Animal translocation:long-term human influences on the vertebrate zoogeography of Australasia (natural dispersal versus ethnophoresy)

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ABSTRACT

A proposed new term ethnophoresy defines a Late Quaternary biological process that occurs when organisms are able to breach geographical barriers and disperse to new areas by hitching a ride in human vessels or cargo. In this paper a combination of literature analysis, historical research and original fieldwork is used to review the impact of ethnophoresy / anthropogenic animal translocation from ancient times to the present on the vertebrate zoogeography of Wallacea, New Guinea and the Northern Melanesian Islands, referred to collectively as the Circum New Guinea Archipelago. The focus of the paper is on translocated wild rather than domesticated vertebrates. The processes through which these species have been either unwittingly, accidentally or deliberately translocated to new areas are reviewed. Three principal categories of introduced wild species are recognised. These include stowaways, ethnotramps and incidentals. Ethnotramps include economically and culturally favoured animals such as Rusa Deer *Cervus timorensis*, Long-tailed Macaque *Macaca fascicularis*, and various civets, cuscuses, wallabies, cassowaries and wild-caught cage birds that are commonly carried around with humans. Stowaways tend to be smaller species such as shrews, rats or herpetofauna that conceal themselves or their eggs in vessels and cargo. While the Oriental region (or broader Indo-Malayan zoogeographic region) appears to have furnished parts of the Circum New Guinea Archipelago with around 58 introduced wild terrestrial vertebrates, translocation from the latter region has had negligible impact on the zoogeography of the former. Some Wallacean islands and New Guinea, however, have been a significant source of species introduced within the Circum New Guinea Archipelago. While vertebrate translocation appears to be largely a Holocene phenomenon, several New Guinea marsupials appear to have been exported to surrounding islands in the Late Pleistocene, with the earliest suspected translocation being that of the Northern Common Cuscus *Phalanger orientalis* to New Ireland between 10,000 and 20,000 years ago. It is postulated that some ancient human influences may be under-recognised due to the ambiguity of the evidence. An appendix presents some contemporary and suggested new terms in ethnozoology and biogeography.

Key words: Circum New Guinea Archipelago; Quaternary vertebrate zoogeography; ethnozoology; introduced species; animal translocation; ethnophoresy; ethnotramp; symbiosis; commensalism; macro-mutualism.

Introduction

The distribution of wild animals across archipelagos of continental and oceanic islands is typically explained by natural processes including vicariance and dispersal. Vicariance refers to the zoogeographic pattern created by the break-up of former continuous ranges of organisms through the creation of new geographical barriers that then facilitate allopatric speciation. For example, when continental drift leads to the breaking up of larger landmasses into smaller islands, or when rising sea levels turn a formerly continuous landmass into an archipelago of isolated islands (Allaby 1991). This contrasts with zoogeographic patterns due to dispersal from a source area, which may include: active dispersal of animals by moving across land-bridges (or ice-bridges in cooler latitudes), swimming and flying across water barriers; or passive dispersal on natural rafts, unaided floating in currents of water, or carriage by strong winds. A further means of dispersal is through carriage in, or on, the body of another animal through a process known as phoresy (Allaby 1991). A common example includes invertebrate ectoparasites such as lice and mites that attach themselves to a visiting fly in order to be transported to new hosts; or which may undergo long distance dispersal by hosts such as migrating birds or bats. With regard to vertebrates, phoresy typically happens when the eggs of fish or frogs, or the mud in which they have been deposited, adheres to the feet or bodies of migrating waterfowl only to be inadvertently shed at a distant location (Tyler 1976). In marine environments, a further vertebrate, the Sucker-fish or Remora *Remora remora* has a pad on its head by which it attaches itself to large fish or sea turtles (Allaby 1991). When attached to carnivorous fish or sharks, the remora gains the added advantage of being able to pick up food debris; but when attached to a sea turtle, manta ray, or whale shark, the principal advantage appears to be conservation of energy and a more efficient means of travel and dispersal.

A further type of phoresy referred to as 'extended-phoresy' or 'ethno-phoresy' is defined here. This is where animals or their eggs hitch a ride in human cargoes, or human vessels such as watercraft, sleds, carts, motor vehicles or aircraft. The aforementioned remora, for example, will sometimes attach itself to the hull of a boat and hitch a free ride for considerable distances. In relation to terrestrial vertebrates, ethnophoresy may occur inadvertently when animals or their eggs become stowaways in vessels or cargo; or it may occur as a result of deliberate human actions when domesticated animals or captive wild species are shipped as cargo or carried as pets. Upon arrival at a destination, such animals may escape captivity or be deliberately liberated, to potentially found a new population.

When dealing with Quaternary zoogeography, an often overlooked alternative explanation for the distribution of certain wild vertebrates is dispersal by ancient human agency through the aforementioned process of ethnophoresy. There is now a growing body of evidence that humans may have been both deliberately and unwittingly carrying species around with them earlier than previously thought (Flannery and White 1991; Spriggs 1997; Heinsohn 1997, 1998a,b). The five principal means by which humans influence zoogeography are: (1) human-induced habitat modification; (2) direct or indirect human-induced decline / extinction of animal species (eg. through predation, competition or disturbance); (3) translocation of pathogens; (4) co-evolution and domestication; and (5) unintentional or deliberate animal translocation by human agency (ethnophoresy). The focus of this paper is on the ancient and recent translocation by human agency of non-domesticated terrestrial vertebrates into and within the chain of islands that extends to the immediate east of Wallace's Line. This is referred to as the Circum New Guinea Archipelago and includes the Lesser Sundas; Sulawesi subregion; Moluccas; New Guinea and its immediate Papuan satellites; the Bismarck Archipelago; and the Solomon Islands (Figure 1).

The central aim of this paper is to assess the extent to which long-term human influences through ethnophoresy may have influenced vertebrate biotas in the Circum New Guinea Archipelago. Time is treated as a continuum, with both the prehistoric and historical period of human impacts analysed. Due to the often incomplete and ambiguous nature of the scientific and historical evidence, such an assessment may not be an exact science, but rather an exercise in scholarly guesswork with regard to the possible magnitude of long-term human influences. In relation to the distribution of individual taxa, in many cases, only probability statements or expressions of possibility can be made regarding natural versus anthropogenic dispersal; and two or more competing theories of equal weight may have to be considered.

Study Area

The dominant natural vegetation of the Circum New Guinea Archipelago, as defined, is Malesian and Papuasian rainforest and monsoon forest. A combination of climate and human impacts, such as frequent burning and deforestation, has also led to sizeable areas of either natural or anthropogenic savanna and savanna-woodland, particularly in drier or more densely populated parts of the archipelago, such as in parts of the Lesser Sundas (Gressitt 1982; Whitten *et al.* 1987; Monk *et al.* 1997).

Apart from the legacy of continental drift and long-distance dispersal, the biogeography of the region has also been influenced by the dramatic sea level changes of the Cainozoic. While Batchelor (1979) proposed that sea levels may have been depressed by about 200 metres during the Pleistocene, the general consensus is that they probably only fell about 130 metres during the Pleistocene epoch (Chappell 1987; Hope 1996). They may, however, have fallen by a greater amount, during the preceding Tertiary period (Haq *et al.* 1987; Hall 2001). Such Late Cainozoic sea level fluctuations led to a periodic narrowing of many permanent water barriers, created continuous landmasses out of many contemporary subregional archipelagos, and led to the formation of land-bridges between New Guinea and Australia, and continental satellites such as Aru. While continental drift, other tectonic processes, volcanism and sea level changes brought about significant palaeogeographic change, it appears, however, that there was never an Upper Cainozoic land-bridge linking Asian Sundaland with Greater Australia (also called Sahul or Meganesia) (Hall 2001). Furthermore, most of the intervening Wallacean Islands of Eastern Indonesia appear also to have remained comparatively insular and exhibit essentially oceanic vertebrate faunas that are transitional between the Oriental faunas of Sundaland and Australo-Papuan faunas of Meganesia (Musser 1987; Whitten *et al.* 1987; Monk *et al.* 1997).

Methods

A combination of literature review, historical research and the results of original zoogeographic survey and ethnozoological fieldwork in Wallacea and the New Guinea / Northern Melanesian region is used to provide a review of wild vertebrate translocation and anthropogenic biological invasions in the Circum New Guinea Archipelago. Some of the evidence considered for translocation of wild vertebrates by humans includes: (1) patchy or improbable distributions; (2) genetic similarity over wide inter-island distributions that may indicate recent introduction; (3) sudden appearances of species in archaeological sequences; (4) a lack of fossil or subfossil material in palaeontological or archaeological sequences that may indicate recent introduction; (5) 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, trade or ceremonial purposes; (6) island assemblages of vertebrates that favour human-associated species over natural dispersal ability; and (7) direct written or oral historical records of translocation. In the face 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. Because dispersal by human-agency can sometimes mimic recent natural dispersal and vice versa, the ambiguities of these two competing possibilities are discussed in detail.

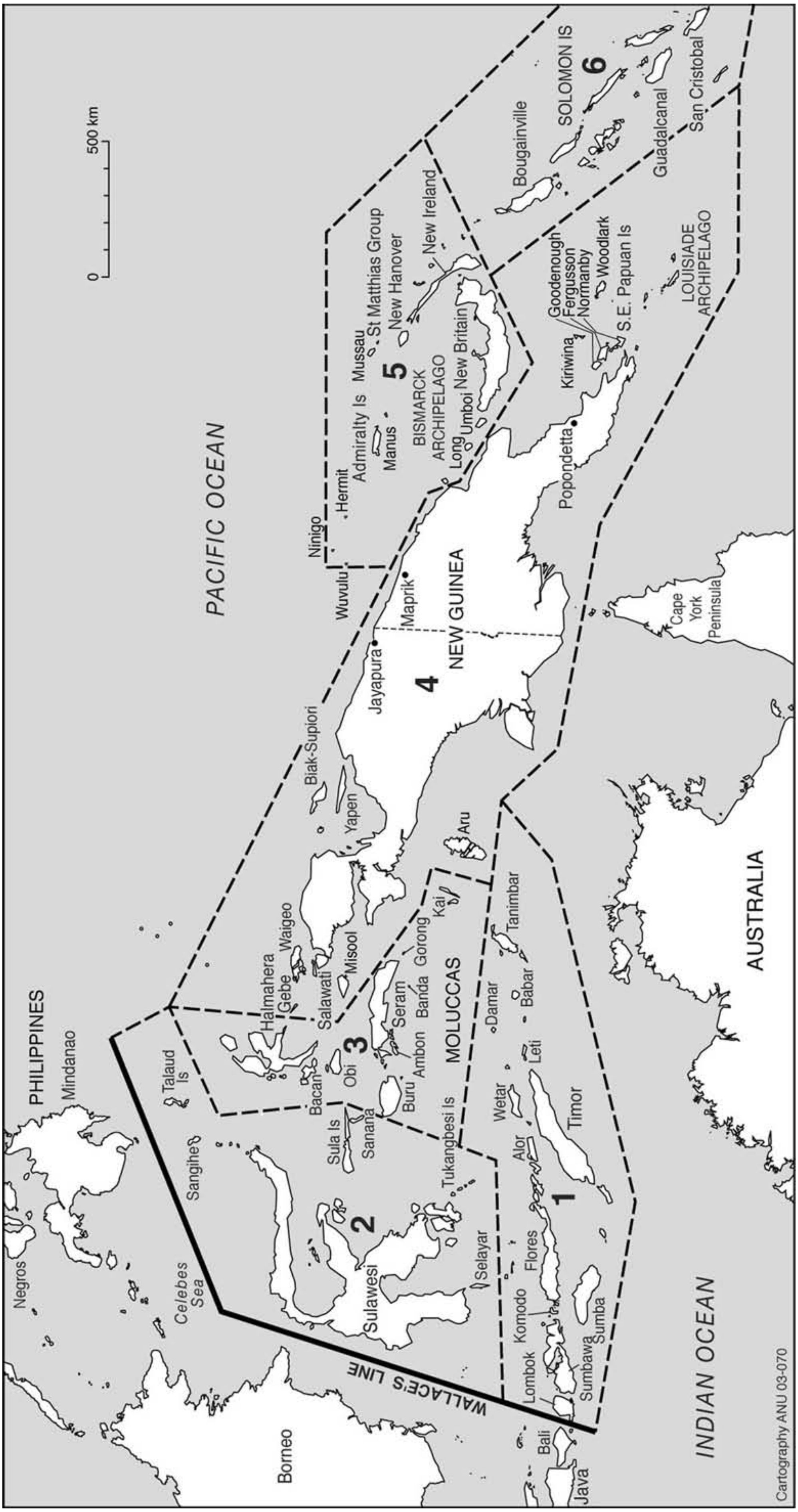

Figure 1. Map of the Circum New Guinea Archipelago. This chain of islands is comprised of the following zoogeographic subregions: (1) Lesser Sundas; (2) Sulawesi; (3) Moluccan; (4) Papuan; (5) Bismarck Archipelago; and (6) Solomon Islands. Wallacea is comprised of (1), (2) and (3).

A captive juvenile male common spotted cuscus (*Spilocuscus maculatus*) being kept as a living larder for future consumption by Nuaulu people in Seram, Indonesia. Utilised throughout most of its range as a game animal, fur-bearing species, food and trade commodity, or pet, this New Guinea centred species appears to have been introduced to much of the oceanic part of its range in the Sulawesi subregion, Moluccas and Bismarck Archipelago through long-term human agency (Photo by Tom Heinsohn).

Motor canoes and other vessels converging on Kavieng market in New Ireland, Papua New Guinea in 1990. Villagers often travel long distances from adjacent archipelagos to sell traditional produce. Cargo may periodically include a variety of captive wild species, such as cuscuses, monitor lizards and birds (Photo by Tom Heinsohn).

Human colonisation and the advent of ethnophoresy in Australasia

The initial invasion of Wallacea and Meganesia (the latter being the combined New Guinean and Australian landmass of the Upper Cainozoic) by *Homo sapiens* is generally thought to have occurred somewhere between 40,000 and 60,000 years ago in the Late Pleistocene (Bellwood 1997; Thorne *et al.* 1999). Recent discoveries on the island of Flores, however, indicate that parts of the Lesser Sundas may possibly have been colonised in the Middle Pleistocene by *Homo erectus* (Bergh *et al.* 1996; Morwood *et al.* 1997; Morwood 2001). In the wake of the colonisation of Meganesia, the Bismarck Archipelago in Near Oceania appears to have been colonised by *Homo sapiens* by about 35,000 years ago, and parts of the Solomon Islands by about 29,000 years ago (Spriggs 1997; Wickler 2001). These initial Pleistocene colonisation episodes may have been significantly aided in places by a narrowing of permanent water barriers due to sea level fluctuations.

Following the relative stabilisation of sea levels in the early Holocene, a further major phase of human colonisation was that of the Austronesian-speaking agricultural and maritime peoples, who expanded into Wallacea, around coastal New Guinea, and into the Pacific Islands in the last 5000 years (Bellwood 1997; Kirch 1997). This was a period that saw the spread of various plant cultivars and the introduction of the domesticated triumvirate of dogs, pigs and chickens into Oceania (Spriggs 1997; Kirch 1997). In Wallacea and Western New Guinea, the Austronesian expansion was followed by ongoing economic and cultural influences from Asia, including the early spice trade, and finally by the impact of the 'modern' spice trade in the last millennium, which involved the mercantile empires of the Chinese, Arabs, Portuguese, Spanish, Dutch and British (Swadling 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). All of these historical phases, including later Australian administration of the Territory of Papua and New Guinea, wartime occupation by the Japanese, and post-war independence for Indonesia, Papua New Guinea and the Solomon Islands have influenced the biotas of the Circum New Guinea Archipelago. The Dutch, British and Germans, for example, contributed to the spread of Rusa Deer *Cervus timorensis* into Melanesia (Downes 1972; Lever 1985; Bentley 1998). Just before the Pacific War, the Australians and British introduced the Cane Toad *Bufo marinus* to Papua New Guinea and the Solomon Islands in a misguided attempt at biological control of agricultural insect pests (Tyler 1994); while during the war the Japanese apparently widely introduced the Giant African Snail *Achatina fulica* in Melanesia as an emergency food source for hungry troops (Downs 1986; Lever 1994; Heinsohn 1998b). Furthermore, Indonesia's ambitious transmigration program of recent decades has probably contributed to the spread of new commensals, such as some murid rats to far provinces, as has recent land and resource development and shipping in Papua New Guinea and the Solomon Islands.

Reconstructions of early prehistoric watercraft are based mostly on images in scattered Australasian rock art sites that appear to depict people in dugout canoes or sitting or standing on rafts. Many appear to be of Holocene age (less than 10,000 years old) or are not adequately dated due to the difficulty of directly dating rock art. Other archaeological evidence in the form of preserved tools, such as shell and stone adzes, has provided possible indirect evidence of prehistoric watercraft-building technology. Another source comes from ethnohistorical and ethnographic records of traditional Asia-Pacific watercraft, such as those documented in Haddon and Hornell (1975) and Hawkins (1982); and those remembered or still made within contemporary cultures. Though contemporary, and not necessarily a direct link with the deep past, such ethnographic information has been used to speculate on possible levels of raft, canoe or sailing vessel technology stretching back into the earlier Holocene and Late Pleistocene (older than 10,000 years). A further impetus for speculation regarding reasonably advanced early watercraft technology comes from the fact that humans appear to have prehistorically colonised some vast oceanic areas, including much of the Bismarck Archipelago and parts of the Solomon Islands during the Late Pleistocene (Spriggs 1997; Wickler 2001), prior to the Holocene colonisation of most of the rest of Oceania (Kirch 1997). Whether early watercraft technology was limited to wood, bark, reed and bamboo rafts or included bark and dugout canoes or wind propulsion may never be known, but the mere act of early inter-island colonisation through the agency of some form of watercraft, makes ancient anthropogenic animal dispersal by early ethnophoresy a distinct possibility.

Prehistoric ethnophoresy is made all the more likely by the agency of inter-island boat traffic involved in various trade networks, that in many cases appears to have intensified in the Upper Holocene following the Austronesian expansion. Salient archaeologically or ethnographically recorded examples include: west to east networks across the Indonesian archipelago from the Asian mainland and western Indonesian islands to as far east as New Guinea; or south to north networks between Indonesia, the Philippines and mainland Asia (Swadling 1996); or well recorded local Melanesian networks such as those of the Vitiaz Strait which linked New Britain, Umboi and the Siassi Islands with the New Guinea mainland (Harding 1967; Lilley 1986); and the Kula network which linked the Southeast Papuan Islands with the adjacent New Guinea mainland (Malinowski 1922; Egloff 1979). As well as carrying manufactured trade goods and agricultural produce, vessels involved in such networks also carried a wide array of extracted natural resources, and sometimes included captive wild animals as part of their cargo. Often intermixed with trading were various long-distance fishing routes, such as those used by the Macassans of South Sulawesi, who travelled vast distances to exploit trepang (sea cucumber) fishing grounds as far east as northern Australia (MacKnight 1976).

A further point is that movements of people were not necessarily completely biased in a west to east direction during the Holocene and Late Pleistocene. There may have been some east to west back-migration by New Guinea centred Papuan-speaking peoples to some of the adjacent Wallacean Islands. Such movements, in combination with trade networks, may have contributed to the westward spread of some introduced Papuan species into Wallacea.

The mechanisms of ethnophoresy in Australasia

The three principal means by which non-domesticated vertebrates are translocated to new landmasses through human agency are: (1) unwittingly as stowaways in vessels or cargo; (2) accidentally as escaped captives or pets; and (3) deliberately as species introduced as part of a 'game-park' or game enhancement strategy. Heinsohn (1997, 1998a,b) recognises three categories of introduced species. These include 'stowaways', 'ethnotramps' and 'incidentals'. 'Stowaways' are usually small animals such as frogs, lizards, snakes, passerine birds, rodents and shrews; they are typically commensal species that live in and around human structures or they may be littoral species that enter canoes and boats that have been beached amidst the vegetation of the sea shore. Beached canoes and boats with thatch shelters on their decks may also be particularly predisposed to stowaways given the propensity of thatch to be colonised by small vertebrates and their eggs (Loveridge 1946; Heinsohn 1998b). Alternatively, stowaways may also include commensal or non-commensal species or their eggs caught up in cargoes carried from inland areas. Potted plants, containers of rice, bunches of bananas, other agricultural produce and traditional building materials such as bundles of timber, bark and thatch are ancient cargoes that are particularly prone to infestation with stowaways. Some examples of stowaways include: commensal frogs such as the Asian Painted Frog *Kaloula pulchra* and Asian Commensal Tree Frog *Polypedetes leucomystax*; commensal lizards such as the Asian House Gecko *Hemidactylus frenatus*; the commensal fossorial Flowerpot Snake *Ramphotyphlops braminus*; the House Sparrow *Passer domesticus* and Tree Sparrow *Passer montanus*; commensal murid rodents such as the Pacific Rat *Rattus exulans* and Black Rat *Rattus rattus*; and shrews such as the House Shrew *Suncus murinus*.

'Ethnotramps' are economically and culturally favoured wild animals that are commonly captured live and carried around with humans as pets or for food, trade or ceremonial purposes (Heinsohn 1997, 1998a). This strong association with humans often leads to greatly expanded geographical ranges as captives escape to establish new populations or are deliberately released as part of a 'game park' strategy. Such strategies may enable new animal products such as meat, pelts, fibre, plumes, bone, horn, antler, and musk to be produced on oceanic islands that are lacking in game; and deliberately introduced predators may provide a valuable service as rat-catchers or agents of biological control. Furthermore, in addition to many commensals that may be captured in the vicinity of settlements, ethnotramps also include species such as cassowaries that are typically captured in the deep bush beyond fields and gardens. Infrequently transported captives that have formed minor rather than widespread introduced populations are referred to as 'incidentals'. Some examples of ethnotramps include: the Rusa Deer *Cervus timorensis*; Long-tailed Macaque *Macaca fascicularis*; Malay Civet *Viverra tangalunga*; Little Civet *Viverricula indica*; Palm Civet *Paradoxurus hermaphroditus*; Northern Common Cuscus *Phalanger orientalis*; Common Spotted Cuscus *Spilocuscus maculatus*; Admiralty Cuscus *Spilocuscus kraemeri*; Northern Pademelon *Thylogale browni*; Dusky Pademelon *Thylogale brunii*; Agile Wallaby *Macropus agilis*; and cassowaries such as the Double-wattled Cassowary *Casuarius casuarius* and Dwarf Cassowary *Casuarius bennetti*. Several species of volant birds within the finch family (Estrildidae), bulbul family (Pycnonotidae), myna family (Sturnidae), pigeon family (Columbidae), parrot family (Psittacidae), and cockatoo family (Cacatuidae) could also be regarded as ethnotramps due to their popularity as traded wild-caught cage birds within the Circum New Guinea Archipelago and their occurrence as introduced species in a number of localities.

Although 'stowaways' and 'ethnotramps' have been differentiated above, it is proposed here that the term ethnotramp be used in a more general sense to include any species that is regularly translocated and dispersed by human agency. Thus classic stowaway species such as the Asian House Gecko *Hemidactylus frenatus*, or deliberately translocated species such as the Rusa Deer *Cervus timorensis* may both be generally referred to as ethnotramps. This then covers species such as the Pacific Rat *Rattus exulans* and Large Spiny Rat *Rattus praetor*, that may have been prehistorically dispersed both deliberately as a food animal, and inadvertently as a stowaway in vessels and cargo (Flannery 1995a; Heinsohn 1998a,b; White *et al.* 2000).

Results

A survey of records of wild vertebrate translocation

In the Circum New Guinea Archipelago, three principal centres of origin are recognised for introduced wild vertebrates. These include: (1) the Oriental zoogeographic region islands of Western Indonesia, and in particular, Java and Bali; (2) the Wallacean / Australasian island of Sulawesi; and (3) the large Australasian island of New Guinea (Northern Meganesia) and its continental satellites which collectively comprise the Papuan zoogeographic subregion. Other minor centres of origin for introduced species include Australia (Southern Meganesia) and various Australasian region oceanic islands and archipelagos with their own endemic species. Certain species, however, such as some widespread or pan-tropical geckos and skinks, are difficult to attribute to any particular centre of origin. A survey of records of actual and postulated translocations of non-volant or weakly volant species from various centres of origin is presented in Table 1. Because strongly volant vertebrates conform less to traditional zoogeographic boundaries and have a more complex pattern of distribution, they are considered separately (Table 2).

Table 1: Records of translocation of non-volant or weakly volant wild terrestrial vertebrates in the Circum New Guinea Archipelago

Species	Original source	Where introduced	Context
Eurasian and Oriental exports			
Cervidae			
Rusa Deer *Cervus timorensis*	Java / Bali	Lesser Sundas; Sulawesi; Moluccas; New Guinea; Bismarck Archipelago	Prehistoric through to historic times. Carried as captives and deliberately introduced to many areas as a venison and game animal (1, 2, 4, 5, 6, 7, 8, 9, 11, 22, 23, 26, 27, 43, 44, 45, 49).
Barking Deer *Muntiacus muntjak*	Western Indonesia / Java / Bali	Lombok	Probably introduced into Lombok in protohistoric / historic times by the Balinese Rajas as a game species (1, 2, 6, 7, 9, 48).
Suidae			
Indonesian Wild Pig *Sus scrofa vittatus*	Western Indonesia	Lombok; Sumbawa; Komodo	Probably introduced prehistorically to its patchy island occurrences in the Lesser Sundas as a food or trade animal (9, 17).
Cercopithecidae			
Long-tailed Macaque *Macaca fascicularis*	Western Indonesia	Lesser Sundas	Prehistoric to protohistoric and historic period. Probably carried as pet and food animal (1, 2, 9, 17, 23, 43, 44, 45, 49).
Silvered Leaf Monkey *Trachypithecus auratus*	Western Indonesia / Java / Bali	Lombok	Probably introduced into Lombok in protohistoric / historic times by the Balinese Rajahs (1, 2, 7, 9, 48).
Viverridae			
Common Palm Civet *Paradoxurus hermaphroditus*	Western Indonesia	Lesser Sundas; Sulawesi Sub-region; Moluccas; Kai; Aru	Probably introduced from the latter part of the Holocene to the protohistoric period as a rat-catcher (1, 2, 4, 5, 6, 7, 8, 9, 11, 17, 21, 22, 23, 26, 43, 44, 45, 49).
Malay Civet *Viverra tangalunga*	Western Indonesia	Sulawesi; Moluccas	Probably introduced from the Late Holocene to protohistoric / early historic period as a trade animal valued as a source of 'civet' a musk-like substance used in perfume (1, 2, 4, 5, 6, 7, 8, 17, 21, 22, 23, 26, 49).
Little Civet *Viverricula indica*	Western Indonesia	Lombok; Sumbawa	Probably introduced from the Late Holocene to protohistoric period as a trade animal valued as a source of 'civet' a musk-like substance used in perfume (1, 2, 4, 6, 7, 9, 17, 49).
Herpestidae			
Small Asian Mongoose *Herpestes javanicus*	Southeast Asia / Java / Bali	Ambon; ?Komodo	Probably introduced in protohistoric or historic times as a rat-catcher (6, 26, 38, 49).
Felidae			
Leopard Cat *Felis bengalensis*	Western Indonesia / Java / Bali	Lombok	Probably introduced during Holocene prehistoric, protohistoric or historic times as pets or traded captives (9, 49).
Manidae			
Malayan Pangolin *Manis javanica*	Western Indonesia / Java / Bali	Lombok	Probably introduced during Holocene prehistoric, protohistoric or historic times as captives traded for their meat, and the medicinal value of their scales (1, 2, 9).
Soricidae			
House Shrew *Suncus murinus*	Asia / Western Indonesia	Lesser Sundas; Sulawesi Sub-region; Moluccas; ?New Guinea; Micronesia; Madagascar; East Africa	Probably introduced to various islands from prehistoric to historic times as a stowaway in cargo, canoes, sailing praus and ships (2, 4, 5, 6, 7, 8, 11, 17, 21, 49, 51).
Javan Shrew *Crocidura maxi*	Southern Indonesian Islands	Ambon; Kai; Aru	Probably introduced as a stowaway in cargo or watercraft (11).
Sunda Shrew *Crocidura monticola*	Western and southern Indonesian islands	Ambon; Obi	Probably introduced as a stowaway in cargo or watercraft (11).

Species	Original source	Where introduced	Context
Hystricidae			
Javan Porcupine *Hystrix javanica*	Java; Madura; Bali	Sulawesi; (?I)Tanahdjampea; (?I)Lombok; (?I)Sumbawa; (?I)Flores	Probably introduced during prehistoric, protohistoric or historic times as captives carried for food or trade (1, 2, 6, 9, 21).
Sciuridae			
Prevost's Squirrel *Callosciurus prevostii*	Western Indonesia	Sulawesi	Probably introduced in Holocene prehistoric, protohistoric or historic times as captives carried as pets or for food, or possibly as stowaways in agricultural cargoes (1, 2, 6, 21).
Plantain Squirrel *Callosciurus notatus*	Western Indonesia	Lombok; Selayar	Probably introduced in Holocene prehistoric, protohistoric or historic times as captives carried as pets or for food, or possibly as stowaways in agricultural cargoes (1, 2, 9, 21, 49).
Muridae			
Pacific Rat *Rattus exulans*	Southeast Asia	Indonesian islands; New Guinea; Melanesia; Polynesia; Micronesia	Probably mostly introduced in the Holocene as a stowaway in canoes and praus and possibly also as a deliberately transported food animal (1, 2, 4, 5, 6, 11, 12, 15, 17, 28, 29, 43, 46).
Himalayan Rat *Rattus nitidus*	Himalayas / Asia	Sulawesi; Seram; New Guinea; Palau	Holocene. Probably introduced as stowaways in cargo and captives kept as food (6, 17, 21).
Asian House Rat *Rattus tanezumi*	Southeast Asia	Micronesia; Moluccas; New Guinea	Holocene. Probably introduced as stowaways in cargo or watercraft and captives kept as food (11, 49).
Rice-field Rat *Rattus argentiventer*	Southeast Asia	Lesser Sundas; Sulawesi Subregion; Moluccas; New Guinea	Holocene. Probably introduced as stowaways in cargo and captives kept as food (4, 5, 6, 9, 11, 12, 17, 21, 29).
Black Rat *Rattus rattus*	East Asia	Throughout the world and study area	Holocene. Introduced mostly as stowaways in cargo and watercraft, with a major expansion during historic times (2, 4, 5, 6, 7, 11, 12, 17, 21, 29).
Brown Rat *Rattus norvegicus*	East Asia	Scattered throughout the world and study area, preferring ports and urban centres	Holocene. Introduced mostly as stowaways in cargo and watercraft, with a major expansion during historic times (2, 4, 5, 6, 7, 11, 12, 17, 21, 29).
House Mouse *Mus musculus*	Eurasian continent	Throughout the world including many parts of the study area	Holocene. Introduced mostly as stowaways in cargo and watercraft, with a major expansion during historic times (2, 4, 5, 6, 7, 9, 11, 12, 21, 29).
Asian House Mouse *Mus castaneus*	Southern Asia	Philippines; Indonesian islands	Introduced from prehistoric times to the present, mostly as stowaways in cargo and watercraft (9, 17).
Ryukyu Mouse *Mus caroli*	Southeast and East Asia	Western Indonesian islands; Flores	Holocene. Probably mostly introduced in protohistoric or historic times as a stowaway in cargo (17).
Phasianidae			
Red Jungle Fowl *Gallus gallus* (Wild form)	Southeast Asia / Western Indonesia	(?I)Wallacea; (Domesticated form widely dispersed beyond Southeast Asia into Oceania)	Probably introduced in prehistoric times as a meat and egg-bearing species. Bird also traded for its plumes and for pets used in the sport of cock fighting (25, 33).
Green Jungle Fowl *Gallus varius*	Southwestern Indonesian islands	Cocos-Keeling Islands; (?I)Some Lesser Sunda islands	??Possibly introduced to parts of Lesser Sundas in prehistoric or protohistoric times as escaped or liberated captives. Valued as a meat, plume and egg-bearing species (33).
Boidae - Pythoninae			
Reticulated Python *Python reticulatus*	Asia / Indonesian Islands	(?I)Some Wallacean islands	This species is a good swimmer and natural disperser, however, as it is carried around as a food animal and rat-catcher, some of its occurrences on Wallacean islands possibly due to human agency (1, 2).

Species	Original source	Where introduced	Context
Elapidae			
Monocled Cobra *Naja naja sputatrix*	West Malaysia / Indonesian Islands	(?I)Some Wallacean islands	As captives are transported for their skins, medicinal products and for ceremonial purposes, some occurrences on Wallacean islands may be due to human agency (1, 2).
Typhlopidae			
Flowerpot Snake *Ramphotyphlops braminus*	Widespread, occuring in Asia; Africa; Mexico; Oceania	Many islands of the Circum New Guinea Archipelago	Probably a comparatively recent introduction in many places as stowaways in horticultural cargoes of potted plants (34, 35, 36, 37, 38, 39, 50).
Varanidae			
Water Monitor *Varanus salvator*	Sri Lanka, India, SE Asia, Southern China, Philippines, Indonesia.	(?I)Some Wallacean islands	This species is a good swimmer and natural disperser, however, as it is carried around as a food animal and is heavily exploited for its valuable skin, some of its occurrences on Wallacean islands may possibly be due to human agency (1, 2).
Gekkonidae			
Asian House Gecko *Hemidactylus frenatus*	Widespread, occurring in Asia; Africa; Central America; Oceania; and some Indian Ocean islands	Many islands of the Circum New Guinea Archipelago	Probably a comparatively recent introduction in many places such as the Solomon Islands where brought in as a stowaway in vessels or their cargo (34, 35, 36, 37, 38, 40, 50).
Bleeker's Gecko *Hemiphyllodactylus typhus*	South and Southeast Asia; and Indo-Pacific archipelagos	Hawaii & some other islands of Outer Oceania; (?I) Some islands of the Circum New Guinea Archipelago	This species may have been introduced to parts of its oceanic range as a prehistoric stowaway in vessels or their cargo (35, 36).
Mourning Gecko *Lepidactylus lugubris*	South and Southeast Asia; Indo-Pacific archipelagos; and Central America	(?I) Possibly introduced to some parts of the Circum New Guinea Archipelago; and some parts of Oceania	This species may have been introduced to parts of its oceanic range as a prehistoric stowaway in vessels or their cargo (2, 50).
Wiegmann's Gecko *Gehyra mutilata*	Widespread occurring in Asia; Mexico; Madagascar; New Guinea; Oceania	Many islands of the Circum New Guinea Archipelago	Probably a recent introduction in many places such as the Solomon Islands where brought in as a stowaway in vessels or their cargo (36, 38, 40, 50).
Schneider's Gecko *Cosymbotus platyurus*	Oriental Region; Indonesian Islands	(?I)Some islands in the Circum New Guinea Archipelago	This commensal species may have been introduced to parts of its range in the Circum New Guinea Archipelago as a stowaway in vessels or their cargo (38, 40).
Scincidae			
Asian Commensal Skink *Mabuya multifasciata*	Oriental Region; Indonesian Islands	(?I)Some islands in the Circum New Guinea Archipelago	This commensal species may have been introduced to parts of its range in the Circum New Guinea Archipelago as a stowaway in vessels or their cargo (38, 40)
Ranidae			
Indonesian Ranid Frog *Rana cancrivora*	Western Indonesian islands	Sulawesi; (?I)Some other Wallacean islands; Western New Guinea	Probably introduced as a stowaway in cargo (21, 38, 51).
Indonesian Ranid Frog *Rana erythraea*	Western Indonesian islands	Sulawesi; (?I)Some other Wallacean islands	Probably introduced as a stowaway in cargo (21).
Oriental Ranid Frog *Rana limnocharis*	Oriental Region; Indonesian Islands	(?I)Some Wallacean islands	Probably introduced as a stowaway in cargo (38).

Species	Original source	Where introduced	Context
Rhacophoridae			
Asian Commensal Tree Frog *Polypedates leucomystax*	Western Indonesian islands	Sulawesi; Timor; (?I)Some other Wallacean islands; New Guinea	Probably introduced as a stowaway in cargo (21, 30, 38, 41).
Microhylidae			
Asian Painted Frog *Kaloula pulchra*	Southeast Asia / Indonesian islands	Sulawesi; Flores; (?I)Some other Wallacean islands	Probably introduced as a stowaway in cargo (21, 38).
Sulawesi exports			
Suidae			
Babirusa *Babyrousa babyrussa*	Sulawesi / Sula Islands	Buru; (?I)Sula Islands	Probably introduced to Buru in the Central Moluccas in prehistoric or protohistoric times as a game species or ceremonial trade animal. Possibly also introduced to the Sula Islands, although the Sula populations may be due to natural dispersal (4, 6, 18, 49).
Celebes Wild Pig *Sus celebensis*	Sulawesi	Halmahera; Flores; Timor; Simeulue Island north-west Sumatra	Probably introduced to its patchy distribution in the North Moluccas, Lesser Sundas and Greater Sundas through traded captives (6, 17).
Cercopithecidae			
Sulawesi Crested Black Macaque *Macaca nigra*	Sulawesi	Bacan	Probably introduced to Bacan in the North Moluccas in prehistoric or protohistoric times through pets carried on trading praus (1, 2, 7, 11, 23, 49).
Phalangeridae			
Sulwesi Bear Cuscus *Ailurops ursinus*	Sulawesi	(?I)Salebabu Island in the Talaud Group	The remote and patchy occurrence on Salebabu Island in the Talaud Group may possibly be due to prehistoric introduction as animals carried for food or trade. Alternatively, the patchy and disjunct Talaud population may possibly be relict and due to natural dispersal (1, 2, 3, 11).
Moluccan exports			
Colubridae			
North Moluccan Water-snake *Tropidonophis truncatus*	Halmahera and satellites	(?I) Salawati	Possibly introduced to Salawati in the Papuan zoogeographic subregion (54).
Lesser Sunda internal translocations			
Crocodylidae			
Indopacific Estuarine Crocodile *Crocodylus porosus*	Indo-Pacific Archipelago: India; Sri Lanka;mainland Southeast Asia; Philippines; Indonesian islands; New Guinea; Melanesian islands; northern Australia	(?I) Lake Ira Lalaro	A reputed crocodile population, probably *C. porosus*, in a topographically isolated semi-montane Lake Ira Lalaro at approximately 250 metres above sea level in far eastern East Timor may be due to human agency, that is, young crocodiles were possibly translocated in from coastal habitats. In parts of Timor the crocodile is regarded as a sacred totemic animal and may have once been used in ceremonial practices (unpublished ethnographic notes). Alternatively, the crocodiles may have entered the lake through subterranean watercourses in the largely limestone terrain or may have been stranded by tectonic processes, although this seems unlikely.
New Guinea / Papuan exports			
Muridae			
Large Spiny Rat *Rattus praetor*	New Guinea	Parts of the Bismarck Archipelago and Solomon Islands	Probably introduced prehistorically as stowaways in watercraft or captives kept as food (11, 12, 15, 16, 46, 52).

Species	Original source	Where introduced	Context
Phalangeridae			
Common Spotted Cuscus *Spilocuscus maculatus*	New Guinea	St. Matthias Group; New Ireland; Selayar; Kai; Buru; Ambon; (?I)Seram; Banda; Pandjang; Tioor	Probably introduced to much of its oceanic distribution from prehistoric to recent times as escaped or liberated captives carried as pets or for food, trade and stock purposes (1, 2, 3, 11, 15, 21, 43, 46, 49).
Admiralty Cuscus *Spilocuscus kraemeri*	?New Guinea / Papuan Subregion	(?I) Admiralty Islands; Hermit Islands; Ninigo Group; and Wuvulu	May have been introduced in prehistoric times, possibly as early as the Late Pleistocene, as escaped or liberated captives carried as pets or for food, trade and stock purposes (1, 2, 3, 11, 46). Alternatively, ancestors of *S. kraemeri* may have naturally dispersed to part of the Manus Province Archipelago on a natural raft, prior to being more widely dispersed across the archipelago by Late Quaternary human agency.
Northern Common Cuscus *Phalanger orientalis*	New Guinea	Solomon Islands; Bismarck Archipelago; Timor; Leti; Wetar; Babar; Kai; Sanana; Buru; Seram; Ambon; Saparua; Gorong; Banda	Probably introduced from Late Pleistocene to Holocene times as escaped or liberated captives carried as pets or for food, trade and stock purposes (1, 2, 3, 11, 15, 16, 17, 19, 43, 44, 45, 46, 49).
Woodlark Cuscus *Phalanger lullulae*	Woodlark Island	(?I)Alcester Island	Possibly transported as a pet or for food, trade or stock purposes (1, 2, 3, 11).
Petauridae			
Sugar Glider *Petaurus breviceps*	New Guinea	(?I)Halmahera; (?I)Some other New Guinea satellites	Possibly introduced in prehistoric or protohistoric times as escaped pets or captive food animals (1, 2, 3, 11, 13, 49).
Macropodidae			
Huon Tree-kangaroo *Dendrolagus matschiei*	New Guinea	Umboi	Probably introduced in Holocene times as escaped or liberated captives carried as pets or for food or trade purposes (1, 2, 3, 5, 19, 20).
Northern Pademelon *Thylogale browni*	New Guinea	Bagabag; Umboi; New Britain; New Ireland; New Hanover	Probably introduced in prehistoric times as escaped or liberated captives carried as pets or for food, trade or stock purposes (1, 2, 3, 11, 14, 15, 16, 20, 46).
Dusky Pademelon *Thylogale brunii*	New Guinea / Aru	Kai Islands	Probably introduced in prehistoric or protohistoric times as escaped or liberated captives carried as pets or for food, trade or stock purposes from Aru (1, 2, 3, 20).
Brown Dorcopsis *Dorcopsis muelleri*	New Guinea / Misool	(?I)Halmahera; (?I)Gebe. Now extinct on both islands.	Possibly introduced in prehistoric times as escaped or liberated captives carried as pets or for food, trade or stock purposes (3, 10, 13).
Agile Wallaby *Macropus agilis*	New Guinea	Goodenough; Fergusson; Normanby; Kiriwina	Probably introduced in prehistoric times as escaped or liberated captives carried as pets or for food, trade or stock purposes (1, 2, 3, 11, 20).
Peroryctidae			
Common Spiny Bandicoot *Echymipera kalubu*	New Guinea	(?I) Admiralty Islands	Possibly introduced to the Admiralty Islands in the Late Pleistocene through escaped or liberated captives carried as food (1, 2, 3, 11, 46).
Rufous Spiny Bandicoot *Echymipera rufescens*	New Guinea / Aru	(?I)Kai Islands	Possibly introduced in prehistoric times as escaped or liberated captives carried for food or trade purposes from Aru (1, 2, 3, 11).
Tachyglossidae			
Short-beaked Echidna *Tachyglossus aculeatus*	New Guinea / Meganesia	(?I) Areas north of New Guinea's central cordillera	Humans may have translocated this species across the formidable mountain barrier of the central cordillera from its natural range in southern New Guinea (12).

Species	Original source	Where introduced	Context
Casuariidae			
Double-wattled Cassowary *Casuarius casuarius*	New Guinea / Aru	Seram	Probably introduced in Holocene prehistoric or protohistoric times as traded captives valued for their meat, plumes and bones (1, 2, 3, 31, 32, 33).
Dwarf Cassowary *Casuarius bennetti*	New Guinea	New Britain	Probably prehistorically introduced as traded captives valued for their meat, plumes and bones (1, 2, 3, 31, 32).
Boidae - Pythoninae			
Amethystine Python *Morelia amethistinus*	New Guinea and some surrounding islands / Northeastern Australia	(?I)Some Circum New Guinea islands	This species is a good swimmer and natural disperser, however, as it is carried around as a food animal, some of its occurrences on Circum New Guinea islands may possibly be due to human agency (1, 2).
Colubridae			
Brown Tree Snake *Boiga irregularis*	New Guinea / Meganesia and satellites	Guam; (?I) Some islands of the Circum New Guinea Archipelago	Recorded to have been historically translocated to Guam in the early 1950s through stowaways in ships, aircraft or their cargo (24). This species appears to be a reasonably good natural disperser on natural rafts etc., however, as it can adopt a semi-commensal niche in and around human settlements and structures, and is known to stowaway in cargoes and vessels, including the hulls and rigging of large sailing canoes and praus, some of its non-continental distributions may be due to long-term human agency, possibly stretching back into the prehistoric past (2, 51)
Varanidae			
Mangrove Monitor *Varanus indicus*	New Guinea and surrounding islands	(?I)Some Circum New Guinea islands	This species is a good swimmer and natural disperser, however, as it is carried around as a food animal, and is extensively exploited for its skin, some of its occurrences on Circum New Guinea islands may be due to human agency (1, 2, 47).
Scincidae			
Northern Skink *Carlia fusca*	New Guinea / New Britain	Bougainville; (?I)Timor;	Probably a comparatively recent introduction into Bougainville as stowaways in cargo (36, 40).
Hylidae			
Papuan Giant Green Tree Frog *Litoria infrafrenata*	New Guinea and some surrounding islands	Java; (?I) some New Guinea satellites	There is a historical record of introduction to Java, possibly as a stowaway in horticultural material or other cargo (53).
Australo-Torresian Giant Green Tree Frog *Litoria caerulea*	Southern New Guinea; and northern and eastern Australia	(?I) Isolated populations on the north coast of New Guinea (eg. Jayapura and Maprik)	Isolated populations on the north coast of New Guinea may be due to translocation of stowaways in shipping, agricultural cargo or possibly Second World War military supplies (30, 41)
Australian exports			
Elapidae			
Eastern Brown Snake *Pseudonaja textilis*	Northern Australia / (?Though apparently absent from Southern New Guinea savanna-woodland areas, it may occur there)	(?I) Northern coast of Southeast Papua, far-eastern New Guinea (Popondetta to Dogura strip)	Possibly an accidental introduction in military cargo brought in during the Second World War, or possibly a natural relict population stranded in the isolated Popondetta to Dogura savanna-woodland area (51).

Species	Original source	Where introduced	Context
American exports			
Bufonidae			
Cane Toad *Bufo marinus*	South and Central America	New Guinea; Bismarck Archipelago; Solomon Islands	Deliberately introduced in the 1930s and 1940s in a misguided effort to control agricultural insect pests (24, 30, 41, 42).

Sources: (1) Heinsohn 1998a; (2) Heinsohn 1998b; (3) Heinsohn 1997; (4) Nowak 1991; (5) Honacki *et al*. 1982; (6) Corbet & Hill 1992; (7) Laurie & Hill 1954; (8) Carter *et al*. 1945; (9) Kitchener *et al*. 1990; (10) Flannery *et al*. 1998; (11) Flannery 1995a; (12) Flannery 1995b; (13) Flannery *et al*. 1995; (14) Flannery 1992; (15) Flannery & White 1991; (16) Flannery *et al*. 1988; (17) Groves 1984; (18) Groves 1980; (19) Koopman 1979; (20) Maynes 1989; (21) Whitten *et al*. 1987; (22) Ellen 1993; (23) Wallace 1869; (24) Lever 1994; (25) Lever 1987; (26) Lever 1985; (27) Bentley 1998; (28) Atkinson 1985; (29) Menzies & Dennis 1979; (30) Menzies 1975; (31) del Hoyo *et al*. 1992; (32) White 1975; (33) Coates & Bishop 1997; (34) Loveridge 1946; (35) Gibbons 1985; (36) McCoy 1980; (37) Edgar & Lilley 1993; (38) Auffenberg 1980; (39) Welch 1988; (40) Welch *et al*. 1990; (41) Zweifel & Tyler 1982; (42) Tyler 1994; (43) Bellwood 1997; (44) Glover 1986; (45) Glover 1971; (46) Spriggs 1997 (47) Green & King 1993; (48) Hartert & Everett 1896; (49) Monk *et al*. 1997; (50) Allison 1996; (51) Menzies 1996 (52) White *et al.* 2000; (53) Tyler 1976; (54) Aplin 1998.

(?I) = Possibly introduced

Table 2: Some recorded translocations of strongly volant wild vertebrates in the Circum New Guinea Archipelago

Species	Main Range	Where introduced?	Context
Eurasian and Oriental exports			
Pycnonotidae			
Sooty-headed Bulbul *Pycnonotus aurigaster*	Southern China to Southeast Asia as far as Java and Bali	Sulawesi; other Wallacean islands; New Guinea	Introduced as escaped or liberated cage birds (1, 2, 3, 12)
Yellow-vented Bulbul *Pycnonotus goiavier*	Southeast Asia, including Philippines, and Greater Sundas and Lesser Sundas.	Sulawesi; (?I)Lombok	Introduced as escaped or liberated cage birds (1, 2, 3)
Passeridae			
Tree Sparrow *Passer montanus*	Eurasian continent; Sumatra; Java; Bali	Sulawesi; Lesser Sundas; Moluccas; New Guinea	Dispersed as cage bird, and stowaway in the cargo holds of ships (1, 2, 3, 10, 12)
House Sparrow *Passer domesticus*	Widespread (originally Eurasian and Mediterranean regions)	New Guinea	Dispersed as cage bird, and stowaway in the cargo holds of ships (1, 2, 4, 12)
Estrildidae			
Java Sparrow *Padda oryzivora*	Java; Bali	Lesser Sundas; Sulawesi; Moluccas	Introduced as escaped or liberated cage birds (1, 2, 3)
Chestnut Munia *Lonchura malacca*	South and southeastern Asia, including Philippines and Greater Sundas	Ambon; (?I)Halmahera	Introduced as escaped or liberated cage birds (1, 2)
Red Avadavat *Amandava amandava*	Southeast Asia including Greater and Lesser Sunda islands	(?I)Populations east of Wallace's Line may be due to early introduction	Introduced as escaped or liberated cage birds (1, 2)
Sturnidae			
Common Starling *Sturnus vulgaris*	Eurasia; Introduced population in Australia	New Guinea	Vagrants from historically introduced population in Australia (4, 6, 12)
Common Myna *Acridotheres tristis*	South and Southeast Asia	New Guinea; Solomon Islands	Acclimatisation effort, or as escaped or liberated cage birds (1, 2, 4, 5, 8, 9, 12)
White-vented Myna *Acridotheres cinereus*	South and Southeast Asia, including Sumatra, Java, Bali, Flores and Sumba	Sumba; (?I)Sulawesi	Introduced as escaped or liberated cage birds (1, 2, 3)
Hill Myna *Gracula religiosa*	South and Southeast Asia including Greater and Lesser Sundas	(?I)Some Wallacean islands	Introduced as escaped or liberated cage birds (1, 2)

Species	Main Range	Where introduced?	Context
Columbidae			
Rock Pigeon *Columba livia*	Europe, Asia, Mediterranean	Many towns and areas in the Circum New Guinea Arcipelago	Introduced as escaped or liberated cage and table birds (1, 2, 5, 10, 12)
Red Collared Dove *Streptopelia tranquebarica*	South and Southeast Asia	(?I)Sulawesi	Introduced as escaped or liberated cage birds (1, 2, 3)
Spotted Dove *Streptopelia chinensis*	South-eastern Asia as far as Western Indonesia and Lesser Sundas	Sulawesi; Moluccas; small islands of Flores Sea; New Britain	Successfully exported from Java to eastern Indonesian islands from 1835 (1, 2, 5)
Zebra Dove *Geopelia striata*	Malay Peninsula; Greater Sundas; Western Lesser Sundas	Ambon; Sulawesi	Introduced as escaped or liberated cage birds (1, 2)
Wallacean and Papuan exports			
Columbidae			
Barred Dove *Geopelia maugei*	Southeast Moluccas; Lesser Sundas	Tomea Island of Tukangbesi Islands in Sulawesi Subregion	Introduced as escaped or liberated cage birds (1, 2)
Western Crowned Pigeon *Goura cristata*	New Guinea; Misool; Salawati; ?Batanta; Waigeo	(?I) Seram	May have been introduced as traded pets or squabs raised for food (2, 12)
Psittacidae			
Blue-streaked Lory *Eos reticulata*	Barbar Island; Tanimbar Islands	(?I)Kai Islands; (?I)Damar	Introduced as escaped or liberated captives trapped for pet trade (1, 2, 7)
Purple-naped Lory *Lorius domicella*	Seram; Ambon	(?I)Buru	Introduced as escaped or liberated captives trapped for pet trade (1, 2, 7)
Ornate Lorikeet *Trichoglossus ornatus*	Sulawesi Sub-region	(?I)Sangihe	Introduced as escaped or liberated captives trapped for pet trade (1, 2)
Blue-naped Parrot *Tanygnathus lucionensis*	Talaud Islands; North Bornean Islands; Philippines	(?I)Sangihe Islands	Introduced as escaped or liberated captives trapped for pet trade (1, 2)
Eclectus Parrot *Eclectus roratus*	Moluccas; Lesser Sundas; New Guinea & satellites; Bismarck Archipelago; Solomon Islands; Australia's Cape York Peninsula	Gorong Island; Banda Islands	Widely captured and translocated for pet trade (1, 2, 7)
Cacatuidae			
Palm Cockatoo *Probosciger aterrimus*	New Guinea; Aru; Australia's Cape York Peninsula	Kai Islands	Introduced as escaped or liberated captives trapped for pet trade (1, 2, 7)
Tanimbar Corella *Cacatua goffini*	Tanimbar Islands	Kai Islands	Introduced as escaped or liberated captives trapped for pet trade (1, 2, 7)
Yellow-crested Cockatoo *Cacatua sulphurea*	Sulawesi Sub-region; Lesser Sundas	Singapore; Hong Kong	Introduced as escaped or liberated captives trapped for pet trade (1, 2)
Sulphur-crested Cockatoo *Cacatua galerita*	New Guinea and some or its satellite islands; Australia	Ambon; Gorong Islands; Kai Islands	Introduced as escaped or liberated captives trapped for pet trade (1, 2)
North Melanesian exports			
Megapodiidae			
Melanesian Scrubfowl *Megapodius eremita*	Bismarck Archipelago	(?I) Some outer islands of the Bismarck Archipelago	This species is a reasonably strong flier and natural disperser, but some of its distribution in the vast Bismarck Archipelago may be due to human agency, as viable clutches of fertilised eggs are commonly carried around by humans for food or trade, and are known to spontaneously hatch to produce exceptionally precocious young (11)

Species	Main Range	Where introduced?	Context
Australian exports			
Artamidae			
Australasian Magpie *Gymnorhina tibicen*	Australia; southern New Guinea	Guadalcanal	Introduced prior to 1945, ? now extinct (1, 2, 9)
Meliphagidae			
Noisy Miner *Manorina melanocephala*	Australia	Solomon Islands	Introduced in the 1950s as escaped or liberated cage birds (5, 9)
Estrildinae			
Star Finch *Neochmia ruficauda*	Australia	New Guinea	Introduced as escaped or liberated cage birds (5)

Sources: (1) Lever 1987; (2) Coates & Bishop 1997; (3) Holmes & Phillipps 1996; (4) Coates 1985; (5) Peckover & Filewood 1976; (6) Beehler *et al*. 1986; (7) Forshaw 1989; (8) Hadden 1981; (9) Doughty *et al*. 1999; (10) Monk *et al*. 1997; (11) Menzies 1996; (12) Coates & Peckover, 2001.

(?I) = Possibly introduced

Discussion

Trends in vertebrate translocation

A number of trends are apparent from the record of translocated vertebrates (Tables 1 and 2). Through translocation by human agency, the Oriental zoogeographic region or broader Indo-Malayan region has supplied parts of the Circum New Guinea Archipelago with about 40 introduced non-volant or weakly volant wild terrestrial vertebrates. This includes two deer; a pig; two monkeys; three civets; a mongoose; a cat; a pangolin; up to three shrews; a porcupine; two squirrels; up to nine murid rodents; up to two jungle fowls; a typhlopid blind snake; at least five geckos, a skink, and five frogs; and possibly a python, an elapid snake and a varanid lizard. In parallel, the large Wallacean island of Sulawesi, with its mixed Oriental and Australasian evolutionary influences, has through translocation by human agency probably supplied the Babirusa *Babyrousa babyrussa* to the Moluccas; another pig *Sus celebensis* to the Moluccas, Lesser Sundas and Simeulue Island near Aceh in north-west Sumatra; a monkey *Macaca nigra* to the Moluccas; and possibly a cuscus *Ailurops ursinus* to the remote Talaud Group. New Guinea (and its Papuan satellites), at the centre of the Australasian zoogeographic region has through translocation by human agency probably supplied approximately 18 non-volant or weakly volant wild terrestrial vertebrates to some surrounding islands, including: a murid rat; up to four cuscuses; possibly a petaurid glider; up to five macropods; up to two bandicoots; two cassowaries; possibly a python and a tree snake; and at least one skink and a frog.

In relation to strongly volant wild terrestrial vertebrates, about 15 species of birds with Afro-Eurasian or Oriental / Indo-Malayan origins have had their ranges extended into or within the Circum New Guinea Archipelago due to translocation by human agency; while ten strongly volant birds (including five psittacid parrots, four cockatoos, a dove and a pigeon) with Wallacean or New Guinea origins have had their ranges expanded within the Circum New Guinea Archipelago through translocation by human agency. In addition, two Australian birds including the Australasian Magpie *Gymnorhina tibicen* and Noisy Miner *Manorina melanocephala* have been introduced to the Solomon Islands, while the Australian Star Finch *Neochmia ruficauda* has been introduced to New Guinea. For the most part, these translocations are due to escaped or liberated captives, and are a by-product of the historically recent pet trade, which in Indonesia, is extensive (Coates and Bishop 1997; Jepson 1997). Some anthropogenic distributions however, particularly in Indonesia, whether recognised as such or not, may be due to a much more ancient traffic in cage birds (Coates and Bishop, 1997) that is at least as old as the spice trade (Swadling 1996; Heinsohn 1998a,b).

Out of all of the above, only a few Australasian species have been successfully translocated by human agency west across Wallace's Line into the Oriental zoogeographic region. These include: the Papuan Giant Green Tree Frog *Litoria infrafrenata* to Java; Sulawesi Wild Pig *Sus celebensis* to Simeulue near Sumatra; and the Wallacean Yellow-crested Cockatoo *Cacatua sulphurea* to Singapore and Hong Kong. Though extralimital to this study, only the historically introduced Australian Red-necked Wallaby *Macropus rufogriseus*, with some wild individuals in the British Isles and a former population in Germany (Grzimek 1967; Lever 1985), stands out as the only Australasian marsupial to have been successfully translocated west of Wallace's Line into the Palaearctic zoogeographic region of Eurasia. Some other Australian marsupials including several macropods and a possum have been translocated eastwards into New Zealand and a single macropod to Hawaii (Lever 1985), but all within the greater Australasian zoogeographic region of which Polynesia is generally considered to be a part.

A further minor trend is that there may have been some internal translocations within the landmasses of some of the larger islands in the Circum New Guinea Archipelago. The Australo-Torresian Short-beaked Echidna *Tachyglossus aculeatus*, for example, may possibly have been assisted across the formidable barrier of New Guinea's high central cordillera to its patchy distribution, north of the watershed, by human agency (Flannery 1995b). A mysterious reputed crocodile population, probably the Indopacific Estuarine Crocodile *Crocodylus porosus* in the topographically isolated semi-montane Lake Ira Lalaro at approximately 250 metres above sea level, in far eastern East Timor, may be the product of translocation by human agency of young crocodiles from coastal habitats. In parts of Timor the crocodile enjoys a sacred totemic status and juveniles or eggs may once have been collected for use in ceremonial practices. Alternatively, the crocodiles may have entered the lake through subterranean channels in the largely limestone terrain or been stranded by geologically recent tectonic processes, although this seems unlikely.

A general trend in Indo-Melanesian zoogeography is one of faunal homogenisation, with a strong probability of ongoing range expansion by various stowaways and ethnotramps. This poses a general threat to insular biodiversity as vigorous introduced vertebrates out-compete or prey on vulnerable insular species, or introduced conspecifics begin to hybridise with restricted insular forms. Occasionally, however, there may be some conservation benefits, such as the spread of locally endangered species to surrogate localities that increase that species' chances of survival. Two such cases of 'ecological surrogacy' include the anthropogenic spread of the endangered Sulawesi Crested Black Macaque *Macaca nigra* to Bacan in the North Moluccas, and the endangered Sulawesi Babirusa *Babyrousa babyrussa* to Buru in the Central Moluccas, where introduced surrogate populations of significant conservation value now occur.

It should also be added that contemporary vertebrate distributions are far from static, with many historically introduced island populations having not yet reached equilibrium. Introduced mammals such as the Rusa Deer in New Guinea, for example, after about a century of liberation, are still consolidating their range (Bentley, 1998); while the historically introduced Common Spotted Cuscus *Spilocuscus maculatus* in New Ireland, after 60 to 70 years since liberation at the far north-western end of the long narrow island has, to date, only invaded a fraction of suitable habitat (Heinsohn 1998a,b, 2000, 2002b, 2003). Similarly, introduced herpetofauna, such as the American Cane Toad *Bufo marinus*, after about 60 years of liberation, has also only invaded a fraction of potentially viable habitat in New Guinea (Menzies 1996). In New Guinea, the invading toxic Cane Toad, which tends to kill predators that naively ingest it, may be responsible, for example, for the apparent decline, within the invasion zone, of the Papuan Black Snake *Pseudechis papuanus* (Parker 1982).

Some salient potential threats to the region's biodiversity include the fact that the introduced Malay Civet *Viverra tangalunga* and Oriental Palm Civet *Paradoxurus hermaphroditus* now occur as far east as Seram and Aru, respectively, and are poised to invade nearby biologically diverse New Guinea should they be given a chance (Heinsohn and Hope 2003). Similarly, the Long-tailed Macaque *Macaca fascicularis*, which is now found throughout the Lesser Sundas, and is carried further afield as a pet, is also poised to invade large biologically diverse islands such as Sulawesi and New Guinea should it be afforded the chance (Heinsohn 2002a). The potential impact of such omnivores and carnivores on the relatively naive faunas of New Guinea could be significant.

With regard to many of the aforementioned utilised ethnotramp species, such as Rusa Deer, Wild Pig, Long-tailed Macaque, and various wallabies and cuscuses; a further trend is that their relationship with humans could be regarded as a form of macro-mutualism. This is because, although individuals within an introduced population may be preyed upon by humans, the species as a whole has its range expanded or maintained by human agency, thus becoming more successful and secure, while humans gain a valuable new resource.

Heterogeneity and ambiguity in island faunas

Analysis of the wild vertebrate faunas of the islands of the Circum New Guinea Archipelago, from Lombok in the west to the outermost Solomon Islands in the east, reveals that all have heterogenous faunas comprised of varying proportions of endemics, native species, self-introduced synanthropic species that colonise in the wake of human disturbance, and species introduced by human agency. A further category recognised here, is that of the 'zoogeographic phantom', a species with an enigmatic island occurrence that may or may not be due to human agency, but for which there is insufficient evidence to decide whether that particular occurrence is due to recent natural dispersal or human agency. A related concept is that of the 'camouflaged exotic', usually an intra-regionally introduced species whose exotic status goes unnoticed because its distribution appears as if it could be natural. Zoogeographic phantoms and camouflaged exotics are similar in concept to the 'cryptogenic species' of uncertain origin, that are neither clearly native nor exotic, as described by Carlton (1996), but mostly applied to invasive marine and aquatic organisms.

A further anthropogenic phenomenon, is that of the 'ethnospecies', an apparent island endemic species or subspecies, that is in fact an artefact of human-induced allopatric differentiation in an insular population that has been isolated for thousands of years following introduction by prehistoric human agency. Here allopatric differentiation may be exaggerated through human-induced founder effect, or through human-induced hybridisation in an introduced founding stock made up of mixed species or subspecies (Heinsohn 1997, 1998a). The enigmatic Admiralty Cuscus *Spilocuscus kraemeri*, with poorly understood New Guinea origins (Singadan 1996), but which is apparently endemic to the oceanic Manus Province Archipelago (Flannery 1994; 1995a), may be an example of an 'ethnospecies' (Heinsohn 1998a, 2003).

Ambiguity of the evidence arises mostly from the fact that introduction by human agency, particularly if it has happened thousands of years ago in the prehistoric past, may in effect, mimic recent colonisation by natural dispersal and vice versa. Furthermore, even the much-touted archaeological evidence of sudden appearances of species in archaeological sequences does not necessarily provide infallible evidence of introduction by human agency. In some cases, such evidence may merely be a reflection of taphonomic processes (archaeological / palaeontological site formation), such as when bones first make it into a site, or are first preserved there, rather than being an actual reflection of first arrival on an island by human agency. Archaeological and palaeontological sites are also often plagued by stratigraphic problems, such as disturbance or contamination, that make accurate dating and interpretation of events difficult. To ameliorate this, archaeologists and Quaternary palaeontologists endeavour to look for consistent trends across a range of sites on an island, and to perform statistical tests on appropriate samples of excavated bone, so as to exclude false results that are in fact an artefact of site disturbance or the displacement of bone fragments during excavation (some of which may fall to lower levels during excavation). Direct dating of bone, using techniques such as AMS radiocarbon dating, may also serve to cross-check broader stratigraphic dating.

One of the best independent checks on archaeological faunas is a parallel natural palaeolontological site, such as a sink-hole, that may serve as a control, by capturing a more random sample of pre-human and post-human fauna. A deep-time, well-stratified archaeological site with deposits that clearly stretch back into prehuman prehistory may also provide a useful control. In reality, however, despite the best efforts of archaeologists and palaeontologists, who often face limited field seasons, there are relatively few places in the Circum New Guinea Archipelago with perfect parallel or continuous palaeontological and archaeological sequences that have been comprehensively excavated. Thus a degree of uncertainty and scholarly guesswork often remains with regard to interpretation of the available archaeological and palaeontological data.

Similarly, the much-touted biochemical and genetic evidence regarding the timing of dispersal episodes leading to new allopatric populations is not exact in its temporal calibration of events and cannot necessarily distinguish between recent natural dispersal and that due to Late Quaternary human agency. Such methods can, in certain circumstances, be used to refute the possibility of introduction by human agency by indicating a much earlier separation event that predates the advent of humans in the area.

Other than high resolution archaeological-palaeontological sequences, or clear historical records of introduction events, one of the best indicators of possible human agency, is animal distributions that seem to far exceed a species' likely natural dispersal ability. Strangely disjunct or patchy distributions can also be indicative of dispersal by human agency, as can incomplete distributions where a newly introduced species has only occupied a limited portion of a landmass, with the biological invasion still in progress. Combined with ethnozoological evidence of that species being highly valued by humans as a resource, or being a commensal that regularly stows away in vessels or cargo, such distributional evidence can provide a compelling case for introduction by human agency.

With regard to distributional and ethnozoological evidence, much can be learned from analogy with historically recorded cases of species introduction. For example, the Australian Brushtail Possum *Trichosurus vulpecula* which was introduced to New Zealand in the mid 19th century to establish a fur industry, was valued enough to be historically introduced to New Zealand's main islands, as well as to many of the smaller satellites, including islands as far afield as the oceanic far eastern Chatham Islands and some far southern oceanic islands (Cowan 1990; Heinsohn 2003). This wide and saturated anthropogenic distribution in New Zealand is the antithesis of a more random and patchy distributional pattern that one would expect from the more stochastic process of natural dispersal. In its natural distributions in and around the Australian mainland, *T. vulpecula* tends only to make it to continental satellite islands with former land-bridge connections. The absence of the Northern Brushtail Possum *T. vulpecula arnhemensis* from not too distant oceanic satellites such as Timor, for example, could be interpreted as indicating relatively poor, over-water dispersal ability in phalangerid possums.

Yet in the Circum New Guinea Archipelago, a further three phalangerid possums, *Phalanger orientalis*, *Spilocuscus maculatus* and *S. kraemeri*, that one would also expect to be poor, over-water dispersers, have vast, sometimes saturated and sometimes patchy oceanic island distributions that even include a number of tiny atolls. *P. orientalis* has oceanic populations that extend from Timor to the Solomon Islands; while *S. maculatus* has populations stretching from Selayar to New Ireland; and *S. kraemeri* is found across most of the vast Manus Province Archipelago (Heinsohn, 2002a,b,c, 2003). Combined with strong ethnozoological and archaeological evidence of long-term utilisation by humans, such improbably wide and often saturated distributions provide compelling evidence of introduction by human agency to much of the non-continental part of their respective ranges. If possums were good natural dispersers then one would perhaps expect a more stochastic pattern with other mainland New Guinea phalangerids, such as the Ground Cuscus *Phalanger gymnotis*, or perhaps some lowland New Guinea pseudocheirid possums to also be represented in adjacent oceanic archipelagos.

A cautionary note with regard to distributional pattern analysis is that there are other groups of vertebrates that are good natural dispersers capable of establishing wide and saturated distributions. For example, there is a suite of widespread oceanic herpetofauna species that are pre-adapted to long-distance over-water dispersal. This is often through the agency of hardy adults or salt-spray resilient eggs that cling to natural rafts of matted vegetation or driftwood that has been washed out to sea by floods and storms. These species can have very wide natural distributions. Examples are various gecko species, some of which are parthenogenetic, a state which greatly enhances the chances of successful colonisation (Gibbons 1985).

However, as some of these widespread oceanic geckos (and other oceanic herpetofauna) may also adopt semi-commensal niches in and around coastal villages, or are found in the vegetation of the sea shore where watercraft are beached, they can also be prone to secondary dispersal by human agency as stowaways in canoes, sailing praus, ships or their cargo. Indeed, some geckos and skinks, such as those listed in Table 1, have exceptionally wide oceanic ranges that probably represent concatenations of interacting natural and anthropogenic dispersal events, and it can be difficult to separate anthropogenic and natural influences on their distributions (Gibbons 1985; Edgar and Lilley 1993; Allison 1996).

A similar problem arises with regard to volant vertebrates such as birds, many of which are adept at natural dispersal, but which may also be subject to a degree of secondary dispersal by human agency. When not historically recorded, such translocations may be difficult to distinguish from natural dispersal. With the aforementioned 'oceanic' herpetofauna, these species probably make up the bulk of camouflaged exotics and phantom vertebrate species. A further source of ambiguity comes from a limited range of essentially 'continental' vertebrates that have managed to raft, float or swim to some of the nearer oceanic islands, but which have failed to colonise the outer Pacific. Such chance colonisations, when recent, may also be difficult to distinguish from introduction by prehistoric human agency, and contribute to the pool of phantom species with indeterminate status.

A more general pattern of heterogeneity, exemplified in the mammal faunas of the islands of the Circum New Guinea Archipelago, shown in Table 3., includes a sample of seven islands including Lombok, Sulawesi, Seram, New Guinea, New Britain, New Ireland and Guadalcanal. With the exception of New Guinea and Sulawesi, all appear to be typically oceanic and have mammal faunas dominated by naturally occurring or self-introduced volant species, that is, microchiropteran and megachiropteran bats; but exhibit a high percentage of introduced species among the non-volant mammals. The most extreme example is provided by Lombok, with up to 94% of its non-volant mammals being introduced, followed by New Ireland, with up to 80% of its non-volant mammals introduced. This compares with a much lower rate of 9% for New Guinea and 16% for Sulawesi of non-volant mammals being introduced, both of which exhibit high levels of endemism and greater diversity among their respective non-volant mammal faunas. In the middle range are islands such as New Britain, for which about half of the non-volant mammal fauna may be introduced.

Both the extreme case of Lombok, and the more moderate case of New Britain, are shown in more detail in Table 4. While Lombok has a non-volant mammal fauna which is probably overwhelmingly anthropogenic, that of New Britain is more ambiguous, with a number of non-volant mammals having an indeterminate status as phantom species. New Britain's two endemic and four indigenous murid rodents represent forms that probably arrived from New Guinea on natural rafts, while another five commensal murids were probably introduced by human agency, as were pigs and deer. The four New Guinean marsupials found on New Britain have a much more enigmatic status, as two, including *Echymipera kalubu* and *Petaurus breviceps*, may have arrived by rafting (or were possibly prehistorically introduced), while *Phalanger orientalis* and *Thylogale browni*, being culturally valued and traded ethnotramp species, may have been introduced by prehistoric human agency. In the absence of corroborating evidence, such as well-preserved archaeological sequences or high-resolution genetic data, it is difficult to confidently assess the status of New Britain's marsupials, and the island's non-volant mammal fauna remains biogeographically enigmatic. Significantly, New Britain also has a single cassowary species, the New Guinea Dwarf Cassowary *Casuarius bennetti*, which was probably introduced by prehistoric human agency, but which also has an ambiguous status due to a current lack of corroborating evidence.

Table 3. Estimated percentage of introduced species in the contemporary mammal faunas of a sample of islands in the Circum New Guinea Archipelago

Island	Total mammal species	Total mammals introduced	Total Non-volant mammals	Non-volant mammals introduced	Source
Lombok	54	(17) 31 %	(18) 33 %	(17) 94 %	1
Sulawesi	136	(12) 9%	(62) 54%	(12) 16%	2
Seram	43	(12-14) 28-33%	(20) 47%	(12-14) 60-70%	3, 4
New Guinea	228	(13) 6%	(141) 62%	(13) 9%	5, 6
New Britain	47	(7-11) 15-23%	(17) 36%	(7-11) 41-65%	4, 7
New Ireland	40	(8) 20%	(10) 25%	(8) 80%	4, 8
Guadalcanal	31	(6) 19%	(9) 29%	(6) 67%	4

*Weakly-volant mammals such as Petaurid gliders are included in the non-volant category.

(1) Kitchener *et al.* 1990; (2) Whitten *et al.* 1987; (3) Macdonald *et al.*1993, (4) Flannery 1995a; (5) Flannery 1995b; (6) Heinsohn & Hope 2003; (7) Downes 1972; (8) Flannery & White 1991.

Table 4. Heterogenous origins of the non-volant mammal fauna of Lombok and New Britain

Species	Origins	Category
Lombok		
Rodentia		
European House Mouse *Mus domesticus homourus*	Introduced from sources originating in Eurasia.	Commensal stowaway ethnotramp.
Asian House Mouse *Mus castaneus*	Introduced from Southeast Asia.	Commensal stowaway ethnotramp.
Ricefield Rat *Rattus argentiventer bali*	Probably introduced from Greater Sundas.	Commensal stowaway / utilised ethnotramp.
Pacific Rat *Rattus exulans*	Probably introduced from Sunda Islands.	Commensal stowaway / utilised ethnotramp.
Black Rat / House Rat *Rattus rattus diardii*	Probably introduced from Sunda Islands.	Commensal stowaway ethnotramp.
Plantain Squirrel *Callosciurus notatus stresemanni*	Probably introduced from Greater Sundas.	Commensal utilised ethnotramp / stowaway. Occasional pet and food animal.
Sunda Island Porcupine *Hystrix javanica*	Probably introduced from Greater Sundas.	Utilised ethnotramp. Game, food and trade animal.
Insectivora		
House Shrew *Suncus murinus*	Probably prehistorically introduced from Southeast Asia.	Commensal stowaway ethnotramp.
Sunda Shrew *Crocidura (?)monticola*	Possibly arrived from adjacent Sunda Islands by dispersal on a natural raft; or possibly introduced.	Possibly indigenous.
Pholidota		
Pangolin *Manus javanica*	Probably introduced from Greater Sundas.	Utilised ethnotramp. Game, food and trade animal. Scales used as medicine.
Artiodactyla		
Wild Pig *Sus scrofa vittatus*	Probably prehistorically introduced from Greater Sundas.	Utilised ethnotramp. Game, food and trade animal.
Barking Deer *Muntiacus muntjak nainggolani*	Probably introduced from Greater Sundas.	Utilised ethnotramp. Game, food and trade animal.
Rusa Deer *Cervus timorenis floresiensis*	Probably prehistorically introduced from Sunda Islands.	Utilised ethnotramp. Game, food and trade animal.
Carnivora		
Little Civet *Viverricula indica baliensis*	Probably introduced from Greater Sundas.	Utilised ethnotramp. Source of civet, a musk-like substance used to make perfume.
Common Palm Civet *Paradoxurus hermaphroditus rindjanicus*	Probably introduced from Greater Sundas.	Utilised ethnotramp. Rat-catcher.
Leopard Cat *Felis bengalensis javanensis*	Probably introduced from Greater Sundas.	Incidental introduction. Occasional juveniles kept as pets.
Primates		
Long-tailed Macaque *Macaca fascicularis sublimitus*	Probably prehistorically introduced from Greater Sundas.	Utilised ethnotramp. Pet, food, game and trade animal.
Silvered Leaf Monkey *Trachypithecus auratus kohlbruggei*	Probably introduced from Greater Sundas.	Incidental introduction. Occasional pet, food, game and trade animal.

Species	Origins	Category
New Britain		
Marsupialia		
Common Echymipera *Echymipera kalubu*	Ancestral stock possibly arrived from New Guinea by over-water dispersal on natural raft; or possibly prehistorically introduced.	Phantom species - context indeterminate. Utilised food and game animal.
Sugar Glider *Petaurus breviceps*	Ancestral stock possibly arrived from New Guinea by over-water dispersal on natural raft; or possibly prehistorically introduced.	Phantom species - context indeterminate. Occasional pet, opportunistically eaten as small game animal.
Northern Common Cuscus *Phalanger orientalis*	Ancestral stock possibly arrived from New Guinea by over-water dispersal on natural raft; or possibly prehistorically introduced.	Phantom species - context indeterminate. Utilised ethnotramp / pet, food, game and trade animal.
Northern Pademelon *Thylogale browni*	Possibly prehistorically introduced from New Guinea.	Utilised ethnotramp / food, game, trade animal and occasional pet.
Rodentia		
New Britain Water-rat *Hydromys neobritannicus*	Ancestral stock probably arrived from New Guinea by over-water dispersal on natural raft or by swimming and floating after being washed out to sea.	Endemic species.
Chestnut Tree-mouse *Pogonomys macrourus*	Probably arrived from New Guinea by over-water dispersal on natural raft.	Indigenous species.
Bismarck Giant Rat *Uromys neobritannicus*	Ancestral stock probably arrived from New Guinea by over-water dispersal on natural raft.	Endemic species.
Lowland Melomys *Melomys platyops*	Probably arrived from New Guinea by over-water dispersal on natural raft.	Indigenous species.
Black-tailed Melomys *Melomys rufescens*	Probably arrived from New Guinea by over-water dispersal on natural raft.	Indigenous species.
Long-nosed Melomys *Melomys cf. M. levipes*	Probably arrived from New Guinea by over-water dispersal on natural raft.	Indigenous species.
Large Spiny Rat *Rattus praetor*	Probably prehistorically introduced from New Guinea.	Commensal stowaway / ?utilised ethnotramp. Possibly eaten in prehistoric times.
Pacific Rat *Rattus exulans*	Prehistorically introduced - from sources originating in Indo-Malayan region.	Commensal stowaway / ?utilised ethnotramp. Possibly eaten in prehistoric times.
Black Rat / House Rat *Rattus rattus*	Historically introduced - from sources originating in Eurasia.	Commensal stowaway ethnotramp.
Brown Rat *Rattus norvegicus*	Historically introduced from sources originating in Eurasia - ?limited occurrence in towns and ports.	Commensal stowaway ethnotramp.
European House Mouse *Mus domesticus*	Historically introduced from sources originating in Eurasia - ?limited occurrence.	Commensal stowaway ethnotramp.
Artiodactyla		
Wild Pig* *Sus scrofa*	Prehistorically introduced - from sources originating in Indonesian Islands.	Utilised ethnotramp. Food, game and trade animal.
Rusa Deer *Cervus timorensis*	Historically introduced - from sources originating in Indonesian Islands.	Utilised ethnotramp. Food and game animal.

Sources: Kitchener *et al*. 1990; Groves 1984; Monk *et al*. 1997; Flannery 1995a; Heinsohn 1998a,b.

*Although the introduced feral pig in New Britain is probably derived from domesticated or semi-domesticated stock, it is included in this table through treatment as a semi-wild species.

In a parallel example to New Britain, on the other side of New Guinea is the large oceanic island of Seram, which has a marsupial fauna consisting of one clearly endemic bandicoot *Rhynchomeles prattorum*, and two possibly prehistorically introduced cuscuses, *Phalanger orientalis* and *Spilocuscus maculatus*, for which there is currently a lack of evidence with which to corroborate their status. Seram also has the region's only other oceanic cassowary population, in this case the Double-wattled Cassowary *Casuarius casuarius*, which is generally considered to have been introduced from New Guinea or Aru (White 1975; del Hoyo *et al.* 1992; Ellen 1993). Other vertebrates on Seram, with Oriental or Indo-Malayan affinities such as *Cervus timorensis*, *Viverra tangalunga*, *Paradoxurus hermaphroditus*, several commensal rats, a couple of shrews, and perhaps a few elements in the herpetofauna, appear to be clearer examples of introduction by human agency (Ellen 1993; Edgar and Lilley 1993; Flannery 1995a), but as with New Britain, more archaeological and biological research is required to resolve the island's biogeographically enigmatic status.

Antiquity of translocation

The antiquity of vertebrate translocation in the Circum New Guinea Archipelago has largely been reconstructed from dated archaeological sequences in which the bones of certain species make sudden appearances in island faunas in the wake of human colonisation. Using such evidence, one of the oldest recorded apparent incidences of animal translocation is that of the Northern Common Cuscus *Phalanger orientalis* to New Ireland from sources in New Britain or New Guinea sometime between about 10,000 and 20,000 years ago in the Late Pleistocene (Flannery and White 1991; Spriggs 1997). This relatively vague date is derived from independent dates for apparent first records of *P. orientalis* at a series of archaeological sites in New Ireland, and reflects some of the uncertainties inherent in site interpretation and dating. Given that the undated possible New Britain source population from which the New Ireland population was probably derived, may also have been introduced (from New Guinea), then initial translocation from New Guinea into the Bismarck Archipelago may have occurred at an even earlier date. Based on archaeological dates from New Ireland, the Bismarck Archipelago was apparently occupied by humans around 35,000 years ago (Spriggs 1997).

Similar evidence of sudden appearances in archaeological records indicates that a further two New Guinean marsupials, the Admiralty Cuscus *Spilocuscus kraemeri* and the Common Spiny Bandicoot *Echymipera kalubu* may have been introduced to the Admiralty Islands in the Terminal Pleistocene, possibly by about 13,000 years ago (Spriggs 1997). This brings the suspected number of Pleistocene introductions from New Guinea to three. However, as the arrival of some probably introduced ethnotramp marsupials on other large New Guinea satellites, such as New Britain and Seram, has not yet been dated through archaeological investigation, there may be some further Pleistocene translocation events yet to be recorded. Most of the other New Guinea exports, recorded in Table 1, were probably translocated prehistorically in the Holocene with some probably being due to the later Holocene movements of the Austronesians (Spriggs 1997; Heinsohn 1998a, 2002a). A recent exception to this is the historically recorded introduction of the Common Spotted Cuscus *Spilocuscus maculatus* to New Ireland in the 1930s or 1940s (Heinsohn 1997, 1998a,b, 2002b, 2003).

In contrast to the New Guinea exports, the Oriental and Sulawesi exports, listed in Table 1, appear on current evidence to be mostly a Holocene phenomenon, with many being associated with the prehistoric Austronesian expansion in the second half of the Holocene; or dating from the later protohistoric and colonial period up to the present (Glover 1971, 1986; White 1975; Lever 1985; Ellen 1993; Bellwood 1997; Heinsohn 1998a). However, it would not be at all surprising if further excavations in the Wallacean Islands, and particularly in parts of the Lesser Sundas, reveal a range of Late Pleistocene introductions of Oriental faunal elements into that region. The Indonesian Wild Pig *Sus scrofa vittatus* for example, may have a long history in parts of the Lesser Sundas, and may have been carried into that region in its wild form at an early date.

Conclusion

Superimposed on the natural vertebrate zoogeography of the Circum New Guinea Archipelago are some significant human influences resulting from animal translocation. The most marked effect is the export of around 58 essentially Oriental or Indo-Malayan wild vertebrate species into various parts of the Circum New Guinea Archipelago. In contrast, only three Australasian vertebrates, the Sulawesi Wild Pig *Sus celebensis*, the Wallacean Yellow-crested Cockatoo *Cacatua sulphurea*, and Papuan Giant Green Tree Frog *Litoria infrafrenata* have been introduced to locations within the Oriental zoogeographic region. While the Oriental zoogeographic region has, through wild vertebrate translocation, had a marked influence on the zoogeography of the Circum New Guinea Archipelago, translocation from the latter region has had negligible influence on the former. Both New Guinea and large Wallacean islands such as Sulawesi have served as significant sources for species translocated within the Circum New Guinea Archipelago. New Guinea, for example, has probably exported around 18 vertebrate species to surrounding islands; whereas Sulawesi has, through translocation, exported three or four endemic vertebrates to various satellites. Furthermore, while the Oriental and Sulawesi exports appear on current evidence to be largely a Holocene phenomenon, with possibly a few yet to be recorded Pleistocene translocations, the export of New Guinea mammals appears to have started in the Late Pleistocene, possibly as early as about 20,000 years ago (Spriggs 1997).

Due to the ambiguity of the evidence there may be many regionally or locally introduced populations of vertebrates, particularly among the herpetofauna (Edgar and Lilley 1993; Allison 1996), that have not yet been recognised as such, because they do not stand out as obvious exotics. Many questions will ultimately only be answered through further biological surveys and genetic studies, coupled with further archaeological excavations and historical research. These are important questions because they address the antiquity and magnitude of human interactions with the biosphere. Prior to the work of the Lapita Homeland Project (Allen and Gosden 1991; Kirch 1997; Spriggs 1997), that fostered so many archaeological discoveries, who would have thought that a humble marsupial *Phalanger orientalis* would vie for the distinction as perhaps the world's oldest recorded ethnotramp? Furthermore, in addition to being recognised as an early alternative centre for plant domestication and agriculture (Spriggs 1997; Denham *et al.* 2003; Diamond and Bellwood 2003), the New Guinea / Northern Melanesian Region can now also be recognised as an early centre for game management / 'game park' strategies through marsupials that were in some instances probably deliberately introduced to oceanic islands previously lacking in faunal resources. Indeed, having collected contemporary oral records of cuscuses being carried to tiny outer islands on motor boats and aircraft for release into patches of bush (Heinsohn 1998b, 2003), this is an ancient ongoing tradition that in the Circum New Guinea Archipelago has probably stretched from the ancient raft / canoe age into the jet age.

In the heavily populated Lesser Sundas, and some other islands at the western end of the Circum New Guinea Archipelago, human impacts are extensive, often with little primary forest or original vegetation left. This is exemplified by Lombok, where up to 94% of the non-volant mammal fauna and 31% of the overall mammal fauna is probably introduced or synanthropic, with strong anthropogenic effects also observable in the bird, reptile and frog faunas. While it would be tempting to overstate the anthropogenic aspect of the vertebrate faunas of the Circum New Guinea Archipelago as a whole, and describe all the islands wholly as artefacts of thousands of years of human intervention, there is actually a spectrum of conditions and a considerable degree of heterogeneity across the archipelago with a number of islands retaining large areas of indigenous habitat, and with both old pre-human faunal elements and newer, introduced species and synanthropes existing side by side. Other than broadscale habitat modification and some recorded extinctions that have simplified some island faunas (Glover 1986; Whitten *et al.* 1987; Monk *et al.* 1997; Spriggs 1997; Aplin 1998; Steadman *et al.* 1999; Heinsohn and Hope, 2003), the most salient effect is that humans introduce a range of small commensal stowaways and some larger continental faunal elements to these mostly oceanic islands.

With regard to large biologically diverse continental islands, such as New Guinea, with its high levels of endemism and vast areas of remaining primary forest, introduced species only account for about 6% of the mammal species and a similarly small fraction of the bird, reptile and frog faunas (Heinsohn and Hope 2003). Furthermore even on oceanic islands such as Seram, New Ireland and Makira (San Cristobal), for example, a night of spotlighting reveals that naturally occurring megachiropteran and microchiropteran bats are by far the most conspicuous nocturnal elements in their respective vertebrate faunas; while a day of sitting by a large forest tree, reveals that in many places native birds and herpetofauna remain as the most conspicuous and predominant faunal elements. Despite thousands of years of human impacts, the old pre-human biotas, though diminished are not yet vanquished.

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APPENDIX I

Appendix I - Glossary of ethnozoological and biogeographical terms

Term	Definition
AMS radiocarbon dating	Accelerator mass spectrometer radiocarbon dating is a method commonly used by archaeologists and Quaternary palaeontologists to directly date small samples of subfossil bone (9).
Camouflaged exotic	An introduced species whose exotic status goes unnoticed because its distribution appears as if it could be natural. Usually an intra-regionally introduced species that does not appear to be out of place (6,7).
Cryptogenic species	Species that are neither clearly native nor exotic (3).
Domestication	The adaptation of plants and animals for life in intimate association with humans (8).
Ecological surrogacy	When an introduced population of a species gains conservation significance due the overall rarity or threatened status of that species in its natural habitat (5).
Edible rat ethnotramps	Refers to two widespread Pacific rats, *Rattus exulans* and *Rattus praetor,* that may have been prehistorically introduced to various oceanic islands as deliberately translocated food animals, in addition to dispersing as stowaways (10).
Ethnophoresy	The process of ethnophoresy or extended-phoresy occurs when an organism is able to breach geographical barriers and establish new populations by hitching a ride in human vessels and cargo (5).

APPENDIX I

Ethnospecies	An apparent island endemic species or subspecies, that is in fact an artefact of human-induced allopatric differentiation in an insular population that has been isolated for thousands of years following introduction by prehistoric human agency. Allopatric differentiation may be exaggerated through human-induced founder effect, or through human-induced hybridisation in an introduced founding stock made up of mixed species or subspecies (6, 7).
Ethnotramp	Economically and culturally favoured wild animals that are commonly captured live and carried around with humans as pets or for food, trade or ceremonial purposes; or commensal species carried unwittingly as stowaways in vessels and cargo, leading to human-assisted dispersal and significantly expanded geographical ranges (6, 7).
Ethnozoology	Study of the traditional use of animals and animal products by various human cultures, and long-term interactions between humans and animal species (8).
Macro-mutualism	Describes the broadscale relationship between humans and deliberately introduced useful ethnotramps, where both benefit at the species level. Although individuals within an introduced population may be preyed upon by humans, the species as a whole has its range expanded or maintained by human agency, thus becoming more successful and secure, while humans gain a valuable new resource (6, 7).
Meganesia	The combined New Guinean-Australian-Tasmanian landmass; particularly that of earlier geological epochs, when low sea-levels exposed much of the Sahul plate on which the continental islands sit, causing them to coalesce into one continuous landmass. Also called 'Greater Australia' or 'Sahul' (2, 4).
Phantom	A species with an enigmatic island occurrence that may or may not be due to human agency, but for which there is insufficient evidence to decide whether that particular occurrence is due to geologically recent natural dispersal or human agency (6, 7).
Phoresy	A method of dispersal in which an animal clings to the body of a much larger animal of another species and is carried some distance before releasing its grip and falling (1).
Protohistoric period	Defined here as the early historical period when strongly literate societies first began to make substantial written historical records of observations in the Circum New Guinea Archipelago. In the eastern part of the archipelago, this equates with the period of first contact with European explorers approximately 500 to 200 years ago (5).
Quaternary biogeography	Biogeography of the last 2 million years, a period that saw the evolution of modern humans and the advent of human influences on the environment. Includes the Pleistocene Epoch from 2 million to 10,000 years ago, and the Holocene Epoch stretching from 10,000 years ago to the present (5).
Stowaway	Defined here as a particular type of ethnotramp, that is usually a small commensal or littoral species that habitually secretes itself or its eggs in human vessels or cargo, leading to unwitting human-assisted dispersal to new areas (5).
Synanthrope	An animal that benefits from environmental modifications made by humans to such as extent that it becomes closely associated with humans, and colonises new areas in the wake of human impacts (1).
Taphonomy	Study of the environmental phenomena and processes that affect organic remains after death, including the processes of fossilisation, in which only a fraction of material may be preserved in a palaeontological or archaeological site (8).

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