# Effect of isolation on coat colour polymorphism of Polynesian rats in Island Southeast Asia and the Pacific

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Populations of vertebrate species introduced onto islands regularly develop similar phenotypic changes, e.g. larger or smaller body size, shortened limbs, duller coats, as well as behavioural changes such as increased tameness and reduced flight-initiation distance. These changes overlap in part with those associated with the 'domestication syndrome', especially tameness and changes in coat patterns, and might indicate a similar neural crest involvement in the concurrent development of multiple phenotypic traits. Here I examine long-term data on free-living populations of wild Polynesian rats from seven mainland countries and 117 islands (n=3034), covering the species' native and introduced range. Mainland populations showed no aberrant coat patterns, with the exception of one albino, whereas aberrant coat patterns were found in 12 island populations. Observed coat colour polymorphisms consisted of leucistic (including singular white patches), melanistic (darkly pigmented) and piebald (mixed) coat patterns. After isolation for at least seven centuries, wild Polynesian rat populations on islands seem to exhibit a trend towards a higher incidence of aberrant coat patterns. These phenotypic changes are here explained as a neutral, non-adaptive process, likely part of the 'domestication syndrome' (via the commensal pathway of domestication), in combination with genetic drift, little or no gene flow between the islands and/or the mainland and a relaxed selection (as a result of the weakening or removal of competitor / predator pressure) under commensality.

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## 11 Abstract
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13  changes, e.g. larger or smaller body size, shortened limbs, duller coats, as well as behavioural
14  changes such as increased tameness and reduced flight-initiation distance. These changes overlap
15  in part with those associated with the 'domestication syndrome', especially tameness and
16  changes in coat patterns, and might indicate a similar neural crest involvement in the concurrent
17  development of multiple phenotypic traits. Here I examine long-term data on free-living
18  populations of wild Polynesian rats from seven mainland countries and 117 islands (n=3034),
19  covering the species' native and introduced range. Mainland populations showed no aberrant
20  coat patterns, with the exception of one albino, whereas aberrant coat patterns were found in 12
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23  isolation for at least seven centuries, wild Polynesian rat populations on islands seem to exhibit a
24  trend towards a higher incidence of aberrant coat patterns. These phenotypic changes are here
25  explained as a neutral, non-adaptive process, likely part of the 'domestication syndrome' (via the
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27  between the islands and/or the mainland and a relaxed selection (as a result of the weakening or
28  removal of competitor / predator pressure) under commensality.

## 29 Introduction
30  Evolution on islands has often led to increased phenotypic variation and phenotypic novelty not
31  observed in closely related mainland forms, inspiring studies on evolution ever since Wallace
32  wrote his influential book (1880). The perhaps most obvious phenotypic variation is observed in
33  body mass, especially in island endemic lineages of the Pleistocene epoch, when rabbit-sized rats

34  and pony-sized elephants and hippos were common elements of island faunas (van der Geer et
35  al., 2010). Body mass evolution of island mammals typically follows a graded trend from
36  gigantism in small-sized species to dwarfism in large-sized species (Foster, 1964; Van Valen,
37  1973; Lomolino, 1985, 2005), where the degree and direction of body size evolution vary in a
38  predictable manner in accordance with characteristics of the ancestral taxon and the levels and
39  nature of various factors like competition, predation, ecological complexity, climate, latitude,
40  island area and isolation (Lomolino et al., 2012, 2013). Other morphological features regularly
41  shared by phylogenetically distant fossil island mammals are proportionally shortened limbs
42  (Sondaar, 1977), reduced brain size (Weston & Lister, 2009; see, however, Lyras et al., 2006),
43  increased convolution of the brain cortex (Desachaux, 1961; Falk et al., 2005), fusions of limb
44  bones (Leinders & Sondaar, 1974; Moyá-Solá, 1979; van den Bergh et al., 2008; van der Geer,
45  2014), high-crowned teeth (Bover, 2004; van den Bergh, 1999; van der Geer et al., 2006; van der
46  Made, 1999), loss of dental elements (Leinders, 1984; Lyras et al., 2006; Boekschoten &
47  Sondaar, 1972), shortened muzzles (van der Geer, 2005; Quintana, Köhler & Moyà-Solà, 2011;
48  Kaifu et al., 2011; van der Geer et al., 2018), increased stereoscopy (van der Geer, 2005) and
49  increased size variation (de Vos & van der Geer, 2002; van der Geer, 2014). Isolated mammal
50  populations may also show shared ecological differences such as increased tameness or
51  ecological naiveté (see also below), higher and more stable population densities, reduced
52  intraspecific aggression, reduced reproductive output (see, however, Raia, Barbera & Conte,
53  2003, who suggested increased reproductive productivity in a dwarf elephant) and reduced
54  dispersal abilities. The suite of ecological and morphological characters often associated with
55  isolated mammal populations is referred to as the 'island syndrome' (Adler and Levins, 1994).
56  Other groups, e.g. lizards, also show trait shifts that are consistent with the 'island syndrome',
57  such as a higher degree of melanism (darkly pigmented skins) (Runemark et al., 2010), increased
58  tameness (Cooper & Pérez-Mellado, 2012), shorter flight initiation distance and reduced sprint
59  speed (Vervust, Grab & van Damme, 2007), smaller clutch sizes (Huang, 2007) and larger
60  bodies (Vervust, Grab & van Damme, 2007; Pafilis et al., 2009). In parallel, insular birds may
61  have smaller clutch sizes (Cody, 1971), dull colours (Omland, 1997), increased tameness
62  (Blondel, 2000), or may become flightless (Roff, 1994).

63  The concomitance of a set of phenotypic alterations, often similar in unrelated groups, is also a
64  common theme in domestication, already noted by Darwin (1868). In mammals, this linked set
65  of alterations has been called the 'domestication syndrome' (Wilkins et al., 2014), and includes
66  increased tameness, shortening of the rostrum, reduced brain size relative to body size (Kruska,
67  2005), floppiness of the ears, curliness of the tail and depigmented skin and fur (Herre & Röhrs,
68  1990). Breeding experiments on silver foxes, *Vulpes vulpes* (Linnaeus, 1758) since 1959
69  (Belyaev, 1969) showed that selection for tameability resulted not only in the desired increased
70  tameness, but also in aberrant pigmentation, floppy ears, rolled and shortened tails, shorter limbs,
71  shortened, flattened and widened rostra, smaller brains, earlier onset of sexual maturity and the
72  ability to perceive human gestures, indicating that these phenotypic features are coupled (Trut,
73  1999; Trut, Plysnina & Oskina, 2004; Trut, Oskina & Kharlamova, 2009; Hare et al., 2005).

74  Similar experiments on brown rats, *Rattus norvegicus* (Berkenhout, 1769), initiated by Belyaev
75  as well also yielded tame and aggressive strains, where, as in the foxes, tame rats have shorter,
76  flatter and wider muzzles (Singh et al., 2017) and a higher frequency of white spots than the
77  aggressive rats (Albert et al., 2009).

78  This morphological covariation of phenotypic features in domestic animals is generally
79  explained as due to particular changes of the neural crest cell migration (Crockford, 2002;
80  Montague et al., 2014; Wilkins, Wrangham & Fitch, 2014; Sánchez-Villagra, Geiger &
81  Schneider, 2016). The selection for tameability results in developmental deficits in the neural
82  crest cells (multipotent stem cells that arise from the dorsal part of the neural tube in vertebrate
83  embryos), which cause most of the characteristics of the 'domestication syndrome' (Wilkins,
84  Wrangham & Fitch, 2014). The variation in pigmentation in domesticates is then likely a
85  pleiotropic effect of alleles influencing traits that are related to tameability.

86  In this respect it is interesting to note the similarity regarding 'naiveté' between the 'island
87  syndrome' and the 'domestication syndrome'. Native island species are often ecologically naive
88  relative to native mainland species. Ecological naiveté is defined as "the tendency for long-term
89  inhabitants of low diversity and disharmonic (unbalanced) islands to lose their capacities for
90  detecting, avoiding or otherwise coping with competitors, predators and parasites from the
91  mainland or otherwise more-balanced and species-rich assemblages - i.e., species at least initially
92  absent from these islands" (cited from Lomolino, 2016:8). An often-cited example is the
93  Falkland wolf (*Dusicyon australis*), initially even considered a feral domestic dog, because of its
94  remarkable tameness and, among others, white on its tail tip, muzzle and lower limbs (Clutton-
95  Brock, 1977), but this was dismissed on the basis of divergence time between this species and its
96  ancestor (Slater et al., 2009; Austin et al., 2013). Darwin (1839) was struck by so much naivety,
97  and foresaw this species' fast extinction, analogous to that of the dodo; indeed, the last individual
98  was killed less than 50 years later.

99  Irrespective of the genetic and developmental background of the 'domestication syndrome', it
100 has been noted that changes in pigmentation are one of the first traits to appear during the
101 domestication of brown rats selected for tameness (Trut, 1999, Trut, Oskina & Kharlamova,
102 2009). Pigmentation changes in the form of increased occurrence of white patches of fur were
103 also observed in a free-living population of wild house mice, *Mus musculus domesticus* Schwarz
104 & Schwarz, 1943, that were experimentally kept at an uninhabited barn, fed *ad libitum* and
105 regularly handled in the course of 14 years (Geiger, Sánchez-Villagra & Lindholm, 2018). The
106 repeated and frequent exposure to humans in combination with abundant food and absence of
107 predators resulted in an indirect selection for tameness (Geiger, Sánchez-Villagra & Lindholm,
108 2018), with as it seems similar covariation of features of the 'domestication syndrome', in this
109 case white fur patches and shorter snouts. Depigmentation might thus be a useful indicator for
110 the detection of the early stages of evolutionary changes in murids which are typical for the
111 'domestication syndrome'. The 'domestication syndrome' might have a partial developmental
112 similarity with the 'island syndrome' as far as increased naiveté (loss of anti-predator strategies)

113 is concerned. If that is the case, one would expect increased depigmentation (especially white
114 patches and brown regions) in natural insular populations on islands with the highest levels of
115 insularity (low biodiversity, small size, high isolation). The opposite, increased pigmentation or
116 melanism, is linked to insularity only in lizards, but the higher prevalence of melanistic colour
117 morphs in more densely settled urban contexts in squirrels (Garroway et al., 2018) and ship rats
118 (Ondrias, 1966), as well as in the latter species on the Galápagos Islands (Patton, Yang, Myers,
119 1975) and Hawaii (Tomich, 1968), suggests that both decreased and increased pigmentation may
120 be expected in insular and/or commensal settings. Here, I examine this hypothesis on wild
121 populations of the Polynesian rat, *Rattus exulans* (Peale, 1848) from the islands of the Pacific
122 and insular Southeast Asia.

123 The Polynesian rat has vastly extended its geographic range through human-mediated transport
124 (Fig. 1) starting c. 4000 years ago (Roberts, 1991) and has been established in mainland
125 Southeast Asia, the Greater and Lesser Sunda islands, the Moluccas, the Philippines, New
126 Guinea, New Zealand and practically all inhabited Pacific islands for at least six centuries
127 (Corbet & Hill 1992; Musser & Carleton 2005); additionally, it has been reported from Taiwan
128 and Miyakojima of the southern Ryukyu Islands (arrival likely less than a century ago;
129 Motokawa et al. 2001) and Adele Island, northern Australia (arrival c. 130 years ago; Boyle et al.
130 2004). On the islands outside its native range, it lives as a human commensal in houses,
131 granaries, gardens, cultivated lands, plantations, anthropogenic scrubland, secondary forest and
132 slightly altered primary forests near habitats maintained by humans (Musser, 1977; Corbet &
133 Hill, 1992), where it is regularly exposed to humans. In this respect it is relevant to note that a
134 number of historical accounts describe this rat as not shy towards humans (e.g. Von Kotzebue,
135 1821 for the Marshall Islands) and easy to catch (Peale, 1848 for the Society Islands).

136 Evolutionary divergence is expected to be greatest in the following populations: those on islands
137 with reduced competitor and predator stress through relaxed selection (Whittaker & Fernandez-
138 Palacios, 2007; Lomolino, Riddle & Whittaker, 2017), those on small islands (Lomolino et al.,
139 2012; van der Geer, 2018) and those with greater residence times (Lomolino et al., 2013; van der
140 Geer, Lomolino & Lyras, 2018). The hypothesis is that these populations of Polynesian rats will
141 show the highest incidence of aberrant coat patterns.

## Materials & Methods

143 Dried and prepared skins of the Polynesian (or Pacific) rat, *Rattus exulans*, were studied at the
144 American Museum of Natural History (New York, US), the Smithsonian Institution
145 (Washington, US) and Te Papa Tongarewa National Museum of New Zealand (Wellington, NZ)
146 (for specimen numbers, see Data S1). Total number of specimens was 3034, of which 370
147 originated from a total of 7 mainland countries (see Table 1 and Data S1 for details). The islands
148 are classified in five biogeographical regions that differ in biodiversity and average colonisation
149 period by the focal species. Numbers of island specimens are as follows per group: Melanesia
150 (n=757 from 21 islands), Micronesia (n=292 from 29 islands), Polynesia (n=424 from 37

151  islands), Sunda Shelf Islands (n=478 from 12 islands) and Wallacea (n=722 from 18 islands).
152  Palawan and its satellites are considered here as part of the Sunda Shelf, following Cranbrook
153  (2000), who maintains a connection with Borneo during the Last Glacial Maximum (see,
154  however, Voris (2000) who dismisses any connection with Borneo during the Late Pleistocene,
155  based on sea-level reconstructions). The remainder of the Philippines are oceanic in origin,
156  except for Mindoro, which originated as a portion of the Asian continental shelf, and have never
157  been connected to a mainland (van der Geer et al., 2010). They are here considered together with
158  Wallacea on grounds of its similar isolation from the Asian and Australian continental shelves.
159  Bali was connected to Java during the Late Pleistocene (Voris, 2000), and is thus classified with
160  the Sunda Shelf Islands. Offshore islands are considered together with the respective main
161  island.

162  The biogeographical regions differ in the composition of their faunas (see Data S2 for number of
163  ecologically relevant native competitors and predators, based on fauna lists provided by van der
164  Geer, Lomolino & Lyras, 2017, 2018). For example, while Sunda Shelf islands (both Greater and
165  Lesser Sunda Islands) and parts of Melanesia have native competitors and predators, Wallacea
166  has only native competitors, whereas Polynesia and Micronesia have no competitors or predators
167  at all. Introduced potentially relevant predators consists of feral cats in this case. Their impact on
168  population dynamics of introduced rats is, however, negligible (Parsons et al., 2018) and their
169  presence is not taken into account here. Time in isolation is taken from Kirch, 1984; Roberts,
170  1991; Matisoo-Smith et al., 1999; Cranbrook, 2000; Anderson & White, 2001; Anderson &
171  Sinoto, 2002; Anderson, 2005, 2008; Green, Jones & Sheppard, 2008; Summerhayes et al., 2010;
172  Hanebuth et al., 2011; Wilmshurst et al., 2011; Burley, Weisler & Zhao, 2012; Denham, Ramsey
173  & Specht, 2012; Carson et al., 2013; Clark et al., 2016; McCoy et al., 2016; West et al., 2017
174  (details per island provided in Data S2; see also Fig. 1) and binned in classes of 1,000 years each,
175  except for the highest class (class 5), which represents time in isolation exceeding 5,000 years
176  without upper limit. Surface area was $\log_{10}$ transformed before statistical analyses.

177  Aberrant coat colour and patterns are those that differ substantially (evaluated by me and, where
178  needed, checked by the photographer and curatorial staff) from those seen in the rest of the
179  population from the same island or country, thus taking natural variation within populations into
180  account. Both upper- and undersides are taken into account. Slightly darker or lighter coat
181  colours are considered normal, taking seasonal variations into account. Dorsal pelage in *R.*
182  *exulans* varies per region between grey-brown to reddish-brown; ventral pelage is dark grey or
183  pale buffy with pale grey or white tips (Tate, 1935; Atkinson & Moller, 1990). White-bellied
184  individuals, lacking grey bases to the white belly hair, are typical for and restricted to Flores
185  (Lesser Sunda Islands; Indonesia) (Schwarz & Schwarz, 1967) and Adele Island (Australia)
186  (Tate, 1951); the mtDNA haplotype (Rx083) is the same in the Flores sample from Liang Bua
187  cave and Adele Island, while different elsewhere (Hingston, 2015), supporting a recent
188  introduction by Indonesian fishermen.

189  I here take the mainland populations as reference, and not those from the Lesser Sunda Islands.
190  Flores was indicated as the place of origin of the *exulans* group (Schwarz, 1960), instead of
191  mainland Southeast Asia (Tate, 1935), based on the presence here of white-bellied forms.
192  Schwarz and Schwarz (1967) considered these  the "wild form" and the ancestor of all
193  commensal types. They interpreted the loss of a white belly as an adaptation to the darker indoor
194  environment. Genomics confirmed this hypothesis was (Thomson et al., 2014),. Note, however,
195  that Musser (1981) did not find significant morphological differences between *R. exulans* from
196  Flores and the rest of the Lesser Sunda Islands; in addition, no fossil or subfossil *R. exulans* have
197  yet been reported from Flores, despite the rich murid fossil record with stratigraphic contexts.
198  Although the exact place of origin has important implications for tracing human migrations
199  through insular Southeast Asia, it has much less relevance to the distribution of coat
200  polymorphisms.

201  Aberrant coat patterns are here defined in terms of leucism and melanism. Leucistic mammals
202  lack pigment to a varying degree, ranging from a few white spots to (nearly) all white or
203  yellowish. In contrast to albinistic mammals, that congenitally lack pigment altogether, eyesight
204  is not usually impaired and the nose, eyes and feet are coloured as typical for the species.
205  Melanistic mammals in contrast show an increased expression of black or brown pigment
206  (melanine). Mixed white and brown / black animals are generally known as piebald.

207  Potentially, three types of sampling biases could have influenced the results presented here.
208  Particular collectors may have either preferred or discarded specimens with an aberrant or
209  otherwise remarkable coat pattern. Particular curators may have discarded particular aberrant
210  specimens during curatorial activities. Finally, sample sizes are not equal for all regions: the
211  samples from Wallacea and Melanesia are twice the size of those from the other three island
212  regions as well as the mainland, potentially increasing the chance of finding abnormalities in the
213  first two regions. I here assume the collector's and curatorial bias to be similar across the
214  regions. Furthermore, the specimens are derived from only three major collections, limiting the
215  curatorial bias to differences among these collections. Overlap in geographical provenance
216  between the collections further reduces this bias.

217  The variables (number of competitors and predators, island area, time in isolation and cases of
218  aberrant coat patterns) were not normally distributed (after testing using the Shapiro-Wilk test;
219  Shapiro & Wilk, 1965; Table S1)), therefore Chi-square tests were used to test whether the
220  aberrant coat patterns were evenly distributed over the archipelagoes and the time bins, and
221  whether there was a relation with the number of native predators and competitors. The groupings
222  were based on biogeographical provinces (Mainland, Melanesia, Micronesia, Polynesia, Sunda
223  Shelf Islands, Wallacea), as this corresponds best to biodiversity and residence time (see above),
224  absence / presence of aberrant coat patterns and residence time (binned in steps of 1,000 years
225  each, see above). The number of native predators was binned as zero, 1, 2 or more predators; the
226  number of native competitors was binned as zero, 1–5, 6–30 or more competitors (see Data S2
227  for the islands; mainlands fall in the latter bins). Regarding island area ($\log_{10}$ transformed), a

228  non-parametric Kruskal-Wallis one-way analysis of variance test (by lack of normality) was used
229  to determine if there was a correlation between coat colour polymorphism (Siegel, 1956), with
230  the number of aberrant coat patterns as grouping variable (three samples: 0, 1 or 2 aberrant coats)
231  and island area, and similarly, to test for a correlation between island area and number of
232  competitors. Statistical analyses were performed using Past 3.16 (Hammer, Harper & Ryan,
233  2001). Significance level alpha = 0.05.

## Results

235  Out of 3034 skins of *R. exulans*, 15 skins showed aberrant coat colour and/or pattern, evenly
236  distributed over the sexes (Tables 2 and 3) and over the geographic distribution (Fig. 2); for
237  summary statistics, see Table S1. The single aberrant coat pattern from the mainland (Vietnam)
238  is an albino (Fig. 3A, B). Albinos are, however, characterised by a congenital failure to produce
239  melanin in otherwise normal melanocytes. In this way, potential changes in the coat colour
240  pattern are not expressed and can thus not be traced. Albinos can further be recognised by their
241  red eyes and pink noses and ears, as a result of this total lack of pigmentation. This specimen is
242  omitted from the analyses. Note that albino specimens are reported in less than 2% of rodent
243  species (Romero et al., 2018), and that the specimen shown here (USNM 357550) is, by my
244  knowledge, the first reported case in *R. exulans*.

245  The aberrant coat colour patterns from the islands by contrast either show signs of increased
246  pigmentation (melanism) or reduced pigmentation (leucism). The depigmentation can be
247  complete (Fig. 3C, D; Fig. S1A), partial (piebald; Fig. 4) or restricted to a single spot (Fig. 5,
248  Fig. S1B) or a few strands of hair (Fig. 2I). The piebald specimen (Hawaii) has normal, wild-
249  type colouration on the head, shoulders and a wide mid-dorsal stripe or band extending to the
250  base of the tail, as typical for the "hooded" phenotype of laboratory rats (*R. norvegicus*);
251  different from the hooded rats is the patchy brown pigmentation on the white parts. Based on the
252  typical light buff colour (pale yellow) of the albino *R. exulans* (Fig. 3A-B) as a result of total
253  lack of melanin in the melanocytes, I here interpret the evenly buff coloured specimens as
254  different phases of leucism with differential expression of melanin, where a total lack
255  corresponds to the colour of the albino (but with different congenital background) (Fig. 3C-D;
256  Fig. S2A). The latter specimens are not albinos because they have black eyes,  coloured ears and
257  toe pads, and presumably black eyes (eyes were removed, but aberrant features are typically
258  noted down, which was not the case here). The melanistic specimens are either evenly darker
259  coloured, including (Fig. 6A-B) or excluding the underside (Fig. 6C-D; Fig. S2B-C), or bear
260  irregular patches of increased pigmentation, either on both upper- and underside (Fig. 6E-F) or
261  only at the underside (Fig. 6G-H).

262  The difference in distribution of aberrant coat colour patterns over the six biogeographical
263  regions is not significant (Chi$^2$, p=0.08, all patterns; p=0.06, melanism and leucism considered
264  separately; Table S2), nor is the distribution different between the mainland and all islands
265  considered together (Chi$^2$, p=0.162). Within Polynesia, coat polymorphisms are restricted to the

266   Hawaiian archipelago and Line Islands, both at the north-eastern limit of the distribution. The
267   majority of aberrant coat patterns are various phases of leucism.

268   Time in isolation cannot predict the occurrence of aberrant coat patterns (Chi$^2$, p=0.673),
269   whereas the numbers of native predators and native competitors as well as log transformed island
270   area are significantly correlated to the number of aberrant coat patterns (Chi$^2$, p = 0.017, Chi$^2$, p =
271   0.002 and Kruskal-Wallis, p < 0.001, respectively). The latter two variables are, however,
272   positively correlated to the number of aberrant coat patterns. This counterintuitive result is
273   probably driven by the positive correlation between island area and competitors (species-area
274   relationship; Kruskal-Wallis, p < 0.001), and the correlation coat polymorphism and island area
275   is here considered redundant. Test results are provided in Tables S1 and S2.

## Discussion

277   Insular populations of Polynesian rats show a higher incidence of individuals with an aberrant
278   coat pattern than those of mainland Polynesian rats, which lacked leucistic and/or melanistic
279   individuals altogether. This higher incidence is, however, not statistically significant, perhaps as
280   a result of the smaller sample size of mainland rats (12% of the total). The coat polymorphisms
281   found on the islands are not significantly correlated with time in isolation. Indeed, although the
282   Philippines and Sulawesi were among the first islands to be reached by the Lapiti people on their
283   way into the Pacific some 3,500–4,000 years ago (Anderson, 2005), and half the reported cases
284   are from these islands, an equal amount of cases of aberrant coats is from Polynesian islands that
285   were reached only some 925–657 years ago (West et al., 2017). Colour polymorphisms seem not
286   to have been facilitated by the sequential colonisation (the founder effect) either, as seen by the
287   lack of a clear distribution pattern of (nearly) identical aberrant coat patterns (Figs 1, 2).
288   However, note that within Polynesia, the aberrant cases are restricted to the most remote part of
289   the north-eastern distribution (Hawaii and Line Islands). A sequence of founding events, such as
290   is the case for the Polynesian dispersal from Near to Remote Oceania is likely to reduce genetic
291   variation (e.g. Clegg et al., 2002). However, this cannot explain the results presented here, as
292   similar polymorphisms would be expected to occur on related islands, which is not the case.

293   The level of predation and murid competition varies substantially between the regions. Whereas
294   Polynesia and Micronesia both lack ecologically relevant native predators and competitors,
295   Wallacea and the Sunda Shelf islands house a suite of native murids to compete with, as well as
296   native predators in the case of the latter islands. The unexpected positive correlation between
297   coat colour polymorphisms and amount of ecologically relevant competitors might be an artefact
298   instead of representing a causal relationship, because these results are strongly influenced by the
299   islands Luzon and Sulawesi, each with two aberrant specimens as well as an exceptionally high
300   number of native murids. A simple mechanism that could explain the observation that the more
301   competitors, the more aberrant coat patterns are present, is that potential expansion of Polynesian
302   rats into non-commensal niches is hampered by resident murid species. I can here only speculate
303   that this obligatory restriction to the human commensal niche, and the inherent reduced fear for

304  humans, caused the higher number of abnormalities on (very) biodiverse islands. For Sulawesi
305  and Luzon, there are indeed indications that this might be valid: its occurrence on Sulawesi was
306  recorded mostly in and around villages, and only sparsely in secondary forest (Musser, 1977) and
307  on Luzon it is considered always associated with human habitation, except when there are few
308  native murids (Heaney et al., 2010). Similar scenarios have been suggested for introduced house
309  mice, which are usually outcompeted by other rodent species in non-anthropogenic habitats (e.g.
310  Berry, Cuthbert & Peters, 1982).

311

312  Depigmentation in the form of white patches on the trunk as presented by Polynesian rats from
313  Java, Hawaii, Kauai, Luzon and Sulawesi has been observed in practically all domestic animal
314  species (mouse, rat, guinea pig, rabbit, dog, cat, fox, mink, ferret, pig, reindeer, sheep, goat,
315  cattle, horse, camel, alpaca and guanaco; Darwin, 1868; Belyaev & Trut, 1989; Gariépy, Bauer
316  & Cairns, 2001; Trut, Oskina & Kharlamova, 2009). In the brown rat, *R. norvegicus*, typically,
317  the irregular white patches occur in particular sites: just below the throat and above the eyes, the
318  paws and the tip of the tail. This is, however, not what we observe in the Polynesian rats, where
319  the patches are predominantly located in the shoulder region and on the back of the thorax. Only
320  the piebald specimen from Hawaii has an irregular placement of white patches all over its body
321  and skull with the exception of the midsagittal region over its entire length, approaching
322  observed colour patterns in domestic brown rats. White patches in rats are generally considered
323  as evolved along the commensal pathway of domestication (Sánchez-Villagra, Geiger &
324  Schneider, 2016), and the Polynesian rat seems to follow this pattern, being a human commensal
325  species in its introduced range, except for islands abandoned by the Polynesians centuries ago
326  (e.g. the Mystery Islands). This pathway is characterized by unintentional selection for tameness
327  (Zeder, 2012a, b; Larson & Fuller, 2014). In the case of island evolution, this tameness may also
328  be a case of ecological naivité driven by the decreased number of predators and competitors
329  relative to the mainland (e.g., the number of native mammalian predators feeding on rats of
330  Vietnam is 24; data from IUCN, 2019). Indeed, a significant correlation was found between
331  native predators and incidence of aberrant coat patterns. This is best illustrated by the presence of
332  the most extreme aberrant coat pattern (the piebald specimen) on an island (Hawaii) without any
333  native mammals, except for bats.

334  In general, evolutionary changes of island mammals in their new environment may have been
335  adaptive as well as non-adaptive (e.g. Whittaker & Fernandez-Palacios, 2007). In that light, a
336  possible scenario for the higher occurrence of melanistic coats on Pohnpei, Kure Atoll and Kauai
337  (Hawaii) could be that darker coat patterns have an adaptive advantage in avoiding birds of prey
338  because such a colour spectrum corresponds to the background colour of their habitats: dark
339  basaltic rocks covered in rain forests. However, the lack of increased melanism on other basaltic
340  islands fails to confirm such a pattern. The lack of a clear pattern and the overall low percentage
341  of melanism seems unable to support a functional explanation. In addition, although piebald coat
342  patterns have the potential to be adaptive in rainforest environments (Hawaii), the high incidence

343    of piebald patterns in domestic animals rather favours an explanation towards a higher degree of
344    tameness under low predatory pressure.

345    The observed colour polymorphisms here are limited to variations in the expression of red-
346    yellow and/or black-brown (distribution, expression, intensity). These two colour ranges in
347    vertebrates are mainly controlled by two genes, being the melanocortin-1 receptor gene (*Mc1r*)
348    and its antagonist, the *Agouti* signalling protein gene (*Asip*) (Hubbard et al., 2010). These genes
349    work together in controlling the pigment expression of eumelanin (black-brown) and
350    pheomelanin (red-yellow) in melanocytes. Melanistic furs in natural populations are most
351    commonly associated with mutations in *Mc1r* (e.g. Mundy et al., 2004), In mice, *Agouti* further
352    regulates the differences between dorsal and ventral pigmentation and may be responsible for the
353    switching off of pigment production altogether (Vrieling et al., 1994). Dark buff or rufous
354    undersides (contrary to the usually white ventral pelage) were observed in the most remote
355    population of the large Japanese field mouse, *Apodemus speciosus* (Temminck, 1844), on the Izu
356    Islands (Tomozawa *et al.*, 2014), explained as the result of loss of genetic variation and changes
357    in the frequency of an allele for a mutation in *Asip*. Laboratory mice with such mutations showed
358    enhanced pigmentation (yellow pheomelanin) of the ventral pelage (Vrieling et al., 1994),
359    similar to the pattern (dark buff with blackish tail) observed in the large Japanese field mouse on
360    Miyake island (Tomozawa et al., 2014). Such a mechanism may explain the Polynesian rat
361    specimen with irregular dark buff patches especially at its underside. White spotting in rats and
362    mice, including hooding, is caused by mutations in one or more of the genes that regulate neural
363    crest-derived melanoblast development (e.g. *Kit*, *Pax3*, *Mitf* and *Sox10*), leading to reduction
364    and/or loss of mature melanocytes (Baxter et al., 2004; Kuramoto et al., 2012). White spots can
365    be associated with disorders in other neural crest derived tissues or elsewhere due to pleiotropic
366    effects, including microphthalmia, deafness, spina bifida and sterility (Baxter et al., 2004), most
367    of which would be fatal or at least severely impact fitness in any wild living rat population. The
368    pale-yellow coat pattern in the Polynesian rat might be explained by the diluting effects of the
369    gene(s) that control the intensity of pigment, in combination with alleles coding for brown
370    instead of black. In mice, this combination is the result of homozygosity for the recessive allele
371    in both genes (Griffiths et al., 2000). In parallel, the ash grey dorsal fur of the Kiritimati
372    specimen might be due to reduced pigment production in combinations with a black colour. In
373    short, a number, or perhaps all, of the aberrant coats in Polynesian rats might be explained
374    simply by loss of genetic variation, due to drift and founder effects.

375    Whereas phases of leucism, including piebald, can all be ascribed to homozygosity for recessive
376    alleles in one or more genes (see above), this is not always the case for melanism. In laboratory
377    mice, for example, mutations in alleles of *Mc1r* leads to dominant melanism, whereas mutations
378    in alleles of *Agouti* usually cause recessive melanism. The latter was found in four
379    geographically widely separated North American deer mouse populations, which suggests that
380    melanism-inducing mutations in *Agouti* might be more common than generally thought
381    (Kingsley et al., 2009). The low incidence (three specimens) of generalised melanism in

382  Polynesian rats indicates such a recessive autosomal inheritance of melanism. The occurrence of
383  two of these, plus the single piebald specimen, in the same archipelago might further indicate a
384  general loss of heterozygosity in this remote destination.

385  In contrast, the absence of coat colour polymorphisms on Borneo and Sumatra may indicate a
386  regular gene flow from the adjacent mainland populations in Southeast Asia. A similar lack of
387  aberrant coat patterns in central east Polynesia (e.g. Society and Cook Islands, Samoa) might be
388  explained by the existence of a broad interaction sphere or a large "homeland region", central to
389  a number of smaller interaction spheres, as indicated by evidence from mtDNA phylogenies
390  (Matisoo-Smith et al., 1998), with the concurrent regular gene flow. By contrast, the Polynesian
391  rats of Hawaii have close affinities with those of the Marquesas and the Society Islands, but
392  whether gene flow continued after the initial introduction(s) remains unclear (Matisoo-Smith et
393  al., 1998). The occurrence of a piebald specimen favours the hypothesis of a high degree of
394  isolation. The limitation of rats with white patches on their dorsal pelage to Luzon, Sulawesi and
395  Java might confirm the existence of a regional interaction sphere including the Philippines,
396  Borneo and Sulawesi, unrelated to that of Oceania, as inferred from the restriction of mtDNA
397  haplogroup I to the Philippines, Borneo and Sulawesi (Matisoo-Smith & Robins, 2004; a
398  cautionary note: Java was not sampled in the latter study). Cytochrome B haplotype distributions
399  also confirm a connection between the Philippines (Negros), Borneo and Sulawesi, all sharing
400  H1, which occurs nowhere else (Thomson et al., 2014). Saipan (Mariana Islands) has the basic
401  Pacific haplotype (H8), which gives no further clue on phylogeny; the other islands of my dataset
402  were not sampled.

## Conclusions

404  Results revealed that populations of the Polynesian rat introduced onto Southeast Asian and
405  Pacific islands show a trend towards a higher incidence of coat polymorphisms, such as white
406  patches, piebald coats, leucism and melanism as compared to mainland populations from their
407  native range, although not statistically significant. No correlation could be found between this
408  incidence and  time in isolation on the focal island. A negative correlation was found between
409  the number of native predators and the incidence of aberrant coat patterns. The higher incidence
410  of abnormal coat patterns on islands with a high level of native murid biodiversity is here
411  tentatively explained as linked to a more exclusively human commensal life. The white patches,
412  including piebald patterns, observed in Polynesian rats, are here explained as a pleiotropic effect
413  of unintentional selection for tameness (commensal pathway of domestication), possibly
414  accelerated by insularity (limited gene flow, lack of predators), whereas melanistic coat patterns
415  are more likely the effect of isolation on gene frequencies and distribution (founding events) and
416  thus not necessarily linked to increased tameness.

## Acknowledgements

418  I thank Darrin Lunde (United States National Museum of Natural History), Neil Duncan, Ross
419  MacPhee, Marisa Surovy, Eleanor Hoeger, Brian O'Toole (American Museum of Natural

History) and Colin Miskelly (Te Papa Tongarewa National Museum of New Zealand) for
permission to access the collections under their care and their technical assistance. I thank
Stergio Intzes for his assistance with the statistical analyses, George Lyras for making the figures
and Tamatea McGlinn for proofreading the text. A special thanks goes to Bartholomeus van der
Geer for much-appreciated technical support, making the photographs and discussing the initial
idea. The reviewers are thanked for their thorough and critical reviews, which helped greatly to
improve the manuscript.

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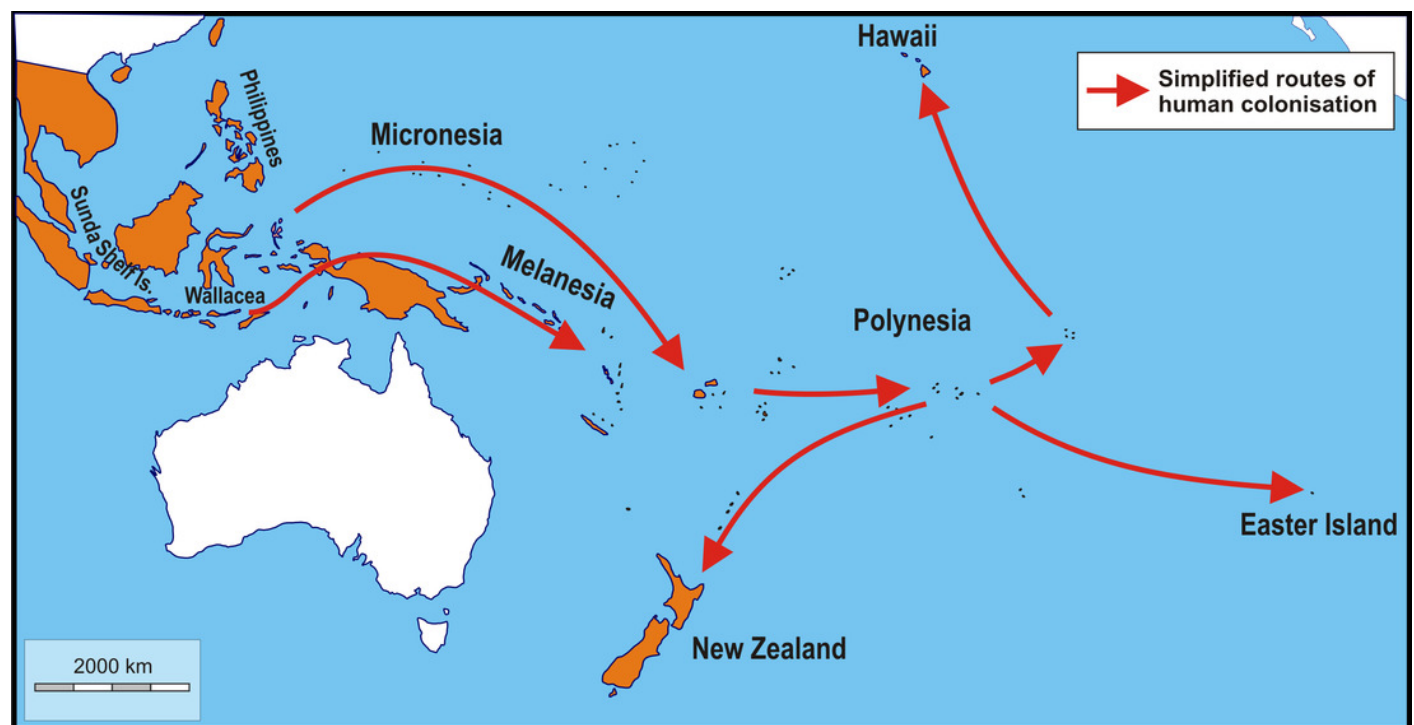
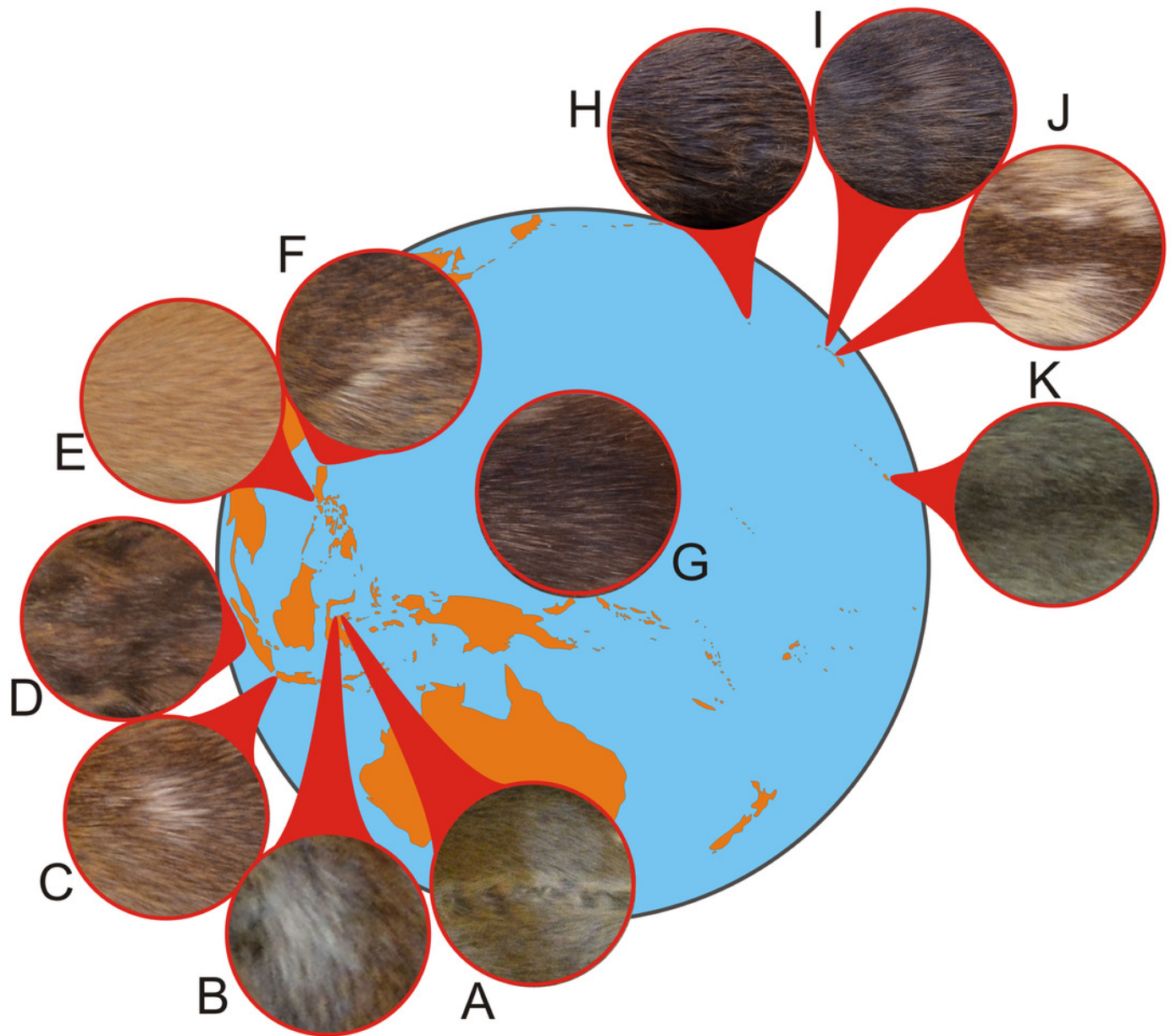
# Figure 1

Schematic map showing simplified routes of human-aided dispersal of Polynesian rats, *Rattus exulans*

Populations on the Sunda Shelf Islands were isolated since the Last Glacial Maximum when sea level rises disconnected these areas from each other and the mainland. Populations in the Philippines and Wallacea were introduced about 4000–3500 BP. Subsequently, more remote areas were reached starting about 3400–3200 BP (Micronesia, Melanesia). The remotest areas of Polynesia (New Zealand, Hawaii and Easter Island), finally, were settled about 820–720 years ago (Roberts, 1991; Matisoo-Smith et al., 1999; Summerhayes et al., 2010; Wilmshurst et al., 2011; West et al., 2017). Orange: native and introduced range. White: areas without Polynesian rats. Image credit: George Lyras. Map credit:https://d-maps.com/carte.php?num_car=3258&lang=en.

# Figure 2

Schematic map showing the distribution of aberrant coat patterns in Polynesian rats.

The distribution of coat polymorphisms is random over the introduced range. No aberrant coat patterns were found in populations from the native range (mainland Southeast Asia), except for an albino specimen from Vietnam (not indicated here; see Fig. 3). The circles show details of ventral (A) and dorsal skins (B); all skins are shown in full in Figs 3-6 and Figs S1-2. (A) Malenge, Togian Islands, Sulawesi. (B) Sulawesi, Indonesia. (C) Java, Indonesia. (D) Batam, Riau Islands, Sumatra. (E) Mindoro, Philippines. (F) Luzon, Philippines. (G) Pohnpei, Caroline Islands. (H) Kure atoll, Hawaii. (I) Kauai, Hawaii. (J) Hawaii, Hawaii. (K) Kiritimati. For specimen details, see Table 2. Image credit: George Lyras.

# Figure 3

Albino (A, B) and complete leucistic (C, D) coat patterns in the Polynesian rat.

(A) Albino specimen from Vietnam (USNM 357550, male), dorsal view. (B) Same specimen, ventral view. (C) Light buff coloured (complete leucism) specimen from Mindoro, Philippines (USNM 278589, male), ventral view. Note that *Rattus vigoratus* as written on the label is a junior synonym for *Rattus exulans* (Polynesian rat), following Wilson & Reeder (2005). (D) Same specimen, dorsal view. Photo credits: Bartholomeus van der Geer.

# Figure 4

Piebald coat pattern in an insular Polynesian rat.

The piebald pattern (a mixture of brown and white) is present on the ventral, lateral and dorsal sides in this specimen from Hawaii (USNM 324887, female). Photo credits: Bartholomeus van der Geer.

# Figure 5

Insular Polynesian rats showing white patches at the shoulder region.

(A) Specimen from Luzon, Philippines (USNM 145823, male). Note that *Epimys querceti* as written on this label and the next is a junior synonym for *Rattus exulans* (Polynesian rat), following Wilson & Reeder (2005). (B) Specimen from the same locality (USNM 145827, female). (C) Specimen from Java, Indonesia (USNM 138794, male). Photo credits: Bartholomeus van der Geer.

# Figure 6

Insular Polynesian rats with different expressions of melanism (increased pigmentation).

(A) Normal-coloured specimen from Ponape, Caroline Islands (USNM 301998; female), ventral side. (B) Melanistic coloured specimen from the same population (USNM 301999, female), captured at the same day, ventral side. (C) Same specimen as (A), dorsal view. (D) Same specimen as (B), dorsal view. (E) Irregular black patches in a specimen from Batam Island, Sumatra (USNM 143251, female), ventral view. (F) Same specimen, dorsal view. Patches are present on both upper- and underside. Note that *Epimys concolor* as written on the label is a junior synonym for *Rattus exulans* (Polynesian rat), following Wilson & Reeder (2005). (G) Irregular dark buff patches in a specimen from Malenge, Togian Islands, Sulawesi (USNM 153296, male), ventral side. (H) Normal-coloured specimen (USNM 153295, female) from the same locality. Photo credits: Bartholomeus van der Geer.

List of mainland countries and islands with number of Polynesian rats sampled in this study.

| Region | Country or Island | Gender | | | | |
|---|---|---|---|---|---|---|
| | | female | male | unknown | subtotal | total |
| **Mainland** | | | | | | 370 |
| | Bangladesh | 2 | 0 | 0 | 2 | |
| | Burma | 3 | 5 | 0 | 8 | |
| | Laos | 3 | 2 | 0 | 5 | |
| | Malaysia | 6 | 5 | 0 | 11 | |
| | Myanmar | 19 | 16 | 0 | 35 | |
| | Thailand | 83 | 60 | 4 | 147 | |
| | Vietnam | 84 | 77 | 1 | 162 | |
| **Melanesia** | | | | | | 757 |
| | Bougainville | 38 | 47 | 0 | 85 | |
| | Efaté | 4 | 2 | 0 | 6 | |
| | Emirau | 1 | 4 | 0 | 5 | |
| | Espiritu Santo | 17 | 18 | 0 | 35 | |
| | Fergusson | 3 | 4 | 0 | 7 | |
| | Fiji (island N/A) | 2 | 1 | 1 | 4 | |
| | Goodenough | 11 | 12 | 0 | 23 | |
| | Grande Terre | 33 | 20 | 0 | 53 | |
| | Guadalcanal | 17 | 27 | 2 | 46 | |
| | Kiriwinia Island | 2 | 0 | 0 | 2 | |
| | Misima Island | 3 | 2 | 0 | 5 | |
| | New Britain | 15 | 15 | 1 | 31 | |
| | New Guinea | 152 | 198 | 30 | 380 | |
| | New Ireland | 2 | 2 | 0 | 4 | |
| | Normanby Island | 11 | 14 | 0 | 25 | |
| | Nusi Island | 0 | 1 | 0 | 1 | |
| | Ontong Java | 3 | 2 | 0 | 5 | |
| | Rossel Island | 9 | 10 | 0 | 19 | |
| | Ugi | 0 | 1 | 0 | 1 | |
| | Vanatinai | 4 | 9 | 0 | 13 | |
| | Woodlark Island | 4 | 3 | 0 | 7 | |
| **Micronesia** | | | | | | 292 |
| | And atoll | 1 | 0 | 0 | 1 | |
| | Arno atoll | 4 | 1 | 0 | 5 | |
| | Babelthuap Island | 3 | 1 | 0 | 4 | |
| | Bikar atoll | 6 | 6 | 1 | 13 | |
| | Bikini Atoll | 3 | 11 | 0 | 14 | |
| | Carlos Island | 1 | 2 | 1 | 4 | |
| | Caroline Islands (island N/A) | 1 | 1 | 0 | 2 | |
| | David Island | 1 | 0 | 0 | 1 | |
| | Dick Island | 1 | 0 | 0 | 1 | |
| | Enewetok Atoll | 1 | 1 | 0 | 2 | |
| | Guam | 20 | 41 | 0 | 61 | |
| | Guguan Island | 0 | 2 | 0 | 2 | |
| | Kalap Island | 1 | 0 | 0 | 1 | |
| | Kapingamarangi Atoll | 2 | 1 | 0 | 3 | |
| | Kayangel Atoll | 0 | 1 | 0 | 1 | |
| | Koror Island | 11 | 10 | 0 | 21 | |
| | Kosrae | 1 | 3 | 0 | 4 | |
| | Kwajalein Atoll | 1 | 0 | 0 | 1 | |
| | Majuro Atoll | 1 | 9 | 0 | 10 | |
| | Moen Island | 3 | 2 | 0 | 5 | |
| | Peleliu Island | 0 | 1 | 0 | 1 | |
| | Pohnpei | 23 | 9 | 0 | 32 | |
| | Ponam | 1 | 0 | 0 | 1 | |
| | Rongelap Atoll | 2 | 4 | 0 | 6 | |
| | Saipan | 7 | 1 | 0 | 8 | |
| | Taka Atoll | 0 | 2 | 0 | 2 | |
| | Tinian Island | 0 | 2 | 0 | 2 | |
| | Ulithi Atoll | 18 | 43 | 0 | 61 | |
| | Wake Island | 8 | 14 | 0 | 22 | |
| **Polynesia** | | | | | | 424 |
| | Atafu Atoll | 2 | 0 | 0 | 2 | |
| | Aunu'U Island | 2 | 5 | 0 | 7 | |
| | Birnie Atoll | 6 | 18 | 0 | 24 | |
| | Fakaofo Atoll | 1 | 1 | 0 | 2 | |
| | Hatutaa Island | 2 | 2 | 0 | 4 | |
| | Hawaii | 18 | 16 | 1 | 35 | |
| | Hen Island | 1 | 3 | 0 | 4 | |

| | | | | |
|---|---|---|---|---|
| Kiritimati | 0 | 1 | 5 | 6 |
| Kanton | 6 | 2 | 2 | 10 |
| Kauai | 1 | 0 | 0 | 1 |
| Kure Atoll | 25 | 36 | 1 | 62 |
| Little Barrier | 18 | 17 | 0 | 35 |
| Manra Island | 1 | 0 | 0 | 1 |
| Macauley | 1 | 1 | 0 | 2 |
| Maui | 7 | 6 | 0 | 13 |
| North Island* | 6 | 7 | 73 | 86 |
| Niuafo'Ou Island | 1 | 2 | 0 | 3 |
| Nukunonu Atoll | 1 | 1 | 0 | 2 |
| Oahu | 13 | 13 | 1 | 27 |
| Ofu | 7 | 3 | 0 | 10 |
| Olosega | 2 | 2 | 0 | 2 |
| Onotoa Atoll | 2 | 3 | 1 | 6 |
| Orona Atoll | 1 | 1 | 1 | 3 |
| Pitcairn | 0 | 3 | 1 | 4 |
| Raoul | 6 | 1 | 1 | 8 |
| Raroia Atoll | 4 | 3 | 0 | 7 |
| Repanga | 2 | 5 | 0 | 7 |
| Rose Atoll | 3 | 5 | 0 | 8 |
| Rurima Rocks | 0 | 0 | 4 | 4 |
| South Island | 1 | 2 | 3 | 6 |
| Stewart | 0 | 2 | 0 | 2 |
| Swains Island | 7 | 4 | 0 | 11 |
| Tahiti | 0 | 0 | 1 | 1 |
| Ta'u Island | 0 | 1 | 0 | 1 |
| Tepoto | 1 | 0 | 0 | 1 |
| Vostok Island | 5 | 5 | 0 | 10 |
| Whakaari | 2 | 5 | 0 | 7 |
| **Sunda Shelf Islands** | | | | **478** |
| Bali | 2 | 5 | 0 | 7 |
| Borneo | 75 | 55 | 3 | 133 |
| Borneo, Pulo Balik Kukup | 10 | 16 | 0 | 26 |
| Java | 53 | 88 | 0 | 141 |
| Palawan | 25 | 27 | 5 | 57 |
| Palawan, Balabac Island | 11 | 11 | 0 | 22 |
| Culion | 3 | 2 | 0 | 5 |
| Sumatra | 19 | 25 | 0 | 44 |
| Sumatra, Banka Island | 1 | 0 | 0 | 1 |
| Sumatra, Batam Island | 4 | 0 | 0 | 4 |
| Sumatra, Nias Island | 4 | 1 | 0 | 5 |
| Sumatra, Simeulue | 5 | 17 | 0 | 22 |
| **Wallacea** | | | | **722** |
| Ambon | 1 | 1 | 0 | 2 |
| Basilan Island | 0 | 3 | 0 | 3 |
| Buru | 0 | 1 | 0 | 1 |
| Busuanga Island | 8 | 9 | 0 | 17 |
| Catanduanes | 1 | 0 | 0 | 1 |
| Halmahera | 10 | 20 | 2 | 32 |
| Leyte | 1 | 0 | 1 | 2 |
| Luzon | 104 | 104 | 10 | 218 |
| Malenge Island | 11 | 14 | 0 | 25 |
| Mindanao | 24 | 15 | 4 | 33 |
| Mindoro | 20 | 23 | 2 | 45 |
| Negros | 11 | 18 | 2 | 31 |
| Panay | 4 | 1 | 0 | 5 |
| Peleng Island | 9 | 4 | 0 | 13 |
| Polillo Island | 0 | 0 | 1 | 1 |
| Samar | 4 | 5 | 0 | 9 |
| Sulawesi | 118 | 147 | 0 | 265 |
| Taliabu | 9 | 9 | 1 | 19 |
| **Total** | | | | **3043** |

Polynesian rats with an aberrant coat pattern.

Specimens are first ordered according to the biogeographic region and then on specimen number. The number of ecologically relevant native predators and competitors and island area (km$^2$) are from van der Geer, Lomolino & Lyras (2017, 2018), except for Batam (Meijaard, 2003) and Malenge (Laurie & Hill, 1954). Area is rounded to the nearest integer.

| Region | Country | | Specimen | | | | sex | aberrant coat pattern |
|---|---|---|---|---|---|---|---|---|
| Mainland | Vietnam | | USNM | 357550 | | | m | albino |

| Region | Island | Area | | | Pred ators | Compet itors | sex | aberrant coat pattern |
|---|---|---|---|---|---|---|---|---|
| Micronesia | Saipan | 123 | USNM | 277708 | 0 | 0 | f | hazelnut colour (dark buff) |
| | Pohnpei | 334 | USNM | 301999 | 0 | 0 | f | melanistic, also underside |
| Polynesia | Hawaii | 10,435 | USNM | 324887 | 0 | 0 | f | piebald, mixture of white and brown, also at underside |
| | Kure | 1 | USNM | 338630 | 0 | 0 | f | very dark, toward melanistic |
| | Kauai | 1435 | USNM | 570868 | 0 | 0 | f | very dark, toward melanistic; few white hairs |
| | Kiritimati | 321 | USNM | 338688 | 0 | 0 | m | ash grey, toward leucism |
| Sunda Shelf Islands | Batam | 399 | USNM | 143251 | 0 | 0 | f | blackish patches, mainly on head and shoulder and median ridge of back; very clear at underside of mandible, left cheek and right front leg |
| | Java | 138,794 | USNM | 481593 | 13 | 7 | m | white spot between the shoulders |
| Wallacea | Malenge | 13 | AMNH | 153296 | 0 | 1 | m | buff coloured, large irregular patches at underside |
| | Sulawesi | 180,681 | AMNH | 153015 | 1 | 36 | f | white patches on both shoulders |
| | Sulawesi | 180,681 | AMNH | 153037 | 1 | 36 | f | white patch sagitally on back |
| | Luzon | 109,965 | USNM | 145823 | 0 | 40 | m | white patch below left shoulder |
| | Luzon | 109,965 | USNM | 145827 | 0 | 40 | f | white patch at left shoulder |
| | Mindoro | 10,572 | USNM | 278589 | 0 | 6 | m | leucism: buff coloured, slightly darker than albino, underside almost white ("aberrant color" on label) |

Percentage of aberrant coat patterns of Polynesian rats per region.

The time spent is an average value, estimated based on the majority of the relevant islands (see Fig. 1). Abnormalities are the combined cases of melanism and leucism. The albino specimen from the Mainland is here excluded (see Results section)

| Region | Time spent in situ (ka) | Number of specimens | Abnormalities | | | |
|---|---|---|---|---|---|---|
| | | | total | % | female | male |
| Mainland | 2200 | 370 | 0 | 0 | 0 | 0 |
| Melanesia | 3.4–3.2 | 757 | 0 | 0 | 0 | 0 |
| Micronesia | 1.75 | 292 | 2 | 0.68 | 2 | 0 |
| Polynesia | 0.80 | 424 | 4 | 0.94 | 3 | 1 |
| Sunda Shelf | 12 | 478 | 2 | 0.42 | 1 | 1 |
| Wallacea | 4–3.5 | 722 | 6 | 0.83 | 3 | 3 |
| **Total** | | **3043** | **14** | **0.46** | **7** | **5** |