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Editor's Note

Another yearly volume of Treubia is published. I have only recently become involved in the publication of this journal and I can say that the research in this issue is increasingly interesting. I hope to remain actively involved in the publication of this journal and that we can continue to reach a larger audience as time goes on.

This volume of TREUBIA contains 5 papers of vertebrates and invertebrates. The contents of these papers vary widely from vocalizations of frogs to tropical forest spider communities. I can only hope in the future that we continue to receive interesting submissions from all areas of zoology of the Indo-Australian Archipelago.

Also this year two esteemed colleagues from LIPI retired from the service of science, Dr. Mas Noerdjito who studied the ecology of birds and Dr. Agustinus Suyanto who dedicated his life to the study of mammals.

Finally I would like to thank all of the co-editors, referees, computing assistants, secretaries and administrative assistants for their collaborative work without which this journal could not be published. I also acknowledge financial support from the Director of Research Center for Biology, LIPI to publish this essential journal.

Cibinong, December 2011

Chief Editor

COMPARISON OF ZOOGEOGRAPHY AMONG RATS, FRUIT BATS AND INSECTIVOROUS BATS ON INDONESIAN ISLANDS

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ABSTRACT

The species number of rat, fruit bat, and insectivorous bat was significantly correlated with island size when five major islands of Irian, Borneo, Sumatra, Sulawesi and Java were included in the analysis, and the z area values were 0.22; 0.19 and, 0.26, respectively. When these islands were excluded, the correlation between species richness and island size was significant in fruit bats and insectivorous bats ($R^2=0.31$, $P<0.01$) but not in rats. Z value declined to 0.07 in rats, 0.14 in fruit bats and 0.19 in insectivorous bats. Zoogeographic boundaries are shown. Wallace's Line seems to be a zoogeographic boundary for all of three mammal groups; Bali and Lombok Islands belong to the cluster of Lesser Sunda in rats but not to the cluster of Greater Sunda in bats. Although Weber's Line also seems to be a zoogeographic boundary for all of the three mammal groups, an effective boundary lies between Sulawesi and Maluku in rats and insectivorous bats but not between northern Maluku and Irian in fruit bats. The fauna of fruit bats in Southern Maluku is more similar to those of Irian. Lydekker's line seems to be a boundary for only rats, though Biak, Owi and Yapen Islands belong to the cluster of Maluku. In addition to those boundaries, Cluster analyses revealed another boundary for rats between Sumatra and western Sumatra islands (Mentawai Islands) and between Lesser Sunda and Sulawesi to Southern Maluku for fruit and insectivorous bats.

Keywords: zoogeography, bats, rats, Indonesia

INTRODUCTION

The Indonesian archipelago lies on 95° to 141° in longitude and comprises of at least 17000 islands and offers a unique opportunity for a biogeographical examination and comparison of various plant and animal distributions. In the geological history of the Indo-Australian Archipelago, the Pliocene collision among the Australian, Pacific and Asian Plates resulted in major geological upheavals and produced the contemporary

positioning of most islands in the region. These events have caused a number of changes, such as fluctuation of the sea levels, seasonality in precipitation and temperature associated with glacial periods (Morley and Flenley 1987; Heany 1991). There are two shelves, Sunda and Sahul, and the fluctuation of sea level influenced the geological and biogeographical dynamics around the Sunda Shelf in the east of Indonesian Archipelago (Audley-Charles 1987, Hall 2002). The Greater Sunda Islands, Sumatra, Borneo and Java often formed a land mass especially in glacial epochs, while many small islands of the Lesser Sundas were selectively independent from the land mass. The Lesser Sundas are composed of outer Banda arc and inner Banda arc which have different geological backgrounds from each other; the outer Banda has the Gondwanic origin while the inner Banda consists of many volcanic islands which emerged more recently than 3 mya (Bunnet *et al.* 1991), though Kitchener (1998) suggested that mammal fauna of the two arcs do not reflect the difference of the geological backgrounds. The isolated major island Sulawesi is geologically complex and has remained isolated from all adjacent islands including Maluku (Hall 2002).

Mostly due to the mixture of Asian and Australian elements, Indonesia is one of the most biologically diverse countries, possessing about 17% of all species and about 12 % of mammal species hitherto discovered in the world (Wilson and Reeder 1993). Rats (Family: Muridae) and bats (Order: Chiroptera) constitute about 55% of 702 mammal species distributed in this country (Suyanto *et al* 2002) and the recent reappraisal of small mammals on the Lesser Sunda and Greater Sunda Islands has represented a dramatically different view of the zoogeographic boundaries in the Oriental and Australian regions from the traditional ones based on Wallace's, Lydekker's and Weber's lines (Kitchener *et al.* 1995ab). In this paper, we will analyze the zoogeography of this archipelago by comparing rats, fruit bats (Sub order: Megachiroptera) and insectivorous bats (Sub order: Microchiroptera) which show different abilities for migration among the islands.

MATERIALS AND METHODS

In addition to data documented among the published literature on the distribution of Indo-Australian mammals (e.g. Laurie and Hill 1954, van der Zee 1979, Taylor *et al* 1982, van Strien 1986, Corbet and Hill 1992, Carleton and Musser 1993, Flannery 1995ab; Kompanje and Moeliker 2001; Kitchener *et al* 2002; Bergmans 2001; Helgen 2005), the zoogeographical data were also collected from Museum Zoological Bogoriense (MZB-LIPI) mammal specimen collection as well as from the

specimens and our data of the joint expeditions between MZB-LIPI and Western Australian Museum (WAM) on Lesser Sunda and Mollucas from Bali to Tanimbar, and Ambon, Kai, Banda and Aru Islands in 1987-1993 (Kitchener and Maryanto 1993, 1994, 1995, Maryanto and Kitchener 1999, Maryanto 2003a,b); Jambi, Riau Sumatra in 1987 (Maryanto *et al.* 2000, Maryanto 2003, 2004), Lore Lindu expeditions in Central Sulawesi in 2000 and 2001 (Maryanto and Yani 2003, Maryanto *et al* 2009); and Kayan Mentarang, Kalimantan-WWF expedition in 2003 (Azlan *et al* 2003). In the expeditions, rats were collected by live and break traps; fruit bats were collected by mist nets and insectivorous bats were collected by mist nets, harp nets or hand catching in the caves or banana fields as their roosting habitats. Accordingly, the data for the zoogeographical analysis were collected from a total of 98 islands. In the analysis however, the data were pooled among some nearby small islands and the total numbers of islands analyzed were 53 for rats, 66 for fruit bats and 61 for insectivorous bats. In the areas which consist many small islands, the data were only observed from the largest island by assuming that it represents the grouped islands zoogeography.

Based on these data, effects of the following four factors on the species richness per island were analyzed using simple and multiple regression analyses: the island size; the distance of the closest approach from the nearest major island, i.e. Sumatra, Borneo, Java, Sulawesi or Irian measured by Arc View 3.1. PC; the volcanic activity (Katili 1963); and the deepest depth of sea isolating the island from the nearest major island (Bakosurtanal 1992). The endemism was calculated by i.e. $100 \times \frac{Ne}{Nt}$ where Ne and Nt are numbers of endemic and all species in the given island. Z area values were calculated from the formula of $S=cA^z$, where S is the number of the species, A is the area of island and c and z are constants (MacArthur and Wilson 1967). In the multiple regression analysis, the species richness (i.e. the number of the species), the island size, the distance and the sea depth were log-transformed. The volcanic activity, was classified as a binary variable, and 1 or 0 were attributed to active-volcano islands and the other islands, respectively. Moreover, clustering of all islands was performed for each group of rats, fruit bats and insectivorous bats using Sørensen similarity index (SI) and UPGMA. The statistical package computer programs NTSYSpc 2.1 and SPSSpc 11 were used for these analyses.

Results

We visited a total of 37 islands including five major islands and collected 58 rat species of 19 genera, 61 fruit bat species of 15 genera and

64 insectivorous bat species of 20 genera. Surveys of specimens and literatures further discovered 125 rat species, 16 fruit bat species and 104 insectivorous bat species not collected in my expeditions. The total numbers of species and genera from 98 islands including mainland of New Guinea Island reached 183 rat species of 52 genera (Rodentia, Muridae), 77 fruit bat species of 21 genera (Chiroptera, Megachiroptera) and 168 insectivorous bat species of 34 genera (Chiroptera, Microchiroptera).

Species richness per island and endemism

The number of species per island ranged from 4 (Ambon) to 79 species (Irian) for rats, from 4 (Enggano) to 28 species (Sulawesi) for fruit bats and from 3 (Rinca) to 80 species (Borneo) for insectivorous bats. *Rattus argentiventer*, *R. tanezumi*, *R. norvegicus*, *R. exulans*, *Mus musculus* (Muridae), *Cynopterus brachyotis*, *Pteropus hypomelanous*, *Rousettus amplexicaudatus*, *Macroglossus sobrinus*, *M. minimus*, *Eonycteris spelaea* (Megachiroptera), *Saccopteryx saccolaimus*, *Megaderma spasma*, *Miniopterus schrebersi*, *M. australis*, *Rhinolophus affinis*, *Myotis adversus* (Microchiroptera) etc., were distributed over a wide range of Indonesian archipelago. However, *Abeomelomys sevia*, *Anisomys imitator*, *Bunomys coelestis*, *B. naso*, *Kadarsanomys sodyi*, *Papagomys armandvillei*, *Rattus haenaldi* (Muridae) *Rousettus linduensis*, *Neopteryx frosti*, *Acerodon humilis* (Megachiroptera), *Otomops johnstonei*, *Nyctophilus heran*, *Hipposideros crumeniferus* (Microchiroptera) etc., were endemic to a single island.

Number of endemic species were found in 16 islands for rats, 6 islands for fruit bats and 11 islands for insectivorous bats and the percentage number of endemism was 0-75.7%, 0-22.7% and 0-36.7%, respectively (Figure 1). Irian exhibited high endemism in all of rats (73.4%), fruit bats (22.7%) and insectivorous bats (36.7%). The endemism in Sulawesi was high in rats (75.7%) and fruit bats (10.7%), but in insectivorous bats (7.8%) lower than in Borneo (25%). When the five major islands Sumatra, Kalimantan, Java, Sulawesi and Borneo and, such medium-sized islands as Timor, Flores, Tanimbar and Seram were excluded, fruit bats had only two endemic species inhabiting a small island Talaud located north of Sulawesi. Endemic rat species have been reported from seven small islands, most of which are distributed between Sulawesi and Irian, excluding Enggano island in Western Sumatra. Endemic insectivorous bat species have been reported from five small islands distributed in Lesser Sunda, western Sumatra (Nias-Batu islands) and eastern Sumatra (Natuna Anamba islands).

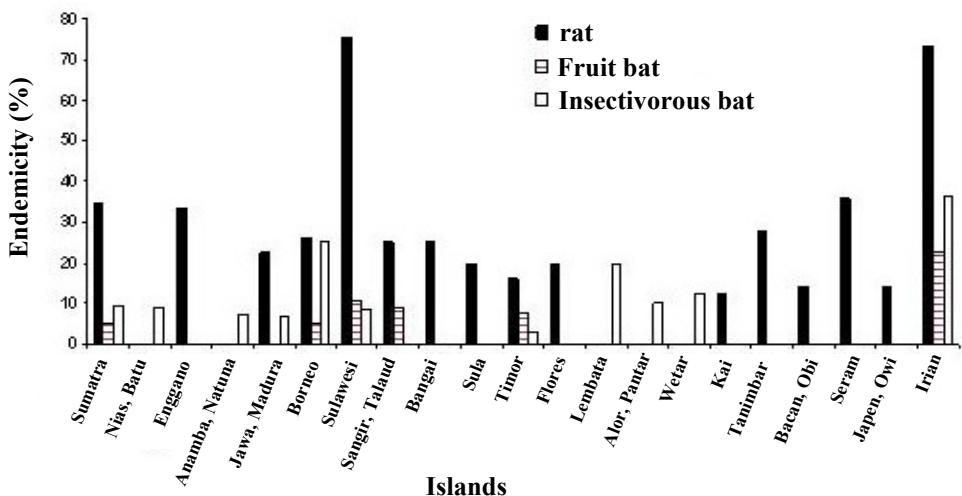


Figure 1. The endemicity of rats, fruit bats, insectivorous bats on each island of Indonesia.

Factors affecting species richness on each island

The island size ranged from 44 km² (Banda islands) to 786,000 km² (Irian). As shown in Figure 2, the numbers of rat, fruit bat, and insectivorous bat species were significantly correlated with island size when five major islands Irian, Borneo, Sumatra, Sulawesi and Java were included in the analysis (rat: $R^2 = 0.52$, $P < 0.01$; fruit bat: $R^2 = 0.51$, $P < 0.01$; insectivorous bat: $R^2 = 0.53$, $P < 0.01$), and z area values (Arthur and Wilson 1967) were 0.22; 0.19 and, 0.26, respectively. When these islands were excluded, the correlation between species richness and island size was significant in fruit bats ($R^2 = 0.29$, $P < 0.01$) and insectivorous bats ($R^2 = 0.31$, $P < 0.01$) but not in rats. Z values declined to 0.07 in rats, 0.14 in fruit bats and 0.19 in insectivorous bats.

Our analysis has identified factors affecting the species richness of non-major islands by multiple regression analysis where the dependent variable was the number of species (Y) and the independent variables were a) island size, b) distance from the nearest major island, c) depth of sea isolating the nearest major island and d) volcanic activity (active volcano island: 1; others: 0). The distance from the nearest major island ranged from 5 km (Bali Island) to 541 km (Roti-Ndao Islands); the deepest depth of sea isolating the given island from the nearest major island ranged from 20 m (Nusa Kambangan Island) to 5,575 m (Barbar Islands); and volcanos were active on Krakatau, Bali, Lombok Flores, Adonara,

Banda etc. In the analysis, the number of species, the island size, the distance from the nearest major island and the sea depth were log-transformed.

In rats, the regression was $\log Y = 0.235\log a - 0.043\log b - 0.604\log c - 0.026d$ and the correlation was significant ($R^2 = 0.49$; $P < 0.001$). The standardized coefficient (SC) was not significant in $\log a$, $\log b$ and, $\log d$ but negatively significant in $\log c$ (Table 1). The sea depth often reflects the history of isolation; that is, shallow seas were often land bridges in glacial epochs while deep seas could be barriers in long time migration. Rats migrate mostly through land bridges and the sea level can be the major factor affecting their species richness. Even if the barrier distance is short, the migration would be difficult between the islands isolated quite long time by deep sea surrounding them.

In fruit bats the regression was $\log Y = 0.423\log a - 0.421\log b + 0.448\log c + 0.333d$ with $\log a$ has significant correlation ($R^2 = 0.52$; $P < 0.001$). SC was negatively significant in $\log b$ and positively significant in other independent variables. Fruit bats have high ability in migration, and their species richness seems to be affected by barrier distance and island size. The positive significance in $\log c$ implies that the long isolation raises the species richness of fruit bats. For the fruit bats with high ability of migration, foraging and nesting may be easier in well isolated islands where competitors like squirrels and predators like snakes are relatively few and the long isolation seems to raise the survival chance of newly immigrated species. The positive significance in $\log d$ implies that volcanic islands have higher species richness of fruit bats than non-volcanic islands whereas the disturbance of ecosystem by eruption is usually thought to damage biodiversity. The decrease of competitors and predators and/or the supply of minerals to the soil by eruption may partly explain the increase of species richness of fruit bats in volcanic islands; however this problem remains for discussion

In insectivorous bats, the regression was $\log Y = 0.41\log a + 0.027\log b - 0.451\log c + 0.265d$ with a significant correlation ($R^2 = 0.46$; $P < 0.001$). SC was negatively significant in $\log c$, positively significant in $\log a$ and d but not significant in $\log b$. Thus, the species richness of insectivorous bats seems to be decreased by long time isolation like rats and increased in large islands and volcanic islands like fruit bats, suggesting that their migration ability is intermediate between rats and fruit bats. The non-significant correlation between insectivorous bats and island size may be partly attributed to their high endemism indicating their relatively more frequent speciation than fruit bats.

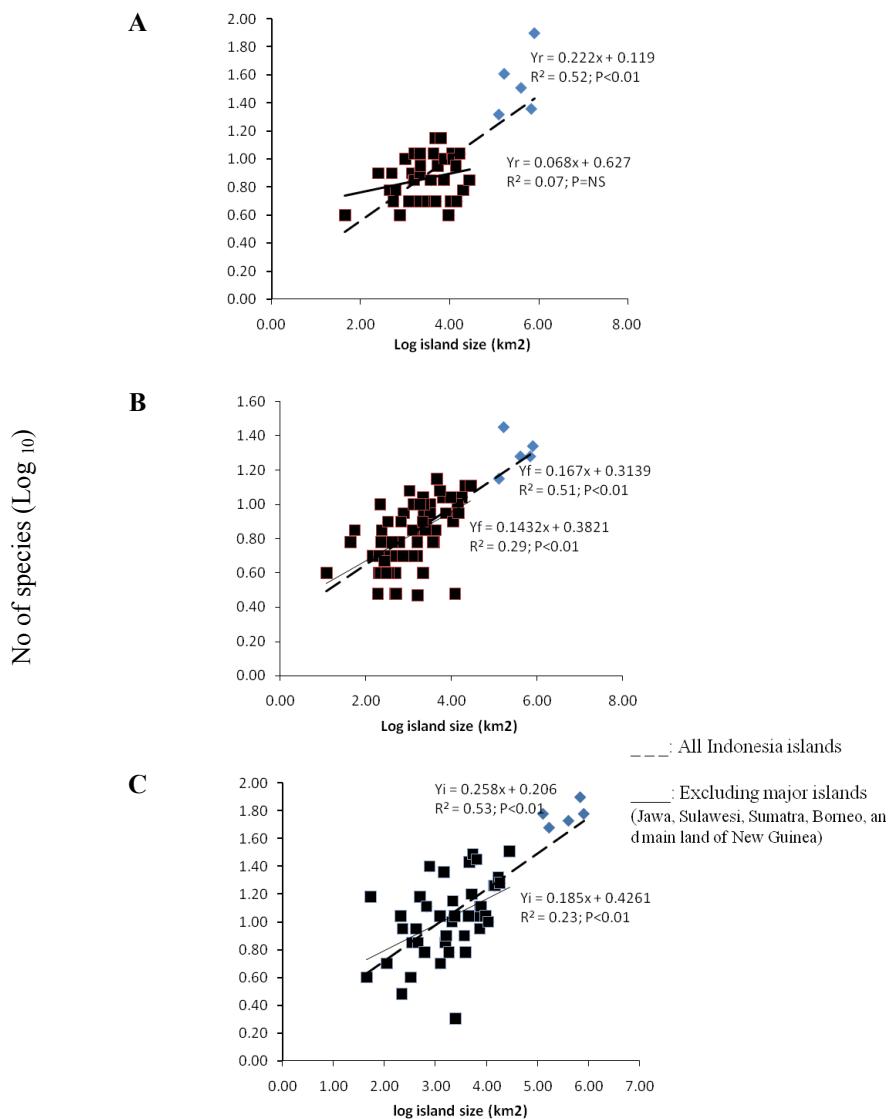


Figure 2. Species-island size relationship in rats (Yr) (A), fruit bats (Yf) (B) and Insectivorous bats (Yi) (C).

Zoogeographic boundaries and clustering of islands

The islands surveyed are distributed from around equator 96° E (western margin of Sumatra) to 140° E (eastern margin of Indonesia arc/Irian island) and Figure 3 shows curves of accumulated numbers of species from west to east along the Indonesian archipelago. In all of rats, fruit bats and insectivorous bats, the curves increased at 115°-120° E and at 125°-130° E, suggesting that both of Wallace's line and Weber's line

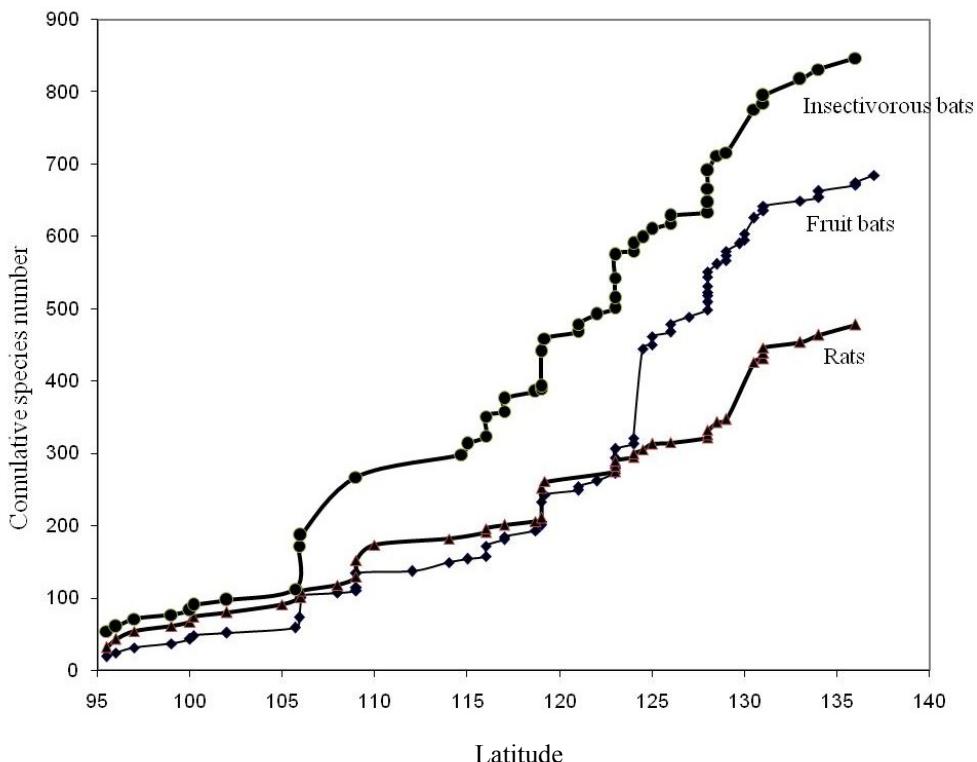


Figure 3. Cumulative species number of rats, fruit bats, and insectivorous bats from west to east Indonesian Archipelago

are zoogeographic boundaries in small mammals including bats. The faunal clustering of islands also suggests the importance of the two zoogeographic boundaries with partial modifications as follows.

Rats:

The 41 islands were grouped into five clusters at the level of Sørensen index ($SI = 0.45$). Cluster A comprises of Greater Sunda Islands though western Sumatra islands belonged to cluster B which mostly consists of Maluku and Lesser Sunda Islands. However, since the western Sumatra islands Pagai, Sipora, Siberut (Mentawai islands) (cluster B1) and Enggano (cluster B2) were separated from the Maluku and Lesser Sunda islands (cluster B3) at the level of $SI = 0.51$, a zoogeographic boundary seems to lie between Greater Sunda and Lesser Sunda (Figure 4). Bali and Lombok belonged to cluster B3, but Sulawesi (cluster D) was independent from cluster B. Cluster C was composed of small islands surrounding Irian which formed cluster E independently. Thus,

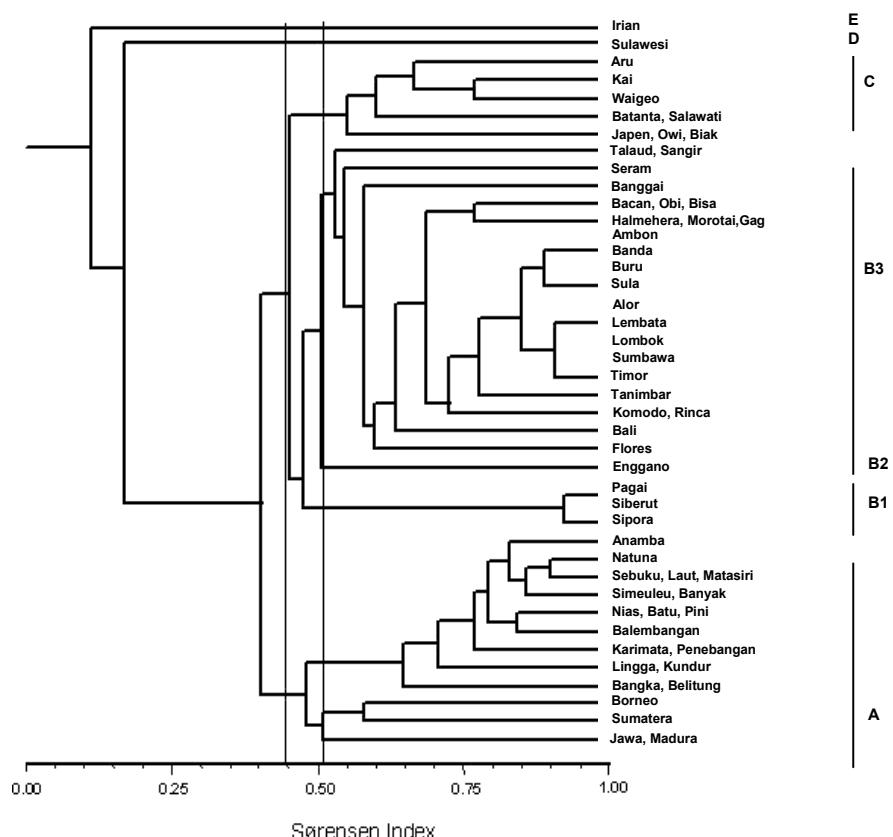


Figure 4. A clustering of Indonesian islands based on rat fauna using Sørensen's similarity index

zoogeographic boundaries seem to lie between Sulawesi and Maluku and between Irian and its surrounding small islands.

Fruit bats:

The 59 islands were grouped into four clusters at the level of $SI=0.32$ (Figure 5). In this clustering, there was no independent islands, and cluster A to D comprised of Greater Sunda islands, Lesser Sunda islands, Sulawesi and Northern Maluku islands and Irian and its vicinity islands, respectively. In this case, Bali and Lombok belonged to the cluster of Greater Sunda; zoogeographic boundary lies between northern Maluku and Irian but not between Northern Maluku and Sulawesi; an obvious boundary was not detected between Southern Maluku and Irian. The increase of the total cumulative species number at around 124° (Figure 3) is attributable to these zoogeographic boundaries.

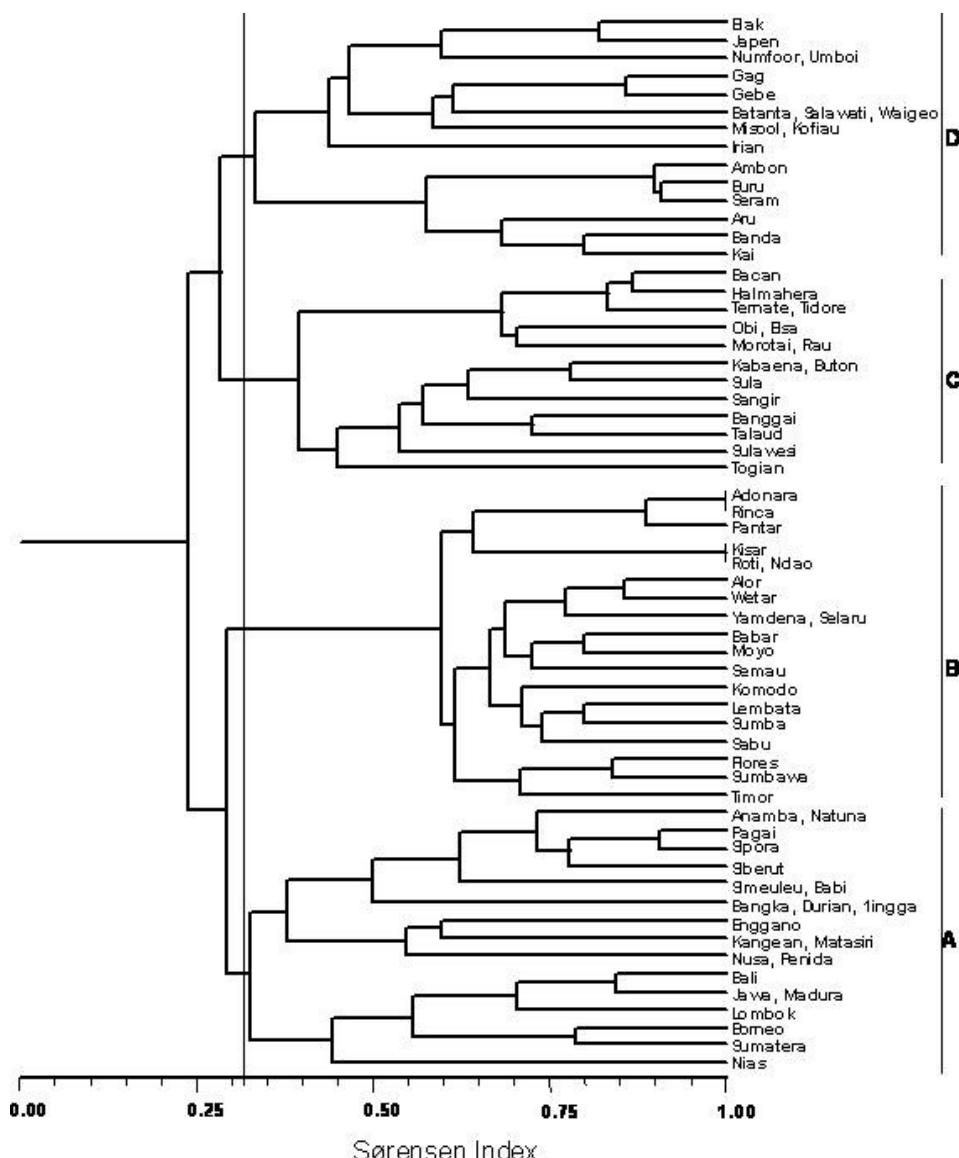


Figure 5. A clustering of Indonesian islands based on fruit bat using Sørensen's similarity index

Insectivorous bats:

The 47 islands were grouped into four clusters at the level of $SI=0.17$ (Figure 6). In this case, Banda island (cluster A) of Southern Maluku is independent from other clusters, mostly because this small island was inhabited by only four species *Pipisterellus tenuis*, *Pipistrellus papuanus*, *Scotophilus collinus* and *Scotophilus kuhlii* which were widely

distributed and very common in Indonesia. This small island is thickly covered by volcanic ash and pumices and has few of caves for roosting of insectivorous bats. Clusters B, C and D were respectively composed of Greater Sunda Islands, Lesser Sunda Islands and Sulawesi-Maluku-Irian Islands. Bali and Lombok islands belonged to the cluster of Greater Sunda; at the level of $SI = 0.33$, the cluster D was divided into Sulawesi and its vicinity islands (cluster D1) and Maluku-Irian islands (cluster D2), suggesting that of a zoogeographic boundary lies between Sulawesi and Maluku but not between Maluku and Irian. The increase of the cumulative species number at around 123°O (Figure 3) is attributable to this zoogeographic boundary.

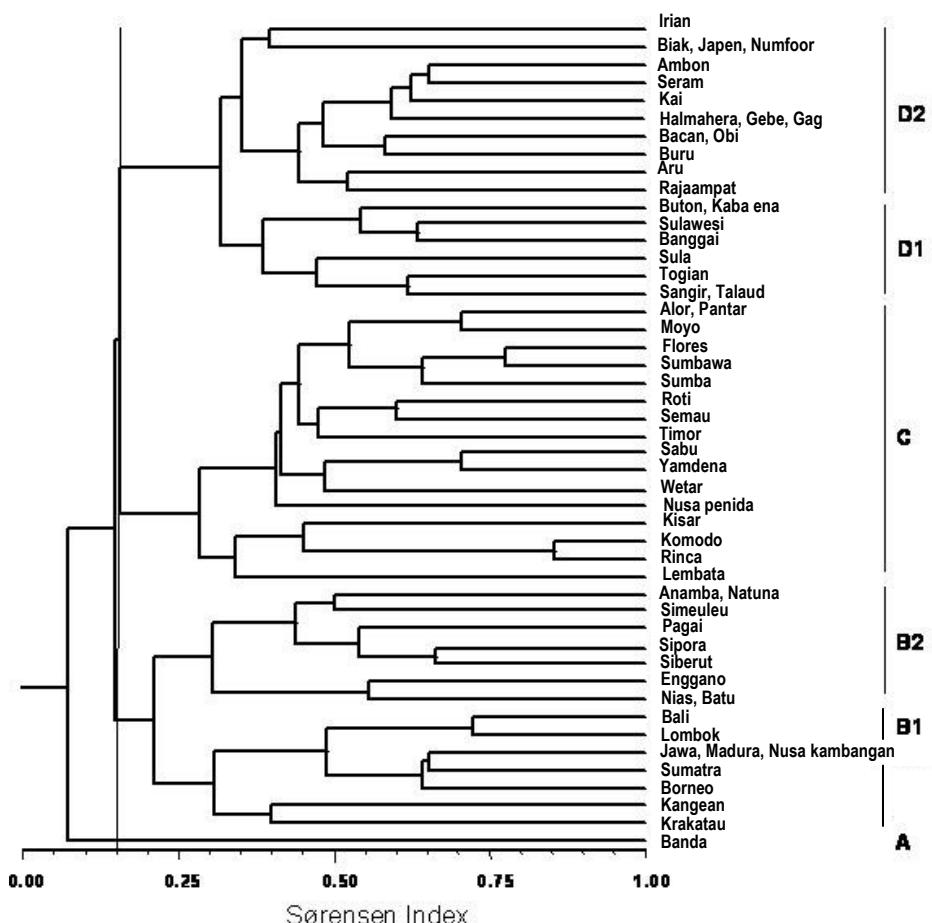


Figure 6. A clustering of Indonesian islands based on insectivorous bat fauna using Sørensen's similarity index

Zoogeographic lines are shown in Figure 7. Wallace's line seems to be a zoogeographic boundary for all of three mammal groups with small modifications. Bali and Lombok belong to the cluster of Lesser Sunda in rats but to the cluster of Greater Sunda in bats. Although Weber's line also seems to be a zoogeographic boundary for all of the three mammal groups, an effective boundary lies between Sulawesi and Maluku in rats and insectivorous bats but between northern Maluku and Irian in fruit bats. The fauna of fruit bats in Southern Maluku is more similar to those of Irian. Lydekker's line seems to be a boundary for only rats, though Biak, Owi and Yapen belong to the cluster of Maluku. In addition to those boundaries, the present study found another boundary for rats between Sumatra and western Sumatra islands.

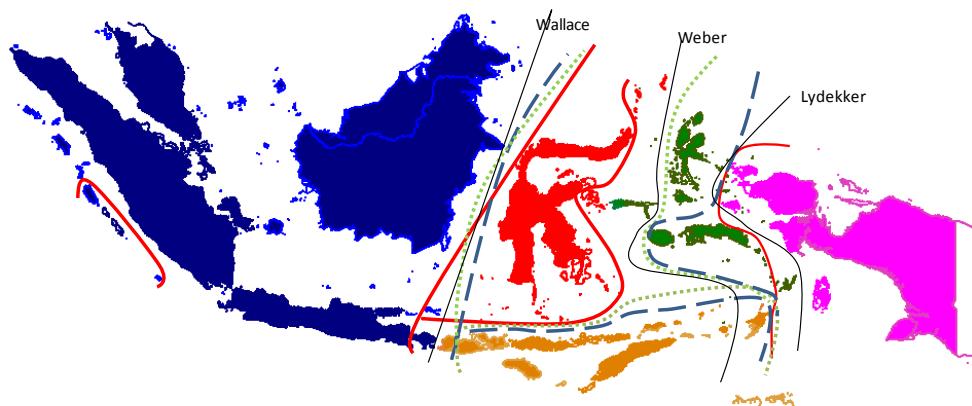


Figure 7. Zoogeographical boundaries in Indonesia for rats (red solid lines), fruit bats (blue broken lines) and insectivorous bats (green dotted lines)

Discussion

As a borderline between Asian and Australian fauna, the Wallace's line has been predicted to lie west of Sulawesi and Philippine, but George (1981) discussed that the position of demarcation line is not a zoogeographic lines for some taxon groups. For instance, Holoway (1987) concluded that, in the distribution of butterflies, there is no sharp Asia-Australia boundary within Wallace's (West Sulawesi). De Boer and Duffels (1996) suggested in the study of cicada distribution that the islands east of Wallace's line show high endemism due to ancient geotectonic dynamics of this area. How and Kitchener (1997) studied the zoogeography of Indonesian snakes and found that the snakes of the

Greater-Lesser Sunda and Sulawesi originated from Asian group, while the snakes of Maluku islands seem close to Papuan group. The present study indicates the importance of Wallace's line and Weber's line for the zoogeography of rats and bats, though there should be a little modification of borderline; thus, it lies between Java and Bali in rats but between Lombok and Sumbawa in fruit bats and insectivorous bats. Such bats as *Megaerops kusnotoi*, *Aethalops alecto*, *Cynopterus horsfieldi*, *C. titthaecheilus* (fruit bats), *Murina cyclotis* and *Rhinolophus pusillus* (insectivorous bats) originated from Greater Sunda but could expand their distribution up to Lombok, while rats of Greater Sunda rarely crossed over the small strait between Java and Bali except in a few species such as *Chiropodomys gliroides*, *Niviventer cremoriventer* and *Niviventer fulvescens*. Even within the Lesser Sunda group, the rat fauna of Bali is independent at Sørensen Index = 0.65 (Figure 4), suggesting that the barrier between Bali and Lombok is still critical for rats.

The importance of Weber's line seems more controversial especially for rats and fruit bats. In rat fauna, the islands of Lesser Sunda are isolated from Sulawesi and belong to the group of Maluku islands, as Turner *et al* (2001) showed based on the study of vicarians that Lesser Sunda is closer to Maluku than Java and Sulawesi is closer to Philippines. In fruit bats, on the other hand, the border lies between northern Maluku islands and southern Maluku islands belonging to the group of Irian and its vicinity islands, mostly because such fruit bats as *Nyctemene keasti*, *Nyctemene papuanus* and *Pteropus macrotis* of Irian could expand their distribution up to southern Maluku islands. The border in insectivorous bats seems almost consistent with Weber's line.

Our research suggests that the migration ability is highest in fruit bats in which the species richness is correlated positively with island size and negatively with distance from a major island. In insectivorous bats, the species richness is positively correlated with island size but not with the distance, suggesting that their migration ability is higher than rats but lower than fruit bats. The expansion of Irian bat species to Maluku islands is evident due to their high migration ability, while the appearance of Lydekker's line in rats seems to reflect their low migration ability.

Indonesia has the world's fifth largest human population size and the small mammals may be frequently transported anthropogenically. Among the factors affecting the distribution of small mammals therefore the effect of human impact on the distribution of small mammals must be discussed. In the study of mammals on Lesser Sunda Islands, Audley-Charles *et al* (1981) argued that the species richness on these islands other than Flores and Timor are low and dominated by such common species as

Rattus tanezumi, and *Mus musculus* which were accidentally introduced by ship. The effect of anthropogenic factors might be limited, and the zoogeographic feature of mammals in Indonesia can be explained by other factors.

The species richness in island archipelagoes is the consequence of colonization, speciation and extinction (Heaney 2000; Lomolino 2000ab, Ward and Thornton 2000) and is influenced by extent of isolation and size of island (Brown and Lomolino 2000). MacArthur and Wilson (1967) stated that the equilibrium number of species found on an island is initially associated with area and isolation of the island and reached when the immigration rate of new species was balanced by the rate of extinction. Our work demonstrates that species richness is highest in fruit bats and lowest in rats on many small islands, suggesting that the high migration ability of fruit bats raises their equilibrium level of species richness, though the difference of extinction rates among the three mammal groups is unknown.

Carvajal and Adler (2005) studied zoogeography of mammals on tropical Pacific islands and indicated that the number of islands larger than 500 km^2 is an important predictor of species richness in the archipelago excluding the major island New Guinea. In the present study, the species richness was significantly correlated with island size in fruit bats and insectivorous bats but not in rats when major islands were excluded, suggesting that the sea depth is more critical to the species richness of rats than the island size. In the Indonesian Archipelago, the species richness seems to be correlated with endemism, and Johnson *et al* (2000) predicted that the endemic species should be greatest on large, isolated islands. In the present study, the endemism of rats, fruit bats and insectivorous bats occur on islands of $> 400 \text{ km}^2$ (Enggano, West Sumatra), $> 2293 \text{ km}^2$ (Sangir-Talaud Is Northern Sulawesi) and $> 1239 \text{ km}^2$ (Lembata, Lesser Sunda), and those islands are isolated from major island by distance and sea depth 114 km and 1539 meter, 194 km and 2540 meter, 428 km and 3885 meter, respectively, supporting the prediction of Johnson *et al* (2000). In addition, the present study demonstrates that the endemism on isolated islands is higher in rats than in bats, exhibiting the correlation between the endemism and the isolation degree attributable to migration ability.

In the Indonesian Archipelago, the migration of rats occurred from continents and among islands throughout the late tertiary and quaternary including the present (Musser 1984, Mahirta *et al* 2004, Shimada *et al* 2005). The low migration ability of rats seems to raise the importance of isolation length reflected by sea depth; that is, shallow seas were often

land bridges in glacial epochs while deep seas could be barriers for migration long time. The sea between the Western Sumatra islands and the major land Sumatra is 289 m (Nias Island) to 1598 m (Siberut Island) deep indicating the long history of isolation. According to Anon (1980) and Mitchell (1981), it is more than half million years since Mentawai islands, Simeulue Island and Enggano Island lost the connection with Sumatra and these islands are inhabited by a large number of unique mammals found nowhere else in the world (Whitten *et al* 1987). Even in Lesser Sunda group, the high endemism in Flores seems due to the long history of isolation. This island is isolated by 252 m deep sea from western Lesser Sunda Islands, by 3497 m deep sea from Timor island and by 4204 m deep sea from Sulawesi island that has been another centre of speciation. Morphological studies of rat genera such as *Komodomys* and *Papagomys* show that those endemics of Flores are closer to Sulawesian endemics than to Javan endemics (Watts and Baverstock 1996).

In the Indonesian Archipelago, volcanos are active on Krakatau, Bali, Lombok, Sumbawa, Flores, Adonara, Banda, Talaud etc and the species richness is positively correlated with the volcanic activity in fruit bats and insectivorous bats but not in rats. The disturbance of ecosystem by eruption is usually thought to damage biodiversity (Ward and Thornton 2000). However, on Krakatau Islands sterilized by eruption in 1883, re-invasion and recovery of such volant mammals as bats was rapid (Tideman *et al* 1991); in particular, widespread insectivorous bats did well (Heaney *et al* 2005). The widespread species of such genera as *Cynopterus*, *Macroglossus*, *Rousettus* (fruit bats), *Rhinolophus* and *Hipposideros* (insectivorous bats) show high colonizing ability, and their early arrival to new habitats may raise their survival chance. In addition to the rapid recovery due to high migration ability, the decrease of competitors, e.g. squirrels, and predators, e.g. snakes, and/or the supply of minerals to the soil by eruption may also explain the increase of species richness of bats on volcanic islands. The fertilities on volcanic islands are partly attributable to the fresh ash falls containing mineral nutrients (Miyauchi and Haruta 1986). The fruit bats have potential to disperse small seeds such as figs (Shilton *et al* 1999), and the supply of minerals to the soil by eruption may induce fast growing of the dispersed plants and partly explain the higher species richness of bats on volcanic islands.

Recently the following factors are often adopted to rank hotspots of biodiversity: 1) number of endemic plant species and endemic vertebrate species 2) area-species curves of endemic plants and endemic vertebrates, 3) habitat richness (Ovadia 2003). Therefore, the information of

z area value is needed to prioritize conservation efforts in the face of the current rapid loss of biodiversity (Myers *et al* 2000). Mac Arthur and Wilson (1967) suggested that the exponent z area typically falls in the range of 0.20-0.35 for islands in archipelago, which is almost consistent with the present result that the z area values of rats, fruit bats and insectivorous bats are 0.22, 0.17 and 0.26, respectively, when major islands of Sumatra, Borneo, Java, Sulawesi and Irian are included in the analysis. The lowest value of fruit bats is probably explained by their high ability of migration, while such non-volant mammals as rats on land bridge islands have z area value of >0.2 (Lawlor 1986). The present study may also contribute to making strategies for the conservation of small mammals including endemics in the Indonesian Archipelago.

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