
CONTRIBUTIONS

A preliminary test of a prediction from the rafting hypothesis for the presence of non-flying mammals on islands

Alexander H. Harcourt¹ and Erik Meijaard^{2,3}

¹Department of Anthropology, Graduate Group in Ecology, University of California, Davis, CA 95616, USA

²People and Nature Consulting International, Ciputat, Jakarta, Indonesia

³School of Archaeology and Anthropology, Australian National University, Canberra, ACT 0200, Australia

Corresponding author: Alexander Harcourt, email: ahharcourt@ucdavis.edu

ABSTRAK

Perangkat kamera telah digunakan sejak tahun 2008 sampai 2012 untuk pemantauan satwaliar di dalam area perkebunan kelapa sawit di Kalimantan timur. Sebanyak 40 perangkat kamera digunakan secara bergilir pada seluruh habitat utama pada lebih dari seratus lokasi yang tersebar pada hutan dengan berbagai tingkatan umur yang telah ditetapkan sebagai hutan konservasi, blok perkebunan dengan umur 4 sampai 12 tahun dalam cakupan wilayah kerja PT REA Kaltim. Secara keseluruhan sebanyak 8628 camera-nights dioperasikan selama lebih dari 4,5 tahun (JANuari 2008 sampai Juni 2012) sepanjang jalur pergerakan satwa atau lokasi sarang orangutan atau tempat dimana ditemui adanya aktivitas satwa. Seabnyak 36 spesies mamalia dari 21 family diidentifikasi dari foto dalam lokasi penelitian. Hampir 54 % dari species yang tercatat dilindungi oleh perundang-undangan di Indonesia. Spesies yang paling banyak terfoto adalah Monyet beruk (*Macaca nemestrina*) total 1450 foto, diikuti oleh Babi jenggot (*Sus barbatus*) dengan foto sebanyak 1126 foto. Beberapa species seperti *Artogalidia bivirgata* tidak pernah terekam dengan menggunakan kamera yang dipasang pada permukaan Tanah. Hasil yang didapatkan menunjukkan pentingnya konservasi spesies, terutama karena relative besarnya jumlah spesies mamalia yang dijumpai pada sekitar 18% hutan asli yang terdapat dalam area konsesi perkebunan. Ringkasa umum setiap aksi yang akan dilakukan dibawah manajemen PT REA Kaltim juga ditampilkan dalam tulisan ini.

ABSTRACT

Non-flying mammals are assumed to have reached oceanic islands by raft from islands of water-edge vegetation. From this hypothesis we can infer that oceanic islands should contain a greater proportion of water-edge species than do continental islands. Without a good sample of mammalian fauna on oceanic islands, we test an altered version of this prediction. At the height of the last ice age, sea levels dropped by 120m. Therefore, immigrants to islands separated by water depths of 120m or more (deep-water islands) should have arrived more often over-water than did immigrants separated by seas of less than 120m depth (shallow-water islands), which immigrants could have reached overland. By comparison to shallow-water islands, deep-water islands should be dominated by water-edge species. We used a multivariate binomial logit generalized linear model accounting for area of island, median body mass of species, predominant habitat of islands, and island region to compare the numbers of water-edge and total species on deep-water islands to the numbers on nearby shallow-water islands (N = 65 species in 42 genera on 16 deep-water islands and 10 shallow-water islands in three regions of Sunda namely Mentawai off the coast of Sumatra, and Palawan and Sulu, north-east of Borneo). The results contradict the rafting hypothesis: if there was a difference between the deep- and shallow-water islands, water-edge species were significantly less common on the deep-water islands instead of more common. We suggest accidental and deliberate transport by humans as a likely means of cross-sea distribution of terrestrial mammals in the Sunda region.

Keywords: Body mass, Habitat, Indonesia, Islands, Mammals, Rafting, Rivers, Sunda

INTRODUCTION

“Hence islands remote from the continent may obtain inhabitants by casualties which ... may occur only

once in many ... thousands of years ... it is obvious that powerful tides, winds, and currents, may sometimes carry along quadrupeds capable ... of preserving themselves for hours in the sea to very considerable distances ...” (Lyell, 1832, Ch. 6, p. 92).

Received 19th August, 2013; Revision accepted 11th December, 2013

Terrestrial mammals inhabit several of the many oceanic islands in south-east Asia (Heaney, 1986;

Meijaard, 2003). Following Lyell, a common assumption is that these species rafted to the islands (Abegg and Thierry, 2002; Brandon-Jones, 1996, 1998). Although a few cases of rafting have been confirmed, for example a correlation of the direction of gene flow among Caribbean island anolis lizards with direction of ocean currents in the region (Calsbeek and Smith, 2003), most suggestions of rafting are hypotheses, especially for terrestrial mammals. The argument is because a terrestrial mammal is on a historically isolated oceanic island, it must have rafted there. Even the Flores Island hominin might have arrived there on the crest of a tsunami (Morwood and Jungers, 2009; Ruxton and Wilkinson, 2012).

In common with several biogeographic patterns (Crisp et al., 2011), the hypothesis of rafting by mammals often remains untested against alternative hypotheses, and few are explicitly tested for the distribution of terrestrial mammals. The absence of terrestrial non-domestic mammals on central Pacific islands could be evidence of the improbability of rafting as a means of their dispersal across water, at least over long distances (Gillespie et al., 2012). Nevertheless, Houle calculated that ocean currents could have transported the founders of the New World primates across the then 1400 km width of the Atlantic in a period of just two weeks (Houle, 1998).

Rivers are believed to be the main launching-point for rafts (Houle, 1998; King, 1962; Krause et al., 1997; Matthew, 1915). The assumption is that river-edge vegetation is dislodged and swept to sea during floods or storms, carrying with it any animals on what has effectively become a raft (Wallace, 1876, Ch. 2).

With respect to terrestrial mammals, Schüle (1993) noted that ungulates inhabiting offshore islands usually belong to swamp or flood plain species, although he provided no examples, lists or analyses. Abegg and Thierry (2002) developed one of the few quantitative predictions to test the rafting hypothesis. They noted that the widespread crab-eating macaque *Macaca fascicularis* is a water-edge and coastal forests species. It is even found in mangrove forest and is a good swimmer (Rowe, 1996). By contrast, the distribution of pig-tail macaque, *Macaca nemestrina*, is limited to interior forest habitats. Abegg and Thierry hypothesized that the wider distribution of the crab-eating macaque resulted from the greater likelihood that it would drift to sea on a vegetation-raft. Their prediction from this hypothesis was that there should be a preponderance of riverine or mangrove taxa on oceanic islands. They

specifically mentioned riverine habitat, as opposed to more general water-edge habitat, because of the idea that rivers might sweep rafts out to sea.

Here we test the Abegg-Thierry prediction using available information on the distribution of the non-flying mammal community of the Sunda region of insular South-east Asia (Meijaard, 2003). Meijaard (2003) listed only two oceanic islands near the Sunda Shelf, Simeulue and Enggano off western Sumatra. Therefore, for the analysis we chose to distinguish between “deep-water” and “shallow-water islands”.

We used Voris’ (2000) calculations of South-east Asian land extent at various ocean depths to separate deep-water from shallow-water islands. Deep-water islands are separated from a main-continent by ≥ 120 m of sea, and shallow-water islands by < 120 m. Using this definition, deep-water islands should still receive more immigrants by rafting than the shallow-water islands, even if sea-levels dropped more than 120m, because the deep-water islands will have been separated from sources for longer than the shallow-water islands. With this assumption, we predicted that deep-water islands should have a preponderance of river edge species in comparison with shallow-water islands.

METHODS

THE ISLANDS

To control for origins of island species, we required deep-water and shallow-water islands nearby the same source, and preferably near one another. Three regions in the species-list that we used (Meijaard, 2003) satisfied the criteria. They are the Mentawai islands and Nias off the potential source of western Sumatra, and the Palawan and Sulu islands off North-east Borneo (Table 1; Fig. 1).

Some consider the Mentawai islands and Palawan island were connected to the Sunda mainland during the last glacial maximum (Meijaard, 2003). If so, the connection must have been brief, given the 145m depth of the channel between Borneo and Palawan, and similarly with the shallowest depth between the northern end of the Mentawai island peninsula and Sumatra (Heaney, 1986; Voris, 2000). Furthermore the high degree of endemism of the Mentawai islands fauna, and to some extent also the Palawan fauna indicates long separation. Nevertheless, we run an analysis excluding Palawan and its neighbouring islands to avoid any biases.

Table 1. Sampled South-east Asian islands and their characteristics. Bracketed areas are estimated from Google maps. Median mass includes *Sus sp.*

Island	Region	Depth	Area (km ²)	Vegetation	Median Mass (kg)	Total #species	#water-edge species	
							Nrw	Brd
Enggano	Mentawai	Deep	800	Non-For.	0.23	2	0	0
N. Pagai	Mentawai	Deep	820	Forest	0.30	14	1	3
Sipura	Mentawai	Deep	845	Forest	0.30	16	1	4
S. Pagai	Mentawai	Deep	920	Forest	2.00	12	1	3
Siberut	Mentawai	Deep	4,030	Forest	0.28	14	1	3
Nias	Mentawai	Deep	4,771	Non-For.	5.00	9	3	5
Bankaru	Mentawai	Shallow	(80)	Forest	0.18	6	1	4
Tuangku	Mentawai	Shallow	(220)	Forest	0.23	11	2	4
Pinie	Mentawai	Shallow	790	Forest	1.10	11	4	6
Tana Masa	Mentawai	Shallow	800	Non-For.	0.83	12	3	8
Tana Bala	Mentawai	Shallow	900	Forest	0.40	16	5	10
Cuyo	Palawan	Deep	(50)	Non-For.	0.16	1	0	1
Bangkalan	Palawan	Deep	(50)	Forest	0.53	1	0	0
Balabac	Palawan	Deep	(300)	Forest	3.26	3	1	2
Culion	Palawan	Deep	320	Forest	2.50	12	3	8
Busuanga	Palawan	Deep	(580)	Forest	0.40	11	1	7
Palawan	Palawan	Deep	14,650	Forest	0.97	21	4	10
Malawali	Palawan	Shallow	(25)	Non-For.	0.08	4	0	1
Balembangan	Palawan	Shallow	(70)	Forest	0.06	7	0	3
Jambangan	Palawan	Shallow	(100)	Non-For.	51.0	2	2	2
Banggi	Palawan	Shallow	440	Forest	0.12	13	3	7
Bongao	Sulu	Deep	(15)	Non-For.	2.00	1	0	0
Sanga-Sanga	Sulu	Deep	(60)	Non-For.	2.00	1	0	0
Simunul	Sulu	Deep	100	Non-For.	2.00	1	0	0
Tawitawi	Sulu	Deep	870	Non-For.	46.00	2	1	1
Sebatik	Sulu	Shallow	452	Non-For.	6.50	1	1	1

Simeulue and Enggano are separated from a potential emigration source (Sumatra) by ocean depths twice the estimated 120m sea level during the last glacial maximum, Simeulue by 420m (Meijaard, 2003), and Enggano by more than 1000m (Natawidjaja, 2003). We omitted Simeulue from the analysis, because suspected that humans introduced all its six terrestrial mammalian species. For instance the Sulawesi *Sus celebensis* was definitely introduced; *Macaca fascicularis* is so closely associated with humans that human-mediated introduction

is a near-certainty (see Discussion); and *Rhizomys sumatrensis* occurs outside of Sumatra in insular SE Asia on only Simeulue, despite being widespread in mainland Asia. We retained Enggano in the sample.

The test-sample consisted of 26 islands, 16 deep-water, and 10 shallow-water. For the three regions of islands, these three values were respectively: Mentawai, 11 islands (6 deep-water, 5 shallow water); Palawan, 10 islands (6 deep, 4 shallow); Sulu, 5 islands (4 deep, 1 shallow).

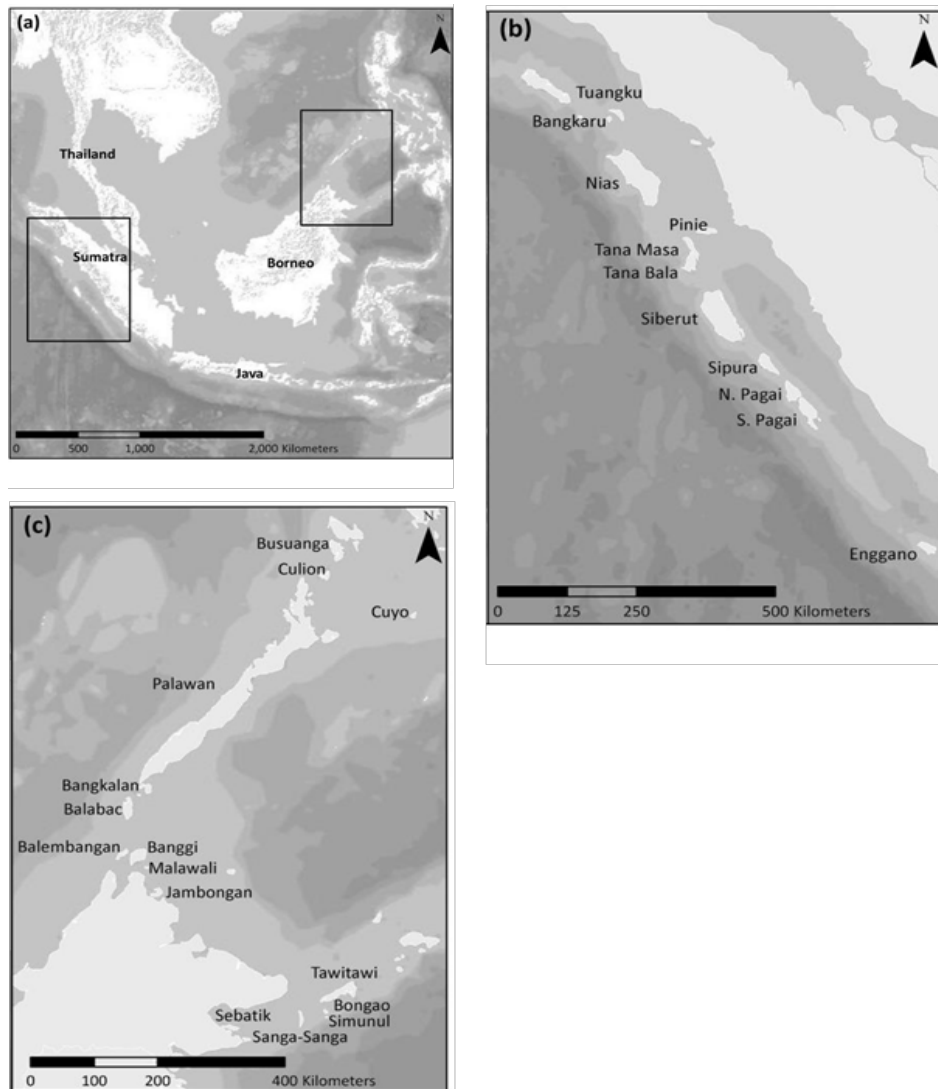


Figure 1. Map of the region analyzed. a) shows regions in map (b), Mentawai (11 islands), and in (c), Palawan (10 islands) and Sulu (5 islands).

MAMMALS ON ISLANDS

We used Meijaard's (2003) detailed analysis and compendium to obtain a list of species on each of the islands (Table 2). *Sus barbatus* has since been seen on Tawitawi (E.M. pers. obsv.). However, the number of species was the unit of analysis, because most genera were represented by only one species on each island (slope of 1.1 for species by genera), and analysis by genera would have produced a very similar result.

Meijaard (2003) excluded 18 species from his listing, including both of the region's macaques, *M. fascicularis* and *M. nemestrina*, because of the likelihood that humans brought them to the islands. Similarly, Heaney (1986) omitted commensals. We excluded Meijaard's

18 species, as well as *Rhizomys sumatrensis* on Simeulue, because we assumed that it is a mainland Asia species and probably introduced.

In total, the sample was 65 species in 42 genera. Per island, median = 7 species, range = 1-21; median = 5 genera, range = 1-18. As expected (Harcourt, 1999), number of taxa, whether genera or species, was strongly related to area of island ($df = 25$, $F > 10.0$, $P < 0.005$).

We accounted for body mass because it could affect both probability of rafting as well as survival post-disembarkation. Heaney (1986) remarked that most of the species on the small south-east Asian islands were rodents. Perhaps a relatively larger number of small-bodied individuals could fit onto a raft, thereby increasing the probability of successful establishment upon arrival (Kappeler, 2000). In addition, smaller animals need smaller rafts, effectively increasing the number of available rafts that could transport small animals. Alternatively, larger bodied animals might survive longer rafting journeys, because

they can better withstand long periods of inclement conditions, such as lack of food and immersion in water (Houle, 1998). And perhaps if the raft breaks up during the voyage, the larger-bodied species are likely to swim longer distances and better survive risky landings at coastal areas with large surfs (Meijaard, 2005). On small islands, small-bodied animals are more likely to achieve sustainable populations than are large ones (Harcourt 1999). The combined result of all these variables suggests that medium sized animal species may enjoy relatively poor rafting success (Meijaard, 2005).

We obtained information on body mass of species

Table 2. Island genera and their characteristics. If more than one habitat, more common given first; body mass is median of congeners.

Genus (# Species)	Water edge		Median	Authority
	Narrow	Broad	Mass (kg)	
<i>Aeromys</i>	No	No	0.28	Robinson & Kloss, 1915
<i>Aonyx</i>	Yes	Yes	4.05	Lesson, 1827
<i>Arctictis</i>	No	No	8.35	Temminck, 1824
<i>Arctogalidia</i>	No	No	2.4	Merriam, 1897
<i>Callosciurus</i>	No	No	0.3	Gray, 1867
<i>Chiropodomys</i> (3)	No	No/Yes	0.03	Peters, 1869
<i>Crocidura</i>	No	Yes	-	Wagler, 1832
<i>Cynocephalus</i>	Yes	Yes	1.1	Boddaert 1768
<i>Exilisciurus</i>	No	No	0.02	Moore, 1958
<i>Hemigalus</i>	No	Yes	2.0	Jourdan, 1837
<i>Herpestes</i>	Yes	Yes	1.4	Illiger, 1811
<i>Hylobates</i>	No	No	5.7	Illiger, 1811
<i>Hylopetes</i> (2)	No	No	0.31	Thomas, 1908
<i>Hystrix</i>	No	Yes	4.6	Linnaeus, 1758
<i>Iomys</i>	No	No	0.09	Thomas, 1908
<i>Lariscus</i> (2)	No	No	0.21	Thomas & Wroughton, 1909
<i>Lenothrix</i>	No	Yes	0.18	Miller, 1903
<i>Leopoldamys</i> (2)	No	No	0.37	Ellerman, 1947
<i>Manis</i>	No	Yes	6.0	Linnaeus, 1758
<i>Maxomys</i> (5)	No	No/Yes	0.15	Sody, 1936
<i>Muntiacus</i>	No	Yes	18.0	Rafinesque, 1815
<i>Mydaus</i>	No	Yes	2.5	F.G. Cuvier, 1821
<i>Nasalis</i>	Yes	Yes	7.0	E. Geoffroyi, 1812
<i>Niviventer</i>	No	Yes	0.08	Marshall, 1976
<i>Nycticebus</i>	No	Yes	2.0	E. Geoffroyi, 1812
<i>Palawanomys</i>	No	No	0.08	Musser & Newcomb, 1983
<i>Petaurista</i>	No	Yes	1.8	Link, 1795
<i>Petinomys</i>	No	No	0.37	Thomas, 1908
<i>Presbytis</i> (2)	No/Yes	No/Yes	6.18	Eschscholtz, 1821
<i>Prionailurus</i>	Yes	Yes	5.0	Severtzov, 1858
<i>Ptilocercus</i>	No	No	0.05	Gray, 1848
<i>Rattus</i> (2)	No	No	0.225	G. Fischer, 1803
<i>Ratufa</i> (2)	No	No	0.5	Gray, 1867
<i>Rhinosciurus</i>	No	No	0.25	Blyth, 1856
<i>Simias</i>	No	Yes	7.9	Miller, 1903
<i>Suncus</i>	No	No	-	Ehrenberg, 1832
<i>Sundamys</i>	No	Yes	0.4	Musser & Newcomb, 1983
<i>Sundasciurus</i> (6)	No/Yes	Yes/No	0.18	Moore, 1958
<i>Sus</i>	Yes	Yes	96	Linnaeus, 1758
<i>Tragulus</i> (2)	Yes	Yes	4.25	Pallas, 1779
<i>Tupaia</i> (7)	No	Yes/No	0.135	Raffles, 1821
<i>Viverra</i>	No	Yes	8	Linnaeus, 1758

from 11 sources (Emmons, 2000; Hayssen, 2008; Lekagul and McNeely, 1977; Meijaard and Groves, 2004; Miller, 1905; Nakagawa et al., 2007; Payne et al., 1985; Sody, 1940; Soligo and Martin, 2006; Yasuma, 1994, 1999). If we could not find the body mass of the species, we used values of the closest relative that we could find of a similar size. This approximation was used to estimate the mass of 32 of the 65 species.

We did not account for phylogeny, but assumed that every rafting was effectively an independent event. Phylogeny is a poor predictor of the co-occurrence of pairs of mammals on islands in insular South-east Asia (Cardillo and Meijaard, 2010).

WATER-EDGE HABITAT OF SPECIES

We divided species into two categories: water-edge and non-water-edge (Table 2). For habitat designations, we used the IUCN Red List of Threatened Species (2012), Lekagul and McNeely (1977), Payne et al. (1985), and Yasuma and Andau (2000). We used a narrow and a broad classification of water-edge. In the narrow classification, we included species with aquatic habitats described as “water-edge”, “occasionally by rivers”, and ‘mangrove’. We excluded species with habitats described as “streams” or “close to water”, assuming that streams and lakes were unlikely sources for ocean-going rafts. If the literature did not highlight “preference for water”, we classified the species as “non-water-edge”. In the broad definition, we classed all species described to have any preference and association with water as “water-edge”, including species with a wide habitat tolerance.

The sample included 11 water-edge species narrowly defined, and 60 non water-edge. Broadly defined, the sample consisted of 32 water-edge species, and 37 non water-edge.

AREA OF ISLANDS

For a water-edge species to survive on an island, we assumed that the island must also have suitable habitat available --- such as water-edge habitat. We did not have information on the vegetation of the islands, but there are plenty of rivers on the islands (Shively, 1997; Whitmore, 1984; Whitten, 1982). As a quantitative measure of potential water-edge habitat, we used area of islands, assuming that larger islands would usually have more coastal perimeter and more rivers, and hence would have a greater area of riverine and water-edge forest. We obtained areas of islands from Harcourt (1999), Heaney (1984), and various online sources,

including maps from Google, from which we calculated areas as length by breadth when we could not find text statements of size.

FOREST ON ISLANDS

Assuming that ocean-going rafts are likely to originate from forests bordering rivers, and therefore carry forest-dependent species, we included whether or not an island harbored forest-dependent species in the multi-factorial analysis. We assumed that, if there were no forest dependent species the resident species were less likely to have arrived by rafting than otherwise. The distribution of forest-dependent species in our data set is as in Fig. 2 in Meijaard (2003).

Another reason to include forest-dependent species in the analysis is because regions of the Sunda Shelf were deforested at the height of the last glacial maximum (Brandon-Jones, 1998, 2001; Heaney, 1991; Meijaard, 2003). However, it seems likely that riverine forest could have remained (Colyn et al., 1991; Dupont and Weinel, 1996), as it does in arid regions nowadays. In the context of probability of successful rafting, the influence of ice-age aridity might be lower than expected. Nevertheless, none of the Sulu islands or their close neighbors have forest-dwelling mammals, perhaps because of recent, near-total clearance of forests on the islands (Stattersfield et al., 1998). Therefore, the Sulu islands should have a significantly different complement of species by comparison to the Mentawai and Palawan island groups.

ANALYSIS

The data were compiled by an assistant who knew of Abegg and Thierry’s (2002) prediction, but not any views we might have had on the probability of rafting as a means of arrival on oceanic islands.

We examined the combined influence of all the hypothesized variables with a binomial logit generalized linear model, with number of water-edge species and total number of species as the response variables, and the category of island (deep-water, shallow-water), area of island, median body mass of species on the island, presence-absence of forest species on the island, and island region as potential determinants.

For a sample of $N = 26$, five potential influences are too many for reliability of the precise resultant values. We used the full model to identify likely and unlikely influences, and then ran the model with only the likely effects to obtain a better idea of their relative strength of influence.

For the multivariate models we provide values for the Akaike Information Coefficient AICc, a measure enabling comparison of how well models performed, i.e. how well the independent variables explain the dependent variable (Burnham and Anderson, 2001). The smallest AICc indicates the best model. AICc, as opposed to AIC, corrects for small samples by penalizing extra parameters. This is important in this case because the number of compared to the sample size.

Table 3a-3d. A) Binomial logit generalized linear model of number water-edge species (NARROW definition) in relation to total number of species as predicted by: deep- or shallow-water islands; median body mass of mammalian fauna on the islands; area of islands; whether islands forested or not, and the island group (Mentawai, Palawan, Sulu). B) Similar to 3A, but results for only significant parameters. C) Similar to 3B, but two outlier islands omitted (one each in Palawan and Sulu groups). D) Similar to 3B, but Palawan group of islands omitted.

A)

Model / Predictors	Estimate	$\sigma_{\bar{x}}$	χ^2	P <	AICc
Whole Model			25.1	0.0004	60.1
Deep / Shallow	1.01	0.29	14.2	0.0003	
Log median body mass	0.71	0.22	12.4	0.0005	
Log area (km ²)	0.20	0.19	1.1	0.3	
Forest / Non-forest	0.35	0.36	1.0	0.3	
Island Group			0.9	0.7	

B)

Model / Predictors	Estimate	$\sigma_{\bar{x}}$	χ^2	P <	AICc
Whole			21.7	0.0001	53.0
Deep / Shallow	0.69	0.22	11.1	0.0009	
Log median body mass	0.64	0.17	17.7	0.0001	

C)

Model / Predictors	Estimate	$\sigma_{\bar{x}}$	χ^2	P <	AICc
Whole			12.9	0.002	51.6
Deep / Shallow	0.62	0.22	8.06	0.005	
Log median body mass	0.57	0.18	10.5	0.002	

D)

Model / Predictors	Estimate	$\sigma_{\bar{x}}$	χ^2	P <	AICc
Whole			13.3	0.002	36.6
Deep / Shallow	0.78	0.27	9.36	0.002	
Log median body mass	0.58	0.22	7.26	0.008	

All statistical tests were performed with JMP 9.0 (SAS Institute Inc., 2011); probabilities are two-tailed; probabilities of 0.1 or more are presented as ‘ns’.

RESULTS

NARROWLY DEFINED WATER-EDGE SPECIES

The complete model, with five potential effect variables, indicated only nature of island (deep- or shallow-water) and median body mass of species on the islands as obvious significant correlates of the number of water-edge species on islands compared to total number of species (Table 3A; Fig. 2). Contrary to the expectation, deep-water islands had fewer water-edge species compared to non-water edge (Fig. 2).

Omitting the three non-significant variables ($P > 0.3$), and reiterating the model with just two variables (a more reasonable number for the sample size) confirms nature of island and average island body mass as statistically significant correlates of the number of water-edge species on islands compared to total number of species, and with a better fit as indicated by the AICc value (Table 3B).

The model had two significant outliers, one Sulu island and one Palawan island, both considered shallow-water islands. If these are omitted, island type and body mass remain as significant predictors, and now with the smallest AICc value (Table 3C)

A reiteration excluding Palawan (e.g. it might not be a true deep-water group of islands) continue to indicate both “type of island” and “body mass” as influential variables, but with island type showing a stronger effect than body mass (Table 3D). Deep-water islands had fewer water-edge species in relation to total number than did shallow-water islands. Island group was not a significant influence ($\chi^2 = 0.1$).

Predictions went both ways in relation to the likely body size of rafting animals, and therefore also to the size of animals on deep-water compared to shallow-water islands. Our results indicated that although narrowly defined water-edge genera were perhaps larger than non-water-edge ($z = 1.7, P < 0.09, N = 10$,

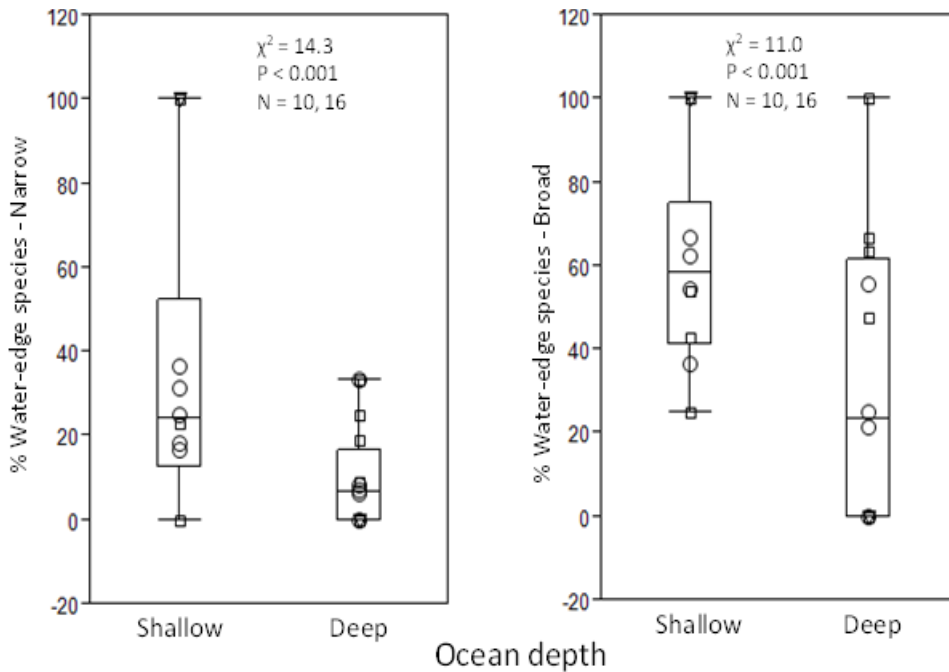


Figure 2. Shallow (N=10) vs Deep (N = 16) islands compared for percentage of “Narrowly” and “Broadly” defined Water-edge species. Circles - Mentawai; triangle - Sulu; square - Palawan. Median, central 50% range and total range shown. Statistics from full model.

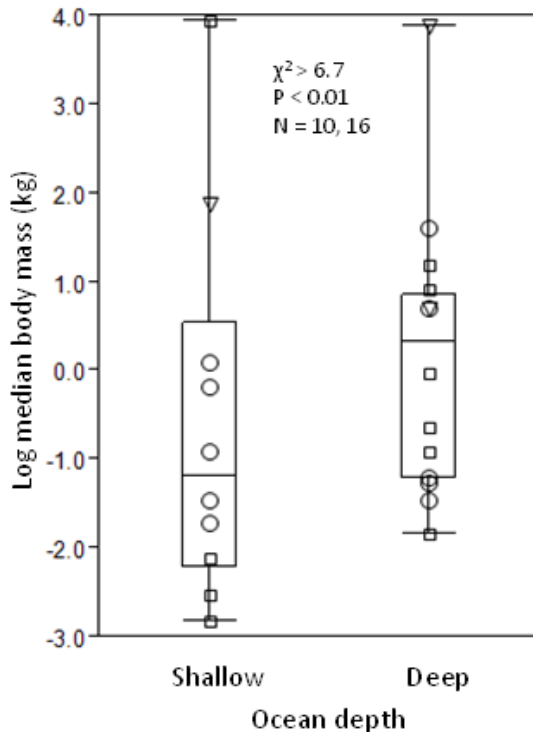


Figure 3. Shallow and Deep islands compared for median body size (kg) of species. Circles - Mentawai; triangle - Sulu; square - Palawan. Median, central 50% range and total range shown. Statistics from full model, for Narrow and Broad definitions of water-edge species.

17, Wilcoxon/Kruskal-Wallis Rank Sums), sample species on deep-water islands were in average larger than those on shallow-water islands (Fig. 3). Water-edge taxa (larger bodied than non-water-edge species) were found on shallow-water islands, whereas large-bodied taxa (water-edge on average) were on found on deep-water islands.

BROADLY DEFINED WATER-EDGE AND NON-WATER EDGE SPECIES

Here, the number of the two types is more similar than when narrowly defined, and island type (deep- vs. shallow-water) and body mass were significant correlates (Table 4A). Omitting the non-

significant correlates, and reiterating the model reveals a better fit (Table 4B). Contrary to our expectations, water-edge species were more common on shallow-water islands than on deep-water islands, even though water-edge genera were larger than non water-edge ($z = 2.4, P < 0.02, N = 17, 10$, Wilcoxon/Kruskal-Wallis Rank Sums), and large-bodied taxa were more common on the deep-water islands (Fig. 3).

With the model’s one significant outlier removed from the sample, sea depth and body mass remained significant predictors of presence on deep-water compared to shallow water islands (Table 4C). A preponderance of heavier taxa were on the deep-water islands.

Even though “island group” was not a significant variable, we made another iteration of the model without Palawan, because the Palawan group of islands might have been separated from a source for a shorter time than the Mentawai and Sulu groups of islands. Island type (deep- vs. shallow-water) and body mass remained significant variables (Table 4D): water-edge species were more common in relation to total number of species on shallow-water islands than on deep-water islands, and larger species were most common on deep-water islands.

Table 4a-4d. A) Binomial logit generalized linear model of number water-edge species (BROAD definition) in relation to total number of species as predicted by five variables: deep- or shallow-water islands; median body mass of mammalian fauna on the islands; area of islands; whether islands forested or not, and the island group (Mentawai, Palawan, Sulu). B) Similar to 4A, but results for only significant parameters. C) Similar to 4B, but one outlier island omitted (in Palawan group). Similar to 4B, but Palawan group of islands omitted.

A)

Model / Predictors	Estimate	$\sigma_{\bar{x}}$	χ^2	P <	AICc
Whole Model			20.9	0.002	80.9
Deep / Shallow	0.64	0.20	11.42	0.001	
Log median body mass	0.49	0.19	7.93	0.005	
Log area (km ²)	0.03	0.14	0.03	0.9	
Forest / Non-forest	0.003	0.27	0.00	1.0	
Island Group			5.41	0.07	

B)

Model / Predictors	Estimate	$\sigma_{\bar{x}}$	χ^2	P <	AICc
Whole Model			15.72	0.0005	77.6
Deep / Shallow	0.53	0.16	10.78	= 0.001	
Log median body mass	0.42	0.14	10.80	= 0.001	

C)

Model / Predictors	Estimate	$\sigma_{\bar{x}}$	χ^2	P <	AICc
Whole Model			17.03	0.0003	74.8
Deep / Shallow	0.55	0.17	11.70	0.001	
Log median body mass	0.44	0.14	11.80	0.001	

D)

Model / Predictors	Estimate	$\sigma_{\bar{x}}$	χ^2	P <	AICc
Whole Model			18.67	0.0001	45.3
Deep / Shallow	0.76	0.21	15.36	0.0001	
Log median body mass	0.45	0.18	6.63	= 0.01	

DISCUSSION

Abegg-Thierry (2002) predicted that, if mammals rafted to islands in the Sunda region, there should be a greater proportion of water-edge species on oceanic islands than on continental islands. The prediction was not supported by our hypothesis. Instead, the analyses indicated the opposite i.e. a smaller number of water-edge species by comparison to total number of species

existed on deep-water islands than on shallow-water islands. The adequacy of the prediction's test depends on deep water islands being disconnected from the source. Excluding the Palawan group of islands from the analysis changes the results for taxa classified as water-edge or not under the broad classification (body size not significant), which suggests that the Palawan group might be different and perhaps more connected to other sources than the other two island groups.

Our study is, of course, only a preliminary test of the rafting hypothesis, given that deep-water continental islands are not as distantly isolated as are oceanic islands. However, the rafting hypothesis for the distribution of mammals in the Sunda region and elsewhere has rarely been rigorously tested either quantitatively or with novel predictions. Therefore, we suggest that our rejection of the Abegg-Thierry prediction should be considered.

In addition to habitat, body size seemed to affect presence on deep-water compared to shallow-water islands in the multi-variate analyses. Deep-water islands had larger-bodied taxa on average than did shallow-water islands.

These are contradictory results. The taxa on deep-water islands are larger than those on nearby shallow-water islands. Water-edge taxa are larger than are non-water-edge. Yet water-edge taxa are less likely on deep-water islands than are non-water-edge taxa. Among the variety of possibilities by which body size could influence mammals reaching or surviving on islands, this anomaly could be explained by the larger bodied animals' better swimming endurance. This might be the case when considering that *Sus*, by far the largest mammal recorded on the islands, is a strong swimmer and recorded to have swum more

than 40km into the ocean (Caldecott et al., 1993). Other factors than those tested might also influence passage to islands.

Over a century ago Wallace (1876, Ch. 13) suggested that humans might have carried Asian species east of what now known as the Wallace Line, a division between the Oriental and the Australian biogeographic regions. Acknowledging the possibility of human agency, both Meijaard (2003) and Heaney (1986) excluded several

species from their lists of island species. For instance, Meijaard excluded the long-tailed, *Macaca fascicularis*, and pig-tailed macaques, *Macaca nemestrina*. People in the region use both species to collect fruit from trees (Sponsel et al., 2002), and transported the long-tailed macaque in colonial times to the eastern-most island in its range, Ngeaur in Palau, east of the Philippines, and hence east of the Wallace Line (Wheatley et al., 2002). If primates constituted part of the human diet, as they do in the Mentawai islands (Fuentes, 2002), it would be common practice in the humid tropics to transport them as “live food”, however, with the possible risk of losing some through escapes. These “escapees” have probably founded new island populations. Meijaard (2003) also excluded the Asian palm civet, *Paradoxurus hermaphroditus*, because the local people often keep it as a pet, as Wallace (1876, Ch. 13) reported.

Several non-flying species on islands are endemics, which suggests that they have been isolated for several thousand years. Nevertheless, that duration does not preclude transport by humans. Wild animals have been traded across hundreds of kilometers for centuries (Somerville et al., 2010), and identified domestication of animals began around 10,000ya (Driscoll et al., 2009). The keeping of wild animals could be a far more ancient practice, bearing in mind that it occurs in traditionally-living societies throughout much of the world (Fuentes and Wolfe, 2002).

Accidental transport of small-bodied species is possible too, even if they were not the commensals that Meijaard (2003) and Heaney (1986) eliminated from their counts. It is easy to imagine some wild mice sought refuge in thatching material and were carried to an island. Such accidental transport could easily explain how the <50g skink, *Lipinia noctua*, dispersed so quickly across much of the Pacific (Austin, 1999). A similar explanation could apply to the 80g Polynesian rat, *Rattus exulans*, although it constituted part of Polynesians’ stable diet (Matisoo-Smith & Robins, 2004) and could have been transported deliberately.

Humans reached Australia at least 45,000 years ago (Gillespie, 2008; Hudjashov et al., 2007; O’Connell and Allen, 1998; Oppenheimer, 2003; Pope and Terrell, 2008). At that time, Australia was separated by 100km of ocean, measured from any part of South-east Asia from which humans could have arrived. In other words, humans have had sea-going craft for at least 45,000 years - assuming that the Australian continent was not populated by humans swept in by tsunamis (Morwood and Jungers, 2009; Ruxton and Wilkinson, 2012).

Fooden (1995) suggested that the various morphological differences between island forms of the long-tailed macaque were sufficiently significant to exclude the possibility of transport by humans. However, if the first humans in the region brought macaques with them, and if a macaque generation time is 10 years, it follows that a time-period of 45,000 years could result in approximately 4,500 generations of macaques. Under significantly different habitat circumstances this is ample evolutionary time to produce forms specific to each island. Most of the other mammals in the region are smaller bodied than are primates, and have shorter life cycles than primates (Harvey et al., 1987; Read and Harvey, 1989). It is reasonable to expect that their generation time is even less than 10 years. McNab (2002) reviews studies that suggest speciation of an oceanic island duck *Chenonetta* in less than 10,000 years, as well as speciation of a 2kg marsupial, *Spilocuscus*, within 2,000-13,000 years.

Transport by humans may indeed explain the apparent discrepancy between the water edge species domination on shallow-water islands and larger-bodied species on deep water islands. But what if water-edge species are larger than non-water-edge species on average? What if humans were more likely to deliberately transport large-bodied live animals to deep-water islands than shallow-water before domestication? This could be due to the former were less easily reached and so required resident food supply? That is pure speculation, of course, but no more so than natural rafting in the absence of any other evidence than the presence of a terrestrial animal on an oceanic island.

Transportation by humans cannot explain the presence of island endemics that arose before humans (or boating hominids) arrived. Examples include the Mentawai island macaques (Abegg and Thierry, 2002; Ziegler et al., 2007). All older origins are irrelevant to the rafting theory, because sea-levels at origin of the Mentawai 2.5mya were lower than in the Pleistocene (Ziegler et al., 2007).

Humans are not the only non-rafting agents of cross-sea transport. “Owls transport mice alive?” wrote Darwin on page 82 of his Notebook B on transmutation of species (Darwin, 1837-1838). Male merlins, *Falco columbarius*, caching food during the breeding season will sometimes leave live lizards in their cache (Jim Tigan, West Coast Falconry Academy, California, pers. comm.). Is transport across water of live animals by raptors less likely than transport by rafts? Even some of the larger mammals could have been so transported,

given that the Philippine eagle, *Pithecophaga jefferyi*, can carry prey weighing more than 10 kg (Birdlife International, 2001), which is larger than all but the bearded pig, *Sus barbatus*, of the species in our dataset.

Our test of the Abegg-Thierry (2002) hypothesis is preliminary. Not only are the deep-water islands in our sample not “true” oceanic islands, but several are very close to the major source islands. The next step should be a comparison of true oceanic islands with shallow-water islands that might have been populated from the same source, or alternatively a comparison of oceanic islands with the adjacent mainland from where the island inhabitants are assumed to have originated from. A good sample might be the mammalian community of the Andaman and Nicobar islands off Thailand in contrast to the community of the shallow-water islands of the Mergui Archipelago along Thailand’s coast, or of the past community of the Thai isthmus. Hypotheses of human transport could be tested by relating dates of arrival of humans as judged by archeological evidence to molecular dates of origins of island forms.

Although our comparison offers only a preliminary test of the Abegg-Thierry prediction, the test is a logical extension of their prediction, and has the benefit of being one of the few explicit tests of the rafting hypothesis for the distribution of mammals in insular South-east Asia.

In conclusion, we do not dismiss the fact that terrestrial mammals could have dispersed by rafts across the South-east Asian islands. We believe, however, to explain the distribution of mammals in the region, rafting is often used as a default explanation void of systematic testing, alternative predictions and in need of more analyses similar to the one we have presented in this paper.

ACKNOWLEDGEMENTS

We thank Margot Wood for collating the data, Mark Grote for statistical advice, Rebecca Runting for her help in producing the maps of Figure 1, and Christophe Abegg, Markus Eichhorn, Andy J. Marshall, Kelly Stewart, Bernard Thierry, and an anonymous reviewer for very helpful commentary that markedly improved the final result.

REFERENCES

Abegg, C. and B. Thierry (2002). Macaque evolution and dispersal in insular south-east Asia. *Biological Journal of the Linnean Society* **75**: 555-576.

Austin, C.C. (1999). Lizards took express train to Polynesia. *Nature* **397**: 113-114.

Birdlife International. (2001). Threatened Birds of Asia: the BirdLife International Red Data Book. Birdlife International, Cambridge.

Brandon-Jones, D. (1996). The Asian Colobinae (Mammalia: Cercopithecidae) as indicators of Quaternary climatic change. *Biological Journal of the Linnean Society* **59**: 327-350.

Brandon-Jones, D. (1998). Pre-glacial Bornean primate impoverishment and Wallace’s line. In *Biogeography and Geological Evolution* (eds R. Hall & D. Holloway), pp. 393-404. Backhuys Publishers, Leiden, The Netherlands.

Brandon-Jones, D. (2001). Borneo as a biogeographic barrier to Asian-Australian migration. In *Faunal and Floral Migrations and Evolution in SE Asia-Australasia* (eds I. M. Metcalfe, J. M. B. Smith, I. Morwood & I. Davidson), pp. 365-372. A. A. Balkema Publ., Lisse.

Burnham, K. P. and D.R. Anderson (2001). Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28**: 111-119.

Caldecott, J.O., Blouch, R.A. and A.A. MacDonald (1993). The bearded pig (*Sus barbatus*). In: *Pigs, Peccaries, and Hippos. Status Survey and Conservation Action Plan.* (ed W. L. R. Oliver), pp. 136 - 145. IUCN/SSC Pigs and Peccaries Specialist group and IUCN/SSC Hippos Specialist Group, Gland, Switzerland.

Calsbeek, R. and T.B. Smith (2003). Ocean currents mediate evolution in island lizards. *Nature* **426**: 552-555.

Cardillo, M. and E. Meijaard (2010). Phylogeny and co-occurrence of mammal species on Southeast Asian islands. *Global Ecology and Biogeography* **19**: 465-174.

Colyn, M., Gautier-Hion, A., and W. Verheyen (1991). A re-appraisal of palaeoenvironmental history in Central Africa: evidence for a major fluvial refuge in the Zaire Basin. *Journal of Biogeography* **18**: 403-407.

- Crisp, M.D., Trewick, S.A., and L.G. Cook (2011). Hypothesis testing in biogeography. *Trends in Ecology and Evolution* **26**: 66-72.
- Darwin, C.R. (1837-1838). Notebook B: [Transmutation of species (1837-1838)]. CUL-DAR121., from <http://darwin-online.org.uk/>.
- Driscoll, C. A., Macdonald, D. W., and S.J. O'Brien (2009). From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences*, **Suppl. 1 106**: 9971-9978.
- Dupont, L.M. and M. Weinelt (1996). Vegetation history of the savanna corridor between the Guinean and the Congolian rain forest during the last 150,000 years. *Vegetation History and Archaeobotany* **5**: 273-292.
- Emmons, L.H. (2000). Tupai. A Field Study of Bornean Treeshrews. University of California Press, Berkeley, California.
- Fooden, J. (1995). Systematic review of southeast Asian longtail macaques, *Macaca fascicularis* (Raffles, [1821]). *Fieldiana Zoology* **81**: 1-206.
- Fuentes, A. (2002). Monkeys, humans and politics on the Mentawai Islands: no simple solutions in a complex world. In *Primates Face to Face. The Conservation Implications of Human-Nonhuman Primate Interconnections* (eds A. Fuentes & L. D. Wolfe), pp. 187-207. Cambridge University Press, Cambridge.
- Fuentes, A. and Wolfe, L.D. (eds.) (2002). *Primates Face to Face. The Conservation Implications of Human-Nonhuman Primate Interconnections*. Cambridge University Press, Cambridge.
- Gillespie, R. (2008). Updating Martin's global extinction model. *Quaternary Science Reviews* **27**: 2522-2529.
- Gillespie, R.G., Baldwin, B.G., Waters, J.M., Fraser, C. I., Raisa, N., and G.K. Roderick (2012). Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology and Evolution* **27**: 47-56.
- Harcourt, A.H. (1999). Biogeographic relationships of primates on south-east Asian islands. *Global Ecology and Biogeography* **8**: 55-61.
- Harvey, P.H., Martin, R.D., and T.H. Clutton-Brock (1987). Life histories in comparative perspective. In *Primate Societies* (eds B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 181-196. University of Chicago Press, Chicago.
- Hayssen, V. (2008). Patterns of body and tail length and body mass in Sciuridae. *Journal of Mammalogy* **89**: 852-873.
- Heaney, L.R. (1984). Mammalian species richness on islands on the Sunda Shelf, southeast Asia. *Oecologia* **61**: 11-17.
- Heaney, L.R. (1986). Biogeography of mammals in southeast Asia: estimates of rates of colonization, extinction and speciation. *Biological Journal of the Linnean Society* **28**: 127-166.
- Heaney, L.R. (1991). A synopsis of climatic and vegetational change in Southeast Asia. *Climatic Change* **19**: 53-61.
- Houle, A. (1998). Floating islands: A mode of long-distance dispersal for small and medium-sized terrestrial vertebrates. *Diversity and Distributions* **4**: 201-216.
- Hudjashov, G., Kivisild, T., Underhill, P.A., Endicott, P., Sanchez, J.J., Lin, A.A., Shen, P., Oefner, P., Renfrew, C., Villems, R., and P. Forster (2007). Revealing the prehistoric settlement of Australia by Y chromosome and mtDNA analysis. *Proceedings of the National Academy of Sciences* **104**: 8726-8730.
- IUCN. (2012). 2012.2 IUCN Red List of Threatened species. IUCN. The World Conservation Union: <http://www.iucnredlist.org/> [accessed 2012].
- Kappeler, P.M. (2000). Lemur origins: rafting by groups of hibernators. *Folia Primatologica* **71**: 422-425.
- King, W. (1962). The occurrence of rafts for dispersal of land animals into the West Indies. *Quarterly Journal of the Florida Academy of Sciences* **25**: 45-52.
- Krause, D.W., Hartman, J.H. and N.A. Wells (1997). Late Cretaceous vertebrates from Madagascar: implications for biotic change in deep time. In *Natural Change and Human Impact in Madagascar* (eds S. M. Goodman and B. D. Patterson), pp. 3-43. Smithsonian Institution Press, Washington D.C.

- Lekagul, B. and J.A McNeely (1977). Mammals of Thailand. Kurusapha Ladproa Press, Bangkok.
- Lyell, C. (1832). Principles of Geology, Vol. 2. John Murray, London.
- Matisoo-Smith, E. and J.H. Robins (2004). Origins and dispersals of Pacific peoples: Evidence from mtDNA phylogenies of the Pacific rat. *Proceedings of the National Academy of Sciences* **101**: 9167-9172.
- Matthew, W.D. (1915). Climate and evolution. *Annals of the New York Academy of Sciences* **24**: 171-318.
- McNab, B.K. (2002). Minimizing energy expenditure facilitates vertebrate persistence on oceanic islands. *Ecology Letters* **5**: 693-704.
- Meijaard, E. (2003). Mammals of south-east Asian islands and their Late Pleistocene environments. *Journal of Biogeography* **30**: 1245-1257.
- Meijaard, E. (2005). Floating islands and frigatebirds on Pulau Derawan. *Forest Science News* **1**: 2-4.
- Meijaard, E. and C.P. Groves (2004). A taxonomic revision of the *Tragulus* mouse-deer (*Artiodactyla*). *Zoological Journal of the Linnean Society* **140**: 63-102.
- Miller, G.S. (1905). The mammals from Enggano Island, West Sumatra. *Proceedings of the United States National Museum* **30**: 819-825.
- Morwood, M. J. and W.L. Jungers (2009). Conclusions: implications of the Liang Bua excavations for hominin evolution and biogeography. *Journal of Human Evolution* **57**: 640-648.
- Nakagawa, M., Miguchi, H., Sato, K., Sakai, S., and T. Nakashizuka (2007). Population dynamics of arboreal and terrestrial small mammals in tropical rainforest, Sarawak, Malaysia. *Raffles Bulletin of Zoology* **55**: 389-395.
- Natawidjaja, D.H. 2003. Neotectonics of the Sumatran fault and paleogeodesy of the Sumatran subduction zone. Ph.D. thesis. California Insititute of Technology, Pasadena.
- O'Connell, J.F. and J. Allen (1998). When did humans first arrive in Greater Australia and why is it important to know? *Evolutionary Anthropology* **6**: 132-146.
- Oppenheimer, S. (2003). Out of Eden. The Peopling of the World. Constable, London.
- Payne, J., Francis, C.M., and K. Phillipps (1985). A Field Guide to the Mammals of Borneo. The Sabah Society, Kota Kinabalu, Malaysia.
- Pope, K.O. and J.E. Terrell (2008). Environmental setting of human migrations in the circum-Pacific region. *Journal of Biogeography* **35**: 1-21.
- Read, A.F. and P.H. Harvey (1989). Life history differences among the eutherian radiations. *Journal of Zoology* **219**: 329-353.
- Rowe, N. (1996). The Pictorial Guide to the Living Primates. Pogonias Press, East Hampton, New York.
- Ruxton, G. D. and Wilkinson, D. M. (2012). Population trajectories for accidental versus planned colonisation of islands. *Journal of Human Evolution* **63**: 507-511.
- SAS Institute Inc. (2011). JMP 9.0. SAS Institute Inc., Cary, North Carolina.
- Schüle, W. (1993). Mammals, vegetation and the initial human settlement of the Mediterranean islands: a palaeoecological approach. *Journal of Biogeography* **20**: 399-412.
- Shively, G.E. (1997). Poverty, technology, and wildlife hunting in Palawan. *Environmental Conservation* **24**: 57-63.
- Sody, H.J.V. (1940). On the mammals of Enggano. *Treubia* **17**: 391-401.
- Soligo, C. and R.D. Martin (2006). Adaptive origins of primates revisited. *Journal of Human Evolution* **50**: 414-430.
- Somerville, A.D., Nelson, B.A., and K.J. Knudson (2010). Isotopic investigation of pre-Hispanic macaw breeding in Northwest Mexico. *Journal of Anthropological Archaeology* **29**: 125-135.

- Sponsel, L.E., Ruttanadakul, N., and P. Natadecha-Sponsel (2002). Monkey business? The conservation implications of macaque ethnoprimateology in southern Thailand. In *Primates Face to Face. The Conservation Implications of Human-Nonhuman Primate Interconnections* (eds A. Fuentes and L. D. Wolfe), pp. 288-309. Cambridge University Press, Cambridge.
- Stattersfield, A. J., Corsby, M. J., Long, A. J., and D.C. Wege (1998). *Global Directory of Endemic Bird Areas*. Cambridge: Birdlife International.
- Voris, H.K. (2000). Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* **27**: 1153-1167.
- Wallace, A.R. (1876). *The Geographical Distribution of Animals, Vol. I*. Harper and Bros, New York.
- Wheatley, B.P., Stephenson, R.A., Kurashina, H., and K.G. Marsh-Kautz (2002). A cultural primatological study of *Macaca fascicularis* on Ngeaur Island, Republic of Palau. In *Primates Face to Face. The Conservation Implications of Human-Nonhuman Primate Interconnections* (eds A. Fuentes and L. D. Wolfe), pp. 240-253. Cambridge University Press, Cambridge.
- Whitmore, T.C. (1984). A vegetation map of Malesia at scale 1:5 million. *Journal of Biogeography* **11**: 461-471.
- Whitten, T. (1982). *The Gibbons of Siberut*. J.M. Dent, London.
- Yasuma, S. (1994). *An invitation to the mammals of East Kalimantan*. Samarinda, Indonesia, : PUSREHUT and JICA.
- Yasuma, S. (1999). *Mammals of Sabah, Field Guide and Identification*. Japan International Cooperation Agency and Sabah Wildlife Department, Kota Kinabalu, Malaysia.
- Yasuma, S. and Andau, M. (2000). *Mammals of Sabah. Part-2. Habitat and ecology*. Kota Kinabalu and Kuala Lumpur, Malaysia: Japan International Cooperation Agency and Sabah Wildlife Department.
- Ziegler, T., Abegg, C., Meijaard, E., Perwitasari-Farajallah, D., Walter, L., Hodges, J.K. and C. Roos (2007). Molecular phylogeny and evolutionary history of Southeast Asian macaques forming the *M. silenus* group. *Molecular Phylogenetics and Evolution* **42**: 807-816.