

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

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

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

## Introduction

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

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

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

## ***Rattus tanezumi***

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

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

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

## ***Rattus norvegicus***

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



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

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

## **Materials and methods**

## **Study sites**

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

## **Survey methods**

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

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

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

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

## Species identification

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

## Results

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

### *Rattus tanezumi*

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

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

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

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

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

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

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

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

### ***Rattus norvegicus***

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

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

periwinkles (Littorinidae) were scattered among the rocks. The intertidal zone in this area also had numerous limpets, crabs, sea stars, sea urchins, kelp plants, and other possible food items. In Daisetsuzan National Park we found one trackway in March in riparian forest of birch (*Betula* sp.) (Fig. 4), and observed one animal in August as it was feeding on Geometridae moths on a paved road through oldgrowth mixed montane forest (Fig. 5), near a small stream lined with alder (*Alnus* sp.). The moths were flying in great numbers that night, and covered the road pavement at densities of up to 3 moths per 1 m<sup>2</sup> of the road (visual estimate). Numerous other mammals, birds and amphibians were also feeding on them.

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

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

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

## Discussion

### *Rattus tanezumi*

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

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



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

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

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

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

### ***Rattus norvegicus***

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

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

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

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

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

#### **Suggested directions of future studies**

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

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

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

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

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## Table legend

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

## Figure legends

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

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

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

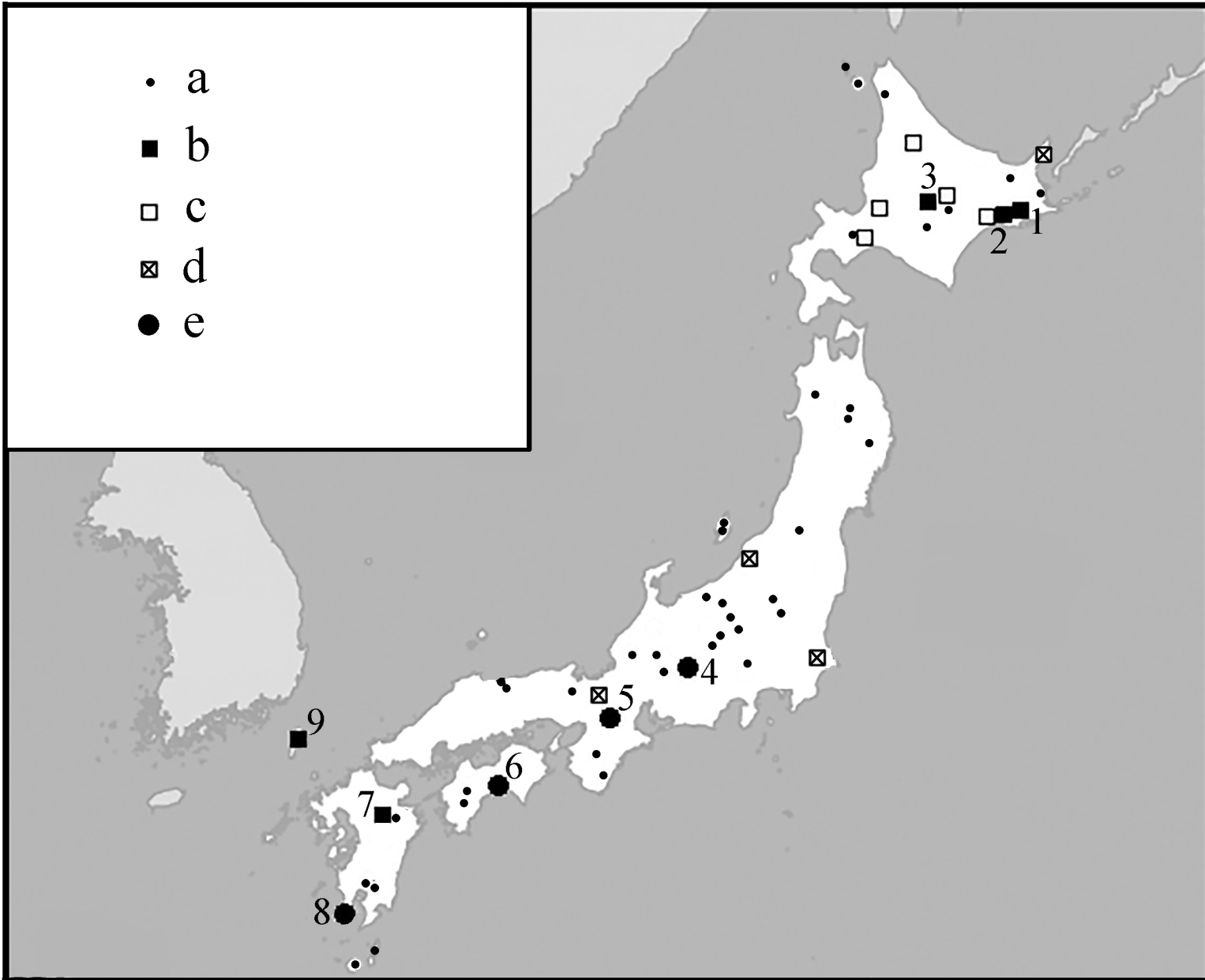
• a

■ 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
<b>Hokkaido and adjacent islands</b>							
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/ <i>14</i>	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/ <i>16</i>	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/ <i>14</i>	forests	-		
Daisetsuzan National Park	43.3368, 143.1578	<u>03</u> *, 08*	61/ <i>42</i>	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/ <i>2</i>	forests, meadows	-		
<b>Honshu and Sado Islands</b>							
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/ <i>4</i>	forests, bogs	-		
Jigokudani Park	36.7326, 138.4620	<u>12</u> , <u>02</u>	4/ <i>4</i>	forests	-		
Karuizawa Wild Bird Park	36.3863, 138.6063	<u>12</u> , <u>02</u> *, 04	19/ <i>14</i>	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	-		
<b>Shikoku</b>							
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	-		
<b>Kyushu</b>							
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
<b>Tsushima Island</b>							
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	-		
<b>Ryukyu Islands</b>							
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

Iheya-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
<b>Ogasawara Islands</b>							
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.