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Marsupials as introduced species: Long-term anthropogenic expansion of the marsupial frontier and its implications for zoogeographic interpretation

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Introduction: Those ‘dull and inferior ... Marsupials’

Traditionally, Southern mammals such as the marsupials and monotremes of Australasia have been viewed as further down the evolutionary tree and thus inferior to the placental mammals of Afro-Eurasia and the Americas. This Eurocentrism or Northern-Hemisphere-centrism is typified in the writings of turn-of-the-century British naturalist McCabe (1910), who wrote a paper entitled ‘Australia – A Museum of Living Antiquities’ in which he characterised the continent as a last bastion for inferior species:

‘...circumstances point to an invasion of Australia by the land-bridge from Asia ... Under the stress of the new carnivores of the northern world the dull inferior Monotremes and Marsupials escaped over the land-bridge to the southern continent.’ (McCabe 1910:44)

Renowned late 19th century German naturalist Haeckel (1893) took Eurocentrism a step further by suggesting that the minute one crosses the Wallace Line, which marks the boundary between the Oriental faunal region of Eurasia and the Australasian (or Australian) faunal region, one is, in effect, stepping back in time to a world of primitive species:

‘Crossing the narrow but deep Lombok Strait [Wallace’s Line] we go with a single step from the Present Era to the Mesozoicum.’ (Haeckel 1893:5)

We now know that there was never a Cenozoic land bridge between the Eurasian continent and Australia, and that marsupials and monotremes reached Australasia via southern Gondwanan connections, but the McCabian and Haeckelian-type views of general Northern evolutionary ascendancy and biological chauvinism lingered on well into the second half of the 20th century (as discussed in Calaby 1984 and Heinsohn 2006a). We now also appreciate that the Australasian marsupial fauna contains a full spectrum of forms adapted to various niches, some of which proved to be quite vulnerable to foreign invasive species such as dingos, foxes, cats, rabbits and humans, and some of which proved to be quite resilient and potentially invasive themselves – for example, Australia's recent challenges in managing the ecological impacts of over-abundant eastern grey kangaroo *Macropus giganteus* populations in peri-urban parks and reserves. Indeed, kangaroos *Macropus* spp. along with many other marsupials have proved highly adapted to the Australian environment, with macropodids discovered to have one of the most energy-efficient modes of locomotion known for a terrestrial mammal (Dawson 1995; Flannery 1997; Tyndale-Biscoe 2005; Van Dyck and Strahan 2008). Similarly, another marsupial, the common brushtail possum *Trichosurus vulpecula*, is renowned for its ability to adapt to both the urban and agricultural environment and actively invades or re-invades these newly created highly anthropogenic landscapes and niches. Ironically, among the vulnerable Australasian native mammals that are now either extinct or threatened are suites of native placental murid rats derived from waif-dispersing Asian ancestors, and this parallels the status of many recently extinct or threatened marsupial species with Gondwanan origins (Flannery et al. 1990; Van Dyck and Strahan 2008). Thus in the biogeography of continents and islands, it is probably evolution in isolation more than phylogenetic history that determines the vulnerability of a species. In modern Australasia with its extensive human impacts, there are both 'losers' and 'winners' among the extant marsupials, just as there are 'losers' and 'winners' among the native placental murid rats (Flannery et al. 1990; Low 2002; Van Dyck and Strahan 2008).

As an inverse test of their adaptability, this paper aims to review the success of Australasian (Australidelphian) marsupials as introduced species on foreign landmasses. This is assessed through literature review combined with some of the author's own fieldwork data on anthropogenic biological invasions by translocated marsupials in the Indo-Australian Archipelago. A significant epistemological problem encountered in such a study is that while marsupial introductions in regional archipelagos during recent historic times for the most part appear to have been historically recorded, those that occurred in the prehistoric past were not. Thus prehistoric marsupial translocations have had to be reconstructed from a combination of palaeontological and archaeological data, combined with other lines of evidence such as molecular systematics and broader ethnozoological and biogeographic contextual analysis. Such an analysis enables the uncovering of prehistorically introduced 'camouflaged exotics' (Heinsohn 1997a) or 'cryptogenic' (Carlton 1996) populations of introduced marsupials on islands, which might otherwise go unnoticed by superficially appearing to be natural. This is referred to as uncovering the 'crypto-anthropogenic factor' of hidden long-term human influences on zoogeography (Heinsohn 1997a, 1998a, 2003, 2006a).

Some of the lines of evidence considered for distinguishing translocated from naturally occurring island vertebrate populations, but here applied to marsupials, are listed below (from Heinsohn 2006a):

1. Patchy, improbable or strangely disjunct distributions;
2. Limited distributions on a landmass, where a species appears to have only arrived comparatively recently and the biological invasion is still in progress;
3. Occurrences on islands that follow a commensal or semi-commensal pattern where species are only found in and around human settlements or other disturbed and highly anthropogenic habitats;
4. Molecular systematics evidence, such as genetic similarity over wide inter-island distributions, that may indicate recent introduction;
5. Sudden appearances of species in archaeological sequences;
6. A lack of fossil or subfossil material in palaeontological or archaeological sequences that may indicate recent introduction;
7. Ethnozoological evidence of long associations between humans and certain wild species that are known to be carried around in watercraft as pets, or for food, utilitarian, trade or ceremonial purposes;
8. Island assemblages of vertebrates that favour human-associated species over natural dispersal ability;
9. Directly documented accounts of species introduction, such as written historical records or oral historical records of translocation and/or subsequent biological invasions by a successfully introduced species;
10. Analogy from biogeographic patterns created by historically documented biological invasions by introduced species; and
11. Big-picture analysis of the global distribution of invasive species and their current invasion frontier, with back-tracing of their probable historic/prehistoric anthropogenic invasion pathway from an original natural source area, so as to distinguish their 'natural' versus introduced/anthropogenic distributions.

In light of the potential ambiguity of single strands of evidence, it is often a combination of some of these indicators that tips the scales of probability in favour of considering translocation by human agency.

Given the problem of camouflaged exotics or cryptogenic populations of marsupials in the Indo-Australian Archipelago, a phenomenon which for the most part has been recognised only recently in relation to marsupials (as reviewed by Heinsohn 2006a), a further aim of this paper is to assess the degree to which the classic zoogeographers and later observers were aware of the aforementioned crypto-anthropogenic factor in marsupial zoogeography. Did varying degrees of naivety or awareness influence their respective interpretations of island marsupial faunas and the placement of various zoogeographic lines (Figure 1)? Thus this interdisciplinary review combines biogeographic analysis with a history of zoogeographic ideas. In particular, this article is juxtaposed with an earlier paper by Gilmore (1977), 'The success of marsupials as introduced species', to show how much our collective knowledge of marsupial biogeography has progressed in the past few decades.

Figure 1. Some traditional zoogeographic boundary lines in the Indo-Australian Archipelago most of which attempt to define the demarcation between Asian and Australian faunas. Simpson's Marsupial Line (1961) is marked in bold. Simpson naively treats this boundary as the natural distributional limit of marsupials in the tropics (after Heinsohn 2006a)

Study area: The realm of the Australidelphian (Australasian) marsupial

The study area includes all of the regions of the world in which Australidelphian (Australasian) marsupials occur as natural or introduced species (not to be confused with the Ameridelphian marsupials of the Americas). For Australidelphian marsupials this includes: (1) Australia and its continental shelf islands such as Tasmania, which together have approximately 158 marsupial species; (2) New Guinea and its fringing Papuan subregion continental shelf islands, which have about 80 species; (3) the oceanic Wallacean islands of Eastern Indonesia, comprising the Lesser Sundas, Sulawesi subregion and the Moluccas, which collectively have about 12 species (seven of which are Wallacean endemics); (4) the oceanic northern Melanesian islands (the Bismarck Archipelago and Solomon Islands) of Near Oceania, which have about seven species (many, or possibly all, of which may be introduced); (5) New Zealand and its satellite islands in southern Remote Oceania, which have six recently introduced species; (6) the Hawaiian Islands in northern Remote Oceania, which have one recently introduced species on Oahu Island; and (7) the British Isles in the European Palearctic region, which has a single recently introduced species (Tomich 1986; Whitten et al. 1987; Corbet and Hill 1992; Flannery 1994; Flannery 1995a, b; Monk et al. 1997; Heinsohn 2001a, 2002a, b, c, 2003, 2004a, b, 2005a, b, c, 2006a; Ziegler 2002; Long 2003; Helgen and Flannery 2004; King 2005; Nowak 2005; Heinsohn and Hope 2006; Harris and Yalden 2008; Van Dyck and Strahan 2008).

A particular focus of this study, however, is the tropical Australasian portion of the Indo-Australian Archipelago that stretches to the east of the Oriental Region. The term 'Indo-Australian Archipelago' can be confusing in that it is generally used as a synonym for 'Malay Archipelago' (islands stretching from the Malay Peninsula to New Guinea), but some authors use it in a broader sense to also include Australia and the islands of Near Oceania (etymology reviewed in Heinsohn 2006a). Some significant recognised boundaries include the Wallace/Huxley Line, which marks the eastern edge of the Sundaic continental shelf and the eastern

limit of complex continental Oriental Region faunas (Figure 2). This is paralleled further east by Lydekker's Line, which marks the western edge of the Meganesian continental shelf and the western limit of complex continental Meganesian (also called 'Greater Australian', 'Sahul' or 'Australo-Papuan') faunas. Between the continental Sundaic region and continental Meganesia lie the oceanic Wallacean islands with depauperate and unbalanced oceanic faunas that exhibit limited Oriental influences from the west and limited Meganesian (Australo-Papuan) influences from the east. To the east of Meganesia lie the oceanic northern Melanesian islands (the Bismarck Archipelago and Solomon Islands) of Near Oceania, which also have depauperate and unbalanced oceanic faunas that exhibit salient New Guinean influences on their biotas (Heinsohn 2006a; Heinsohn and Hope 2006; Morwood and Van Oosterzee 2007). For a delineation of specific tropical Australasian zoogeographic subregions to the immediate east of the Wallace Line, see Figure 3.

Figure 2. Indo-Australian Archipelago showing land and sea during the Last Glacial Maximum at c. 19,000 BP when sea levels may have fallen by 120 m to 130 m. The Wallace/Huxley Line essentially marks the eastern edge of the Sunda continental shelf and eastern limit of complex Oriental continental faunas; while Lydekker's Line essentially marks the western edge of the Sahul/Greater Australian continental shelf and the western limit of complex Australo-Papuan continental faunas. Between these two lines lie the oceanic Wallacean Islands (after Heinsohn 2006a)

Figure 3. Map of the zoogeographic subregions to the immediate east of the Wallace Line. (1) Lesser Sunda; (2) Sulawesi Subregion; (3) Moluccas; (4) Papuan Subregion; (5) Bismarck Archipelago; and (6) Solomon Islands. Wallacea is comprised of subregions 1, 2 and 3; while Near Oceania is comprised of subregions 5 and 6 (after Heinsohn 2003)

During times of significantly lowered sea levels, such as the Last Glacial Maximum (LGM) at about 19,000 BP, when sea levels fell by 120 m to 130 m, large areas of both the Asian Sunda shelf and the Greater Australian Sahul shelf became exposed (Figure 2). In the west, this caused the Greater Sunda islands of Sumatra, Java, Bali and Borneo to coalesce with each other and the Asian mainland to form a continuous land bridge stretching from the Malay Peninsula to Bali and Borneo-Palawan. In the east, this caused New Guinea and its continental satellites such as Aru to coalesce with Australia and Tasmania to form a single Meganesian or Greater Australian continental landmass. Despite some limited internal coalescences, however, the intervening Wallacean islands (Lesser Sundas, Sulawesi subregion and Moluccas), separated by deep channels and seas, remained insular and this prevented the formation of a land bridge from Asia to Australia (Figure 2). Similarly, due to a series of deep intervening channels and seas, the northern Melanesian islands (the Bismarck Archipelago and Solomon Islands) of Near Oceania, despite internal coalescence within some island groups, also remained insular and oceanic and never formed land bridges with New Guinea or between principal island subregions. Furthermore, the Philippines (other than Palawan with its Bornean connections), despite some internal coalescences, also remained significantly insular and oceanic and thus could almost be viewed as a northern extension of oceanic Wallacea (Chappell and Shackleton 1986; Chappell 1987; Haq et al. 1987; Fairbanks 1989; Hope 1996; Hall 2001; Inger and Voris 2001; Heinsohn 2006a; Morwood and Van Oosterzee 2007).

The dominant natural vegetation of the tropical Indo-Australian Archipelago (excluding Australia) is Malesian and Papuan rainforest and monsoon forest, but with sizeable areas of either natural or anthropogenic savannah and savannah woodland, particularly in drier parts of the archipelago such as across much of the Lesser Sundas and southern New Guinea. The highest mountains in the region occur in the central cordillera of New Guinea, which has peaks approaching 5000 m in altitude, with the island supporting a spectrum of lowland to montane, subalpine and alpine habitats, including sizeable areas of montane anthropogenic grasslands. In other stretches of the archipelago, such as in parts of Wallacea and the northern Melanesian islands, there are island mountain ranges that reach between 2000 m and 3000 m in altitude, many of which support significant areas of montane forest, and upland anthropogenic grasslands (Whitten et al. 1987; Hope 1996; Monk et al. 1997; Heinsohn and Hope 2006).

The earliest recorded human occupation in the Indo-Australian Archipelago is that of *Homo erectus* in Java to the west of the Wallace Line at about 1.2 million years ago, where both fossil remains and stone tools have been found (Bellwood 1997). However, recent discoveries of ancient stone tools, possible early anthropogenic faunal extinction (turnover) horizons, and the fossil remains of *Homo floresiensis* on the Lesser Sunda island of Flores, variously dating between 880,000 and 18,000 years ago, have indicated the presence of pre-modern hominids to the east of the Wallace Line in Wallacea (Morwood and van Oosterzee 2007). Indeed, the *H. floresiensis* remains recently have been interpreted as possibly belonging to a relictual pre-*Homo erectus* hominid population that was probably once widespread in Asia and was able to hang on in Flores until about 18,000 BP. Indeed, suspected possible Middle Pleistocene stone-tool assemblages and/or possible Middle Pleistocene anthropogenic faunal extinction (turnover) horizons from places such as Timor, Sulawesi and the Philippines may be indicative that early pre-*H. erectus* hominids akin to *H. floresiensis* reached other parts of Wallacea and more northerly oceanic areas such as the Philippines (Morwood and Van Oosterzee 2007; Morwood pers comm. 2009, Mulvaney Lecture, Australian National University, 13 May 2009). If this is the case, then Sulawesi, with its ancient endemic marsupials, may be the first place where hominids and marsupials came into contact.

In contrast to the above early hominid record, the initial invasion of Wallacea and Meganesia (Greater Australia or Sahul) by modern *Homo sapiens* is generally thought to have occurred between 40,000 and 55,000 years ago in the late Pleistocene, with the islands of the Bismarck Archipelago in Near Oceania also being colonised within a broadly similar timeframe

(c. 40,000 BP), but slightly later for the Solomon Islands at about 32,000 BP (Bellwood 1997; Thorne et al. 1999; Wickler 2001; Leavesley and Chappell 2004; Morwood and van Oosterzee 2007; Summerhayes 2007). Following the relative stabilisation of sea levels in the lower Holocene, a further major phase of human colonisation was Austronesian-speaking agricultural and maritime peoples' expansion into Wallacea, around coastal New Guinea, into Near Oceania and the more distant Pacific islands of Remote Oceania in the past 4000 years, probably reaching New Zealand in the last millennium (Bellwood 1997; Kirch 1997; Spriggs 1997; Summerhayes 2007). This was a period that saw the rapid spread of various plant cultivars and the domesticated triumvirate of dogs, pigs and chickens into Oceania, along with anthropogenic spread of commensal murids such as the Pacific rat *Rattus exulans* (Kirch 1997; Spriggs 1997; Summerhayes 2007).

In the Indo-Australian Archipelago as far as western New Guinea, the aforementioned expansion was followed by ongoing economic and cultural influences from South and Southeast Asia, including the early spice and produce trade, and finally by the impact of the 'modern' spice trade in the past millennium, which involved the mercantile empires of the Chinese, Arabs, Portuguese, Spanish, Dutch and British (Swadling 1996; Black 1999). In Australasia, Australia and New Zealand were progressively colonised by British settlers from the late 18th and early 19th centuries respectively (Derbyshire 1993; Nile and Clerk 1996). Most of New Guinea and northern Melanesia remained as scattered indigenous realms until the 19th century when colonial rivalries and the lure of copra and gold led the Dutch, Germans and British to establish territories and colonial outposts (Souter 1963; Derbyshire 1993; Black 1999). The activities of the colonial acclimatisation societies in the 19th and early 20th centuries led to the deliberate introduction of a whole range of Eurasian, American and Australian vertebrate species to New Zealand, and a range of mostly Eurasian vertebrates to Australia, with significant impacts on both landmasses (Lever 1992; McDowall 1994; Young 2004; Heinsohn 2006a). In the tropical Indo-Australian Archipelago and Oceania, Dutch, German, British, Australian and French colonists contributed to the further spread of Oriental vertebrates such as the Javan rusa deer *Cervus timorensis*, adding to a traditional long-term process of translocation of multiple Oriental vertebrate species eastwards into Wallacea and Oceania by the native population, which had also carried some New Guinean/Australo-Papuan vertebrate species, including some marsupials, westwards into Wallacea (Glover 1971, 1986; Groves 1984; Heinsohn 1997a, 1998a, b, 2001a, 2002a, 2003, 2004a, 2005a, b, 2006a; Heinsohn and Hope 2006). This is the deeper historical and cultural backdrop to the anthropogenic translocation of Australasia's Australidelphian marsupials.

Results and discussion: A survey of records and postulations of long-term Australidelphian marsupial translocation

Based on literature review and some of the author's own field observations, Table 1 summarises records and postulations of historic and prehistoric Australidelphian marsupial translocations, while Table 2 summarises the postulated impact of translocation on the composition and status of island marsupial faunas. Analysis reveals that there are three principal putative source areas for translocated Australidelphian marsupials: (1) continental Australia (including continental shelf islands such as Tasmania and the Bass Strait islands); (2) continental New Guinea and the broader Papuan subregion (including continental shelf satellites such as Aru, Misool, Salawati and the southeast Papuan islands); and (3) oceanic Wallacea (specifically Sulawesi). These are discussed separately below.

Table 1. Records and postulations of anthropogenic translocation of Australasian (Australidelphian) marsupials during historic and prehistoric times (Table 1 continues on pages 141-148)

Taxa/species and value/ reason for translocation	Presumed natural distribution	Where thought to be introduced	Historical context	References
New Guinea / Papuan exports				
Dasyuridae				
New Guinea quoll (<i>Dasyurus albopunctatus</i>) [? Pet, trade animal, bilas fur, food and small game species, rat-catcher]	New Guinea	(?)1) Malai Island in the Siassi group	Lilley (1986) reports finding the bones of a small game animal, the New Guinea quoll (normally restricted to the New Guinea mainland) from Holocene deposits on Malai Island in the oceanic Siassi group (near Umboi) in the Vitiaz Strait. This may merely represent a captive animal or preserved salted or smoked carcass/carcass portion transported in from the New Guinea mainland. Or it may represent a now-extinct naturally occurring population due to waif dispersal on a natural raft, or possibly a now-extinct ephemeral population of animals derived from anthropogenic translocation.	Lilley 1986; Heinsohn 2006a
Peroryctidae				
Common echymipera or common spiny bandicoot (<i>Echymipera kalubu</i>) [? Food and small game species, trade animal]	New Guinea and some adjacent islands	(?)1) Manus Is.; (?)1) Some other oceanic New Guinea satellites	Slightly ambiguous archaeological evidence indicates that the population on Manus Is. in Northern Melanesia may have been introduced in the Terminal Pleistocene at around 13,000 BP (Spriggs 1997; Summerhayes 2007). Alternatively, Manus Is. and other oceanic populations may represent unaided dispersal on natural rafts washed out to sea during floods, storms, king tides or tsunamis.	Flannery 1995b; Spriggs 1997; Heinsohn 2003; Long 2003; Heinsohn 2006a; Summerhayes 2007
Rufous echymipera or rufous spiny bandicoot (<i>Echymipera rufescens</i>) [? Food and small game species, trade animal]	New Guinea; Aru Is.	(?)1) Kai Is.	Possibly introduced to the oceanic Kai Is. through captives carried for food, trade or stock purposes from Aru. Alternatively, the Kai population may represent unaided dispersal on natural rafts washed out to sea during floods and storms.	Flannery 1995b; Heinsohn 1997a; Heinsohn 2003, 2006a
Petauridae				
Sugar glider (<i>Petaurus breviceps papuanus</i>) [Papuan region subspecies] [? Pet, trade animal, bilas fur, delicacy]	New Guinea & some Papuan Region satellite islands	(?)1) Halmahera; (?)1) Bacan; (?)1) Gebe; (?)1) Some other New Guinea satellites	Populations on Halmahera and Bacan, and on some other oceanic New Guinea satellites may possibly be due to long-term human agency through captives carried as pets or as a small mammal food delicacy; or possibly through stowaways in traditional cargos such as large bunches of bananas.	Flannery 1994b; Flannery 1995b; Flannery et al. 1995; Monk et al. 1997; Heinsohn 2003; Long 2003; Heinsohn 2004a, 2006a

Phalangeridae				
Common spotted cuscus (<i>Spiloglossus maculatus</i>) [Pet, trade animal, bilas fur and fibre, food and game animal]	New Guinea	Selayar; Buru; Ambon; Seram and satellites; Banda; Kai; St. Mathias group; New Ireland; ?New Britain (adventive populations)	Probably introduced to much, or all, of its oceanic distribution through long-term human agency, through captives carried as pets or for food, trade and stock purposes. Archaeological evidence from the St. Mathias group indicates that it was probably introduced there within the past few thousand years (Kirch 1988, 1997). Populations in New Ireland appear to have been introduced sometime in the decade leading up to the commencement of the Second World War (Flannery and White 1991; Heinsohn 1998a, b, 2004a), and the species is still spreading down the island from its suspected original release point at Kavieng at the far northwestern tip of the long narrow island (main invasion frontier reaching as far south as Lemakot area), but with secondary introduced populations derived from cuscuses carried further on in motor vehicles or boats now starting to appear in other more southern locations (eg. Pangeifua area to the southwest of the main invasion frontier and the Weiten River Valley in far southern New Ireland). These separate populations will eventually coalesce and speed up the rate of complete colonisation of New Ireland by <i>S. maculatus</i> (Heinsohn 2006a). A recent development is that adventive populations of <i>S. maculatus</i> , probably carried across the St. George Strait from New Ireland in boats in the late 20 th century and early 21 st century, have begun to appear in adjacent northern New Britain (Sebastian Högberg pers comm. 2009) and these will probably go on to establish invasion beachheads on that island.	Musser 1987; Whitten et al. 1987; Kirch 1988; Flannery 1990a; Flannery and White 1991; Flannery 1994b; Flannery 1995a, b; Monk et al. 1997; Spriggs 1997; Emmons and Kinbag 2001; Long 2003; Heinsohn 1997a, 1998a, b, 2002a, b, 2003, 2004a, b, 2006a
Admiralty cuscus (<i>Spiloglossus kneri</i>) [Pet, trade animal, bilas fur and fibre, food and game animal]	Ancestors may be from New Guinea or fringing Papuan subregion islands	(?) Admiralty Is.; Hermit Is.; Ninigo group.; Wuvulu [All of the above are a part of the Manus Province Archipelago] ?(1) Bali Is., Witu Is., West New Britain Province?	May have been introduced to the aforementioned islands of the Manus Province Archipelago through long-term human agency through captives carried as pets or for food, trade and stock purposes (Flannery 1994, 1995b; Heinsohn 2004a). Spriggs (1997) and Summerhayes (2007) interpret archaeological evidence from the site of Pamwak on Manus Island to conclude that <i>S. kneri</i> may have been introduced there in the terminal Pleistocene at around 13,000 years ago, presumably from unknown sources in the Papuan subregion/northern New Guinea. Author considers it possible that the apparent uniqueness of <i>S. kneri</i> may be due to anthropogenic admixture/introduction of a mixed <i>Spiloglossus</i> spp. founding stock leading to a differentiated hybrid population. Alternatively, <i>S. kneri</i> may have naturally rafted to part of the Admiralty Islands, such as Greater Manus Island where it differentiated, and was then subsequently spread by human agency to other islands in the vast Manus Province Archipelago, such as the Hermit Is., Ninigo group and Wuvulu. On the basis of a single specimen, an adventive population derived from Manus Province trade animals may now also occur on Bali Is., Witu Is. of West New Britain Province to the southeast of Manus Province	Flannery 1994b; Flannery 1995b; Spriggs 1997; Anthony 2001; Long 2003; Heinsohn 1997a, 1998a, b, 2003, 2004a, 2006a; Helgen and Flannery 2004; Summerhayes 2007

Taxa/species and value/ reason for translocation	Presumed natural distribution	Where thought to be introduced	Historical context	References
Northern common cuscus, grey cuscus or brown cuscus (<i>Phalanger orientalis</i>) [Pet, trade animal, bilas fur and fibre, food and game animal]	New Guinea	Timor; Leti; Wetar; Sanana; Buru; Ambon; Seram and satellites; Banda; Kai; Bismarck Archipelago; Solomon Is.; some other oceanic New Guinea satellite islands	Probably introduced to much, or all, of its oceanic distribution through long-term human agency through captives carried as pets or for food, trade and stock purposes. Archaeologists of the Lapita Homeland Project consider, on the basis of material from a range of cave sites in New Ireland in the Bismarck Archipelago, that <i>P. orientalis</i> may have been introduced there as early as 23,500 to 20,000 BP in the Late Pleistocene (Flannery and White 1991; Spriggs 1997; Summerhayes 2007), while archaeological evidence from Timor (Glover 1971, 1986) and the North Solomons (Wickler 2001; Summerhayes 2007) indicates that the species may have been introduced to those areas in the middle to upper Holocene respectively. Long Island off the north of New Guinea is reported to have been deliberately restocked with northern common cuscus <i>P. orientalis</i> following a cataclysmic volcanic eruption three centuries ago that wiped out virtually all animal life. Diamond (as cited by Koopman 1979) and Mayr and Diamond (2001), citing oral historical evidence from the inhabitants of Long Island, report that this happened in the 19 th century through the efforts of a man called Ailimai, apparently from sources on Tolokiwa Island to the east.	Glover 1971; Koopman 1979; Ball and Hughes 1982; Groves 1984a; Glover 1986; Menzies and Pernetta 1986; Flannery et al. 1988; Flannery and White 1991; Flannery 1993b; Flannery 1994b; Flannery 1995ab; Monk et al. 1997; Spriggs 1997; Mayr and Diamond 2001; Wickler 2001; Heinsohn 2002c; Heinsohn 2003; Long 2003; Heinsohn 2004a, 2005ab, 2006a; Summerhayes 2007
Woodlark cuscus (<i>Phalanger lullulae</i>) [Pet, trade animal, bilas fur and fibre, food and game species]	Woodlark Is.	(?) Alcester Is.	Possibly introduced to Alcester Is. through captives from Woodlark Is. carried as pets, or for food, trade, ceremonial or stock purposes	Flannery 1994b; Flannery 1995b; Heinsohn 2003; Long 2003; Heinsohn 2004a, 2006a
Macropodidae				
Huon tree-kangaroo (<i>Dendrolagus matschiei</i>) [Pet, trade animal, food and game species, bilas fur and fibre; bones, teeth and other animal products]	New Guinea	(?) Umboi; (?) ?New Britain	Probably introduced through long-term human agency through captives carried as pets or for food or trade purposes. Juveniles captured during hunting are often kept for a while as pets, with some subsequently escaping.	Koopman 1979; Honacki et al. 1982; Maynes 1989; Flannery 1995a, b; Flannery et al. 1996; Heinsohn 2003; Long 2003; Martin 2005; Heinsohn 2006a
Brown dorcopsis				
(<i>Dorcopsis muelleri</i>) [Pet, trade animal, food and game species, bones, teeth, pelt and other animal products]	New Guinea; Misool	(?) Halmahera; (?) Gebe. Now extinct on both islands	May have been introduced from an adjacent Papuan region continental shelf satellite island such as Misool or Salawati, or the New Guinea mainland in the early to middle Holocene through captives carried as pets, or for food, trade or stock purposes, but now extinct on Halmahera and Gebe.	Flannery et al. 1995; Flannery et al. 1998; Heinsohn 2003, 2006a; Summerhayes 2007

Northern pademelon (<i>Thylogale brownii</i>) [Pet, trade animal, food and game species, bones, teeth, pelt and other animal products]	New Guinea	Bagabag; Umboi; New Britain; New Ireland; New Hanover Now extinct introduced populations appear to have occurred within recent historic times on a string of New Ireland satellites, including Tabar Is., Lihir group, Tanga Is. and Feni Is. (Heinsohn 2005c)	Probably introduced through long-term human agency through captives carried as pets, or for food, trade, ceremonial or stock purposes. Archaeological evidence from cave sites in New Ireland indicates that it may have been introduced there around 8400 to 7000 BP (Flannery and White 1991; Spriggs 1997; Summerhayes 2007). Egloff (1975, 1979) and Flannery et al. (1988) discuss archaeological evidence of macropodid translocation in the Northern Melanesian Islands during the Holocene.	Egloff 1975; Koopman 1979; Flannery et al. 1988; Maynes 1989; Flannery and White 1991; Flannery 1992; Flannery 1995a, b; Spriggs 1997; Heinsohn 2003; Long 2003; Heinsohn 2005c, 2006a
Dusky pademelon (<i>Thylogale brunii</i>) [Pet, trade animal, food and game species, bones, teeth, pelt and other animal products]	Aru Is.; New Guinea	(?) Kai Is.	Possibly introduced to the oceanic Kai Is. through captives carried from Aru as pets, or for food, trade or stock purposes.	Maynes 1989; Heinsohn 1997a; Heinsohn 2003; Long 2003; Heinsohn 2006a
Agile wallaby (<i>Macropus agilis</i>) [New Guinea form of this Australo-Papuan macropodid is sometimes described as the subspecies <i>M. a. papuanus</i>] [Pet, trade animal, food and game species; bones, teeth, pelt and other animal products]	Northern and northeastern Australia; Southern New Guinea	(?) Goodenough; (?) Fergusson; (?) Normanby; (?) Kiriwina; (?) Savannah woodland areas in mainland southeast Papua to the north of New Guinea's Central Range	May have been prehistorically introduced to the aforementioned islands of Southeast Papua from the New Guinea mainland through captives carried as pets, or for food, trade, ceremonial or stock purposes. Possibly also introduced to the isolated savannah/savannah-woodland patches of the Southeast Papuan mainland to the north of New Guinea's Central Cordillera. Egloff (1975, 1979) discusses archaeological evidence of macropodid translocation in the Southeast Papuan Islands during the Holocene.	Brass 1956; Brass 1959; van Deusen 1972a, b; Schodde and Calaby 1972; Liem 1977; Ziegler 1977; Egloff 1979; Maynes 1989; Flannery 1995b; Heinsohn 2003; Long 2003; Heinsohn 2006a
Sulawesi exports				
Sulawesi bear cuscus (<i>Ailurops ursinus</i>) [Pet, trade animal, food and game species, pelt, fur, fibre, bones, teeth and other animal products]	Sulawesi and some close satellite islands	(?) Salebabu Island in the remote Talaud group	The remote and patchy occurrence on Salebabu Island in the oceanic Talaud group may possibly be due to long-term human agency through captives carried as pets, or for food, trade, ceremonial or stock purposes. Alternatively, the patchy and disjunct Talaud population may possibly be relict and due to natural dispersal such as on rafts washed out to sea by floods, storms and surges.	Flannery 1994b; Flannery 1995b; Heinsohn 1997a, 1998a, b, 2001a, b, 2003, 2004a, 2006a

Taxa/species and value/ reason for translocation	Presumed natural distribution	Where thought to be introduced	Historical context	References
Australian exports to Remote Oceania				
Phalangeridae				
Common brush-tail possum (<i>Trichosturus vulpecula</i>) [Pelt for fur industry]	Tasmania and mainland Australia	New Zealand (North Is.; South Is.; Stewart Is.; Chatham Is. and other small NZ satellite islands)	Deliberately introduced to New Zealand from Tasmania and mainland Australia starting in the mid 19 th century to establish a fur industry. Due to selective over-browsing on New Zealand's mammalian-foliivore-naïve forests leading to the death of certain palatable tree species from exhaustion following repeated defoliation, <i>T. vulpecula</i> is reported to have caused possum-induced die-back and changes in forest composition in many areas of the North and South islands. Other impacts include predation on native invertebrates and small vertebrates such as nestling birds, and competition with indigenous species such as birds for tree-hollows and other habitat space.	Thomson 1922; Donne 1924; Wodzicki 1950; Murphy 1951; De Vos et al. 1956; Pracy 1962; Davidson 1965; Poole 1970; Gibb and Flux 1973; Tyndale-Biscoe 1973; Bull and Whitaker 1975; Gilmore 1977; King 1984; Lever 1985; Cowan 1990; King 1990; Holmes 1993; Flannery 1994b; McDowall 1994; Montague 2000; Isern 2002; Long 2003; Heinsohn 2004a; Cowan 2005; Heinsohn 2006a; Heinsohn and Barker 2006
Brush-tailed rock wallaby or black-tailed rock wallaby (<i>Petrogale penicillata</i>) [Acclimatisation movement and menagerie escapees]	Eastern Australia	Kawau Is., Rangitoto Is. and Motutapu Is. off the coast of the North Island of New Zealand; Oahu Is. in the Hawaiian Is.	Deliberately introduced to small satellite islands in New Zealand commencing in the early 1870s as a part of acclimatisation efforts. Also found on Oahu Island in Hawaii, as a result of a male and female that escaped from a private menagerie in 1916.	Tinker 1941; Wodzicki 1950; De Vos et al. 1956; Gilmore 1968; Tomich 1969; Poole 1970; Kramer 1971; Gibb and Flux 1973; Tyndale-Biscoe 1973; Bull and Whitaker 1975; Gilmore 1977; Lazell 1980; Tinker 1980; Lazell 1981; Lazell et al. 1984; Archer et al. 1985; Lever 1985; Moulton and Pimm 1986; Tomich 1986; Maynes 1989; King 1990; Flannery 1995b; Ziegler 2002; Long 2003; King 2005; Warburton 2005c; Heinsohn 2006a
Swamp wallaby or black wallaby (<i>Wallabia bicolor</i>) [Acclimatisation movement]	Eastern Australia	Kawau Is., off the coast of New Zealand's North Island	Probably introduced to Kawau Is. by Sir George Grey in circa 1870 as a part of acclimatisation efforts.	Wodzicki 1950; De Vos et al. 1956; Gilmore 1968; Poole 1970; Gibb and Flux 1973; Bull and Whitaker 1975; Gilmore 1977; Lever 1985; Maynes 1989; King 1990; Flannery 1995b; Long 2003; King 2005; Warburton 2005f; Heinsohn 2006a
Bennett's wallaby, red-necked wallaby, brush wallaby or scrub wallaby (<i>Macropus rufogriseus</i>) [Acclimatisation movement]	Tasmania and eastern Australian mainland	New Zealand's South Island (Wairarapa and Hawke districts)	Deliberately introduced to the Hunters Hills area of New Zealand's South Island in 1874 as a part of acclimatisation efforts, with the population growing and spreading to occupy a large area of the central South Island to the east of the Southern Alps.	Murphy 1951; Davidson 1965; Gilmore 1968; Poole 1970; Gibb and Flux 1973; Tyndale-Biscoe 1973; Bull and Whitaker 1975; Gilmore 1977; Lever 1985; Maynes 1989; King 1990; McDowall 1994; Flannery 1995b; Long 2003; King 2005; Warburton 2005b; Heinsohn 2006a

Tamar wallaby, dama wallaby, Kangaroo Island wallaby or silver-grey wallaby (<i>Macropus eugenii</i>) [Acclimatisation movement]	Southwestern Western Australia and southern South Australia	Kawau Is. and Rotorua district of New Zealand's North Island	Introduced to Kawau Island by Sir George Grey in circa 1870 as a part of acclimatisation efforts; and subsequently introduced to the Rotorua area of the North Island in circa 1912 from whence it continues to expand its range.	Wodzicki 1950; De Vos et al. 1956; Gilmore 1968; Poole 1970; Gibb and Flux 1973; Bull and Whitaker 1975; Gilmore 1977; Lever 1985; Maynes 1989; King 1990; McDowall 1994; Flannery 1995b; Long 2003; King 2005; Warburton 2005a; Heinsohn 2006a
Parma wallaby, white-throated wallaby or small brown wallaby (<i>Macropus parma</i>) [Acclimatisation movement]	Northeastern and central eastern New South Wales, Australia	Kawau Is. off the coast of New Zealand's North Island	Probably introduced circa 1870 as a part of acclimatisation efforts.	Gilmore 1968; Poole 1970; Wodzicki and Flux 1971; Gibb and Flux 1973; Tyndale-Biscoe 1973; Bull and Whitaker 1975; Gilmore 1977; Honecki et al. 1982; Archer et al. 1985; Lever 1985; Maynes 1989; King 1990; McDowall 1994; Flannery 1995b; Long 2003; King 2005; Warburton 2005c; Heinsohn 2006a
Black-striped wallaby or scrub wallaby (<i>Macropus dorsalis</i>) [Acclimatisation movement]	Eastern Australia	?Kawau Is. off the coast of the North Island of New Zealand	This species is presumed to have been liberated on Kawau Is. by Sir George Grey circa 1870 and may have persisted there for more than 80 years with the last apparently authenticated record in 1954, but the species may now be either extinct or extremely rare on Kawau. There is, however, ongoing debate as to whether <i>M. dorsalis</i> ever occurred on Kawau, with possible misidentification of other introduced macropodid species on the island leading to a false record of its occurrence there.	Wodzicki 1950; De Vos et al. 1956; Gilmore 1968; Poole 1970; Gibb and Flux 1973; Bull and Whitaker 1975; Gilmore 1977; Lever 1985; Maynes 1989; King 1990; Flannery 1995b; Long 2003; King 2005; Warburton 2005d; Heinsohn 2006a
Australian exports to Europe				
Bennett's wallaby, red-necked wallaby, brush wallaby or scrub wallaby (<i>Macropus rufogriseus</i>) [Zoo and menagerie escapees, and acclimatisation movement]	Tasmania and eastern Australian mainland	Great Britain (virtually extinct); Germany (extinct)	(UK) A series of escapes and deliberate liberations from the latter half of the 19 th century to the first half of the 20 th century led to a number of ephemeral populations in Great Britain. A small and dwindling extant population in the Peak District is derived from an escape of five animals from an enclosure in Staffordshire in 1939-40. (Germany) A series of acclimatised ephemeral populations also existed at scattered locations in Germany from the late 19 th century until the 1940s.	Boertger 1943; Grzimek 1967; Mallon 1970; Yalden and Hosey 1971; Tyndale-Biscoe 1973; Corbet 1974; Gilmore 1977; Lever 1977; Yalden 1982; Lever 1985; Maynes 1989; Baker 1990; Corbet and Harris 1991; Yalden 1999; Long 2003; Heinsohn 2006a; Harris and Yalden 2008
Australian exports to local Continental Shelf islands				
Dasyuridae				
Southern dibbler (<i>Paramechthys apicalis</i>) [Conservation]	Southwestern Western Australia	Escape Is. off the west coast of Western Australia	Deliberately introduced between 1998 and 2001 as a part of conservation efforts, with the species appearing to become established.	Long 2003; Heinsohn 2006a

Taxa/species and value/ reason for translocation	Presumed natural distribution	Where thought to be introduced	Historical context	References
Peramelidae				
Long-nosed bandicoot (<i>Perameles nasuta</i>) [? Reason]	Eastern Australia	(?) Badu Is. (Mulgrave Is.) in the Torres Strait, Australia	Long-nosed bandicoots may have been introduced to Badu Is. 'within living memory'.	Long 2003
Eastern barred bandicoot (<i>Perameles gunnii</i>) [Conservation]	Southeastern Australia, including Tasmania	Maria Is. off the coast of Tasmania.	Fifty-five individuals were introduced in 1971 as a part of wildlife management efforts.	Weidenhofer 1977; Rounsevell et al. 1991; Long 2003; Heinsohn 2006a
Southern brown bandicoot (<i>Isodon obesulus</i>) [Conservation]	Australia, including Tasmania	Maria Is. off the coast of Tasmania	Apparently introduced to Maria Is. off the Tasmanian coast in 1971 as a part of wildlife management efforts.	Weidenhofer 1977; Rounsevell et al. 1991; Long 2003; Heinsohn 2006a
Vombatidae				
Common wombat (<i>Vombatus ursinus</i>) [Conservation]	Southeastern Australia, including Flinders Is. and Tasmania	Maria Is. off the coast of Tasmania	Between 1969 and 1971 28 individuals of the subspecies <i>V. ursinus ursinus</i> from Flinders Is. were introduced to Maria Is. off Tasmania as a part of wildlife management efforts.	Weidenhofer 1977; Long 2003; Heinsohn 2006a
Southern hairy-nosed wombat (<i>Lasiorhinus latifrons</i>) [Conservation]	Central southern Australia	Wedge Is. off the coast of South Australia.	Introduced in 1971 as a part of wildlife management efforts.	Copley 1995; Long 2003; Heinsohn 2006a
Phascolarctidae				
Koala (<i>Phascolarctos cinereus</i>) [Conservation]	Eastern Australia	Kangaroo Is.; Phillip Is.; French Is.; some other small continental islands	Introduced to Phillip Is. and French Is. in 1920 in Victoria, and to Kangaroo Is. in South Australia between 1923 and 1958, becoming successfully established. Over-population on islands such as Kangaroo Is. has caused habitat damage such as high mortality rate for rough-barked manna gum <i>Eucalyptus viminalis</i> through over-browsing.	Condon 1967; Inns et al. 1979; Kemper 1985; Archer et al. 1987; Lee and Martin 1988; Phillips 1990; Backhouse and Crouch 1991; Copley 1995; Inns 2002; Long 2003; Heinsohn 2006a

Petauridae				
Sugar glider (<i>Petaurus breviceps breviceps</i>)	Australia	Tasmania	Probably introduced into Tasmania in the middle years of the 19 th century through escaped pets imported from Victoria.	Gunn 1851; Lord 1919; Lord and Scott 1924; Smith 1973; Honecki et al. 1982; Rounsevell et al. 1991; Lever 1985; Flannery 1994b; Long 2003; Heinsohn 2004a, 2006a
[Southern and eastern Australian subspecies of the Australo-Papuan sugar glider]				
[Escaped pets]				
Pseudocheiridae				
Common ringtail possum (<i>Pseudocheirus peregrinus</i>)	Eastern Australia, including Tasmania	Kangaroo Is. off the coast of South Australia in 1926; Maria Is. off the coast of Tasmania in 1971	Deliberately introduced as a part of acclimatisation and conservation efforts.	Waite and Jones 1927; Condon 1967; Inns et al. 1979; Kemper 1985; Rounsevell et al. 1991; Copley 1995; Inns 2002; Long 2003; Heinsohn 2004a, 2006a
[Acclimatisation movement and conservation]				
Potoroidae				
Tasmanian bettong (<i>Bettongia gaimardi</i>)	Southeastern Australia (extinct); and Tasmania (extant)	Maria Is. off the coast of Tasmania	Between 1969 and 1971, 123 individuals were released on to Maria Is. as part of wildlife management efforts, with the species becoming successfully established there.	Weidenhofer 1977; Long 2003; Heinsohn 2006a
[Conservation]				
Brush-tailed bettong (<i>Bettongia penicillata</i>)	Australia	Venus Bay Island 'A'; Baird Bay Is.; St. Peter Is.; Wedge Is. off the coast of South Australia	Introduced to islands off South Australia in the last quarter of the 20 th century as a part of conservation efforts.	Long 2003; Nelson et al. 1992; Copley 1995; Short et al. 1992; Delroy et al. 1986; Heinsohn 2006a
[Conservation]				
Macropodidae				
Rufous hare-wallaby or Mala (<i>Lagorchestes hirsutus</i>)	Western and central Australia	Trimouille Is., Montebello group off the coast of Western Australia	Thirty individuals were successfully introduced to Trimouille Is. in the Montebello group in 1998 as a part of conservation efforts.	Long 2003; Heinsohn 2006a
[Conservation]				
Tasmanian pademelon (<i>Thylogale billardieri</i>)	Southeastern Australia (extinct); Tasmania and larger islands of the Bass Strait (extant)	Maria Is. off the coast of Tasmania	Thirteen individuals were released on Maria Is. in 1971 as part of wildlife management efforts.	Weidenhofer 1977; Long 2003; Heinsohn 2006a
[Conservation]				

Taxa/species and value/ reason for translocation	Presumed natural distribution	Where thought to be introduced	Historical context	References
Black-footed rock wallaby (<i>Petrogale lateralis</i>) [Conservation]	Western and central Australia; some islands off South Australia.	Central Pearson Is., South Pearson Is., Thistle Is., Wedge Is., off the coast of South Australia.	Subspecies <i>Petrogale lateralis pearsoni</i> is endemic to North Pearson Is., South Australia, but was translocated to other islands off South Australia in the latter part of the 20 th century as a part of conservation efforts.	Long 2003; Copley and Alexander 1997; Copley 1995; Short et al. 1992; Heinsohn 2006a
Rothschild's rock wallaby (<i>Petrogale rothschildi</i>) [Conservation]	Northwestern Australia in the Hamersley Range area, including some rocky offshore islands of the Dampier Archipelago	West Lewis Is. off the coast of northwestern Western Australia	Deliberately re-introduced to West Lewis Is. in 1981 as a part of conservation efforts.	Strahan 1995; Pearson and Kinnear 1997; Long 2003; Heinsohn 2006a
Bennett's wallaby, red- necked wallaby, brush wallaby or scrub wallaby (<i>Macropus rufogriseus</i>) [Conservation]	Tasmania and eastern Australia	Maria Is. off the coast of Tasmania	Between 1969 and 1970, 127 Tasmanian Bennett's wallabies (<i>Macropus rufogriseus rufogriseus</i>) were successfully introduced to Maria Is. off Tasmania as a part of wildlife management efforts.	Weidenhofer 1977; Long 2003; Heinsohn 2006a
Tammar wallaby, dama wallaby, Kangaroo Island wallaby or silver-grey wallaby (<i>Macropus eugenii</i>) [Food animal and conservation]	Southwestern Western Australia and southern South Australia	Greenly Is. off the coast of South Australia; North Island in the Abrolhos Archipelago of Western Australia	<i>M. eugenii</i> was introduced to Greenly Island off the coast of South Australia in about 1905, apparently to provide an emergency food supply for shipwreck survivors; and introduced to North Island in the Abrolhos Archipelago of Western Australia in the latter half of the 20 th century.	Inns et al. 1979; Short et al. 1992; Copley 1995; Long 2003; Heinsohn 2006a
Eastern grey kangaroo (<i>Macropus giganteus</i>) [Tasmanian subspecies <i>M. giganteus tasmaniensis</i>] [Conservation]	Eastern Australia, including northeastern Tasmania	Maria Is. off the coast of Tasmania	Between 1969 and 1971, 45 individuals of the Tasmanian subspecies <i>Macropus giganteus tasmaniensis</i> subspecies were successfully introduced to Maria Is. as a part of conservation efforts.	Wapstra 1976; Weidenhofer 1977; Rounsevell et al. 1991; Long 2003; Heinsohn 2006a
Western grey kangaroo (<i>Macropus fuliginosus</i>) [? Reason]	Southwestern and southern Australia west of the Great Dividing Range	Woody Is. in the Recherche Archipelago of Western Australia	Successfully introduced to Woody Is. in 1948.	Short et al. 1992; Long 2003; Heinsohn 2006a

(?) = May be introduced. ? = May occur on that landmass.

Australian exports

The translocation of Australian marsupials to new landmasses can be broken down into three categories: (1) species introduced to Europe in recent historic times; (2) species introduced to Pacific islands in Remote Oceania in historically recent times; and (3) species introduced locally to Australia's own continental shelf islands in historically recent times. Currently, there is very little information on possible prehistoric translocation of strictly Australian (as opposed to Australo-Papuan) marsupial species, other than, for example, postulations by McNiven and Hitchcock (2004) based on archaeological and ethnohistorical evidence that Torres Strait Island peoples may have enhanced macropodid populations on some of the Torres Strait islands during insular post-land-bridge Holocene times through introductions or re-introductions of macropodid species, including the Australian common wallaroo *Macropus robustus*. While this is quite plausible, such postulation currently runs into the problem of clearly distinguishing between natural relictual macropodid populations left over from when the islands were part of the Australo-Papuan Torresian land bridge, and possible subsequently introduced/re-introduced populations. This could potentially be resolved through more extensive archaeological sampling of the area, and molecular systematics analysis of DNA extracted from subfossil bone/teeth and from tissue samples from extant regional macropodid populations.

Only one Australian marsupial species has been successfully introduced to Europe – the red-necked wallaby *Macropus rufogriseus* from eastern and southeastern Australia and Tasmania, with Tasmanian stock principally used. Several small populations were successfully established in Germany and the United Kingdom in the latter half of the 19th century and the first half of the 20th century, through deliberate acclimatisation efforts and escapees from zoos and private menageries. With successful reproductive recruitment, these populations appeared to be naturally viable and able to withstand Palearctic predators such as foxes and dogs, but for the most part, apart from the impacts of some severe winters, they eventually dwindled because of human predation (especially during the hungry war years in Germany) and the indirect impacts of high human population densities. Today, out of all of these former introduced populations, there are probably only a few animals left, such as in the Peak District of England in the United Kingdom (Long 2003; Heinsohn 2006a; Harris and Yalden 2008).

Seven species of marsupials have been successfully translocated to Pacific islands in Remote Oceania. These include one phalangerid, the common brushtail possum *Trichosurus vulpecula*, and six macropodids including the swamp wallaby *Wallabia bicolor*, red-necked wallaby *Macropus rufogriseus*, tammar wallaby *M. eugenii*, parma wallaby *M. parma*, and black-striped wallaby *M. dorsalis* to New Zealand; and the brushtailed rock wallaby *Petrogale penicillata* to both New Zealand and Hawaii. Of these, *T. vulpecula* is now almost ubiquitous in New Zealand, having been introduced to the North Island, South Island, Stewart Island and many satellite islands, including the remote eastern Chatham Islands (pers obs. 2009). Introduction of this folivorous possum began in the mid 19th century to establish a fur industry, with both Tasmanian and mainland Australian stock being imported before use of New Zealand-bred stock for later liberations (Thompson 1922; Donne 1924; Wodzicki 1950; Pracy 1962; Montague 2000; Heinsohn 2004a; Cowan 2005; Tyndale-Biscoe 2005). In New Zealand, the possum has become an invasive over-abundant pest species with a significant impact on ecosystems and biodiversity. The principal impact is selective over-browsing on New Zealand's mammalian-folivore-naïve forests (there were no native mammalian folivores in New Zealand), leading to the death of certain palatable tree species from exhaustion following repeated defoliation. This is reported to have caused possum-induced die-back and changes in forest composition in many areas of the North and South Islands. For example, species such as rata *Metrosideros* spp., fuchsia *Fuchsia excorticata*, titoki *Alectryon excelsa* and kamahi *Weinmannia racemosa* have declined in many areas. Possums can also affect plant recruitment in a number of species through consumption of seedlings on the ground or through eating the palatable

bark on favoured saplings, effectively ring-barking young trees, and this, too, can contribute to changes in plant community composition. Other possum impacts include predation on native invertebrates such as snails and insects and on small vertebrates such as nestling birds, and competition with indigenous species such as birds for tree hollows and other habitat space (King 1984; Montague 2000; Heinsohn 2004a; Cowan 2005; Tyndale-Biscoe 2005; Amanda Baird pers comm. 2009).

In comparison, New Zealand's six macropodids were all introduced as a part of 19th century or early 20th century acclimatisation efforts, and have much more restricted ranges, and limited impacts. Indeed, three species, including *W. bicolor*, *M. parma* and *M. dorsalis*, have been restricted to Kawau Island in the Hauraki Gulf of the North Island since being liberated there by Sir George Grey in c. 1870, and one, *M. dorsalis*, appears to have died out in the mid 20th century after persisting there for 80 years. A further two species, *P. penicillata* and *M. eugenii*, were also introduced to Kawau Island by Sir George Grey in c. 1870, where they still persist, but were additionally introduced to other parts of New Zealand. Specifically, in c 1870, *P. penicillata* was also introduced to Rangitoto and Motutapu Islands in the Hauraki Gulf, where it persisted for about 120 years until being exterminated in the 1990s; while *M. eugenii* was additionally introduced to the Rotorua area of the North Island in c. 1912, where it is now firmly established and from where it continues to expand its range. In contrast, New Zealand's sixth wallaby, *M. rufogriseus*, was introduced to the Hunters Hills area of the South Island in 1874, and is now firmly established in a considerable area of the central South Island to the east of the Southern Alps. It is the only macropodid in the south, and was never established in northern New Zealand (Wodzicki 1950; Lever 1985; Maynes 1989; Long 2003; King 2005; Warburton 2005a, b, c, d, e, f).

Of the aforementioned Australian macropodids introduced to temperate New Zealand, the brushtailed rock wallaby *Petrogale penicillata* is now also established on the Hawaiian island of Oahu in tropical Remote Oceania. This occurred as a result of a single male and female pair that escaped from a private menagerie in 1916. A small, apparently viable population persists to this day in steep rocky terrain on Ewa Kalihi in the lower Ko'olau Range on Oahu Island, where it is somewhat contained by geography and habitat (Kramer 1971; Tinker 1980; Lazell 1981; Lazell et al. 1984; Lever 1985; Moulton and Pimm 1986; Tomich 1986; Maynes 1989; Ziegler 2002; Long 2003; Heinsohn 2006a).

Of the approximately 20 Australian marsupial species translocated locally to surrounding continental shelf islands in historically recent times, most were introduced or re-introduced to island reserves and refuges in the 20th century for species management and conservation purposes. These mostly fairly minor translocations include: a carnivorous dasyurid; three species of bandicoot; two wombat species; koalas; sugar gliders; common ringtail possums; two bettong species; a hare wallaby; Tasmanian pademelons; two species of rock wallaby; and four wallabies/kangaroos in genus *Macropus* (Long 2003; Heinsohn 2004a, 2006a; Van Dyck and Strahan 2008) (see Table 1). Of the above, probably the most significant introduction in terms of the scale of the subsequent biological invasion is the mainland Australian sugar glider *Petaurus breviceps* to Tasmania in the mid 19th century through escaped pets brought from Victoria. After initial escapes in northern Tasmania, perhaps with some further human-assisted dispersal, it is recorded to have spread across the entire length of the island by the early 20th century, and today *P. breviceps* occupies virtually all areas, other than non-congenial habitats such as parts of the damp southwest region (Gunn 1851; Lord 1919; Lord and Scott 1924; Lever 1985; Rounsevell et al. 1991; Flannery 1994; Long 2003; Heinsohn 2004a; Van Dyck and Strahan 2008).

Curiously, the introduction of the koala *Phascolarctos cinereus* to Kangaroo Island in South Australia in the 1920s has had some parallels to the impact of the brushtail possum *T. vulpecula* in New Zealand, in that this fairly large arboreal folivore has become over-

abundant on the island and is responsible for the death of certain palatable tree species such as rough-barked manna gum *Eucalyptus viminalis* through over-browsing. Repeated defoliation through excessive browsing by over-abundant koalas eventually causes a significant proportion of palatable trees to die from exhaustion, thus bringing about changes in forest composition (Inns 2002; Heinsohn pers obs. 2008). Kangaroo Island has a second introduced arboreal folivore, the common ringtail possum *Pseudocheirus peregrinus*, also introduced in the 1920s (Waite and Jones 1927; Copley 1995; Inns 2002; Long 2003; Heinsohn 2004a), and this species may possibly contribute to cumulative browsing pressures on palatable plant species.

New Guinea and Papuan subregion exports

With an estimated 80 marsupial species, New Guinea, including its fringing Papuan subregion satellite islands, is the world's second major centre for Australidelphian marsupial radiation (after Australia, which has nearly 160 species) (Table 2). Despite having half the number of marsupials, the Papuan subregion is, however, the world's greatest exporter of translocated marsupials to surrounding oceanic archipelagos, with 10 or more of its species suspected to have been exported through long-term human agency (Table 1). Furthermore, nearly all of these postulated translocations, including the export of two peroryctid bandicoots, a petaurid glider, several phalangerid possums and several macropodids, are thought to have occurred in prehistoric times. Several of these postulations regarding prehistoric translocations are based principally on archaeological evidence of sudden appearances of skeletal material in archaeological sequences, while other postulations, often regarding areas where little archaeological sampling has occurred, are based on broader ethnozoological and biogeographic contextual analysis, sometimes also including available evidence from the emerging field of molecular systematics.

The oldest postulated marsupial translocation in the region, based on archaeological evidence, is that of the New Guinean northern common cuscus *Phalanger orientalis* to New Ireland in the outer northwestern arm of the Bismarck Archipelago in Near Oceania at 23,500 BP to 20,000 BP in the late Pleistocene (Flannery and White 1991; Flannery 1993; Spriggs 1997; Leavesley 2005; Summerhayes 2007). This is also the world's oldest recorded anthropogenic animal translocation event, making *P. orientalis* the world's oldest known 'ethnotramp', an animal species dispersed through human agency (as defined in Heinsohn 1997a, 1998a, b, 2001a, 2003, 2004a, 2006a). Furthermore, as *P. orientalis* may have been translocated through New Britain to New Ireland, populations on the former, if also introduced, may have been translocated at an even earlier date. Other Pleistocene marsupial translocations postulated on the basis of archaeological evidence include the introduction of the New Guinean common spiny bandicoot *Echymipera kalubu* and the ancestors of the Admiralty cuscus *Spilocuscus kraemeri* to Manus Island in the northeastern Bismarck Archipelago, possibly at around 13,000 BP in the terminal Pleistocene (Spriggs 1997; Summerhayes 2007). This compares with archaeological evidence for prehistoric Holocene marsupial translocations in Near Oceania which supports postulated introduction of: the New Guinean northern pademelon *Thylogale browni* to New Ireland between 8400 and 7000 BP; the New Guinean common spotted cuscus *Spilocuscus maculatus* to the St. Matthias group in the far northern Bismarck Archipelago in the late Holocene; and secondary introductions of *P. orientalis* to Nissan and the Solomon Islands in the middle to upper Holocene (Kirch 1988; Flannery 1995b; Kirch 1997; Spriggs 1997; Summerhayes 2007).

There is also historical and archaeological evidence of further ephemeral (now extinct) introduced *T. browni* macropodid populations on some of the smaller New Ireland satellites, including Tabar Island, the Lihir group, Tanga Island and Feni Island, and archaeological evidence of possible ephemeral (now extinct) introduced populations of this macropodid on Buka in the North Solomons, and Eloaue Island in the St. Matthias group in the upper

Holocene (Egloff 1975; Flannery et al. 1988; Flannery 1995b; Spriggs 1997; Heinsohn 2005c; Summerhayes 2007). Combined archaeological, ethnozoological and biogeographic evidence also indicates that another macropodid, the Australo-Papuan agile wallaby *Macropus agilis*, may have been introduced to its contemporary island range in the continental southeast Papuan islands during mid to late Holocene times (Brass 1956, 1959; Egloff 1979; Maynes 1989; Flannery 1995b; Heinsohn 2003; Long 2003; Heinsohn 2006a).

To the immediate west of New Guinea in the oceanic Moluccas of Wallacea, there has been considerably less archaeological investigation, but limited excavations from places such as Halmahera in the north Moluccas and Gebe, an adjacent oceanic Papuan subregion outlier, indicate that a now extinct, probably introduced, macropodid population of the Papuan brown dorcopsis *Dorcopsis muelleri* occurred on the aforementioned islands in the early and middle Holocene respectively (Flannery et al. 1995; Flannery et al. 1998; Summerhayes 2007). Further archaeological evidence of marsupial translocation comes from Timor in the eastern Lesser Sundas, where more extensive archaeological excavations indicate that the New Guinean northern common cuscus *Phalanger orientalis* was probably introduced there in the

Table 2. Proportions of introduced marsupials on landmasses in the Indo-Australian Archipelago, Oceania and Europe

	Marsupial species	Number introduced	Percentage introduced
Continental Meganesia			
Australia	158	0	0%
New Guinea	80	0	0%
Oceanic Wallacea			
Halmahera	2	? 1	? 50%
Seram	3	2	66%
Buru	2	2	100%
Kai Is.	5	? 3 to 5	? 60% to 100%
Sulawesi subregion			
(Sulawesi and satellites including Selayar and Peleng)	4	1	25%
Timor			
(and Lesser Sundas as a whole)	1	1	100%
Near Oceania			
Admiralty Islands	2	? 0 to 2	? 0% to 100%
New Ireland	3	3	100%
New Britain	? 6	? 3 to 6	? 50% to 100%
Umboi	4	? 3 to 4	? 75% to 100%
Solomon Is.	1	1	100%
Remote Oceania			
New Zealand	6	6	100%
Hawaiian Is.	1	1	100%
European Continental islands			
British Isles	1	1	100%

References: Tomich 1986; Whitten et al. 1987; Corbet and Hill 1992; Flannery 1994b; Flannery 1995a, b; Monk et al. 1997; Heinsohn 2001a, 2002a, b, c, 2003, 2004a, b, 2005a, b, c, 2006a; Ziegler 2002; Long 2003; Helgen and Flannery 2004; King 2005; Nowak 2005; Heinsohn and Hope 2006; Harris and Yalden 2008; Van Dyck and Strahan 2008

middle Holocene (Glover 1971, 1986; Flannery 1995b; Bellwood 1997; Monk et al. 1997; Heinsohn 2003; Summerhayes 2007).

Other than palaeontology and archaeology, a further line of evidence for anthropogenic translocation of New Guinea region marsupials is provided by ethnohistorical and contemporary records of live animals being carried around in watercraft, as pets, living-larder food animals, trade commodities and sources of animal products such as decorative pelts, fibre, bone and teeth. While diminutive marsupials such as young sugar gliders *Petaurus breviceps* are principally kept as pocket pets (pers obs.), other larger marsupials such as bandicoots, cuscuses, and macropodids can provide significant parcels of bush meat, while in some areas spotted cuscuses *Spiloguscus* spp. in particular are highly valued for their often colourful pelts, which are worn as esteemed body adornments ('bilas' in New Guinea pidgin), with some tree kangaroo *Dendrolagus* spp. pelts also prized as bilas (pers obs.). Marsupial fur is also valued as a source of traditional fibre used to make products such as woven bilum bags and hats, with cuscuses and some other possums being plucked for this purpose. Young cuscuses including *Spiloguscus* spp. and *Phalanger* spp. are also popular pets, although virtually any young marsupial, including wallaby and tree-kangaroo joeys captured during hunting, may be kept for a while as ephemeral pets or live-animal trade commodities and carried about. Any carriage of pets, trade stock, or living-larder captives increases the chance of escapees establishing new populations beyond their natural range, particularly given the flimsy or less-than-secure state of various cages, baskets, sacks, woven bags and bindings used to restrain captive marsupials (Heinsohn 1997a, 1998a, b, 2001a, 2003, 2004a, b, 2006a, pers obs.).

There are also contemporary and ethnohistorical records of deliberate attempts to introduce various marsupials such as cuscuses and wallabies to faunally depauperate islands as part of a game-enhancement strategy to provide a future source of food and other animal products. This parallels the well-recorded tradition of European sailors, fishermen and whalers who are historically known to have left breeding stock of goats, pigs and fowls on stop-over islands to ensure a future food supply. The author, for example, recorded details of late 20th century attempts by local Melanesians to introduce the common spotted cuscus *S. maculatus* to Djaul Island off New Ireland, and the Admiralty cuscus *S. kraemeri* to small satellites such as Bipi Island off Manus, while there is also ethnohistorical evidence that local people traditionally kept some of New Ireland's satellite islands deliberately stocked with northern pademelons *Thylogale browni*, restocking from larger source populations on the adjacent New Ireland mainland (Heinsohn 1998b, 2005c).

A further recorded case of probable deliberate translocation of New Guinea region marsupials during the historical period is that of the northern common cuscus (*Phalanger orientalis*) being introduced (or re-introduced) to Long Island off the northeast coast of New Guinea some time in the past 300 years. The oral traditions of local people indicate that the island was deliberately restocked with *P. orientalis*, a valued food animal, following a cataclysmic volcanic eruption of Krakatoan magnitude that occurred three centuries ago and destroyed virtually all life (Koopman 1979; Ball and Hughes 1982; Ian Hughes pers comm. 1990). Jared Diamond (as cited by Koopman 1979:3), reporting on the testimonies of the island's inhabitants, considers that this restocking may have happened in the 19th century, from phalangerid sources on Tolokiwa Island to the east. This is subsequently elaborated on in Mayr and Diamond (2001:18): 'Even the name of the person who introduced *Phalanger orientalis* to Long Island in the 19th century is known: a man called Ailimai.'

There are also historically recorded cases of secondary marsupial introductions in the Bismarck Archipelago that apparently happened as a result of accidental escape of captive marsupials. This underscores the diversity of likely scenarios for the introduction of New Guinea region marsupials to surrounding archipelagos. Thus, while a great many introductions in the prehistoric past may have been deliberate, as a part of game enhancement strategies to

add to the faunal resources on islands, a proportion of introductions may have occurred as a result of pets, living-larder food animals, captive trade stock, or simply a hunter's live catch (caught in traps, snares or by hand) that escaped captivity on arrival at a destination (Heinsohn 1997a, 1998a, b, 2001a, 2003, 2004a, b, 2006a).

*Contemporary anthropogenic spread of *Spiloglossus maculatus* in the Bismarck Archipelago*

The first recorded translocation of the New Guinean common spotted cuscus *S. maculatus* into the Bismarck Archipelago is its prehistoric introduction to the remote St. Matthias group in the late Holocene, where the animal remains strongly established to this day (Kirch 1988, 1997; Flannery and White 1991; Heinsohn 1998b). A salient historical case of marsupials apparently established on an island through escaped captives is provided by the story of how *S. maculatus* subsequently made it to New Ireland from sources in the St. Matthias group. Flannery and White (1991:111) were the first to report in any detail on this case:

'Sanila Talevat, a senior man of Madina, related the facts of the introduction of this species as they were known to him: several *S. maculatus* were brought to Kavieng, northern New Ireland, in 1929 from the St. Matthias Group by Australian Government officials (or possibly their Melanesian employees). [The population on the St. Matthias Group itself results from human introduction.] The animals subsequently escaped. They are now found over a large area of northern New Ireland ... Sanila suggests that they had not spread much farther south than the narrowest part of New Ireland, ~60km south of Kavieng.' (Flannery and White, 1991:111, reporting on data collected in 1988)

The contemporary and ongoing human-induced spread of *S. maculatus* provides an illuminating analogy for anthropogenic biological invasions in the past. The author's own spotlighting survey and oral historical investigation of the distribution of *S. maculatus* in New Ireland revealed that by 1990, it had invaded about 40 km to 50 km down the long narrow island (Heinsohn 1998b, 2004a, 2006a) (Figure 4). However, even then, there were reports of isolated adventive populations, apparently mostly derived from escaped or liberated pets carried in by boat or motor vehicle, that were beginning to appear at scattered localities beyond the main invasion front, such as one near Pangeifua some 20 km further south (Heinsohn 1998b, 2004a). By the mid 1990s, an adventive population of *S. maculatus* had been recorded in lower elevations of the Weiten River Valley of far southern New Ireland (Emmons and Kinbag 2001). This far southern record is more than 200 km to the south of the main invasion frontier, and probably also represents an adventive population established fairly recently through secondary boat or vehicle transport of pets and captives (author's assessment), and no doubt will go on to form a further invasion beachhead, with such anthropogenic secondary invasion beachheads eventually coalescing to speed up the complete colonisation of New Ireland by *S. maculatus* (Heinsohn 2006a). Indeed, rapid development of oil palm plantations and the spread of logging activities to far corners of New Ireland has probably hastened the spread of *S. maculatus* through greatly increased vehicular and boat traffic and movement of people, including cashed-up workers who buy the animals at markets for use as food or popular status-enhancing pets.

The latest development is that recently translocated adventive populations of *S. maculatus*, probably from introduced sources in adjacent New Ireland, have begun to appear around villages and plantations in northern New Britain (Sebastian Högberg, pers comm. 2009). Thus, the predicted anthropogenic spread of *S. maculatus* from New Ireland to New Britain has already begun. Adventive populations may also be starting to appear on other New Ireland satellites, such as New Hanover (Lavongai). For a reconstruction of the historical invasion

of New Ireland and some adjacent islands by *S. maculatus*, see Figure 4 (Heinsohn 1998b, 2004a, 2006a).

Figure 4. Ongoing biological invasion of the Bismarck Archipelago by the introduced northern New Guinean subspecies of the common spotted cuscus *Spilocuscus maculatus maculatus*. Inset – This species was prehistorically introduced to the St. Matthias group in the Bismarck Archipelago in the late Holocene, from whence it was subsequently historically introduced to Kavieng at the far northwestern tip of New Ireland in the decade leading up to the commencement of the Second World War. Main map – Reconstruction of the subsequent biological invasion of New Ireland in the latter half of the 20th century. Dot at Pangeifua represents an adventive population beyond the main invasion front. Inset – Dot at the far southern end of New Ireland shows an isolated secondary adventive population of *S. maculatus* recorded at lower elevations in the Weiten River Valley of far southern New Ireland in the mid 1990s more than 200 km beyond the main invasion front. This is probably due to a secondary introduction of animals brought in from the north by boat or motor vehicle. Dot in northern New Britain represents secondary adventive populations of *S. maculatus* that have recently appeared in and around villages and plantations on that part of the island, probably through boat traffic from adjacent New Ireland. Adventive populations may now also occur on other New Ireland satellites such as New Hanover (Lavongai) marked by a dot (after Heinsohn 2006a)

In New Ireland, it was found that recent biological invasion by a slightly larger and more generalist *S. maculatus* had caused a slight niche contraction in pre-existing prehistorically introduced populations of *P. orientalis* (see Figures 5 and 6). Principally, in broad sympatry with *S. maculatus* within the northwestern New Ireland invasion zone, *P. orientalis* tended to retreat to core habitats within closed forest, whereas in allopatry beyond the invasion zone, where it was the sole cuscus species, it exhibited a more relaxed niche that also included plantations and some open forest areas. In contrast, the invading *S. maculatus* tended to occupy the full spectrum of closed forest, open forest and plantation, displacing *P. orientalis* from the more marginal plantation and open-forest habitats (Heinsohn 1998a, b, 2004 a, b). It is likely that this pattern will be repeated as *S. maculatus* invades New Britain and other adjacent islands that were once the sole reserve of *P. orientalis*.

The big picture of postulated anthropogenic export of Papuan region marsupials is summarised below.

Summary of postulated anthropogenic Papuan marsupial exports to surrounding oceanic islands

Taking all of the above contextual information into account, broad ethnozoological and biogeographic analysis indicates that:

1. Possibly all of the oceanic distribution of the New Guinean northern common cuscus *Phalanger orientalis* in the Bismarck Archipelago and Solomon Islands in Near Oceania; on Seram, Buru and satellites in the Central Moluccas; on the Kai Islands in the South Moluccas; on Sanana Island in the Sulawesi subregion; and on Timor and its satellites in the Lesser Sundas is due to long-term human agency;
2. Possibly all of the oceanic distribution of the New Guinean common spotted cuscus *Spilocuscus maculatus* in the St. Matthias group, New Ireland and New Britain in the Bismarck Archipelago; on Seram, Buru and satellites in the Central Moluccas; in the Kai Islands in the South Moluccas; and on far-flung Selayar Island in the Sulawesi subregion is due to long-term human agency;
3. All of the oceanic distribution of the Admiralty cuscus *Spilocuscus kraemeri* in the Admiralty Islands and other Manus Province Archipelago islands in the Bismarck Archipelago may be due to long-term human agency, with the distinctive specific status possibly being due to human-induced hybridisation and founder effect caused by anthropogenic admixture or introduction of a mixed *Spilocuscus* spp. founding stock from New Guinea or Papuan subregion sources;
4. The oceanic distribution of the Australo-Papuan sugar glider *Petaurus breviceps* in the north Moluccas and on some other oceanic New Guinea satellites such as New Britain may be due to long-term human agency;
5. The oceanic distribution of the New Guinean common spiny bandicoot *Echymipera kalubu* on Manus Island in the Bismarck Archipelago, and on some other oceanic New Guinea satellites such as New Britain, may be due to long-term human agency;
6. The oceanic distribution of the New Guinean rufous spiny bandicoot *Echymipera rufescens* in the Kai Islands of the south Moluccas may be due to long-term human agency;
7. The oceanic distribution of the New Guinean Huon tree kangaroo *Dendrolagus matschiei* on Umboi Island, and possible occurrence on New Britain, in the Bismarck Archipelago, is probably due to human agency;
8. The oceanic distribution of the New Guinean northern pademelon *Thylogale browni* in the Bismarck Archipelago is probably due to long-term human agency;
9. The oceanic distribution of the New Guinean dusky pademelon *Thylogale brunii* in the Kai Islands of the south Moluccas is probably due to long-term human agency;
10. The oceanic distribution of past populations of the New Guinean/Papuan subregion brown dorcopsis *Dorcopsis muelleri* in the north Moluccas can probably be attributed to long-term human agency;
11. The distribution of the Australo-Papuan agile wallaby *Macropus agilis* in the continental southeast Papuan islands is probably due to long-term human agency; and
12. The secondary occurrence of the endemic Woodlark Island cuscus *Phalanger lullulae* on Alcester Island may be due to long-term human agency (See Table 1).

Figure 5. Introduced New Guinean common spotted cuscus *Spiloglossus maculatus maculatus* invading New Ireland. Photograph by T. E. Heinsohn

Figure 6. Northern common cuscus *Phalanger orientalis* in New Ireland, where archaeological evidence indicates that it was probably first introduced between 23,500 and 20,000 years ago in the late Pleistocene. This is the oldest known case of anthropogenic translocation of an animal species making *P. orientalis* the world's oldest known ethnotramp. Photograph by T. E. Heinsohn

Wallacean exports

After Australia and New Guinea, including fringing islands of the Papuan subregion, the third largest centre for Australidelphian marsupial radiations is the oceanic Wallacean islands, which currently have a dozen recorded marsupial species, seven of which are endemic. These seven Wallacean endemics are: (1) three phalangerid possums endemic to the Sulawesi subregion – the Sulawesi bear cuscus *Ailurops ursinus*, the small Sulawesi cuscus *Strigocuscus celebensis*, and the Peleng cuscus *Strigocuscus pelengensis*; (2) three phalangerids endemic to the north Moluccan area, the ornate cuscus *Phalanger ornatus*, the Obi cuscus *Phalanger rothschildi*, and the Gebe cuscus *Phalanger alexandrae*; and (3) one bandicoot, the Ceram bandicoot *Rhynchomeles prattorum*, endemic to Seram in the central Moluccas. Gebe is a relatively small oceanic island lying near the boundary between the Moluccan and Papuan subregions. Principally because of its avifaunal composition, it is traditionally placed in the latter subregion and treated as an oceanic Papuan outlier (Rand and Gilliard 1967; Coates and Bishop 1997). However, because the Gebe cuscus *P. alexandrae* is closely related to the ornate cuscus *P. ornatus* of adjacent Halmahera in the north Moluccas, it is treated here as a part of the oceanic Wallacean marsupial fauna.

Apart from the Wallacean endemics, as discussed in greater detail above, the other non-endemic marsupials in Wallacea may all have been introduced from New Guinea and its fringing Papuan subregion islands through long-term human agency. These include two probably introduced New Guinean phalangerid possums *Phalanger orientalis* and *Spilocuscus maculatus*, one probably introduced Australo-Papuan petaurid glider *Petaurus breviceps*, one possibly introduced New Guinean bandicoot *Echymipera rufescens*, and one probably introduced New Guinean macropodid *Thylogale brunii* (Table 1).

Out of the aforementioned endemic Wallacean marsupials, only one, the Sulawesi bear cuscus *Ailurops ursinus*, is postulated to have possibly been subjected to human-assisted dispersal beyond its natural range on Sulawesi and some close satellite islands, to Salebabu Island in the remote oceanic Talaud (or ‘Talaud’) group:

‘*A. u. melanotis* from the Talaud Group is small, and the fur is more profusely tipped with yellow than in other forms. It is provisionally recognised here as a distinct subspecies. However, it is apparently restricted to a single island in the distant Talaud Group, north of Sulawesi, which suggests that it may have been introduced there prehistorically by humans’ (Flannery 1994:160)

Indeed, its apparent distinctiveness as a subspecies on Salebabu (as with *Spilocuscus kraemeri* and *Phalanger orientalis breviceps* in the northern Melanesian islands of Near Oceania) could possibly be an artefact of long-term human-induced founder effect or anthropogenic allopatric differentiation resulting from thousands of years of isolation on oceanic Salebabu Island following long-term prehistoric introduction there. However, further research, including more extensive zoological surveys, molecular systematics and greater archaeological/palaeontological sampling of regional fossil/subfossil sites, is required to determine whether the outlying Salebabu Island, Talaud group, *A. ursinus* population is relict and due to ancient natural dispersals or an artefact of Quaternary human agency (Heinsohn 2004a, 2006a). Regarding its ethnozoological status, in Sulawesi *A. ursinus* is used for bush meat and sometimes carried about live as a living-larder trade commodity or pet (pers obs.), thus making it a candidate for possible deliberate or accidental introduction to adjacent islands via liberated or escaped captives.

Diagnosing the natural marsupial frontier: The problem of ambiguous oceanic marsupial faunas

In attempting to define the natural marsupial frontier, a line that marks the natural (as opposed to anthropogenic) distributional limits of Australidelphian marsupials, researchers encounter the problem of ambiguous marsupial faunas on certain fringing oceanic islands where there is currently insufficient evidence to determine whether all or some of the marsupial fauna is due to introduction by human agency, or indigenous and due to natural processes such as sweepstakes dispersal on natural rafts. This is because in the absence of historical records or adequate archaeological sampling, prehistorically introduced species, in particular, can mimic recently dispersed naturally occurring species (and vice versa), thus creating cryptogenic populations of unknown status or camouflaged exotic species which appear natural. In the Indo-Australian Archipelago, principally due to insufficient archaeological sampling, cryptogenic marsupial populations occur on New Britain and the Admiralty Islands in the Bismarck Archipelago of Near Oceania, and on Salebabu Island in the Talaud group in the Sulawesi subregion of Wallacea. The ambiguous zoogeographic status of various marsupials on these islands is described in Table 3.

Table 3. Ambiguous marsupial faunas on oceanic islands at the marsupial frontier (Table 3 continues on pages 160 and 161)

Species	Putative origins and zoogeographic context	Zoogeographic and ethnozoological status
<i>Near Oceania</i>		
New Britain	Non-volant mammal fauna is oceanic and unbalanced. Several endemic murid rats recorded, but depauperate compared to New Guinea mainland (4).	
<i>Marsupials</i>		
Common echymipera <i>Echymipera kalubu</i> (New Britain)	(a) Possibly arrived from New Guinea by over-water dispersal on a natural raft, or (b) possibly introduced through long-term human agency.	Cryptogenic – origins unclear on current evidence. Utilised food and game animal. Source of bush meat. (1, 2, 4, 8)
Sugar glider <i>Petaurus breviceps</i> (New Britain)	(a) Possibly arrived from New Guinea by over-water dispersal on a natural raft, or (b) possibly introduced through long-term human agency.	Cryptogenic – origins unclear on current evidence. Occasional pet and eaten as small game animal delicacy. (1, 2, 4, 8, 9)
Northern common cuscus <i>Phalanger orientalis</i> (New Britain)	(a) Possibly arrived from New Guinea by over-water dispersal on a natural raft, or (b) possibly introduced through long-term human agency.	Cryptogenic – origins unclear on current evidence. Utilised ethnotramp. Pet, food, game and trade animal. Source of animal products such as bush meat and bilum fibre. (1, 2, 4, 8, 9)
Common spotted cuscus <i>Spiloglossus maculatus maculatus</i> (New Britain)	This species appears to have been recently introduced to northern New Britain in the very late 20 th century and/or very early 21 st century, probably from adjacent sources in New Ireland.	Recently introduced species with adventive populations established. Utilised ethnotramp. Pet, food, game and trade animal. Source of animal products including bush meat, decorative fur pelts, and bilum fibre. (11)

Species	Putative origins and zoogeographic context	Zoogeographic and ethnozoological status
<p>?Admiralty cuscus</p> <p>? <i>Spilocuscus kraemeri</i></p> <p>(New Britain)</p> <p>Probably not a part of the New Britain fauna.</p>	<p>If pets or small adventive populations of this Admiralty Islands species do occur anywhere on New Britain or on any of its small satellite islands such as Bali Island, Witu group, then these are likely to be due to trade animals carried in from the Admiralty Islands where live animals are extensively traded for bush meat, other animal products and pet-keeping purposes (pers obs.). The author disagrees with the theory put forward by Helgen and Flannery (2005) that <i>S. kraemeri</i> may be endemic to New Britain, the original source, but is cryptic there and thus not recorded (13). This seems extremely unlikely as <i>S. kraemeri</i> is an adaptable and prominent species, which, like <i>S. maculatus</i>, tends to be easily located during spotlighting surveys (pers obs.). As such, it is unlikely to have gone undetected on New Britain until now.</p>	<p>?Introduced species if present in New Britain. Utilised ethnotramp. Pet, food, game and trade animal. Source of animal products including bush meat, decorative fur pelts, and bilum fibre.</p>
<p>Northern pademelon</p> <p><i>Thylogale browni</i></p> <p>(New Britain)</p>	<p>Probably introduced from New Guinea through long-term human agency (as this species is not a likely candidate for rafting, floating or swimming).</p>	<p>Prehistorically introduced species. Utilised ethnotramp. Food, game and trade animal, and occasional pet. Source of bush meat. (1, 2, 4, 8, 10)</p>
<p>Tree-kangaroo</p> <p><i>Dendrolagus matschiei</i></p> <p>(New Britain)</p>	<p>Probably introduced from New Guinea through human agency, possibly from secondary introduced sources on Umboi Island (as this relatively large marsupial is not a likely candidate for rafting, floating or swimming).</p>	<p>?Introduced species. Traditional source of bushmeat and pelts. Juveniles kept as occasional pets. (5, 7)</p>
Admiralty Islands	<p>Non-volant mammal fauna is oceanic and depauperate. One endemic murid rat recorded (4).</p>	
Marsupials		
<p>Admiralty cuscus</p> <p><i>Spilocuscus kraemeri</i></p> <p>(Admiralty Islands)</p>	<p>(a) Ancestral stock possibly arrived in the Admiralty Islands from New Guinea by over-water dispersal on a natural raft, or (b) ancestral stock was possibly introduced through long-term human agency. Distinctiveness may possibly be due to human-induced founder effect such as anthropogenic hybridisation in a mixed founding stock. Helgen and Flannery (2004) theory of introduction from undiscovered populations in New Britain (13) seems unlikely as this is a highly visible and adaptable species (pers obs.) that is unlikely to have remained undiscovered on New Britain.</p>	<p>Cryptogenic – origins unclear on current evidence. Apparently endemic to Manus Province Archipelago, but paradoxically also possibly introduced. Utilised ethnotramp. Pet, food, game and trade animal. Source of animal products including bush meat, decorative fur pelts and bilum fibre. (1, 2, 4, 6, 8, 9). In Seventh Day Adventist parts of the Admiralty Islands where there is reduced hunting pressure, the species is reported to become overabundant and become a minor pest in food gardens. (12)</p>
<p>Common echymipera</p> <p><i>Echymipera kalubu</i></p> <p>(Admiralty Islands)</p>	<p>(a) Possibly arrived from New Guinea by over-water dispersal on a natural raft, or (b) species was possibly introduced through long-term human agency.</p>	<p>Cryptogenic – origins unclear on current evidence. Utilised food and game animal. Source of bush meat. (1, 2, 4, 8)</p>

Species	Putative origins and zoogeographic context	Zoogeographic and ethnozoological status
<i>Sulawesi Subregion</i>		
Talaud Islands	Non-volant mammal fauna is oceanic and depauperate. Two endemic murid rats recorded. (4)	
<i>Marsupials</i>		
Sulawesi bear cuscus <i>Ailurops ursinus melanotis</i> (Salebabu Island, Talaud Group)	(a) Ancestral stock may have arrived from Sulawesi or one of its near satellites by over-water dispersal on a natural raft, or (b) possibly introduced to Talaud Islands through long-term human agency.	Cryptogenic – origins unclear on current evidence. Utilised food and game animal. Occasional pet and sometimes traded. (1, 2, 3, 4, 8, 9)

Sources: (1) Tate et al. 1945; (2) Laurie and Hill 1954; (3) Corbet and Hill 1992; (4) Flannery 1995b; (5) Flannery et al. 1996; (6) Helgen and Flannery 2004; (7) Martin 2005; (8) Heinsohn 1998a, 2003, 2006a; (9) Heinsohn 2004a, 2005b; (10) Heinsohn 2005c; (11) Sebastian Högberg, pers comm. 2009; (12) Heinsohn 1998b, 2004a; (13) Helgen and Flannery 2004.

Thus the marsupial fauna of the Talaud group, consisting of a single species *A. ursinus*, may be wholly introduced or wholly natural, while the marsupial fauna of the Admiralty Islands, comprised of two species *S. kraemeri* and *E. kalubu*, may be wholly introduced, 50% introduced, or wholly natural. New Britain, with up to seven, but probably six recorded species, has a marsupial fauna that may be wholly introduced or partially introduced, but not wholly natural, as the most recent introduction, that of *S. maculatus*, is historically recorded. In contrast to ambiguous New Britain, where there has been a lack of zooarchaeological sampling at appropriate sites, the marsupial fauna of neighbouring New Ireland, due to thorough archaeological sampling and historical records, is known to be wholly introduced (Flannery and White 1991; Flannery 1995b; Spriggs 1997; Heinsohn 1998b; Summerhayes 2007).

However, given that all of the marsupial species occurring in the Bismarck Archipelago are utilised or traded ethnotramp species (Heinsohn 2003, 2004a), with even the diminutive sugar glider *Petaurus breviceps* kept as a pocket pet, and given the lack of stochastic arrival of other non-ethnotramp marsupials such as pseudocheirids and dasyurids by sweepstakes dispersal during the late Cenozoic, the author considers it quite possible that the entire marsupial population in the archipelago was introduced through long-term human agency. Indeed, given all of the known precedents of marsupial translocation in the Bismarck Archipelago and the Solomon Islands, an application of the Occam's razor principle of looking for the simplest explanation could support attribution of the entire marsupial population of Near Oceania to long-term human agency, with the same principle also applied to the outlying *A. ursinus* population in the remote and oceanic Talaud Group. This leads to the author's proposed line of actual natural marsupial distributional limits marked by the bold broken line in Figure 7. This contrasts with Figure 8 which depicts the contemporary line of Australasian marsupial distributional limits when one takes into account all natural and introduced marsupial populations in the region. This represents a considerable anthropogenic expansion of the marsupial frontier into Near Oceania, Remote Oceania and southern Wallacea.

On the basis of the Occam's razor principle of parsimonious explanation and some ethnozoological and ecological considerations, the plausibility of the recent Helgen and Flannery (2004) radical hypothesis regarding possible New Britain origins for the Admiralty cuscus *Spiloglossus kraemeri* in the Bismarck Archipelago is questioned below. *S. kraemeri* is recorded from the Admiralty Islands and some outlying satellites such as the Hermit Islands, the Ninigo group and Wuvulu in the vast oceanic Manus Province Archipelago of Papua New Guinea (Laurie and Hill 1954; Flannery 1994, 1995b; Heinsohn 2004a). The species has the curious status of being apparently endemic to the Manus Province Archipelago, but paradoxically also considered to have been possibly introduced there from unknown sources in the New Guinea region (Flannery 1994, 1995b). On the basis of limited archaeological

sampling from the Pamwak site on Manus Island, it is considered that this may have happened in the terminal Pleistocene (Spriggs 1997; Summerhayes 2007). The author has postulated that the apparent distinctiveness of *S. kraemeri* may be due to anthropogenic founder effect and genetic drift which have exaggerated allopatric differentiation since introduction thousands of years ago, and that this founder effect possibly may have involved anthropogenic hybridisation or admixture following introduction of a mixed *Spilocuscus* spp. founding stock from sources in the New Guinea region (Heinsohn 1997a, 1998a, b, 2003, 2004a, 2006a). A regional precedent for this model is provided by the introduced pigs of New Guinea which may be derived from hybrids of *Sus scrofa vittatus* and *Sus celebensis* carried in from sources in the Indonesian Archipelago during the Holocene (Groves 1981; Flannery 1995a). If humans can inadvertently almost create a new taxon with ethnotramp pigs, then why not with ethnotramp phalangerids? A further possibility, however, regarding the origins of *S. kraemeri* in the Admiralty Islands is that it is due to natural waif dispersal of ancestral founding stock from New Guinea or its fringing Papuan subregion islands in the prehistoric past via animals washed out to sea on natural rafts as a result of floods, king tides, storms or tsunamis. However, even if *S. kraemeri* did make it to the Admiralty Islands by natural means, at least part of the animal's distribution within the vast Manus Province Archipelago, such as that on the outlying Hermit Islands, the Ninigo group and Wuvulu, is probably due to human agency, as the species is extensively traded at markets in that province, and to this day continues to be carried about in traditional vine baskets and other cages (pers obs.; Heinsohn 1998a, b, 2003, 2004a, 2006a).

A radical new hypothesis regarding the origins of *S. kraemeri* in the Admiralty Islands was presented by Helgen and Flannery (2004), who on the basis of two specimens, one bought at a New Britain market and reputed to come from Bali Island in the Witu group of West New Britain and a further museum specimen labelled 'New Britain', proposed that the species differentiated in New Britain becoming an island endemic, and was subsequently introduced to the Admiralty Islands by prehistoric human agency. Furthermore, they proposed that the species may still be in New Britain, but is cryptic there, thus remaining undiscovered and unrecorded on that island or its near satellites (Helgen and Flannery 2004). The author's own view is that the above hypothesis is improbable as it is extremely unlikely that New Britain would have been home to a prominent species such as *S. kraemeri* without it being firmly recorded by science over recent centuries. This is underscored by the fact that in the Admiralty Islands, *S. kraemeri* (as with *S. maculatus* in New Ireland) is a highly adaptable animal found in primary and secondary forest habitats as well as spreading into plantations and gardens, with its presence being well known by local villagers and hunters, and other than where locally over-hunted, is also relatively easily detected by biologists with spotlights and head torches (pers obs.; Heinsohn 1998b). Thus, it is extremely unlikely not to have been discovered on New Britain if present there.

It is much more likely that the few specimens of *S. kraemeri* with a New Britain provenance represent animals traded in from the Admiralty Islands. After all, if *S. kraemeri* can be traded as far as the Wuvulu, Ninigo and Hermit groups far to the west of the main Admiralty Islands, as is well recorded, then one would also consider it quite likely for animals to be traded to the southeast as far as New Britain and satellites such as Bali Island in the Witu group of West New Britain Province, the latter of which is about the same distance from the Admiralty Islands as Wuvulu. Indeed, confusion caused by the uncertain provenance of trade animals or naive acquisition-point labelling of specimens collected from traders is a well-recorded epistemological problem in the interpretation of historical museum systematics collections (as discussed in Heinsohn 2006a).

Helgen and Flannery (2004) do offer a possible explanation for the cryptic nature of putative undiscovered New Britain *S. kraemeri* populations, such as competitive suppression by local populations of *Phalanger orientalis breviceps*, making them rare. However, in the

Figure 7. Author's postulated actual natural marsupial distribution when one subtracts probably or possibly introduced marsupial populations (bold dashed line). This represents an older natural marsupial frontier prior to prehistoric and historic human influences on zoogeography. The bold broken line represents the maximum degree to which the natural marsupial frontier retreats if ambiguous marsupial faunas on New Britain, Admiralty Islands and the Talaud Group turn out to be introduced. Fainter dotted line extensions represent the degree to which the natural marsupial frontier expands if ambiguous elements of the New Britain, Admiralty Islands and Talaud marsupial faunas turn out to be naturally occurring through waif dispersal such as on natural rafts (after Heinsohn 2006a)

Figure 8. Line of actual marsupial distributions in Australasia taking into account all natural and introduced marsupial populations. This represents the contemporary human-influenced marsupial frontier in Australasia (after Heinsohn 2006a)

author's own observations of interspecific interactions between sympatric populations of slightly dwarfed island populations of *Spilocuscus maculatus maculatus* and *Phalanger orientalis breviceps* in northwestern New Ireland during a six-month field season, it was the larger *Spilocuscus* that had a competitive suppressing effect on *Phalanger*, rather than the other way around, with *Spilocuscus* being generally easier to detect in northwestern New Ireland than *Phalanger* (Heinsohn 1998b, 2004a, b). As *S. kraemeri* is only slightly smaller than *S. maculatus maculatus*, and probably a little larger than island populations of *P. orientalis breviceps*, it is unlikely for *P. orientalis breviceps* to cause competitive suppression of *S. kraemeri* should the two come into sympatric contact. Thus, the Helgen and Flannery (2004) theory is regarded as implausible on ecological and ethnozoological grounds.

Thus two apparent records of *S. kraemeri* on Bali Island, the Witu group, West New Britain Province, and on the New Britain mainland respectively are most likely due to trade animals carried in from Manus Province. However, this does raise the possibility that adventive populations of *S. kraemeri* derived from escaped or liberated trade animals from Manus Province may have become established in places such as the Witu islands of West New Britain Province. Furthermore, if recently introduced adventive populations of both *S. maculatus* and *S. kraemeri* are beginning to appear on New Britain or some of its satellite islands, then this may eventually lead to interbreeding and the creation of a new hybrid *Spilocuscus* population, thus setting off a new evolutionary concatenation in the anthropogenic island biogeography of phalangerids in Near Oceania. Thus, as has probably happened in the past, humans may again be on the verge of creating new taxa through anthropogenic hybridisation.

Discussion and conclusions: Implications of recent recognition of long-term marsupial translocation in the Indo-Australian Archipelago

As discussed above, in the Indo-Australian Archipelago, up to five out of 12 extant oceanic Wallacean marsupials (~42%) may have been introduced from New Guinea or fringing Papuan subregion islands through long-term human agency (the other seven ~58% being Wallacean endemics). This compares with the oceanic Bismarck Archipelago and Solomon Islands of Near Oceania, where possibly all of the marsupials may have been introduced from New Guinea or Papuan subregion sources. However, this strong long-term anthropogenic effect on Indo-Australian oceanic marsupial faunas has only recently been uncovered. This started with the 1960s archaeological work of Glover (1971, 1986) in Timor, who revealed that the island's single marsupial, the New Guinean northern common cuscus *Phalanger orientalis*, had probably been introduced in the mid Holocene. Following this revelation, came the 1980s and 1990s work of the Lapita Homeland Archaeological Project, which revealed that a whole range of marsupials in Near Oceania (the Bismarck Archipelago and Solomon Islands) had also been prehistorically introduced, some as early as the late Pleistocene (Allen and Gosden 1991; Flannery and White 1991; Kirch 1997; Spriggs 1997; Summerhayes 2007). This exposed the naivety of early marsupial biologists and most of the classic zoogeographers who had failed to imagine that tropical Indo-Australian marsupials, as economically valued commodities (in common with various placental species such as rusa deer *Cervus timorensis*), might also have been subject to long-term anthropogenic translocation and range expansion (Heinsohn 1997a, 1998a, b, 2001a, 2003, 2006a).

As late as 1977, marsupial biologist Gilmore, for example, in an essay entitled 'The success of marsupials as introduced species', while showing great awareness of historically recent Australidelphian marsupial introductions to the United Kingdom, New Zealand and Hawaii, automatically attributed the occurrence of all other far-flung oceanic populations, such as those in the Solomon Islands to 'natural spread' (Gilmore 1977:169). Furthermore,

as late as the 1960s, world-renowned zoogeographer Simpson, in an essay entitled 'Historical Zoogeography of Australian Mammals' (Simpson 1961) and in a subsequent book 'The Geography of Evolution' (Simpson 1965), defined his marsupial line, which purported to show the natural distributional limits of Australasian marsupials (see Figure 1). Other than excluding the obviously introduced marsupials in New Zealand and Hawaii, the Simpson Marsupial Line treated all other oceanic marsupial distributions in the Indo-Australian Archipelago and Australasia as natural.

Going further back in time, while classic 19th century zoogeographer Alfred Russel Wallace demonstrated a precocious awareness that various Oriental placental mammals such as Javan rusa deer *Cervus timorensis*, long-tailed macaque *Macaca fascicularis* and Malay civet *Viverra zibetha* had been translocated into various parts of Wallacea, he demonstrated an almost complete blind spot regarding the possibility of marsupial translocation, assuming all island marsupial distributions to be natural (Wallace 1869; Heinsohn 1997a, 1998b, 2006a). One cannot help but wonder whether, had Wallace recognised that much of the Wallacean marsupial biota was introduced, he would, in addition to recognising the Wallace Line as the eastern limit of complex Oriental continental faunas, have also perceived the current Lydekker's Line as the western limit of complex Australo-Papuan continental faunas. Instead, however, while getting the Wallace Line substantially right, he erroneously viewed the Wallacean islands as vicariant remnants of a western extension of a sunken 'great Pacific continent', thus mistakenly treating oceanic Wallacea as continental in origin (Wallace 1860, 1869, 1876). Furthermore, virtually all of the other classic 19th century zoogeographers, such as Salomon Müller, Philip Lutley Sclater, Thomas Henry Huxley, Andrew Dickson Murray, Max Wilhelm Weber and Richard Lydekker, who proposed various faunal boundary lines demarcating the Asian and Australian faunas (Figure 1) in their various writings, treated all marsupial faunas in the Malay Archipelago as natural (Heinsohn 2006a). Indeed, even by the mid 20th century, the only classic zoogeographer known to have demonstrated faint early awareness that some marsupial populations in Wallacea may have been introduced through long-term human agency was Philip Jackson Darlington, who in his classic tome *Zoogeography: The Geographical Distribution of Animals* (1957:468) said, 'Whether some of these marsupials may be introduced on some islands I do not know.'

Latter-day recognition of the status of some oceanic marsupials as introduced species also changes society's ecological perceptions of them. They go from being automatically treated as a benevolent natural part of the environment to being viewed as perhaps out-of-place translocated exotics which may have caused an anthropogenic impact. For example, just as the introduced folivorous common brushtail possum *Trichosurus vulpecula* is recorded to have caused a considerable impact on New Zealand's indigenous forests and wildlife, so to some degree may have another phalangerid possum, the northern common cuscus *Phalanger orientalis*, when it first arrived in New Ireland 23,500 to 20,000 years ago, or when it and other phalangerids were first introduced to other tropical oceanic Indo-Australian islands through long-term human agency. For example, during ecological field work in New Ireland in 1990, the author did notice some indications of possum impacts on some trees due to combined browsing pressure from introduced populations of both *P. orientalis* and the common spotted cuscus *S. maculatus*, with cuscuses actually observed in the process of defoliating the branches of favoured food trees such as *Intsia bijuga* (Heinsohn 1997a, 1998b, 2004a, b).

Indeed, both *P. orientalis* and *S. maculatus*, as adaptable and widely introduced ethnotramp possums in Wallacea and Near Oceania, could be viewed as invasive species, which, among other impacts, could potentially threaten the region's island-endemic phalangerids such as the Papuan subregion's restricted Woodlark Island cuscus *Phalanger lullulae*, or the restricted north Moluccan and Sulawesi subregion phalangerids through interspecific competition. In other instances, the threat may arise from both competition and possible hybridisation, should, for example, the closely related *S. maculatus* be introduced to the island realm of the

endemic Waigeo Island cuscus *Spilocuscus papuensis*. Whatever the case, adaptable ethnotramp species such as *P. orientalis* and *S. maculatus*, and possibly also *S. kraemeri*, particularly with the advent of modern rapid transportation in the region such as motor boats and air services and in the absence of effective biosecurity measures, are likely to continue to expand their ranges. *S. maculatus*, for example, will rapidly invade all of New Ireland, having been subject recently to secondary translocation into the far southern Weiten River Valley (Emmons and Kinbag 2001; Heinsohn 2006a), far beyond the original northern New Ireland invasion frontier (Heinsohn 1998b, 2004a), with new secondary invasion beachheads eventually coalescing until all suitable habitats on New Ireland are occupied and animals spread further afield to other New Ireland satellites such as New Hanover (Lavongai). From New Ireland, *S. maculatus* trade animals and pets will continue to be carried across the St. George's Channel to neighbouring New Britain, where further adventive populations will become established, and these will coalesce eventually into new invasion fronts from whence locally sourced animals will be traded and carried to other parts of New Britain to repeat the whole process of complete invasion of a new landmass. Then New Ireland and New Britain may become launching platforms for the future spread of *S. maculatus* to Bougainville Province and the Solomon Islands, with the species eventually invading much of Near Oceania. Furthermore, a widely traded *S. kraemeri* from Manus Province may increase its range through anthropogenic translocation to other parts of the Bismarck Archipelago, perhaps even coming into contact with *S. maculatus* in some locations to form new hybrid populations.

In the Lesser Sundas, introduced populations of *P. orientalis* on Timor and some of its satellites, where it is used as a valued game animal sold at markets and kept as a pet (pers obs.), may gradually spread to other adjacent islands, perhaps eventually making their way westwards along the Lesser Sundas chain; while in the Solomon Islands, the species may eventually be spread to some of the last uninvaded islands such as those in far southern Rennell and Bellona Province, or those of far eastern Temotu (Santa Cruz) Province, or perhaps even beyond to Vanuatu. Thus, owing to some highly adaptable ethnotramp species and anthropogenic translocation, the marsupial frontier is likely to expand rather than contract and contribute to the general homogenisation of biotas during this recent era of accelerated anthropogenic impacts that some have dubbed the Homogenocene (Samways 1999) or Anthropocene (Crutzen and Stoermer 2000; Ruddiman 2003).

However, such translocations are not necessarily always deleterious to all aspects of an island's biota. Introduction of *P. orientalis* to the Solomon Islands in the mid to upper Holocene, just as many of that archipelago's large endemic murid rats were in decline or going extinct under human impacts (Flannery and Wickler 1990; Flannery 1995b; Spriggs 1997; Flannery and Roberts 1999), may have allowed a timely prey-switch for the endemic Sanford's eagle *Haliaeetus sanfordi* and the fearful owl *Nesasio solomonensis*, both of which are now recorded to habitually prey on the archipelago's introduced cuscuses (Hadden 1981, 2004; Coates 1990; Doughty et al. 1999). Furthermore, even in places such as New Ireland that lacked giant endemic murids, local populations of the white-breasted sea eagle *Haliaeetus leucogaster* have learned to prey regularly on both *P. orientalis* and *S. maculatus*, which now provide a locally abundant additional source of prey (Heinsohn 2000; Beehler et al. 2001). A similar prey-shift by various raptors may have occurred also in Timor, with the mid-Holocene introduction of *P. orientalis* and recorded upper-Holocene extinction (Glover 1971, 1986) of a whole suite of giant endemic murid rats.

Another observation that highlights the adaptability and potential invasiveness of some marsupials is the fact that some successfully established populations of both phalangerids and macropodids have arisen from very small founding populations. The entire population of brushtailed rock wallabies *Petrogale penicillata* on Oahu Island, Hawaii, for example, was established from a single pair that escaped in 1916; while the population of red-necked wallabies *Macropus rufogriseus* that established in the Hunters Hills area of New Zealand's

South Island is attributed to a single male and two females released in 1874 (Maynes 1989; Warburton 2005b). Similarly, the entire population of New Guinean common spotted cuscus *Spiloglossus maculatus* in New Ireland, which now occupies a large swath of the 300 km long island and probably numbers in the tens of thousands, was probably established from only a few individuals, possibly as few as a single pair, or even just a single gravid female or mother with pouch young (Heinsohn 1998b, 2004a, b). Furthermore, in its most far-flung introduced population on Selayar Island in the Sulawesi subregion, *S. maculatus* even manages to coexist with introduced Oriental placental mammals, including scansorial viverids such as the common palm civet *Paradoxurus hermaphroditus*, arboreal sciurids such as the plantain squirrel *Callosciurus notatus* and moderately dense human populations in a highly anthropogenic island environment (Heinsohn 2002a, 2004a). Similar adaptability is demonstrated by *P. orientalis* in Timor, where that species shares that island's significantly anthropogenic environment with the introduced viverid *P. hermaphroditus* and a scansorial cercopithecoid monkey, the long-tailed macaque *Macaca fascicularis* (Heinsohn 2004a, 2005a, b).

On high oceanic islands such as Seram, Buru, Timor, New Britain, New Ireland, Bougainville and Guadalcanal, introduced populations of *P. orientalis* in relative competitive release have also demonstrated considerable ecophysiological adaptability by exhibiting a much greater altitudinal range than occurs in their natural continental context on the New Guinea mainland. For example, whereas *P. orientalis* is found from sea level to 1500 m in New Guinea where its altitudinal range appears to be restricted by competition with specialised montane cuscuses, on Seram it is recorded to occur right up to the limits of forest, just below the 3020 m rocky summit of Mount Binaiya, with these higher altitude populations exhibiting thicker coats than their lowland counterparts (Heinsohn 2005a, b; Heinsohn and Hope 2006).

Just as some marsupials have proved highly vulnerable to threatening processes and extinction, others have proved in the right circumstances to be highly adaptable invasive species that as translocated ethnotramps are bringing about an overall expansion of the marsupial frontier. See the contrast between Figure 7 and Figure 8, the first showing the author's postulated line of natural marsupial distributions, compared with the latter depiction of the contemporary greatly expanded anthropogenic marsupial frontier. Marsupials also push some ethnozoological temporal 'frontiers', in that the world's oldest recorded anthropogenic translocation of an animal is that of the New Guinean cuscus *P. orientalis* to New Ireland in Near Oceania at 23,500 to 20,000 BP. Thus, the world's oldest known ethnotramp species is a humble marsupial that may have been deliberately harnessed for use on oceanic islands as part of an ancient late-Pleistocene game-enhancement production system. Removal of a traditional Eurocentric theoretical blind spot in relation to Australasian mammals reveals that there may be much more to the humble marsupial than meets the eye. They carry a long human history in their pouches.

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