

1 **Noble savages: human-independent *Rattus* rats in Japan**

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8 **Abstract** Brown (*Rattus norvegicus*) and black (*R. rattus* sensu lato) rats are among the world's
9 most widespread and important invasive animals; however, there are very few studies of their
10 natural history in natural habitats within their native ranges. Both taxa are native to Japan and
11 still occur in natural habitats there, but have been traditionally treated by zoologists working in
12 the country as invasive pests limited to cities and agricultural lands. We used thermal imaging
13 and snow tracking to conduct the first study of status, distribution and behavioral ecology of
14 remnant human-independent populations of these species in Japan. We found both species still
15 living in natural habitats away from human settlements: brown rat is a rare species of wetlands
16 on the main islands and of upland forests on Hokkaido, while the native taxon of *R. rattus*
17 species complex, the Asian house rat (*R. tanezumi* sensu stricto) inhabits remnant deciduous old-
18 growth forests, as well as evergreen subtropical forests in the south of the country. Such
19 knowledge is critically important for understanding the rats' evolutionary history, invasion
20 biology and behavior. Future molecular studies should aim to clarify the origin of these
21 populations, possibly Pleistocene relicts threatened by hybridization with rats of related non-
22 native taxa.

23 **Keywords:** black rat, brown rat, habitat, invasive species, Oriental field rat, origin

24 **Introduction**

25

26 Three or four (depending on classification) species of *Rattus* rats (*R. exulans*, *R. rattus* sensu
27 stricto, *R. [rattus] tanezumi*, and *R. norvegicus*) are among the world's most widespread
28 mammals, thanks to being exceptionally capable of using humans for dispersal and of colonizing
29 human-created habitats. They are also among the world's most studied organisms, being the
30 subject of more than half a million papers and books according to Google Scholar. However,
31 virtually all that research is focused on domesticated, human-dependent (living in human
32 settlements or agricultural habitats) or feral (secondarily wild, living in natural habitats outside
33 the species' native range) populations (see, for example, the bibliographies in Burgin 2017a,b,c).
34 Except for general rodent surveys, there are very few studies of the populations of these rat
35 species that still live within their respective native ranges independently of humans. These
36 ancient populations hold keys to understanding numerous aspects of the rats' biology,
37 evolutionary history, unique invasive success, and interactions with humans, because most of
38 these aspects have likely evolved prior to the rats becoming human commensals (Hulme-Beaman
39 *et al.* 2016).

40 Pacific (or Polynesian) rat *Rattus exulans* (Peale 1848), native to the island of Flores
41 (Thomson *et al.* 2014) but introduced throughout Southeast Asia and Oceania (Burgin 2017d),
42 has been recorded in Japan only once, on Miyakojima Island in 1955, and has never been found
43 there during subsequent surveys (Motokawa *et al.* 2001, Iwasa 2015a), including our quick
44 survey of the island in 2018 (see below). “Western” black (or ship) rat, *Rattus rattus* (Linnaeus,
45 1758) sensu stricto, is native to India (Baig *et al.* 2018), but has been introduced worldwide
46 (Burgin, 2017b); in Japan it occurs only in a few port cities and in human settlements on some

47 small remote islands (Kambe *et al.* 2011). Our research focused on the other two taxa of *Rattus*
48 present in Japan. We tried to determine where they live independently of humans, which natural
49 habitats they inhabit, and how their habitat preferences in Japan correspond to those known from
50 other parts of their presumed native ranges.

51

52 *Rattus tanezumi*

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54 “Eastern” black (or Asian/Oriental house) rat *Rattus tanezumi* Temminck, 1844, originally
55 described from Japan, is closely related to *R. rattus* sensu stricto, but is usually considered a full
56 species, although such treatment renders one or both taxa polyphyletic (Aplin *et al.* 2011) and
57 the two forms can hybridize (Lack *et al.* 2012, Conroy *et al.* 2013), in Japan among other
58 locations (Chinen *et al.* 2005). We’ll be discussing only *R. tanezumi* sensu stricto (Lineage II in
59 Aplin *et al.* 2011), hereafter *Rt*. Introduced throughout the Oriental region and locally elsewhere
60 (Burgin 2017c), *Rt* is thought to originate from Yunnan and northern Indochina, where its
61 genetic diversity is the highest among mainland populations (Guo *et al.* 2019) The earliest fossils
62 are from Early Pleistocene cave deposits of Thailand (Chaimanee and Yaeger 2001); in Korea it
63 is known from Middle and Late Pleistocene (Yeong-Seok 2015) while in central China it doesn’t
64 appear until Late Pleistocene (Zheng 1993); in all three cases the fossils were identified as *R.*
65 *rattus* sensu lato, but likely belong to *Rt* based on geography. In Japan the earliest (Middle
66 Pleistocene) fossils possibly of this taxon are from Honshu, where they predate the human
67 arrival; there are also Late Pleistocene and Holocene fossils assigned to *R. rattus* sensu lato from
68 Honshu and Kyushu (Kawamura 1989, Iwasa 2015c). Fossil record shows *Rt* to be an ancient
69 introduction in the central and southern Ryukyu Islands, where it was not present prior to the

70 human arrival (Kowalski and Hasegawa 1976, Otsuka and Takahashi 2000). In historic times *Rt*
71 has been introduced to many other islands, including Hokkaido in the 20th century (Ota 1968)
72 and the remote Ogasawara Islands (Kambe *et al.* 2011).

73 *Rt* occurs in human settlements and agricultural areas (its scientific name *tanezumi* means
74 “ricefield rat” in Japanese), but also in forests on all main islands of Japan except Hokkaido and
75 on many smaller islands where it is often the most abundant non-volant forest mammal (see
76 Results). However, *Rt* in Japan has only been studied in urban and agricultural habitats, with the
77 exception of very cursory studies of forest populations in southern Ryukyu Islands (see
78 bibliography in Iwasa 2015c).

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80 ***Rattus norvegicus***

81

82 Brown (or Norway) rat *Rattus norvegicus* (Berkenhout 1769), hereafter *Rn*, first described from
83 Europe, originates from Southeast Asia (Zeng *et al.* 2018) or, more likely, the Far East (Puckett
84 and Munshi-South 2018); in any case it is native to northern China, Mongolia, Korea and
85 Russian Far East, as evidenced by high genetic diversity in those areas (Puckett *et al.* 2016,
86 Puckett and Munshi-South 2018), and has been introduced worldwide (Amori and Cristaldi
87 1999, Burgin 2017a). East Asian *Rn* are smaller, browner (with lighter pelage in winter), and
88 shorter-tailed than those in the Western Palearctic, and have been described (from Transbaikalia)
89 as *R. caraco* (Pallas, 1778), now usually considered a subspecies; introduced *Rn* on other
90 continents are either *R. n. norvegicus* or a mixture of the two forms (Kuzyakin 1951); the latter
91 also appears to be the case in Tokyo (Ohno *et al.* 1994).

92 *Rn* is a native species in the main islands of Japan: there are Middle Pleistocene fossils (pre-
93 dating the human arrival) from Honshu, as well as Late Pleistocene-Holocene fossils from
94 Honshu and Kyushu (Kawamura 1989, Iwasa 2015b). Elsewhere the earliest fossils are from
95 Late Pleistocene of Korea (Yeong-Seok 2015) and Late Pleistocene of central China (Zheng
96 1993). Today *Rn* occurs on all four main islands of Japan and on Tsushima (Iwasa 2015b). It is
97 also present on almost all other islands of Japan (with the notable exception of Amami-oshima),
98 but those populations are purely human-associated and presumably introduced (Iwasa 2015b);
99 extensive fossil record from the central and southern Ryukyu Islands shows that *Rn* arrived there
100 much later than humans (Otsuka and Takahashi 2000). It largely replaced *R. rattus* in European
101 cities during the Industrial Revolution (Amori and Cristaldi 1999), and in North American cities
102 in the 18th century (Lack *et al.* 2013), but it is unknown if a similar replacement of *Rt* by *Rn* has
103 ever taken place in the cities of the main Japanese islands; in parts of China and certain other
104 regions the opposite might be happening (Zhang *et al.* 2000, King 2019).

105 Some field zoologists have always recognized *Rn*, Japan's only native semi-aquatic rodent, as
106 an integral element of the country's native fauna (Abe *et al.* 1971), but Japanese zoological
107 literature often treats it as an invasive species confined to human settlements and agricultural
108 habitats (see, for example, Iwasa 2015b), despite the fact that it has been recorded during surveys
109 in remote mountain forests and large natural wetlands on Hokkaido (Ota 1968, Abe *et al.* 1971,
110 Maekawa *et al.* 2002).

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112

113 **Materials and methods**

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115 **Study sites**

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117 The survey was conducted at 70 locations throughout Japan in 2017-2019 (Table 1, Fig. 1). We
118 tried to choose sites that were as distant from human-created habitats (fields, tree plantations,
119 recently logged forests, and buildings) as possible, and to sample diverse plant communities
120 (forests of different composition, wetlands with different types of vegetation, coastlines with
121 different structure). In most cases our minimal criteria were the absence of human settlements
122 and agricultural fields within 1 km, and of isolated non-residential structures (abandoned cabins,
123 unmanned utility buildings) within 200 m. However, no natural lowland wetland in Japan outside
124 Hokkaido is more than 500 m from human settlements, which made distinguishing between
125 human-dependent and human-independent *Rn* populations uncertain. Forest sites were more
126 remote; it is worth noting that in Japan, humans temporarily visiting forests almost never leave
127 food scraps and other litter that could support rodent populations, so rat populations living in
128 forests can be considered human-independent even if these forests are frequented by human
129 visitors.

130

131 **Survey methods**

132 Our main survey method was nighttime visual search using Pulsar Quantum Lite XQ30V
133 thermal imager (Yukon Advanced Optics Worldwide, Ltd., Lithuania). The imager allowed
134 locating rats at distances of up to 30-50 m in dense forests and up to 200-300 m in more open
135 habitats. After detection, SRT7GT handheld flashlight (Nitecore, China) was turned on to
136 identify the animal to species. If a rat was detected in cluttered habitat where seeing it well

137 without the imager was difficult, we observed it until it moved into an opening, and then turned
138 on the flashlight.

139 We evaluated the efficiency of this method by comparing its results with using Sherman traps
140 at two locations: flooded forest along the shores of Lake Biwa, where *Rn* was common and the
141 only rodent present (there are no other native semi-aquatic rodents in Japan), and Ono Forest on
142 Miyakojima Island, where *Rt* was abundant and the only rodent present (there are no other forest
143 rodents on the island). At each of these two locations we used 25 Sherman traps (folding,
144 aluminum 76 x 82 x 230 mm) placed at least 100 m apart along a 5-km route; each trap had the
145 door removed, was left in place for 4 nights, and disappearance of the bait (a mix of oats and
146 peanut butter) was counted as detection (even if some other species removed the bait, it would
147 only lead to overestimating the efficiency of Sherman traps). Visual surveying was conducted for
148 one night along the same route. The comparisons showed that visual surveying produced more
149 detections than 100 trap-nights (12 vs. 0 at Lake Biwa and 162 vs. 6 in Ono Forest). Spotlighting
150 without the thermal imager resulted in much fewer, if any, sightings, even in places where the
151 rats were extremely abundant, so it was almost never used.

152 When snow was present, we searched for rat tracks during visual surveys at night and also
153 during daytime (Table 1). We considered snow tracking important because when thick snow
154 layer is present, murine rodents spend most of time under snow cover and are unlikely to be
155 detected visually (Dinets and Rotshild 1998), but winter records were necessary to determine if
156 the rats remain in natural habitats year-round, rather than overwinter in human houses – a pattern
157 observed in some non-native populations (Kuzyakin 1951). Driving at night along backcountry
158 roads was also used but proved ineffective, except once on Hokkaido (see Results).

159

160 **Species identification**

161 *Rattus* rats are easy to distinguish visually from other rodents of Japan. Squirrels (*Sciurus* and
162 introduced *Callosciurus*) and giant flying squirrels (*Petaurista*) have different build and fluffy
163 tails; Ryukyu giant rat (*Diplothrix*) is larger and has very long guard hairs and conspicuous white
164 tail tip; locally introduced nutria (*Myocastor*) is much larger with flattened tail; introduced
165 muskrat (*Ondatra*) has very limited distribution, different built, smaller ears, and flattened tail;
166 all other Japanese rodents are obviously smaller than *Rattus* (Ohdachi *et al.* 2015). *Rt* is not
167 distinguishable in the field from *R. rattus*, but the latter has very limited distribution in Japan and
168 is known only from urban habitats (Kambe *et al.* 2011). Tracks were identified using track
169 descriptions in Formozov (1974) and hindfoot measurements of Japanese rodents in Ohdachi *et*
170 *al.* (2015). Hindfoot length is larger in *Rn* than in *Rt* (27-42 mm vs. 22-35 mm, Iwasa 2015b,c);
171 there is some overlap but none of 6 trackways we found (5 *Rn*, 1 *Rt*) were in the overlap range.
172 There is, however, a possibility that the single recorded trackway with hindfoot size of *Rt*
173 actually belonged to juvenile *Rn*; the webbing between toes which is present only in *Rn* is
174 sometimes visible in tracks on soft mud but not on the snow (pers. obs.).

175

176

177 **Results**

178

179 Both *Rt* and *Rn* were recorded in natural habitats, with winter records indicating their presence in
180 such habitats year-round.

181

182 *Rattus tanezumi*

183 *Rt* was observed on three of the main islands (Table 1, Fig. 1), and also on many small islands
184 where it is known to be non-native.

185 On Honshu, one individual was observed for ~5 min in August in a relict grove of giant
186 Japanese horse chestnuts (*Aesculus turbinata*) at Torii Pass (Fig. 7); it repeatedly carried large
187 rounded objects (presumably horse chestnuts) from the crown of a very large tree to a hollow
188 ~20 cm in diameter, ~4 m above ground. Another *Rt* was observed in September climbing a large
189 oak (*Quercus* sp.) in Kasuga Primeval Forest near Nara (the oldest forest in Japan). A trackway
190 was found on fresh snow in Yacho-no-Mori deciduous forest near Karuizawa, but that location
191 was within 100 m of residential buildings.

192 On Shikoku, three *Rt* were observed in August in Hokigamine Forest Park near Kochi, in a
193 habitat transitional between subtropical evergreen and deciduous forest (Hämet-Ahti *et al.* 1974).
194 Two of them were moving through subcanopy tree crowns 4-5 m above ground, while the third
195 one was feeding on acorns (*Quercus* sp.) on the ground.

196 On Kyushu, *Rt* was surprisingly common (8 sightings in 2 nights) in subtropical evergreen
197 forests around Bonotsu in the far south of the island (Fig. 8, 9); all animals were observed in tall
198 shrubs or subcanopy trees 1-3 m above ground.

199 In the Ryukyu Islands *Rt* was abundant year-round in all surveyed forests on Amami-Oshima,
200 Miyakojima and Ishigaki Islands. On Okinawa it was common in small forest fragments in the
201 south but virtually absent from larger forests in central and northern parts of the island, such as
202 Yanbaru National Park. On Iriomote it was apparently rare in natural habitats and confined to
203 forest edges. We also recorded it in remnant forest patches on Ie-jima, Kume-jima, Minami-
204 Daito and Yonaguni, but not on Tokunoshima, Yakushima or Iheya-jima. More than 2/3 of all
205 sightings (N=137) were in trees. Many rats were observed feeding; identified food items

206 included acorns (*Quercus* sp.), fruit of itajii (*Castanopsis sieboldii*), figs (*Ficus* sp.), and a cave
207 cricket (Rhaphidophoridae). *Rt* was never found in Ryukyu pines (*Pinus luchuensis*) or pine-
208 dominated forests that are common on the islands.

209 *Rt* was common in forests of Chichijima and Hahajima (Ogasawara Islands); all observed
210 animals (N=13) were in trees 1-5 m above ground. The only identified food item was a fig (*Ficus*
211 sp.).

212 Exposed arboreal nests, like those known for *Rt* in the Philippines (Stuart *et al.* 2012) and for
213 *R. rattus* in the Caucasus region (Bernstein 1959) and North America (Reid 2006), were never
214 observed, but 11 animals on Ryukyu and Ogasawara Islands were observed entering and/or
215 exiting tree hollows. All such hollows had entrances 9-25 cm in diameter and were located 2-4 m
216 above ground, in trees that were 30-60 cm in diameter at ~1.5 m above ground.

217

218 *Rattus norvegicus*

219 *Rn* was detected in natural habitats on three of the main islands and on Tsushima Island (Table 1,
220 Fig. 1).

221 On Hokkaido, we found two trackways in March and observed one animal (Fig. 2) in August
222 in Kushiro Marsh, the largest remaining natural wetland in Japan. All three records were along
223 the edges of wood patches surrounded by reedbeds, tall grass, and patches of open water (Fig. 3).
224 One trackway was found in March in Kiritappu Marsh (a similar but smaller wetland) in a large
225 reedbed ~50 m from the edge of mixed forest. We also found one trackway in December on a
226 snow-covered beach in Shiretoko National Park, but it was less than 1 km from residential
227 buildings. That trackway appeared to be a well-used path ~30 m long, connecting a burrow in the
228 coastal cliff with intertidal zone, where more than a hundred fragments of broken shells of

229 periwinkles (Littorinidae) were scattered among the rocks. The intertidal zone in this area also
230 had numerous limpets, crabs, sea stars, sea urchins, kelp plants, and other possible food items. In
231 Daisetsuzan National Park we found one trackway in March in riparian forest of birch (*Betula*
232 sp.) (Fig. 4), and observed one animal in August as it was feeding on Geometridae moths on a
233 paved road through oldgrowth mixed montane forest (Fig. 5), near a small stream lined with
234 alder (*Alnus* sp.). The moths were flying in great numbers that night, and covered the road
235 pavement at densities of up to 3 moths per 1 m² of the road (visual estimate). Numerous other
236 mammals, birds and amphibians were also feeding on them.

237 On Honshu and Kyushu *Rn* was recorded only in wetlands. On Honshu, at least 6 individuals
238 were seen in June walking and feeding (on unidentified small seeds) along the edges of reedbeds
239 of Tone River near Sasagawa, 1 was observed in August running across an opening in a small
240 wetland on Niigata Plain, and 12 were seen in December running and swimming in flooded
241 woodlands along the shores of Lake Biwa. However, all those locations were within 1 km of
242 residential buildings and/or ricefields.

243 On Kyushu, one *Rn* was seen in December running across a sedge meadow in Bogatsuru
244 Marsh, a unique high-elevation wetland inside a volcanic crater in Aso-Kuji National Park.

245 On Tsushima, two *Rn* were observed in August feeding on crabs in the intertidal zone in Aso
246 Bay Park, along a shoreline lined with deciduous forest and wetlands (Fig 6). One was seen
247 entering a burrow in a steep clay slope ~3 m from the water edge at high tide; the burrow had
248 likely been built by the rat, as similar waterside burrows are commonly built in riverbanks by
249 human-independent *Rn* in Russian Far East (Kuzyakin 1951). Local people reported rats to be
250 common along the island's coast.

251

252

253 **Discussion**

254

255 *Rattus tanezumi*

256 *Rt* is apparently common in evergreen subtropical forests (Hämet-Ahti *et al.* 1974) that grow in
257 the southernmost parts of the main islands (southern Shikoku and southernmost Kyushu). In
258 central Kyushu and in the southwestern half of Honshu it was found only in exceptionally well-
259 preserved patches of very old deciduous forests, while in the northeastern half of Honshu it
260 wasn't detected even in the most pristine forest habitats still existing. It is also common in
261 evergreen subtropical forests on many small islands further south, where it is not native. It is
262 remarkably arboreal (even considering a certain bias towards exposed locations unavoidable
263 when searching for animals using a thermal imager).

264 Localized distribution of *Rt* in natural habitats on the main islands of Japan likely results from
265 the loss of high-quality habitat in the suboptimal northern part of the range, and small extent of
266 warmer areas (characterized by subtropical evergreen forest) where it can live in lower-quality
267 habitat. It might be speculated that following the widespread logging during the Edo Period
268 (Morris-Suzuki 1995) it was replaced in much of its former range by two species of large native
269 mice (*Apodemus speciosus* and *A. argenteus*) which are capable to live at high densities in all
270 forest types and are by far the most abundant forest rodents on the main islands of Japan
271 (Ohdachi *et al.* 2015; also pers. obs.). Alternatively, the present range of *Rt* in natural habitats
272 might be confined to areas where non-coniferous forests survived during the last glacial
273 maximum (Tsukada 2017). It is also possible that all *Rt* present in Japan today originate from an
274 ancient introduction rather than from the Pleistocene rats, which were driven to extinction by ice

275 ages and/or the massive Akahoya Eruption, which covered much of southern Japan with volcanic
276 ash in 4,500 BC (Maeno and Taniguchi 2005).

277 Small human-independent populations of *Rt* on the main islands of Japan might be under
278 threat from feral cats and introduced Siberian weasels (*Mustela sibirica*), northern raccoons
279 (*Procyon lotor*), and masked palm civets (*Paguma larvata*) (Ohdachi *et al.* 2015). Hybridization
280 with introduced *R. rattus* has been recorded in some Japanese cities and small islands (Chinen *et*
281 *al.* 2005, Kambe *et al.* 2013) and might eventually threaten the genetic integrity of native
282 populations. On some of the Ryukyu Islands *Rt* is now the most common non-volant forest
283 mammal, and an important food source for endangered Iriomote cat (*Prionailurus bengalensis*
284 *iriomotensis*) (Sakaguchi and Ono 1994). Its rarity in northern Okinawa might be a result of
285 mongoose eradication program that started in 2000 (Yamada *et al.* 2015), as thousands of *Rt* per
286 month were caught in mongoose traps and removed (Kambe *et al.* 2012); however, a similar
287 program on Amami-oshima doesn't seem to have had such effect.

288 The distribution of *Rt* in natural habitats in its presumed native range in mainland Asia is
289 difficult to elucidate from published literature. It is usually unclear which populations are
290 human-independent because, like in Japan, it is often impossible to find forests with no human
291 settlements nearby (Lekagul and McNeely 1977). Another problem is the complicated and
292 rapidly evolving taxonomy of *R. rattus* sensu lato; in many cases multiple taxa with different
293 habitat preferences are mentioned but it's unclear what exactly they are. Some mainland *Rt* differ
294 from Japanese animals phenotypically. In China they often have yellowish spots on the throat,
295 and are considered to be two separate species – *R. fulvipectus* (Milne-Edwards, 1872) and *R.*
296 *yunnanensis* (Anderson, 1879) – by many Chinese zoologists; these forms are treated as
297 subspecies or synonyms in non-Chinese literature (Ying *et al.* 2002, Musser and Carleton 2005),

298 and have identical karyotypes (Mikhail Kosoy pers. comm.). Yellowish throat spots are common
299 in some Indochinese populations of *Rt* as well (Abramov *et al.* 2007). In mainland Asia and
300 elsewhere *Rt* is mostly confined to human-modified habitats (Zhan 1982, Zhang *et al.* 2000,
301 Stuart *et al.* 2012). In Korea it occurs in forests on small Ulleung Island (VD pers. obs.), but not
302 on larger Jeju Island or the mainland (Jo *et al.* 2012, Jo *et al.* 2019). China it is largely absent
303 from forests as far south as Hong Kong (Chung and Corlett 2006) and Taiwan (Yu 1994).
304 However, in southernmost China (Yunnan and Guanxi) and northern Indochina, where *Rt* is
305 apparently native (Guo *et al.* 2019), it is an uncommon but widespread component of forest
306 fauna (Zhang *et al.* 2000). At the northern edge of its native range in China it occurs at low
307 densities in primary montane subtropical forests of central Yunnan, where the habitat is
308 remarkably similar to the sites where we found it on Honshu (Wu and Deng 1988, Wenbo Chen
309 pers. comm., VD pers. obs.). *Rt* also occurs at low densities in evergreen tropical forests of
310 southern Yunnan, where animals in primary and secondary forest are phenotypically different
311 (Wu *et al.* 1996), and in deciduous tropical forests and karst forests in northern Thailand
312 (Chaisiri *et al.* 2010, Latinne *et al.* 2011). Note that we found it in karst forests in Okinawa
313 (Table 1). *Rt* is apparently absent from forests in mainland Vietnam (Lunde and Truong Son
314 2001); no *Rt* have been recorded during an extensive camera trapping survey of primary forests
315 of Pu Mat National Park in north-central Vietnam (VD and Nicholas Wilkinson, in prep.). *R.*
316 *rattus* sensu lato has been reported to be common in primary forests on islands off southern
317 Vietnam (Abramov *et al.* 2007), in karst and mangrove forests of southern Thailand (Lekagul
318 and McNeely 1977, Latinne *et al.* 2011), and in other natural (but mostly disturbed) habitats of
319 southern Indochina (Lekagul and McNeely 1977, Aplin *et al.* 2011); these populations are
320 currently thought to be taxa different from *Rattus tanezumi* sensu stricto based on mtDNA and

321 sometimes phenotypical differences (van Peenen *et al.* 1970, Pagès *et al.* 2010, Aplin *et al.*
322 2011, Balakirev and Rozhnov 2012, Abramov *et al.* 2018), but nuclear DNA data contradict this
323 (Pagès *et al.* 2013). Some forms of *R. rattus* sensu lato, possibly *Rt*, are common in disturbed
324 forests of Laos (Aplin and Singleton 2003) and unlogged forests of Myanmar (Thazin Wai *et al.*
325 2018). Unlike *Rattus rattus* sensu stricto, *Rt* is not known from natural habitats outside Asia; all
326 records from other continents are from human settlements (Aplin *et al.* 2011, Bastos *et al.* 2011,
327 Lack *et al.* 2012).

328

329 ***Rattus norvegicus***

330 *Rn* appears to be a rare species of pristine upland forests (mostly alder and birch groves along
331 streams), natural wetlands, and possibly seashores on Hokkaido, natural wetlands on other main
332 islands, and seashores on Tsushima. Such habitat preferences correspond to its distribution in
333 other parts of its native range (see below).

334 It is puzzling that *Rn* occurs in forests of Hokkaido but not in the mountains of Honshu where
335 the climate is similar; possible explanations include the availability of invertebrate prey or the
336 duration of snow cover, which is important for *Rn* in the forests of Russian Far East (Kuzyakin
337 1951). It is also possible that *Rn* of Hokkaido are not related to those known from Pleistocene
338 fossils from Honshu and Kyushu, but have colonized Hokkaido from mainland Asia via Sakhalin
339 Island, like most other native mammals of Hokkaido (Kuroda 1939). Unfortunately, Pleistocene
340 fossil record of small mammals from Hokkaido is very fragmentary (Kawamura 1991).
341 Similarly, *Rn* of Tsushima might be relatively recent natural colonizers from Korea, like some
342 other mammals of the island (Ohdachi *et al.* 2015).

343 Dependence on wetlands and pristine forests make human-independent populations of *Rn*
344 vulnerable to extinction in Japan, where virtually all primary forests have been logged during the
345 Edo Period (Morris-Suzuki 1995), and very few large natural wetlands remain, particularly
346 outside Hokkaido (Washitani 2007). Daisetsuzan National Park (the largest protected natural
347 area in Japan) and Kushiro-Shitsugen National Park (the largest remaining wetland in the
348 country), where *Rn* was detected by previous surveys (Ota 1968, Abe *et al.* 1971) as well as in
349 our study, appear to be the main strongholds of human-independent *Rn* in Japan. Populations in
350 Hokkaido wetlands might be under threat from introduced American mink (*Neovison vison*),
351 while on other main islands they now have to compete with introduced coypu (*Myocastor*
352 *coipus*) (Ohdachi *et al.* 2015). Declines in human-independent populations of *Rn* have been
353 noted in other parts of its native range: it is now virtually extinct in Transbaikalia where it was
354 locally common in the 20th century (Karaseva *et al.* 1990), and on some of the southern Kuril
355 Islands where it used to be abundant (Grigor'ev 2008). Replacement of native subspecies *caraco*
356 by invading *ssp. norvegicus* from the west has been noted in Siberia (Kuzyakin 1951), and might
357 be happening in Japan, where differences in mtDNA between brown rats in ports/large cities and
358 the backcountry have been reported (Ohno *et al.* 1994).

359 In its presumed native range outside Japan, *Rn* occurs in upland forests (mostly alder groves
360 along streams), riparian forests, tallgrass floodplain meadows, and seashore habitats on southern
361 Kuril Islands, where virtually all bodies of water once had *Rn* living along their shores (Surkov
362 1986, Dinets and Rotshild 1998); in mixed forests (particularly with alder) and tallgrass
363 meadows near streams on Sakhalin Island (Surkov 1986); in floodplain and streamside forests
364 (sometimes in pristine areas very far from human habitat) in Ussuriland (Maak 1861, Karaseva *et*
365 *al.* 1990, Anna Gritsuk pers. comm., Anastasia Kadetova pers. comm.); along forest streams with

366 large salmon runs in the lower Amur River basin (Khamaganov 1965); in riparian forests and
367 sedge-reed marshes around oxbow lakes in Transbaikalia (Radde 1862, Kuzyakin 1951,
368 Karaseva *et al.* 1990); in reedbeds with forested islands in Manchuria (VD pers. obs.), and in
369 coastal wetlands in Korea (VD pers. obs.). Note that the oldest Ussuriland record is from the
370 mid-19th century when there were no cities or agriculture there (Maak 1861); there are also mid-
371 19th century records from Sakhalin, where human presence at the time was largely limited to
372 small villages of native hunter-gatherers (Yegerov 1946). In its non-native range in western
373 Eurasia and North America *Rn* also readily colonizes reedbeds, riverbanks and other wetlands,
374 and sometimes deciduous forests and seashores (Kuzyakin 1951, Karaseva *et al.* 1990, Amori
375 and Cristaldi 1999, Dinets 2015).

376

377 **Suggested directions of future studies**

378 Presence of the two species of *Rattus* in natural habitats on the main islands of Japan raises
379 important questions. Are these rats genetically distinctive from those in cities and ricefields, or
380 do they freely interbreed and fully mix with their conspecifics in urban and agricultural areas?
381 What role did native Japanese rats play in rat colonization of Japanese cities and in the global
382 spread of *Rt* and *Rn*? Are these small populations descendants of Pleistocene rats, recent
383 invaders, or a mix of both?

384 A genetic study would answer all these questions. But for now, even the origin of urban rats
385 of Japan is poorly understood. The recent studies of worldwide genetics of *Rn* (Puckett *et al.*
386 2016, Puckett and Munshi-South 2018, Zeng *et al.* 2018, Ullrich and Tautz 2020) did not include
387 any Japanese samples, although ancient lineages detected only on the west coast of North
388 America (Puckett *et al.*, 2016) could be of Japanese origin (Jason Munshi-South pers. comm.). In

389 their study of *Rattus rattus* complex, Aplin *et al.* (2011) found three Japanese samples of *Rt*
390 (from Amami-oshima, Mizayki City on Kyushu, and downtown Tokyo) to cluster with samples
391 from Taiwan, coastal China and Indochina, indicating relatively recent introduction (a specimen
392 from Hokkaido clustered with *R. rattus sensu stricto*). Kambe *et al.* (2013) studied *Rt* from a few
393 Japanese cities, as well as outlying islands including the Ryukyus and the Ogasawaras; they
394 found haplotype diversity of urban rats on the main islands to be very low, suggesting recent
395 introduction, possibly via the Ryukyus. But rats living in natural habitats on the main islands of
396 Japan are yet to be sampled.

397 The tradition of ignoring *Rattus* rats in studies of native mammals of eastern Asia goes back
398 at least to the early 20th century. For example, Kuroda (1939) didn't even mention them in his
399 detailed overview of mammals of the Japanese Empire. The accounts for *Rn* and *Rt* in the most
400 recent monograph on Japanese mammal fauna (Ohdachi *et al.* 2015) are among the shortest of all
401 species accounts: the occurrence of *Rn* in natural habitats is not mentioned at all (Iwasa 2015b),
402 and for *Rt* it is very briefly mentioned that it occurs in forests on three of the Ryukyu Islands –
403 ironically, not even the ones where it is most common (Iwasa 2015c). Similar omissions exist in
404 many overviews of mammals of Korea (i. e. Jo *et al.* 2018) and China (i. e. Smith and Xie 2013).
405 Such limited approach has created an unfortunate lack of knowledge about two of the most
406 important rodents in the region. In the former Soviet Union human-independent *Rn* in its native
407 range has been studied by many researchers, but not since 1987 (see bibliography in Karaseva *et*
408 *al.* 1990).

409

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417

418 **References**

419 Abe H, Kobayashi T, Maeda K, Hayata I (1971) Faunal survey of the Mt Daisetsu Area, JIBP
420 Main Area-II (Annual report of JIBP/CT-S for the fiscal year of 1970). Contributions from
421 JIBP-CT 105:13–23.

422 Abramov AV, Kalinin AA, Morozov PN (2007) Mammal survey on Phu Quoc island, southern
423 Vietnam. *Mammalia* 71:40–46.

424 Abramov AV, Kruskop SV, Shchinov AV (2018) Mammals of Con Son Island, southern
425 Vietnam. *Russ. J Theriol* 17:1–16.

426 Amori G, Cristaldi M (1999) *Rattus norvegicus*. In: Mitchell-Jones AJ (ed) *The atlas of*
427 *European mammals*. Academic Press, London, pp. 278–279.

428 Aplin KP, Singleton GR (2003) Balancing rodent management and small mammal conservation
429 in agricultural landscapes: challenges for the present and the future. In: Singleton GR et al.
430 (eds) *Rats, mice and people: rodent biology and management*. Australian Centre for
431 International Agricultural Research, Canberra, Australia, pp. 80–88.

432 Aplin KP, Suzuki H, Chinen AA, Chesser RT, Ten Have J, Donnellan SJ et al. (2011) Multiple
433 geographic origins of commensalism and complex dispersal history of black rats. *PloS One*
434 6:e26357.

435 Baig M, Khan S, Eager H, Atkulwar A, Searle JB (2019) Phylogeography of the black rat *Rattus*
436 *rattus* in India and the implications for its dispersal history in Eurasia. *Biol Invasions* 21:417–
437 433.

438 Balakirev AE, Rozhnov VV (2012) Contribution to the species composition and taxonomic
439 status of some *Rattus* inhabiting Southern Vietnam and Sundaland. *Russ J Theriol* 11:33–45.

440 Bastos AD, Nair D, Taylor PJ, Brettschneider H, Kirsten F, Mostert E, Von Maltitz E, Lamb JM,
441 Van Hooft P, Belmain SR, Contrafatto G (2011) Genetic monitoring detects an overlooked
442 cryptic species and reveals the diversity and distribution of three invasive *Rattus* congeners in
443 South Africa. *BMC Genetics* 12:26.

444 Bernstein AD (1959) [Some features of the black rat biology in Abkhazia]. *Bull Moscow Soc*
445 *Nat Explor (Biology)* 64, 5–14 [in Russian].

446 Burgin CJ (2017a) 659. Brown rat. *Rattus norvegicus*. In: Wilson DE et al. (eds) *Handbook of*
447 *the mammals of the World. Vol. 7. Rodents II.* Lynx Edicions, Barcelona, Spain, pp. 829–
448 830.

449 Burgin CJ (2017b) 660. Roof rat. *Rattus rattus*. In: Wilson DE et al. (eds) *Handbook of the*
450 *mammals of the World. Vol. 7. Rodents II.* Lynx Edicions, Barcelona, Spain, pp. 830–831.

451 Burgin CJ (2017c) 661. Oriental house rat. *Rattus tanezumi*. In: Wilson DE et al. (eds)
452 *Handbook of the mammals of the World. Vol. 7. Rodents II.* Lynx Edicions, Barcelona,
453 Spain, p. 831.

454 Burgin CJ (2017d) 669. Pacific rat. *Rattus exulans*. In: Wilson DE et al. (eds) *Handbook of the*
455 *mammals of the World. Vol. 7. Rodents II.* Lynx Edicions, Barcelona, Spain, pp. 833–834.

456 Chaimanee Y, Jaeger J (2001) Evolution of *Rattus* (Mammalia, Rodentia) during the plio-
457 pleistocene in Thailand. *Histor Biol* 15:181–191.

458 Chaisiri K, Chaeychomsri W, Siruntawineti J, Ribas A, Herbreteau HV, Morand S (2010)
459 Gastrointestinal helminth infections in Asian house rats (*Rattus tanezumi*) from northern and
460 northeastern Thailand. *J Trop Med Parasitol* 33:29–35.

461 Chinen AA, Suzuki H, Aplin KP, Tsuchiya K, Suzuki S (2005) Preliminary genetic
462 characterization of two lineages of black rats (*Rattus rattus sensu lato*) in Japan, with evidence
463 for introgression at several localities. *Genes Gen Systems* 80:367–375.

464 Chung KP, Corlett RT (2006) Rodent diversity in a highly degraded tropical landscape: Hong
465 Kong, South China. *Biodiv Conserv* 15:4521–4532.

466 Conroy CJ, Rowe KC, Rowe KM, Kamath PL, Aplin KP, Hui L, James DK, Moritz C, Patton JL
467 (2013) Cryptic genetic diversity in *Rattus* of the San Francisco Bay region. *Calif Biol*
468 *Invasions* 15:741–758.

469 Dinets V (2015) Peterson field guide to finding mammals in North America. Houghton Mifflin
470 Harcourt, Boston, MA.

471 Dinets V, Rotshild E (1998) [Mammals of Russia]. 2nd edn. ABF, Moscow, Russia [in Russian].

472 Formozov AN (1974) [Tracker’s Companion.] Detskaya Literatura, Moscow, USSR [in
473 Russian].

474 Grigor’ev EM (2008) [Small mammals of southern Kuril Islands]. Doctoral dissertation, Institute
475 of Biology and Soil Science, Vladivostok, Russia [in Russian].

476 Guo S, Li G, Liu J, Wang J, Lu L, Liu Q (2019) Dispersal route of the Asian house rat (*Rattus*
477 *tanezumi*) on mainland China: insights from microsatellite and mitochondrial DNA. *BMC*
478 *Genetics* 20:11.

479 Hämet-Ahti L., Ahti T, Koponen, T (1974) A scheme of vegetation zones for Japan and adjacent
480 regions. *Ann Bot Fennici* 11:59–88.

481 Jo YS, Kim TW, Choi BJ, Oh HS (2012) Current status of terrestrial mammals on Jeju Island. J
482 Species Res 1:249–256.

483 Jo YS, Baccus JT, Koprowski JL (2018) Mammals of Korea: a review of their taxonomy,
484 distribution and conservation status. Zootaxa 4522:1–216.

485 Iwasa MA (2015a) *Rattus exulans* (Peale, 1848) In: Ohdachi SD et al. (eds) The wild mammals
486 of Japan. 2nd edn. Shoukadoh Book Sellers, Kyoto, Japan, p. 182.

487 Iwasa MA (2015b). *Rattus norvegicus* (Berkenhout, 1769). In: Ohdachi SD et al. (eds) The wild
488 mammals of Japan. 2nd edn. Shoukadoh Book Sellers, Kyoto, Japan, p. 180.

489 Iwasa MA (2015c) *Rattus rattus* (Linnaeus, 1758). In: Ohdachi SD et al. (eds) The wild
490 mammals of Japan. 2nd edn. Shoukadoh Book Sellers, Kyoto, Japan, p. 181.

491 Kambe Y, Nakata K, Yasuda SP, Suzuki H (2012). Genetic characterization of Okinawan black
492 rats showing coat color polymorphisms of white spotting and melanism. Genes Gen Syst
493 87:29–38.

494 Kambe Y, Suzuki S, Yabe T, Nakata K, Maezono Y, Abe S, Ishida K, Tanikawa T, Hashimoto
495 T, Takeda M, Tsuchiya K (2013) Introgressive hybridization of two major lineages of
496 invasive black rats, *Rattus rattus* and *R. tanezumi* on the Japanese Islands inferred from *Mclr*
497 sequences. Mammal Sci 53:289–300.

498 Kambe Y, Tanikawa T, Matsumoto Y, Tomozawa M, Aplin KP, Suzuki H (2011) Origin of
499 agouti-melanistic polymorphism in wild black rats (*Rattus rattus*) inferred from *Mc1r* gene
500 sequences. Zool Sci 28:560–567.

501 Karaseva, EV, Kozlov AN, Melkova VK, Trahanov DF, Turov IS, Novatny I (1990) [Habitat].
502 In: [Brown rat: Systematics, Ecology, Population Control]. Nauka, Moscow, pp. 85–127 [in
503 Russian].

504 Kawamura Y (1989) Quaternary rodent faunas in the Japanese Islands (Part 2). In: Memoirs of
505 the Faculty of Science, Kyoto University, Series Of Geology & Mineralogy, Vol. LIV., pp. 1–
506 235.

507 Kawamura Y (1991) Quaternary mammalian faunas in the Japanese Islands. *Quaternary Res*
508 (Daiyonki-Kenkyu) 30:213–220.

509 Khlyap L, Glass G, Kosoy M (2012) Rodents in urban ecosystems of Russia and the USA. In:
510 Triunver A, Scalise D (eds) *Rodents: habitat, pathology and environmental impact*. Nova
511 Science Publishers, Inc., Hauppauge, NY, pp. 1–21.

512 Kowalsky K, Hasegawa Y (1976) Quaternary rodents from Japan. *Bull Nat Sci Mus (Tokyo)*,
513 Series C (Geology) 2:31–66.

514 Kuroda N (1939) Distribution of mammals in the Japanese Empire. *J Mammal* 20:37-50.

515 Kuzyakin AP (1951) History of expansion, recent distribution, and habitation sites of the
516 Norway rat in the USSR. In: Formozov AN (ed) *Fauna and ecology of rodents*. Vol. 4. MOIP,
517 Moscow, pp. 22–81 [in Russian].

518 Lack JB, Greene DU, Conroy CJ, Hamilton MJ, Braun JK, Mares MA, van den Bussche RA
519 (2012) Invasion facilitates hybridization with introgression in the *Rattus rattus* species
520 complex. *Mol Ecol* 21:3545–3561.

521 Lack JB, Hamilton MJ, Braun JK, Mares MA, Van Den Bussche RA (2013) Comparative
522 phylogeography of invasive *Rattus rattus* and *Rattus norvegicus* in the US reveals distinct
523 colonization histories and dispersal. *Biol Invasions* 15:1067–1087.

524 Latinne AS, Waengsothorn SV, Herbreteau V, Michaux J (2011) Thai limestone karsts: an
525 impending biodiversity crisis. In: *The 1st EnvironmentAsia international conference on*
526 “Environmental supporting in food and energy security: crisis and opportunity”, Thai Society

527 of Higher Education Institutes on Environment, 22-25 March 2011, Bangkok, Thailand, pp.
528 176–187.

529 Lekagul B, McNeely JA (1977) Mammals of Thailand. Sahakarnbhat, Bangkok.

530 Lunde D, Truong Son N (2001) An identification guide to the rodents of Vietnam. American
531 Museum of Natural History, New York.

532 Maak RK (1861) [Journey Along the Ussuri River Valley]. Vol. 2. Bezobrazov, Saint Petersburg
533 [in Russian].

534 Maekawa K, Dewa H, Maeda K (2002) Animals of Nayoro. In: New Nayoro City history, Vol. 3.
535 Nayoro City, Nayoro, Japan, pp. 49-74.

536 Maeno F, Taniguchi H (2005) Eruptive history of Satsuma Iwo-jima Island, Kikai Caldera, after
537 a 6.5ka caldera-forming eruption. Bull Volc Soc Japan 50:71–85 [in Japanese].

538 Morris-Suzuki T (1995) Sustainability and ecological colonialism in Edo period Japan. Japanese
539 Stud 15:36–48.

540 Motokawa M, Liu KH, Harada M, Lin LK (2001) New records of the Polynesian rat *Rattus*
541 *exulans* (Mammalia: Rodentia) from Taiwan and the Ryukyus. Zool Stud 40:299–304.

542 Musser GG, Carleton MD (2005) Superfamily Muroidea. In: Wilson DE, Reeder DM (eds)
543 Mammal species of the World: a taxonomic and geographic reference (Vol. 1). John Hopkins
544 University Press, Baltimore, pp. 894–1532.

545 Ohdachi SD, Ishibashi Y, Iwasa MA, Fukui D, Saitoh T (eds) (2015) The wild mammals of
546 Japan. 2nd edn. Shoukadoh Book Sellers, Kyoto, Japan.

547 Ohno K, Niwa Y, Kato S, Kondo K, Oda Si, Inouye M, Yamamura H (1994) Establishment of
548 new inbred strains derived from Japanese wild rats (*Rattus norvegicus*). Experimental
549 Animals 43:251–255.

550 Ota K (1968). Studies on the ecological distribution of the murid rodents in Hokkaido. Research
551 Bull College Experiment Forests Hokkaido Univ 26:223–295. [In Japanese with English
552 abstract].

553 Otsuka H, Takahashi H (2000) Pleistocene vertebrate faunas in the Ryukyu Islands: their
554 migration and extinction. *Tropics* 10:25–40.

555 Pagès M, Bazin E, Galan M, Chaval Y, Claude J, Herbreteau V, Michaux J, Piry S, Morand S,
556 Cosson JF (2013) Cytonuclear discordance among Southeast Asian black rats (*Rattus rattus*
557 complex). *Mol Ecol* 22:1019–1034.

558 Pagès M, Chaval Y, Herbreteau V, Waengsothorn S, Cosson JF, Hugot JP, Morand S, Michaux J
559 (2010) Revisiting the taxonomy of the Rattini tribe: a phylogeny-based delimitation of species
560 boundaries. *BMC Evol Biol* 10:184.

561 Puckett EE, Munshi-South J (2019) Brown rat demography reveals pre-commensal structure in
562 eastern Asia before expansion into Southeast Asia. *Genome Res* 29:762–770.

563 Puckett EE, Park J, Combs M, Blum MJ, Bryant JE, Caccone A, Costa F, Deinum EE, Esther A,
564 Himsworth CG, Keightley PD (2016) Global population divergence and admixture of the
565 brown rat (*Rattus norvegicus*). *Proc Royal Soc B: Biol Sci* 283:20161762.

566 Radde GFR (1862) *Reisen im Suden von Ost-Sibirien. Vol. 1. Die Säugethierfauna.* Buchdr. der
567 Kaiserlichen Akademie der Wissenschaften, Vienna [in German].

568 Reid FA (2006) *Peterson's guide to mammals of North America.* Houghton Mifflin Harcourt,
569 New York.

570 Sakaguchi N, Ono Y (1994) Seasonal change in the food habits of the Iriomote cat *Felis*
571 *iriomotensis*. *Ecol Res* 9:167–174.

572 Smith AT, Xie Y (eds) (2013) *Mammals of China.* Princeton University Press, Princeton, NJ.

573 Stuart AM, Prescott CV, Singleton GR (2012) Natal nest locations of the Asian house rat (*Rattus*
574 *tanezumi*) in lowland rice–coconut cropping systems: a coconut penthouse or rice bunds with
575 water frontage?. *Wildl Res* 39:496–502.

576 Stuart AM, Singleton GR, Prescott CV (2015) Population ecology of the Asian house rat (*Rattus*
577 *tanezumi*) in complex lowland agroecosystems in the Philippines. *Wildl Res* 42:165–175.

578 Surkov VS (1986) [Some ecological traits of brown rat in Sakhalin and the southern Kurils].
579 [Brown rat (Ecology and Distribution)] 1:114–128 [in Russian].

580 Thazin Wai K, Sukmasuang R, Trisurat Y (2018) Comparison of small mammal communities in
581 logged and unlogged areas in the proposed Mahamyaing Wildlife Sanctuary, Myanmar. *J*
582 *Trop Forest Res* 1:1–20.

583 Thomson V, Aplin KP, Cooper A, Hisheh S, Suzuki H, Maryanto I, Yap G, Donnellan SC
584 (2014) Molecular genetic evidence for the place of origin of the Pacific rat, *Rattus exulans*.
585 *PLoS One* 9:e91356.

586 Tsukada M (1985) Map of vegetation during the last glacial maximum in Japan. *Quatern Res*
587 23:369–381.

588 Ullrich KK, Tautz D (2020) Population genomics of the house mouse and the brown rat. In:
589 Dutheil JY (ed) *Statistical population genomics*. *Methods Mol Biol* 2090:435–452.

590 Van Peenen PFD, Cunningham ML, Duncan JF (1970) A collection of mammals from Con Son
591 Island, Vietnam. *J Mammal* 51:419–424.

592 Washitani I (2007) Restoration of biologically-diverse floodplain wetlands including paddy
593 fields. *Global Envir Res* 11:135–140.

594 Wu D, Deng X (1988) The community structure of myomorpha rodents in the tropical and
595 subtropical mountainous forests in Yunnan Province. I. Species diversity, relative abundance,
596 density and biomass. *Acta Teriol Sinica* 8:25–32 [in Chinese with English abstract].

597 Wu D-L, Luo J, Fox JB (1996) A comparison of ground-dwelling small mammal communities in
598 primary and secondary tropical rainforests in China. *J Trop Ecol* 12:215–230.

599 Yamada F, Ogura G, Abe S (2015) *Herpestes auropunctatus* (Hodgson, 1836). In: Ohdachi et al.,
600 (eds) *The wild mammals of Japan*. 2nd edn. Shoukadoh Book Sellers, Kyoto, Japan, pp. 272–
601 274.

602 Yegerov DB (1946) [Sakhalin Island]. *Gidrometeoizdat*, Moscow [in Russian].

603 Yeong-Seok J (2015) *Mammals of Korea: Conservation and management*. Doctoral Dissertation,
604 Texas Tech University. <https://ttu-ir.tdl.org/handle/2346/66132>, Accessed 28 August 2020.

605 Ying B, Kosoy MY, Maupin GO, Tsuchiya KR, Gage KL (2002) Genetic and ecologic
606 characteristics of *Bartonella* communities in rodents in southern China. *American J Trop Med*
607 *Hygiene* 66:622–627.

608 Yu HT (1994) Distribution and abundance of small mammals along a subtropical elevational
609 gradient in central Taiwan. *J Zool* 234:577–600.

610 Zeng L, Ming C, Li Y, Su LY, Su YH, Otecko NO, Dalecky A, Donnellan S, Aplin K, Liu XH,
611 Song Y (2018) Out of Southern East Asia: origin of the brown rat revealed by large-scale
612 genome sequencing. *Mol Biol Evol* 35:149–158.

613 Zhan S-C (1982) Preliminary survey of the distribution and breeding habits of predominant
614 species of rodents in the area of Dai-yun Mountain Range. *Wuyi Sci J* 13:25–32 [in Chinese
615 with English abstract].

616 Zhang MW, Guo C, Wang Y, Hu ZI, Chen AG (2000). The buff-breasted rats (*Rattus*
617 *flavipectus*) in China. *Zool Res* 21:487–497.
618 Zheng SH (1993) Quaternary rodents of Sichuan-Guizhou area, China. Science Press, Beijing [in
619 Chinese with English abstract].

620

621 **Table legend**

622 **Table 1** Sites of surveying for *Rattus* rats in Japan in 2017-2019.

623

624 **Figure legends**

625 **Figure 1** Locations of study sites in Japan. **a** – sites more than 1 km from human habitat where
626 no *Rattus* rats were detected; **b** – sites where brown rat (*Rattus norvegicus*) was detected more
627 than 1 km from human settlements; **c** – records of brown rat far from human settlements by
628 earlier surveys (Ota 1968, Abe *et al.* 1971, Maekawa *et al.* 2002); **d** – sites where brown rat
629 was detected in natural habitats but less than 1 km from human settlements, **e** – sites where
630 Asian house rat (*R. tanezumi*) was detected more than 1 km from human settlements within
631 possible native range; 1 – Kiritappu Marsh, 2 – Kushiro Marsh, 3 – Daisetsuzan National
632 Park, 4 – Torii Pass, 5 – Kasuga Primeval Forest, 6 – Hokigamine Forest Park, 7 – Bogatsuru
633 Marsh, 8 – Bonotsu area, 9 – Aso Bay Park. Omitted are records of Asian house rat from the
634 Ogasawara Islands and central and southern Ryukyu Islands, where it is known to be non-
635 native.

636 **Figure 2** Brown rat (*Rattus norvegicus*) in Kushiro Marsh, Japan’s largest remaining wetland.

637 **Figure 3** Habitat of brown rat (*Rattus norvegicus*) in large natural wetland, Kushiro-Shitsugen
638 National Park, Hokkaido.

639 **Figure 4** Habitat of brown rat (*Rattus norvegicus*) in riparian birch forest, Daisetsuzan National
640 Park, Hokkaido.

641 **Figure 5** Habitat of brown rat (*Rattus norvegicus*) in mixed upland forest, Daisetsuzan National
642 Park, Hokkaido.

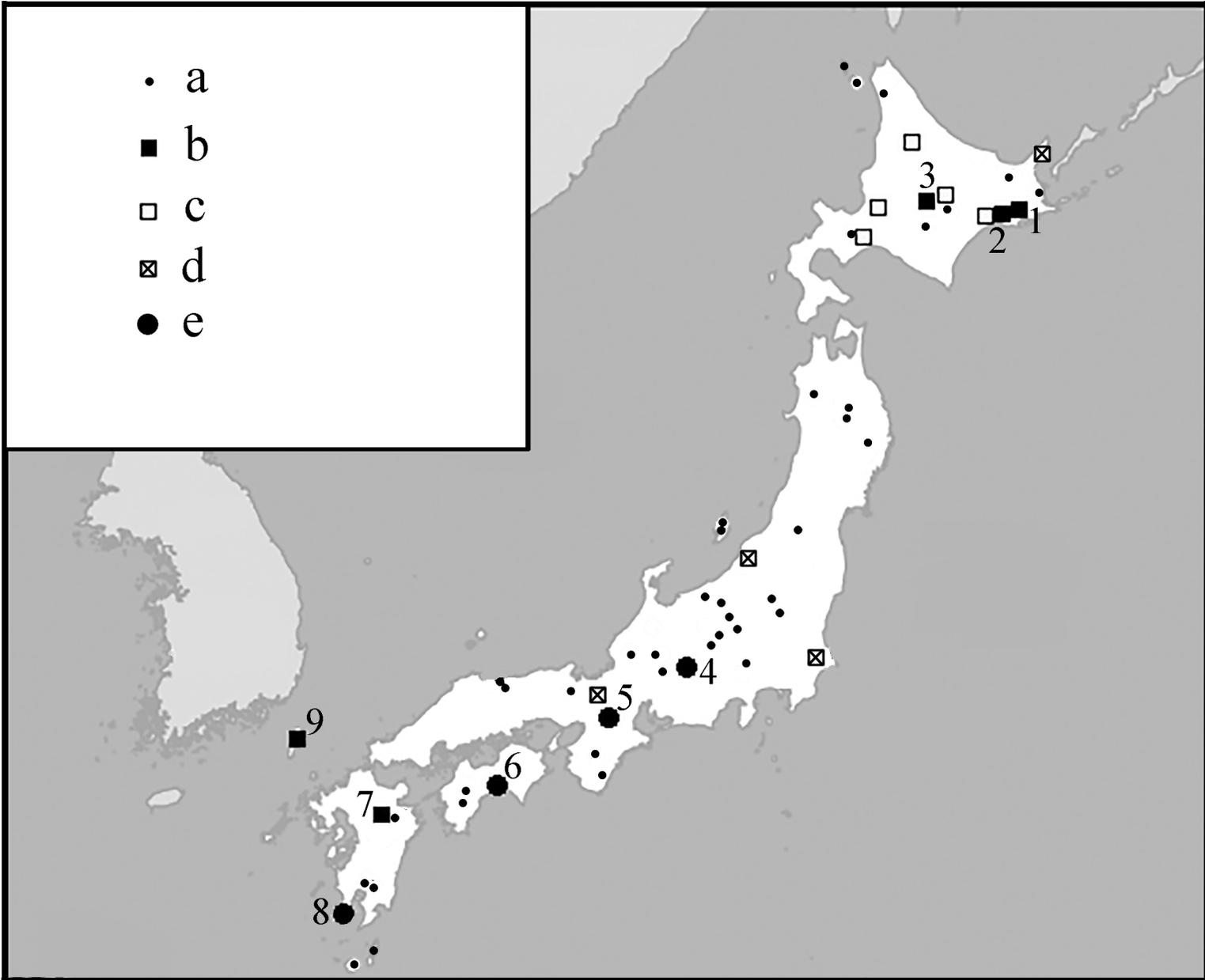
643 **Figure 6** Habitat of brown rat (*Rattus norvegicus*) along forested seashore with tidal wetlands,
644 Aso Bay Park, Tsushima.

645 **Figure 7** Habitat of Asian house rat (*Rattus tanezumi*) in ancient forest of giant Japanese horse
646 chestnuts (*Aesculus turbinata*) at Torii Pass, Honshu.

647 **Figure 8** Asian house rat (*Rattus tanezumi*) in subtropical evergreen forest near Bonotsu,
648 Kyushu.

649 **Figure 9** Habitat of Asian house rat (*Rattus tanezumi*) in subtropical evergreen forest near
650 Bonotsu, Kyushu.

- a
- b
- c
- ⊠ d
- e



















Site	Latitude, longitude	Months (months of detections marked with *; months when snow tracking was possible <u>underlined</u>)	Hours of nighttime surveying (daytime hours of survey for tracks on the snow in <i>italics</i>)	Habitat types	Detection of <i>Rattus</i> rats (<i>Rn</i> – <i>R. norvegicus</i> , <i>Rt</i> – <i>R. tanezumi</i>)	Habitats at detection site(s)	Distance to human settlements and/or fields, km
Hokkaido and adjacent islands							
Sarobetsu Plain	45.1120, 141.6997	08	12	marshes, meadows	-		
Rishiri Island	45.2223, 141.2127	08	7	forests	-		
Rebun Island	45.4241, 141.0391	08	8	forests, meadows	-		
Shiretoko National Park	44.1979, 145.3322	<u>03</u> , 08, <u>12</u> *	41/14	forests, meadows, seashores	1 <i>Rn</i> trackway	rocky beach	0.8
Notsukefurendo Natural Park	43.3260, 145.3245	08	4	coastal dunes, marshes	-		
Kiritappu Marsh	43.0944, 145.0712	<u>03</u> *	4/6	marshes	1 <i>Rn</i> trackway	reedbed	2.1
Kushiro Marsh (Kushiro-Shitsugen National Park)	43.0979, 144.3656	<u>03</u> , 08*, <u>12</u> *	38/16	forests, marshes	1 <i>Rn</i> seen, 2 <i>Rn</i> trackways	wet deciduous forest, reedbed	3.1-3.5
Akan-Matsu National Park	43.4502, 144.2019	08, <u>12</u>	12/14	forests	-		
Daisetsuzan National Park	43.3368, 143.1578	<u>03</u> *, 08*	61/42	forests, talus slopes	1 <i>Rn</i> seen, 1 <i>Rn</i> trackway	riparian forest, road along alder-lined stream	4-8
Lake Oketo	43.6138, 143.3789	08	5	forests, meadows	-		
Lake Utonai Park	42.7049, 141.7096	03	12	forests, wetlands	-		
Shimukappu	43.1155, 142.3980	<u>03</u>	14/2	forests, meadows	-		
Honshu and Sado Islands							
Oraise Gorge	40.5331, 140.9749	04	12	forests	-		
Lake Towada	40.4343, 140.8934	04	12	forests, meadows	-		
Shirakami Range	40.5227, 140.1774	05	20	forests	-		
Ryusen-do	39.8602, 141.7969	04	60	forests	-		
Lide Hot Springs	37.9557, 139.7040	06	7	forests	-		
Osado Ishina Ancient Forest (Sado I.)	38.1955, 138.4146	04, 08	7	forests	-		
Nyugawa Valley (Sado I.)	38.1576, 138.3700	04, 08	6	forests, rocky slopes	-		
Echigo Plain	37.8143, 138.8740	08*, 12	4	marshes, forest fragments	1 <i>Rn</i> seen	lakeshore marsh	0.1
Oze National Park	36.8900, 139.2000	06	10	forests, marshes, meadows	-		
Nikko National Park	36.7695, 139.4521	06, <u>01</u>	28/4	forests, bogs	-		
Jigokudani Park	36.7326, 138.4620	<u>12</u> , <u>02</u>	4/4	forests	-		
Karuizawa Wild Bird Park	36.3863, 138.6063	<u>12</u> , <u>02</u> *, 04	19/14	forests	1 <i>Rt</i> trackway	deciduous forest	0.5
Mt. Naeba	36.8545, 138.6627	07	4	forests, meadows	-		
Ikenotaira Marsh	36.4280, 138.4136	07	3	marshes, meadows	-		
Norikura Plateau	36.1042, 137.6265	04, 06	16	forests, marshes, meadows	-		
Yatsugatake Mts.	36.0058, 138.3648	06	6	forests	-		

Mt. Ontake	35.8736, 137.5024	08	8	forests, meadows	-		
Torii Pass	35.9509, 137.7952	08*	6	forests	1 <i>Rt</i> seen	very old deciduous forest	1
Akasawa Natural Forest	35.7292, 137.6257	08	8	forests	-		
Tone River	35.8523, 140.6544	06*	4	open floodplain	6 <i>Rn</i> seen	edges of reedbeds	0.1-0.2
Mt. Fuji	35.3364, 138.7368	06	6	forests, lava flows	-		
Mt. Nogohaku	35.7794, 136.5184	11	10/4	forests, meadows	-		
Lake Biwa	35.4459, 136.1897	12*	12	wooded lakeshores	12 <i>Rn</i> seen	flooded deciduous woodland	<0.1
Beechney Primary Forest	35.3534, 135.7820	11	49	forests	-		
Kasuga Primeval Forest	34.6856, 135.8628	12, 09*	25	forests	1 <i>Rt</i> seen	very old mixed forest	1.1
Dorokyo Gorge	33.9102, 135.8814	02, 03, 10	52	forests, rocky slopes	-		
Mt. Koyasan	34.1862, 135.6044	03, 10	48/14	forests, meadows	-		
Mt. Daisen	35.3913, 133.5336	09	5	forests	-		
Kagamiganaru Wetland	35.3449, 133.5916	09	6	wooded wetlands	-		
Shikoku							
Hokigamine Forest Park	33.6712, 133.6915	08*	8	forests	1 <i>Rt</i> seen	oldgrowth evergreen forest	1.5
Ishizuchi Ropeway	33.8032, 133.1483	08	4	forests, meadows	-		
Ashizuri-Uwakai National Park	32.8661, 132.8502	08	4	forests	-		
Kyushu							
Mt. Kurodake	33.0962, 131.3021	07	8	forests	-		
Bogatsuru Marsh	33.0996, 131.2611	12*	4	wetlands	1 <i>Rn</i> seen	grassy marsh	2
Lake Miiike	31.8843, 130.9564	01, 06	21	forests	-		
Mt. Takachinomine	31.8859, 130.8960	06	4	forests, shrubs, talus slopes	-		
Bonotsu	31.3090, 130.2421	06*	17	forests	8 <i>Rt</i> seen	evergreen forest	1-1.2
Tsushima Island							
Aso Bay Park	34.3067, 129.3517	08*	12	wooded seashores	2 <i>Rn</i> seen	rocky shoreline	1-2
Sago Valley	34.6554, 129.4098	08	5	forests	-		
Ryukyu Islands							
Tanegashima Island	30.4481 130.9718	05	4	forests, meadows	-		
Yakushima Island	30.3800, 130.5741	05	13	forests	-		
Mangrove Primeval Forest, Amami I.	28.2570, 129.4108	04*	2	forests	6 <i>Rt</i> seen	evergreen forest, mangroves	0.1-0.5
Amami Natural Forest Park, Amami I.	28.4524, 129.5931	04*	8	forests	8 <i>Rt</i> seen	evergreen forest	0.5-0.7
Tokunoshima Island	27.8725, 128.9503	04	10	forests	-		
Daisekirinzan Park, Okinawa I.	26.8590, 128.2530	02*, 06	16	karst forest	1 <i>Rt</i> seen	evergreen forest on limestone	1
Yambaru National Park, Okinawa I.	26.7528, 128.2408	01-12 (06*)	195	forests	1 <i>Rt</i> seen	evergreen forest	3
Seifa-Utaki Sacred Forest, Okinawa I.	26.1722, 127.8262	03*, 07*	4	karst forest fragment	3 <i>Rt</i> seen	evergreen forest on limestone	0.2
Peace Memorial Park, Okinawa I.	26.0930, 127.7220	07*	2	forest fragment	2 <i>Rt</i> seen	evergreen forest	0.1
Onna Hills, Okinawa I	26.4594, 127.8358	01-12	17	forests	-		
Mt. Gusuku, Ie-jima I.	26.7198, 127.8070	09*	8	forests, rocky slopes	2 <i>Rt</i> seen	evergreen forest	0.1

Ihaya-jima Island	27.0287, 127.9558	05	16	forests, palm groves	-		
Darumayama Forest, Kumejima I.	26.3609, 126.7640	08*	4	forests	2 <i>Rt</i> seen	evergreen forest	0.5-0.6
Ono Forest, Miyakojima I.	24.8016, 125.3228	10*	24	forests	162 <i>Rt</i> seen	evergreen forest	0.1-0.3
Banna Park, Ishigaki I.	24.3754, 124.1569	11*	8	forests	19 <i>Rt</i> seen	evergreen forest	0.1-0.4
Mt. Omotodake, Ishigaki I.	24.4252, 124.1996	11*	2	forests	12 <i>Rt</i> seen	evergreen forest	0.1-0.9
Iriomote Island	24.2978, 123.8651	11*	22	forests, meadows	4 <i>Rt</i> seen	forest edges and clearings	0.1-2
Mitsudahara Forest, Yonaguni I.	24.4563, 122.9757	2*	8	forests	3 <i>Rt</i> seen	evergreen forest	0.2-0.3
Tsukumi Park, Minami-Daito I.	25.8374, 131.2343	8*	4	wooded wetlands	2 <i>Rt</i> seen	forested lakeshore	0.1
Ogasawara Islands							
Ogamiyama Park, Chichijima I.	27.0986, 142.1953	8*	6	forests	9 <i>Rt</i> seen	evergreen forest	0.1-0.2
Hahajima Island	26.6470, 142.1540	8*	10	forests	4 <i>Rt</i> seen	evergreen forest	0.2-3

Table 1 Sites where surveying for *Rattus* rats was conducted in Japan in 2017-2019.