Chapter 13
A Comparative Zoogeographic View on the Animal Biodiversity of Indonesia and Japan

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Abstract The Indonesian Archipelago harbors unique fauna with a high level of species diversity and endemism. In this report, we provide basic information on the spatial and temporal aspects of the animal ecosystem in the Indonesian Islands. We discuss four zoogeographic topics, including (1) lineage dispersal events from the continents to the Islands, (2) speciation processes in the insular area, (3) accelerated phenotypic evolution and (4) human impact on commensal animals compared to previous cases in the Japanese Archipelago, in which the same eustatic geological events and global climatic changes have occurred.

Keywords Biogeography • Indonesia • Japan • Molecular phylogeny • Mammals • Evolution

13.1 Introduction

The Indonesian Islands are situated on the southeastern side of the Eurasian continent and harbor ecosystems with high species diversity and endemism, consisting of two biodiversity hotspots—namely, "Sundaland" (western Indonesia and Malay Peninsula) and "Wallacea" (eastern Indonesia, Papua New Guinea, and Melanesia), representing important biological areas, together with the nearby regions of "Philippines" and "Indo-Burma" (Myers et al. 2000; Mittermeier et al. 2004). The two hotspots Sundaland and Wallacea include around 3,000 vertebrate species, accounting for 10 % of the world's species (half of which are endemic) (Sodhi et al. 2004). Notably, the proportion of endemic bird species in the Philippines may be

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M. Osaki, N. Tsuji (eds.), *Tropical Peatland Ecosystems*,
DOI 10.1007/978-4-431-55681-7_13

much higher than current estimations (Lohman et al. 2010), and many local lineages have been re-evaluated as endemic or cryptic species. This may also apply to other vertebrate taxa in hotspot regions in the area (Gorog et al. 2004; Lohman et al. 2011). However, why these geographic areas show such high levels of species diversity and endemism remains unclear. In this report, we provide basic information on Indonesian biodiversity. We also compare Indonesian biodiversity with the Japanese Islands, another biodiversity hotspot situated on the eastern side of the Eurasian Continent at a higher latitude that stretches from the humid subtropics to the boreal zone, resulting in a wide variety of climates and ecosystems (Mittermeier et al. 2004). This comparison highlights the extreme Indonesian biodiversity by comparing the insular domains to areas with high levels of biodiversity.

13.2 Evolutionary Consequences of Dispersal Events from the Continents

The appearance and disappearance of land bridges are important for the historical assemblage of insular ecosystems. Recently, Kirihara et al. (2013) performed phylogenetic inference using mitochondrial gene sequences, focusing on four Japanese mole species. The Japanese mole fauna is thought to have been structured by frequent dispersal events from the continent to Japan (Tsuchiya et al. 2000; Shinohara et al. 2004). It is believed that the fluctuating sea levels over time resulted in dispersal events across the deep seas (>100 m in depth; Kirihara et al. 2013); rapid, marked sea-level drops are thought to have occurred ca. 5.6, 3.5, 2.4,1.6, 1.3, and 0.9 million years ago (mya) (Haq et al. 1987; Woodruff 2003; Kitamura and Kimoto 2006). Based on this assumption, together with estimated divergence times from the cytochrome *b* gene (*Cytb*) sequences of mitochondrial DNA (mtDNA), the dispersal of ancestral lineages of the four Japanese moles of *Euroscaptor mizura*, *Mogera tokudae*, *M. imaizumii* and *M. wogura* are considered to have occurred 5.6, 3.5, 2.4, and 1.3 (or 1.6) mya, respectively (Kirihara et al. 2013; Fig. 13.1). The resultant phylogenetic tree implies that the dispersal event of the Taiwanese mole *M. insularis* may be coincident with *M. tokudae*. This assumption may be applicable to other insularlineages. For example, it is possible that the two Japanese wood mouse

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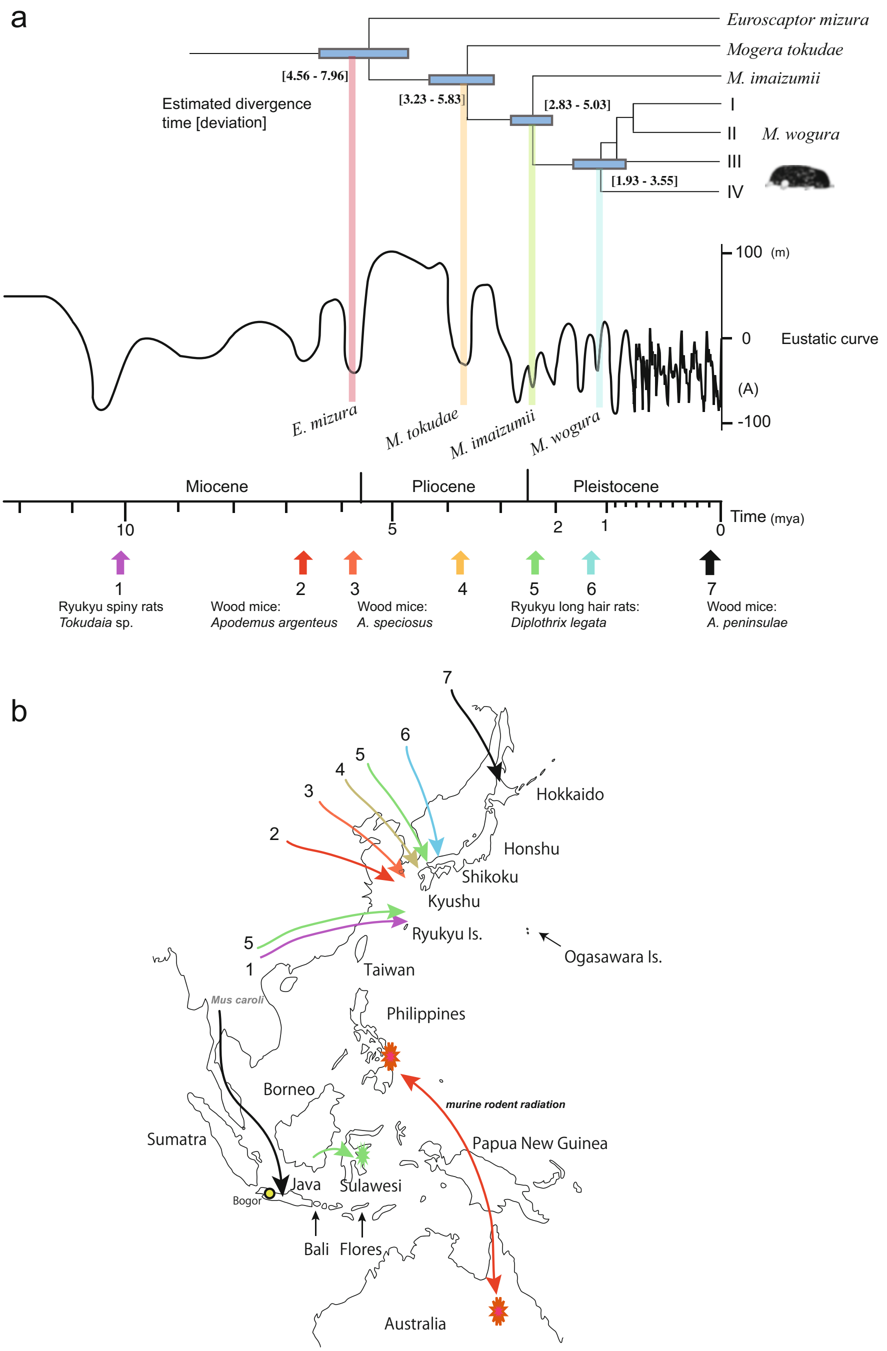
Fig. 13.1 A zoogeographic view on the migration events of the ancestral lineages leading to endemic lineages in respective geographic regions, focusing on Indonesia, Philippines, Australia and Japan. Eustatic changes in the global sea level during the last 10 million years (Woodruff 2003; Berggren et al. 1995), which were suggestive of marked sea level decreases 5.6, 3.5, 2.4, and 1.3 mya (**a**). Estimated divergence times of the four Japanese endemic mole lineages (*vertical line*: means; *horizontal line*: confidence interval) are in good accordance with the worldwide sea level changes (See Kirihara et al. 2013 for details). Schematic representation of the inferred evolutionary history of small mammals in the eastern part of the Eurasian landmass and its adjacent islands (**b**)


a
Euroscaptor mizura
Mogera tokudae
M. imaizumii
I
II
III
IV
M. wogura
[4.56 - 7.96]
[3.23 - 5.83]
[2.83 - 5.03]
[1.93 - 3.55]
Estimated divergence time [deviation]
100 (m)
0
Eustatic curve
(A)
-100
E. mizura
M. tokudae
M. imaizumii
M. wogura
Miocene
Pliocene
Pleistocene
10
5
2
1
0
Time (mya)
1
Ryukyu spiny rats
Tokudaia sp.
2
Wood mice:
Apodemus argenteus
3
Wood mice:
A. speciosus
4
5
6
Ryukyu long hair rats:
Diplothrix legata
7
Wood mice:
A. peninsulae
b
7
6
5
4
3
2
Hokkaido
Honshu
Shikoku
Kyushu
5
1
Ryukyu Is.
Ogasawara Is.
Taiwan
Mus caroli
Philippines
murine rodent radiation
Borneo
Sumatra
Papua New Guinea
Java
Sulawesi
Bogor
Bali
Flores
Australia

species *Apodemus argenteus* and *A. speciosus* came to Japan across land bridges, which would have been built 6–7 and 5.6 mya, respectively (Fig. 13.1), based on the estimated divergence times from the molecular phylogenetic inference (Serizawa et al. 2000; Suzuki et al. 2003, 2008). The eustatic changes in sea level may have had a significant impact on faunal compositions of terrestrial animals found on the continent-associated islands, such as Japan and Taiwan, on which ancient migration events of terrestrial animals should be examined (e.g. Suzuki 2009; Hosoda et al. 2011). This may also be observed in Indonesia, as discussed below.

In the Northern Hemisphere, global climate change has shaped fauna composition; the climate has become cool and arid during the last 10 million years (Zachos et al. 2001) and assisted the expansion of temperate taxa 6–7 mya (Cerling et al. 1997) and subsequently boreal taxa 2–3 mya (Einarsson and Albertsson 1988). The Japanese Islands received continental lineages at different geological times; tropical or subtropical lineages came to Ryukyu Islands in ancient times, followed by temperate lineages to Honshu/Shikoku/Kyushu at moderately ancient times, and finally boreal lineages to Hokkaido rather more recently (Fig. 13.1; Suzuki 2009). The estimated divergence time for the Ryukyu Island endemic species, Ryukyu spiny rats *Tokudaia* sp. and Amami rabbits *Pentalagus furness*, is almost 10 mya (Suzuki et al. 2000; Yamada et al. 2002). Mammals found in the central landmass of Japan; namely, Honshu, Shikoku, and Kyushu, are thought to have come to Japan during the last 6–7 million years (Suzuki 2009). The northern-most island of Japan, Hokkaido, harbors both temperate and boreal lineages that originated recently (within the last 1 million years) from the continent and Honshu (e.g. *A. argenteus* and *A. speciosus*, respectively).

On the contrary, the most prominent geological event explaining the Indonesian fauna is the formation of the Indonesian Islands through collision between the Asian and Australian continental plates. The collision, which is thought to have occurred around 25 mya (Hall 2002, 2012), may explain the co-occurrence of both lineages from Asian and Australian components in the Indonesian biota, which are represented by eutherians (e.g. macaques) from the Asian side and marsupials (e.g. possums) from the Oceanian side. This may have facilitated the introduction of a large number of plant and animal taxa that originated in Asia into Australia over the past 20 million years (Byrne et al. 2011).

To explore the nature of the Indonesian ecosystem, murine rodents (subfamily Murinae) harboring a large number of species (approximately 500; 10 % of mammalian species that belong to this single subfamily) (Carleton and Musser 2005) should be examined since Indonesia and its neighboring regions are the primary geographic areas harboring the rodent taxon. In particular, the *Rattus* and its allele genera (tribe Rattini), the largest lineage of the murine rodents, is an ideal study group that includes more than 120 species. This group has three major subgroups, *Rattus*, *Niviventer*, and *Maxomys*, the first of which extended its descendent lineages to the Ryukyu Islands (*Diplothrix legatta*) and Australia. Recent molecular phylogenetic analyses revealed spatio-temporal patterns of the dispersal events of the Rattini lineages (e.g. Steppan et al. 2005; Jansa et al. 2006;

Rowe et al. 2008, 2011). The initiation of the radiation events of the murine rodents is rather old (10 mya), but migration of the rodents into the Philippines and Australia is estimated to have occurred 5 mya. The estimated times for migration of the Indonesian Rattini are 2–3 mya. This is in good accordance with the mouse taxon genus *Mus*. An ancestral lineage belonging to the subgenus *Coelomys*, with its homeland in Southeast Asia (Suzuki and Aplin 2012), extended its lineage to *Mus crociduroides* in Sumatra and *Mus vulcani* in Java approximately 2–3 mya. Oscillation of the Quaternary glacial and warm periods is thought to have contributed to the dispersal events from the Asian Continent to the Indonesian Islands. For example, molecular phylogeographic analyses indicated that the Southeast Asian mouse *Mus caroli* of the Java population shows a natural habitation. Intraspecies radiation of mtDNA in this species is known to have occurred half a million years ago, yielding several intraspecies local lineages that have extended from Myanmar to Vietnam, as well as to Java, in which the lineage is equally distinct from the continental lineages, contrary to the initial belief that the presence of this species in Indonesia is due to human-mediated introduction (Shimada et al. 2007). Overall, it is possible that the major assemblage of the Indonesian rodents (and perhaps the majority of other terrestrial animals) is young, dating back only 2–3 million years (see Esselstyn et al. 2013).

13.3 Speciation Processes

The number of murine rodent species in Indonesia exceeds 173 (Suyanto et al. 2002; Carleton and Musser 2005). An important feature of Indonesian fauna is the ability to promote the rapid speciation processes observed in murine rodents, as discussed above. For the Japanese Islands, the number of endemic murine rodent species is limited; only two species are found in the main areas of Japan (Honshu, Shikoku and Kyushu) (Fig. 13.2). Indonesia includes seven geographic areas; Sumatra, Kalimantan (most of Borneo), Jawa, Sulawesi, Lesser Sunda, Maluku, and Papua (the western half of Papua New Guinea). These islands harbor a large number of endemic species, indicative of promotion by specific systems of rapid speciation events, as seen in the murine rodents and shrews (Achmadi et al. 2013; Esselstyn et al. 2009, 2013). In particular, Sulawesi and Papua show high levels of endemicity in Rattini, excluding the six commensal species *Rattus argentiventer*, *R. exulans*, *R. nitidus*, *R. norvegicus*, *R. rattus* (and its related lineages) and *Mus musculus* (Suyanto et al. 2002; Fig. 13.2). Based on the phylogenetic tree of murine rodents, we observed several nested divergent clusters at various times from 1 to 3 mya, indicative of intermittent radiation events associated with the Indonesian Islands. Each of the clusters tended to include a Sulawesi endemic lineage. This is suggestive of unidirectional dispersal events toward Sulawesi, which fostered the migrant lineages to become indigenous species, resulting in the absence or limited migration of the Sulawesi lineages to other islands in the subsequent time period. In contrast,

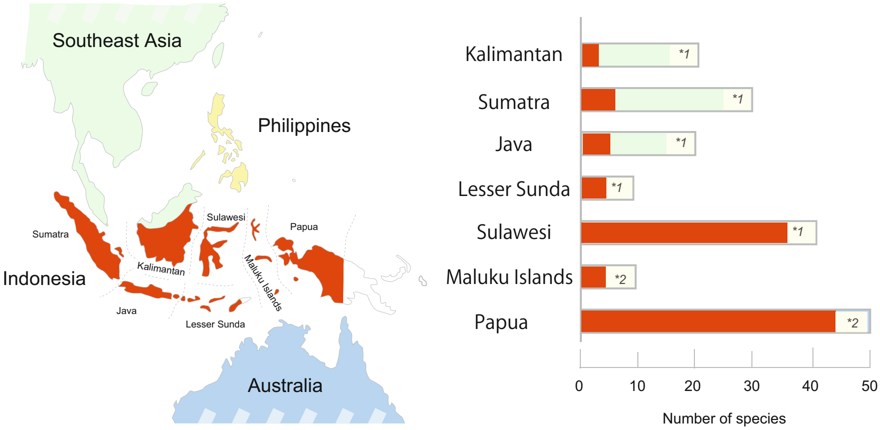


Fig. 13.2 Frequency histogram showing the number of species of Indonesian murine rodents described in the checklist published by Suyanto et al. (2002). Although the checklist requires revision, it can be used to characterize heterogeneous patterns in the endemic species (*red*) among the following seven geographic regions: Kalimantan, Sumatra, Java, Lesser Sunda, Sulawesi, Maluku Islands and Papua, as well as the distribution of species sets of invasive introduced rodents; *1: *Mus musculus*, *Rattus argentiventer*, *R. exulans*, *R. norvegicus* and *R. rattus*, and *2: species set *1 plus *R. nitidus*

the three islands Sumatra, Borneo, and Java showed limited numbers of endemic species, indicative of a strong influence of dispersal events among the three islands and the Asian continental region.

The several cycles of connection and disconnection of the landmasses during the late Pliocene to the early Pleistocene (e.g. 1–3 mya) would have affected lineage differentiation within the Sulawesi Islands, which can be divided into several insular-like landmasses (see Stelbrink et al. 2012). Sea level changes are thought to cause geographic isolation and hence mediate speciation processes, which can be seen in a variety of terrestrial animals, including *Rattini* rodents and macaques (Evans et al. 2003; Stelbrink et al. 2012). In the Japanese Islands, the genetic subdivision is thought to have been accelerated along with the insular domains of Honshu, Shikoku and Kyushu with the changes in sea level, which may also have affected the western Japanese mole, *M. wogura* (Kirihara et al. 2013).

The multiple separations and mixing of the Indonesian islands during the Quaternary may also have contributed to the extreme biodiversity in animal groups. Notably, the richness of the marine fish fauna of the East Indian region (Indonesia, New Guinea, and the Philippines) may be been caused by multiple cycles of sea level decreases and increases over the last 700,000 years (Randall 1998). Further investigations are required to explore the factors involved in speciation episodes using speciose animals such as bats (Maryanto and Yani 2003) and parrots (Astuti et al. 2006).

13.4 Specificity of the Ecological Features and Ongoing Phenotypic Evolution

Both the Japanese and Indonesian archipelagos, comprised of numerous islands, can contribute to evolutionary studies of natural selection and genetic drift. Rapidly changing species compositions due to frequent dispersal events would have forced rapid phenotypic changes due to adaptation to “new” environments, as well as interspecific (evolutionary arms race) and intraspecific competition (sexual selection), yielding phenotypic and functional variation within species.

The murine rodents, in particular Rattini rodents, show significant phenotypic evolutionary changes with respect to morphological characteristics. In fact, although the species lineages are young, many of the Rattini lineages that have different morphological appearances are classified as distinct genera. For example, in the Okinawan long-haired rat *Diplothrix legata*, the largest rodent in Japan, the divergence time from *Rattus* species dates back only 2–3 mya (Suzuki et al. 2000). One remarkable case is the Indonesian Rattini, the Flores giant rat, *Papagomys armandvillei*, with a head and body size of greater than 40 cm, whereas the small rat *Rattus exulans* has a head and body length of only 12 cm (Fig. 13.3). Rattini appears to be in a mid-period of phenotypic evolution in the ecosystems of Lesser Sunda, Sulawesi and Papua New Guinea, and a comprehensive view of the evolutionary patterns from both ecological and genetic perspectives is not yet available. The murine rodent evolved into the shrew-rat species with no cheek teeth, *Paucidentomys vermidax*, found in Sulawesi, which feeds on earthworms exclusively (Esselstyn et al. 2012). The newly discovered rodent *Waiomys mamasae* from Sulawesi represents a semi-aquatic and carnivorous rodent, which was previously found only on the continent of Sahul, showing a strong example of convergent evolution in the Indo-Australian Archipelago (Rowe et al. 2014).

Phenotypic variation in coat color is also a visible indicator of the evolutionary dynamics in each geographic area (e.g. Suzuki 2013). The Japanese Islands from north to south exhibit a number of coat color variations within species. A common example of coat color variation is seen in the Japanese hare, which shows apparent pelage color variation with the presence or absence of massive snowfall during

Fig. 13.3 Dorsal view of two skin specimens of rats, *Papagomys armandvillei* (*top*) and *Rattus exulans* (*bottom*), showing their markedly different size characteristics

the winter season (Nunome et al. 2010). The Japanese marten also shows spatial variation in the winter season based on hair pigmentation (Sato et al. 2009). On Hokkaido, the northern-most island, the sables show marked differences in body colors in the winter season, from bright yellow to dark brown (Hosoda et al. 2005). The five macaque species found in Sulawesi show remarkable interspecies phenotypic variation in coat color. Current studies are exploring the causative mutation of color variation (Nakayama et al. 2008).

The continuously changing ecosystems, such as are observed in Indonesia and Japan, will provide numerous opportunities to explore the factors shaping phenotypic changes. Genetically polymorphic states provide an opportunity to identify the responsible gene and causative mutation underlying phenotypic changes. In the Hokkaido sable, the causative mutation for the total yellow hair color is known to be replacement of a conserved cysteine residue at codon site 35 in the coat-color-related gene, melanocortin 1 receptor (Ogawa et al. unpublished). The identification of a causative mutation allows us to assess the involvement of natural selection by surveying accelerated rates of amino acid changes (e.g., Shimada et al. 2009) and the signatures of selective sweeps around a causative mutation.

13.5 Human Impact on Biodiversity

It is important to understand how human activity has altered the evolutionary patterns of wild life, including their geographic ranges, gene introgression, and phenotypic changes. In this context, the evolutionary dynamics of commensal rodents should be explored. Commensal rats are generally considered alien species, which are expected to harbor microorganisms related to a variety of zoonotic infections. Stowaway introduction of commensal rodents has now become a serious problem in ecosystems. However, commensal rodents provide valuable information on prehistoric human movements. In this section, we discuss the following two influential commensal rodents: the house mouse *Mus musculus* and the ship rat (or black rat) *Rattus rattus* or the *Rattus rattus* species complex.

The homeland (natural range) of the wild house mouse *M. musculus* is thought to have been a specific area of west Asia, and the historical human movements originating from Africa are thought to have mediated the global expansion of three subspecies groups of house mice onto the entire Eurasian Continent in prehistoric times (Bonhomme and Searle 2012). The three major subspecies that show long-range dispersal are *Mus musculus domesticus* (DOM), *M. m. castaneus* (CAS), and *M. m. musculus* (MUS), which are found in western Europe, southern Asia, and northern Eurasia, respectively. Molecular phylogenetic studies of the mitochondrial sequences revealed two subspecies lineages of CAS and MUS on the Japanese Islands with skewed distribution of CAS in the northern area; namely, Hokkaido and northern Honshu (Yonekawa et al. 1988; Terashima et al. 2006). The exact origins of the parental lineages remain unclear. A recent study using relatively long mitochondrial sequences revealed that Japanese CAS and MUS are closely related to haplotypes from South China, near areas of the Pearl River and the Korean Peninsula, respectively (Suzuki et al. 2013; Kuwayama et al. unpublished). This allows us to examine ancient movements of humans who propagated agriculture from the Asian continent to the Japanese Islands. The mtDNA analyses of Indonesian mice from five localities revealed CAS haplotypes unique to Indonesia that belong to a clade, designated CAS-1, with low nucleotide diversity and a wide distribution range in Southeast Asia, South China and Indonesia, and an estimated time for radiation of 8,000–4,000 years ago (Suzuki et al. 2013). This is suggestive of an ancient colonization event, spreading to Java, Bali, and Flores, which is somewhat concordant with the archaeological record of agriculture. Previous studies demonstrated the domestication of cereal crops, including rice and millet, by about 9,000 years ago in several parts of southern and eastern Asia (Khush 1997). This hypothesis requires verification, and the possible impact of Indonesian mice on the neighboring areas of the Philippines and Australia should be examined.

Meanwhile, nuclear gene analyses revealed relatively long DOM haplotypes of >2 Mb in some areas near ports and airports (Kushiro, Kyowa, and Atsugi), which is indicative of the introduction of eastern European lineages in modern times (Nunome et al. 2010; Kuwayama et al. unpublished). This so-called "stowaway introduction" is more common than initially believed. The western European lineage of the mtDNA, DOM, has been detected in Bogor. Mice collected from Bogor by 1990 contain CAS mtDNA haplotypes, while mice captured since 2000 are of western European type, DOM (Terashima et al. 2006; Suzuki et al. 2013). This unexpected occurrence of DOM haplotypes may be explained by long-distance dispersal events associated with human activities in somewhat modern times. This suggests that introgression of the DOM mtDNA is ongoing in this city. It is possible that the genetic structure of the house mouse is unstable over time due to stowaway introduction.

The evolutionary dynamics of the black rats (ship rats or roof rats), the *Rattus rattus* species complex, in ancient and present times should be explored. Black rats, the species complex, include two major members (*Rattus rattus* with $2n = 38$ and *R. tanezumi* with $2n = 42$). *Rattus rattus* is believed to have originated in western India (Yosida 1980), which is supported by recent mtDNA phylogeographic studies of *Rattus rattus* (sensu lato; Robins et al. 2007; Pagès et al. 2010; Aplin et al. 2011). In the Japanese Islands, two species can be found; the initial resident *R. tanezumi* and the new *R. rattu*s. Molecular phylogenetic analyses revealed *R. tanezumi* haplotypes throughout the Japanese Islands, as expected, as well as the sporadic appearance of *R. rattus* haplotypes. In the northernmost island, Hokkaido, the *R. rattus* colony is confined to specific buildings, perhaps due to the unpleasant environment during the winter season. In Honshu and Kyushu, the *Rattus rattu*s species is found in ports (e.g. Kagoshima) and shows urban habitation in large cities (e.g. Tokyo). In the Ryukyu Islands, represented by Okinawa and Amamioshima Islands, the introduction of *R. rattus* in the subtropical natural forests is not observed (Kambe et al. 2011, 2012, 2013), implying that the high-density habitation of *R. tanezumi* rats prevents introduction of the new *R. rattus*. In the Ogasawara Islands with subtropical climate, black rats inhabit areas, including numerous tiny islands, without human residency, contrary to the general belief that black rats always co-inhabit with humans. Subtropical natural forests lacking humans and congeneric competitors are likely the optimal habitats. Recent mtDNA studies revealed natural habitation of the black rat lineages in the Indonesian Islands and human-associated migration events during both prehistoric and historic times (Aplin et al. 2011). It is believed that alien lineages of black rats emerged from human-mediated introduction of established colonies, and may affect wildlife by eating seabird eggs. Further studies, including an intensive survey of the influence of colonization of black rats on the numerous Indonesian Islands, irrespective of human residency, are required.

Acknowledgements We would like to thank all members of the Museum Zoologicum Bogoriense, Research Center for Biology – LIPI, especially Dwi Aswti, Ibnu Maryanto, Martua H. Sinaga and Agustinus Suyanto for their hospitality in the field investigation and valuable suggestions. We would also like to thank Alejandro A. Chinen, Seigo Higashi, Tomofumi Shimada and Hidenori Takahashi for their valuable comments. This study was supported in part by a Grant-in-Aid for Scientific Research (B) from Japan Society for the Promotion of Science (JSPS) to H. S. (2440513).

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