Origin, Dispersal Routes, and Geographic Distribution of *Rattus exulans*, with Special Reference to New Zealand¹

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ABSTRACT: Current anthropological theory and archaeological evidence have led to a reappraisal of the hypothesized route of dispersal of the Polynesian rat, *Rattus exulans*, through the Pacific and to New Zealand. This commensal rodent seems to have entered the Fiji-Tonga-Samoa region by way of Melanesia, in association with the people of the Lapita cultural complex. The hypothesized migrations of those people and hence presumably of *R. exulans* throughout Near and Remote Oceania are presented here, along with a brief review of this rat's history and current distribution in New Zealand, the last settled and southernmost landmass in its range.

THE WIDESPREAD AND UNIFORM DISTRIBUTION of the Polynesian rat, Rattus exulans (Peale), throughout the insular Pacific is at variance with the observed distribution of noncommensal animals; this has given rise to the hypothesis that its dispersal occurred in association with human movements. The archaeological evidence supports this theory; for instance, the Pleistocene mammalian fauna of New Ireland includes two fruit bats, a phalanger, a wallaby, Rattus mordax, and Rattus praetor. Rattus exulans appears later, along with the commensal pig, dog, and chicken, at around 3100-2500 Before Present (B.P.). The temporal specificity of artifacts and faunal remains found in the sites led Allen et al. (1989) to conclude that apart from the bats, all appear to be human introductions. Anthropological information also suggests that the dispersal of R. exulans throughout the Pacific took place (accidentally or deliberately) in association with the migrations of the ancestral peoples of this region. From the New Zealand perspective then, questions concerning the origin of this rat become a question of the origin of the Maori, and hence of the Polynesian peoples. Based on this presumed relationship, two previous

accounts in the literature (Tate 1935, Schwarz and Schwarz 1967) that deal with the origin and dispersal of this species both reflect the then-prevailing anthropological view (e.g., 1938) that the Proto-Polynesians entered the Pacific by way of Micronesia and not Melanesia. For example, after studying the comparative anatomy and morphology of numerous specimens of the Polynesian rat collected from throughout its geographical range, Tate (1935) related this species to the concolor group of Rattus, whose geographical range includes the Malay states, Sumatra, Java, Borneo, the Philippines, Celebes, New Guinea, and the Pacific islands including New Zealand, but excluding mainland Australia. He went on to suggest that speciation of R. exulans occurred in the Philippine-Borneo-Java region, and from there this rat dispersed eastward into the Pacific (Figure 1). He pointed out that "since all have been carried by man, whether voluntarily or involuntarily, they must have followed his colonization tracks" and that the "original course from the mainland [of Southeast Asia] was probably from Borneo and the Philippines via the Caroline Islands rather than through New Guinea and the Solomon Islands" (Tate 1935:169). Schwarz and Schwarz (1967) suggested that the origin of the R. exulans series of commensals was from a wild subspecies, Rattus rattus wichmanni, of Flores in the Lesser Sunda Islands (Figure 1).

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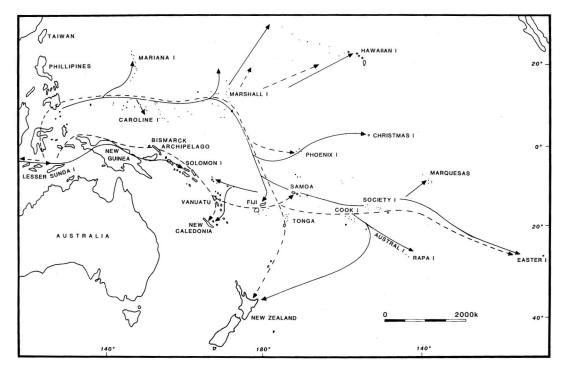


FIGURE 1. Hypothesized insular Pacific dispersal routes of *Rattus exulans*. Solid lines modified after Tate (1935); dashed lines according to Schwarz and Schwarz (1967).

Divergence and spread then occurred to the west (mainland Southeast Asia) and to the north and east (the insular Pacific). Although those authors traced one of those lines of descent east through the Bismarck Archipelago and Solomon Islands region to New Caledonia and Samoa (Schwarz and Schwarz 1967:150), they derived the New Zealand stock as follows (p. 151): "it is possible to trace rats ... that now stand as R. r. exulans Peale from Palau to the Caroline and Marshall Islands; from there south to the Tonga Islands and New Zealand ..." (Figure 1).

Archaeological evidence of this rat from the postulated center of origin somewhere in island Southeast Asia comes from the Neolithic period, dating around 5000 B.P. Mammals associated with or immediately preceding Neolithic pottery assemblages dated at 4100–3700 B.P. in East Timor include the pig, civet cat, macaque monkey, and R. exulans (Spriggs 1989). The emergence of R. exulans from ancestral Rattus stock must therefore

have occurred before that time. By 6000 B.P., rising sea levels had resulted in the formation of an island Southeast Asia from the ancient land masses of Sundaland and Sahulland (Bellwood 1985; Green, in press). The consequent reduction in land area and hence population size of *Rattus* stock may have created a "bottleneck effect" leading to a speciation event (Val 1988) from which *R. exulans* might have been derived.

Whatever the impetus for speciation, the dispersal of both flora and fauna from Southeast Asia eastward into the Pacific has been impeded in regard to both space and time. Reasons for this include the difficulty in crossing water, the distances between islands, and the failure to find suitable habitats or chance extinctions following colonization. Biotic zones have been described on the basis of the observed inequities in species number and composition of the animal and plant biotas between islands in that region. For example, "Wallacea," lying between Borneo and Irian

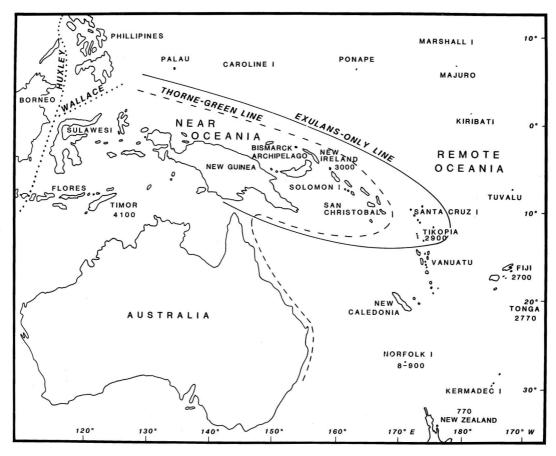


FIGURE 2. Geographical locations of the "Thorne-Green" line and the "exulans-only" line within Near and Remote Oceania. The radiocarbon dates (time Before Present) are the earliest estimates for *Rattus exulans*.

Jaya (or more definitively, between the Wallace-Huxley line and Weber's line), marks a major faunal transition between the Oriental and Australian faunas. In fact, the Wallace-Huxley line (Figure 2) separates one of the richest vertebrate faunas in the world from one of the poorest; beyond it to the east there is a continuing trend toward faunal impoverishment. This is true for both invertebrates (Laird 1956) and for vertebrates (Darlington 1957). For instance, from New Guinea, 520 species of birds have been recorded; the Solomons, 127; Fiji, 54; Samoa, 33; the Society Islands, 17; the Marquesas, 11; and Henderson, 4 (Thorne 1963). Of mammals, four orders including the Rodentia are indigenous to New Guinea. Approximately 24

rodent genera occur there, including 16 species of Rattus. This reduces to only three genera in the Bismarck Archipelago, where three Rattus species have been identified from prehistoric sites in Balof, New Ireland (Allen et al. 1989) (i.e., R. mordax, R. praetor, and R. exulans, the last-mentioned at around 3000 B.P. [Figure 2]). In fact, all nonvolant mammals other than Rattus sp. and Mus musculus reach the easternmost limit of their distribution in the Solomon Islands (Thorne 1963). Pawley and Green (1973) have delineated the eastern boundary of this faunal distribution with a line passing between the southeastern end of the Solomon Islands (San Cristobal) and the Santa Cruz group 350 km to the east, thus separating Near Oceania (New Guinea, the

Bismarck Archipelago, and the Solomon Islands) from Remote Oceania (eastern Melanesia, Polynesia, and Micronesia). They noted that this line (referred to as the "Thorne-Green" line in Figure 2) marks "a major cutoff point in the natural distribution of animal and plant species." Beyond this the only nonvolant mammals to proceed (by way of human assistance) were one or two rat species and the domesticated dog, pig, and chicken. For example, the 2900-year-old mammalian fauna of Tikopia on the Remote Oceania side of this line includes the dog, pig, Rattus exulans, R. praetor, and two species of fruit bats (Pteropus spp.), with only the bats likely to have been present before human colonization (Flannery et al. 1988). Approximating the "Thorne-Green" line but slightly farther to the east, a line can be drawn between the Santa Cruz Islands and Fiji indicating the boundary beyond which the only rat species known to have been introduced prehistorically is R. exulans. This line is labeled the "exulans-only" line in Figure 2.

Modern anthropological theory now accepts that the ancestors of the Polynesians entered the Pacific by way of Melanesia (Bellwood 1979). Their dispersal eastward from the Bismarck Archipelago to Tonga and Samoa between ca. 3600 and 3000 B.P. coincides with the introduction of their commensals (the dog, pig, chicken, and rat) as has been detailed above for New Ireland and Tikopia. The cultural complex of these particular people has been called "Lapita" (Green 1979) in reference to the distinctive pottery recovered from sites in the Bismarck Archipelago and the Solomon Islands east to Santa Cruz, Vanuatu, New Caledonia and the Loyalty Islands, Fiji, and on to western Polynesia (Tonga and Samoa). The archaeological evidence suggests that the eastward dispersion of R. exulans across the biogeographical boundaries denoted by the "Thorne-Green" and the "exulans-only" lines was made possible by the increasingly accomplished longdistance voyaging of these Lapita people. The dates for R. exulans bones from Fiji (Best 1984) and from Tonga (Poulsen 1987) given in Figure 2 allied with the dates for earliest human settlement in Remote Oceania (Figure 3) confirm this association. Along with their pottery and animals, those people entered the Fiji-Tonga-Samoa triangle sometime after 3500 B.P. but probably by 3000 B.P. (G. Irwin, pers. comm.). In that region, a cultural lineage was developed that subsequently dispersed farther east and whose descendants are known today as Polynesians. On the far-flung islands of Polynesia, the only indigenous mammals present (if any at all) were one or two species of bats. The rat, dog, pig, and chicken accompanied humans on those voyages, but not all of those species survived each colonization event. For example, only the dog and rat apparently made it to New Zealand (Pawley and Green 1973), but R. exulans is the only vertebrate found in archaeological deposits (dated at 800-900 B.P.) on Norfolk Island (Meredith et al. 1985).

Figure 3 summarizes these hypothesized dispersal events through Near and Remote Oceania as outlined above. All dates are radiocarbon estimates of time of first human settlement (although the date for Easter Island may be later than the time of first settlement). Some explanatory comments need to be made. As the dates indicate. New Guinea. the Bismarck Archipelago, and the northern Solomon Islands were all settled in the Pleistocene, but the rest of the insular Pacific was settled much later. The line linking Vanuatu to the Marshall and Caroline islands is a language-based inference. The people of western Micronesian island groups (the Marianas, Palau, Yap) all speak languages of Western Austronesian (island Southeast Asian) type, and thus they were presumably settled from island Southest Asia. Eastern Micronesians (Caroline and Marshall islands, Kiribati, Tuvalu) speak Oceanic (i.e., Eastern Austronesian) languages. Those peoples thus seem to be most closely related to those of northern Vanuatu and the southeastern Solomon Islands (Blust 1984–1985). The settlement dates of the Cook and Society islands and the Tuamotu Archipelago are unknown, but it is very likely to be earlier than the settlement date of the Marquesas (ca. 2000 B.P.). Although it is uncertain which particular island group was first settled in central-eastern Polynesia, the information in Figure 3 follows the

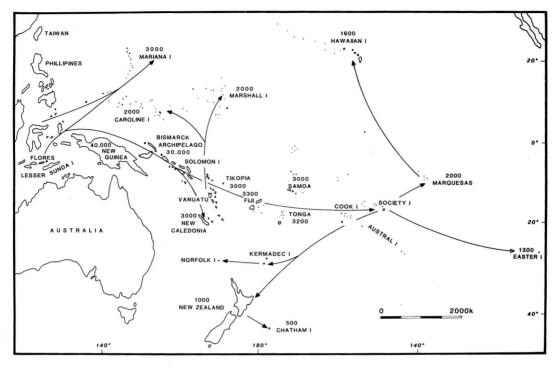


FIGURE 3. Reconstruction of the hypothesized insular Pacific dispersal routes of *Rattus exulans*, based on radiocarbon estimates (time Before Present) of time of first human settlement.

assumption that the island groups were settled in order of accessibility from West Polynesia, according to recent theories of East Polynesian colonization (Irwin 1989). New Zealand, the last major world landmass to be settled by humans, was reached by ancestral Maori ca. 1000 B.P. (Irwin et al. 1990). The earliest rodent evidence (presumably of R. exulans) in New Zealand comes from ratgnawed berries of hinau (Elaeocarpus dentatus) dated at 770 ± 50 B.P. recently discovered at an archaeological site in Auckland (S. Best, pers. comm., 1990).

Distribution

The complete geographical distribution of *R. exulans* is illustrated in Figure 4. The oceanic records shown here are detailed in Atkinson (1985). As can be seen, this rodent has a fairly circumscribed distribution, seldom being found beyond the confines of the tropics. Its westernmost boundary is marked

by the Andaman Islands (92° E long.) off the west coast of Southeast Asia, while in the east it has reached Easter Island (109° W long.). To the north it is found in Burma (25° N lat.) and in Hawaii (28° N lat.), while the southernmost limit of its distribution is New Zealand, where it ranges as far south as Stewart Island (47° S lat.). Although it has been recorded from two offshore islands of northern Australia (Taylor and Horner 1973), that continent remains the only major landmass in the Southeast Asia–Pacific region that has not been colonized by this species, possibly because its preferred grassland habitat was already occupied (Gressitt and Ziegler 1973).

Distribution within New Zealand

Rattus exulans is known in New Zealand by its Maori name, "kiore." Ethnographic accounts of the arrival of this rat in New Zealand include those of the Maori people, whose oral histories have been recorded by

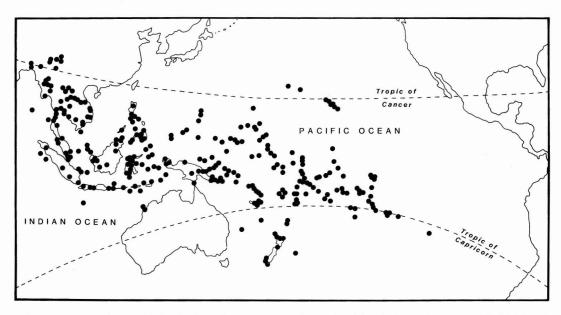


FIGURE 4. Recorded world distribution of *Rattus exulans*. Reproduced by kind permission from Wodzicki and Taylor (1984).

many authors. One of these, Best (1942), makes reference to a tradition that names Aotea as the canoe into which R. exulans, the sweet potato (Ipomoea batatas), swamp hen (Porphyrio melanotus), and seeds of the karaka tree (Corvnocarpus laevigata) were placed before its departure from Hawaiki (the ancestral homeland). Other tribal traditions give the name of this canoe as the Horouta and also refer to methods used by the Maori for trapping and cooking this rat, giving credence to the possibility that its use as a supplementary food source led to its deliberate introduction and distribution. A. C. Ziegler (pers. comm.) has recently suggested that these rats might also have served as a food source for the domesticated dog, based on the discovery of bone fragments of R. exulans in the stomach region of a dog skeleton recovered from a Hawaiian burial site.

After the introduction by Europeans of other rodent species (Rattus rattus, R. norvegicus, and Mus musculus) to New Zealand, there was a marked decline in the abundance of R. exulans on the main islands, so that by the end of the nineteenth century it was considered virtually extinct (Taylor

1975). Earlier, in 1840, this species had become sufficiently scarce over much of the North Island for Hutton (1879) to resort to material collected from middens to describe it as Mus maorium. The current distribution within New Zealand has been well documented by Watson (1956), Taylor (1978), Atkinson (1986), and Atkinson and Moller (1989). In brief, the only remaining mainland populations of R. exulans are in parts of South Westland and Fiordland in the South Island. However, many offshore island populations still persist, ranging from the Kermadec Islands north of New Zealand (considered part of territorial New Zealand) to Stewart and nearby islands in the south. On many of the more northern offshore islands, R. exulans is the only rodent species present, and, on a number of these, it is also the only mammal present. On a few of the larger islands it coexists with one or more of the other rodent species, but nowhere in New Zealand do all four rodent species co-exist. After an appraisal of the historical decline of kiore on New Zealand's mainland and an examination of the various combinations of rodent species on the offshore islands, Taylor (1975, 1984)

suggested that strong competitive interactions between species may be followed by displacement and even exclusion. On New Zealand's two main islands mice in particular seem to have been a major factor associated with the disappearance of *R. exulans*. Such interactions and their effects are postulated to be more severe in New Zealand than in tropical latitudes (where all four species can and do co-exist) because these islands are at the extreme southern limits of this originally tropical rat's range (Taylor 1975).

CONCLUSIONS

The origin of R. exulans from ancestral stock somewhere in island Southeast Asia, as postulated by Tate (1935) and Schwarz and Schwarz (1967), remains unchallenged. However, current anthropological and archaeological information allow a reconstruction of their views concerning the probable historical dispersal route of R. exulans throughout the insular Pacific and, in particular, to New Zealand. This modern hypothesis, outlined in Figure 3, differs from that of earlier authors (Figure 1) by deriving the New Zealand stock not from a migration line passing through Micronesia, but from one that passes through Near to eastern Remote Oceania and thence south to New Zealand. In addition to updating theories concerning the dispersal routes of R. exulans in the Pacific, Figure 2 presents radiocarbon dates for the estimated arrival times of R. exulans in Near Oceania and western Polynesia. The figure is intended to stimulate interest in the accuracy (or otherwise) of the "exulans-only" line and to elicit more information relating to the prehistory of this species elsewhere in the insular Pacific.

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