substantial quantities of lithics imported from the probable migration source areas to the west (Sheppard and Walter 2006), i.e. Western Melanesia and west Polynesia, respectively. The implication is one of large or frequent migration into the proximate areas, but small or infrequent movement further east. As these data do not sustain the null hypothesis for the broad extent of either of the main migration phases it must be rejected.

### Transportability

The propagule pressure hypothesis is particularly germane in the Remote Oceanic context, because all long-range introduction depended upon the operation of seafaring, which critically controlled the level of propagule pressure. The role of seafaring is, however, open to several interpretations. One is that that highly capable seafaring, as in the orthodox model, created a broadly undifferentiated propagule pressure in space and time. If so, then the varied distribution of introductions is attributable to some other factor. It could have been temporal variation in the species sources. This was almost certainly the case for the

dog prior to about 2000 BP. There is an intriguing possibility that none of the other three species were available in the source area of the initial West Micronesian migrants, probably in the southern Philippines or eastern Indonesia, at 3500 BP. The rat, chicken and probably the pig were available to the early Lapita migrants at about 3000 BP, but they may not have been sufficiently established in the western archipelagos to contribute equally to the movement very soon afterward to Fiji and west Polynesia. Similarly, all four species may have been abundant in west Polynesia when migration began into east Polynesia, but were too scarce to supply continuing migration equally beyond the central area.

Alternatively, less capable seafaring (Anderson 2000c, 2001) may have been unable to create approximate equality of propagule pressure amongst the species. Differential constraints on seafaring capability are often attributed to large-scale variation in wind directions and frequencies (e.g. Di Piazza et al. 2007). Thus, recent simulation (e.g. Callaghan and Fitzpatrick 2007) shows that the West Micronesian and Lapitan migrations could have occurred by downwind drift voyages, whereas probabilities of success were lower toward the east where the southeast trades are more persistent. Later migration into east Polynesia on downwind passages may have depended upon long term trends in ENSO frequency and strength which, similarly, were more effective in central east Polynesia than toward the eastern margins or south of the tropics (Anderson et al. 2006). In other words, in each of the main migrations, it was much easier to reach, and move about amongst, the nearer than the more remote islands. In that case, colonising success at destinations might have reflected variation in the size or transportation frequency of propagules. For example, rats, embarked intentionally and unintentionally, were nutritionally adaptable and fast-breeding on passage, so colonising populations were probably often in the tens of individuals or larger, whereas pigs being large, nutritionally demanding and relatively slow breeding, may seldom have been landed as more than a few individuals.

There is an additional consideration of transportability which is whether some animals were embarked and nurtured preferentially because they were of symbolic significance or valued as companions. The extent to which dogs, especially, were

treated as pets ethnographically is hardly surprising and both they and chickens appear frequently in Polynesian rock art and other decorative or symbolic contexts, whereas pigs and rats are almost absent.

## Conclusions

The overall history of translocation amongst the four domestic animal taxa that reached Remote Oceania prehistorically conforms only in part to the expectations of the orthodox colonisation model. There are so few data concerning the migration phase around 2000 BP that its internal characteristics cannot be described, except to note that it may have been the mechanism by which the dog was introduced to Remote Oceania, although whether through a Micronesian or a Melanesian route is yet unclear. Potentially, it was a movement of more consequence than it seems currently, especially if some propositions about ceramic change across the central Pacific are sustained (Spriggs 2003 but see Bedford and Clark 2001).

Within the two main phases of initial migration, c. 3500–2800 BP and c. 1000–700 BP, the expected pattern of animal introduction in the orthodox colonisation model can be observed at the early, proximate, stage. In the later, distal, stage, of each migration phase the evidence suggests patchy, partial distributions of domestic animals. Consideration of the invasibility, invasiveness and transportability characteristics of the four domestic taxa suggests several hypotheses that might account for this apparent time/distance decay of that faunal suite.

One is that there is a general pattern of declining resource diversity and biomass related to island size and isolation eastward across the tropical Pacific, which favoured rats, especially and was more challenging for pigs, even if the precise reasons are still unclear. Similarly, the domestic taxa of larger body-size were at a relative disadvantage in terms of selective filters and adaptive mechanisms that favoured invasiveness. Of these, the propagule pressure effect is the most important, and in the current context it operated crucially through the cultural phenomenon of seafaring. It may have done so in several ways. If seafaring was as capable as is assumed in the orthodox colonisation model, then the patchy distribution of domestic animals could reflect

the availability of populations at source for migrant voyaging. If seafaring was less capable, then the patchy distribution could reflect the differential probability amongst domestic taxa of landing a successful colonising propagule upon those destinations that were much more difficult to reach.

These conclusions represent no more than a sketch of issues involved in evaluating the archaeology of introductions to Remote Oceania. Databases are still very limited, even for domestic animals, and given the functional inter-relationships between those taxa and others that were introduced, notably food plants and commensal weeds and invertebrates, any conclusions about domestic animal introduction must be qualified accordingly. Nevertheless, this preliminary evaluation of current evidence, and of propositions that might account for it, suggests that invasion biology offers a more comprehensive and searching methodology than that of earlier archaeological approaches within which to frame questions and develop hypotheses about the introduction history of exotic fauna in Pacific islands. It carries the additional advantages of bringing the archaeological evidence into the larger arena of modern introduction biology and, conversely, of emphasizing the importance of changing cultural patterns of seafaring in the development of island-invasion trajectories.

**Acknowledgments** I thank Terry Hunt and Don Drake for inviting me to the conference in Honolulu, and Stuart Bedford, Simon Best, Geoffrey Clark, Lisa Matisoo-Smith, Nick Porch, Matiu Prebble and Alice Storey for scholarly assistance.

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