

Genetic assessment of Borneo elephants: origin and conservation implications

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Abstract The origin of elephants on Borneo has been controversial, with competing suggestions that they were introduced by humans, or indigenous to the island. Genetic analysis of Borneo elephants and comparison to other Asian elephant populations across their range has shown that they are genetically unique and divergent from all other populations (Fernando *et al.*, 2003). The genetic uniqueness of Borneo elephants suggests that elephants colonized Borneo in the Pleistocene and that they have had an independent evolutionary trajectory since then. Here we discuss the possible factors limiting the distribution of the species in Borneo, and the conservation implications of their newly discovered genetic status.

Introduction

The origin of elephants (*Elephas maximus*) in Borneo is controversial. While some authors have suggested elephants were not indigenous to Borneo but introduced by humans (Shoshani & Eisenberg, 1982), others (Deraniyagala, 1950; 1955) have postulated a natural origin. With a land area of approximately 745,000 km², Borneo is the third largest island in the world. Sabah, a state in the federation of Malaysia, occupies the north-eastern tip of Borneo, while contiguous and to the south

is the Indonesian province of East Kalimantan (Fig. 1). Elephants are restricted to north-east Borneo (eastern Sabah and the northern part of East Kalimantan) within an area approximately 5% of the island. The north-east, south-west orientation of the longitudinal axis of Borneo, makes this area the farthest part of the island from the closest free ranging elephant populations outside of Borneo, in Sumatra and Peninsular Malaysia (Fig. 1).

The earliest detailed description of Borneo by a visitor to the island is that of Antonio Pigafetta, the Italian chronicler of Magellan's Spanish fleet, which sailed into Brunei on the north-west coast of Borneo, in 1521. Pigafetta's group was taken to visit the sultan of Brunei on two tame elephants (Harrisson & Harrisson, 1971). There have been no subsequent reports of elephants in Brunei or western Borneo. The next published record of elephants in Borneo is that of Dalrymple, who reported in 1767 that "the eastern part of Unsang abounds with wild elephants". Tanjung Unsang, presumably the Unsang mentioned by Dalrymple, is near the eastern-most tip of Sabah. In 1811 Hunt reported that wild elephants occurred at Kenibatangan (= Kinabatangan), Unsang and Sabahan, and that ivory was traded from Kinabatangan. The reports of Dalrymple (1767) and Hunt (1811) suggest the presence of a large free ranging elephant population in northeastern Borneo in mid 18th century. Ivory from Borneo is reported to have been imported into China in the middle ages (Laufer, 1925). The massive expeditions of Admiral Cheng Ho, which sailed from southern China to South-east Asia in 1405, may have visited the southern Philippines and possibly Kinabatangan (Harrisson & Harrisson, 1971) but did not leave a written record concerning elephants or ivory.

Were elephants introduced?

There are two factors that suggest elephants may not be indigenous to Borneo. Firstly, it is the common belief, of uncertain but long-standing origin, among people who live or work within the Borneo elephant range (J. Payne pers. obs.). Secondly, it seemingly offers a parsimonious explanation for the limited and unusual distribution of the species in Borneo.

Many authors have commented on the possible

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anthropogenic origin of elephants in Borneo. Among them, Silva (1968) mentions "...the popular presumption that they are the progeny of elephants given to the Sulu Sultan by the East India Company in 1750..." but provides no reference. Harrisson & Harrisson (1971) summarize: [among] "...the many and conflicting statements we have heard on the subject at various places in Sabah... [during the 1950s-1960s]... a long time ago the Sultan of Sulu, who had previously received some elephants as a gift, decided to move them from his small island and place them on the Borneo coast. The purpose of this act was that these elephants were his representatives in a territory which he claimed to control..." These animals presumably originated from India, as the operations of the East India Trading Company were mostly in India, and it was a center of elephant commerce. Medway (1977) quotes earlier authors (Müller, 1839-1840; Everett, 1893; Banks, 1931) who made similar but unsubstantiated assumptions. Hunt (1811) reported the presence of elephants on Sulu island (southern Philippines), where he spent six months, and he states that these elephants were imported from Banjarmasin (in Borneo) by Banjar settlers. There is also evidence that a flourishing regional trade in elephants existed, with large numbers caught and exported from Sumatra in and before the 16th century (Marsden, 1811) and from the west coast of Peninsular Malaysia in and before the 18th century (Andaya, 1977).

A 'natural' origin?

In antiquity, Borneo formed part of a single land mass referred to as Sundaland, which also included peninsular Malaysia and the islands of Java, Sumatra and many smaller islands of the western Indo-Malayan archipelago (Holloway & Hall, 1998). Sea level fluctuation during Pleistocene glaciations periodically disconnected and reconnected the Sunda islands through submersion and emergence of low lying parts of the Sunda shelf (Holloway & Hall, 1998; MacKinnon *et al.*, 1996). A savannah corridor which allowed faunal and floral migrations from the mainland to the Sunda islands, is thought to have existed between southeast Asia and Borneo during the highly seasonal climates of the late Tertiary and mid-Pleistocene (MacKinnon *et al.*, 1996). Therefore, it is possible that Borneo was colonized by elephants, through land connections with the mainland and other Sunda islands, and that the current population is descended from those early founders.

There have been a few subfossil or fossil remains in Borneo indicative of a pre-historic elephant population. Ribs and a femur of an animal assumed to be *E. maximus*, now in Lambung Mangkurat Museum, Banjarbaru, South Kalimantan. They have not been dated but appear to be relatively recent and not fossilized. A portion of a right upper first molar of *E. maximus*, said to have come from a cave in Belait District, Brunei is believed "more likely to be Pleistocene than Holocene" (Hooijer, 1972). Other fossils found in Borneo and reported to be

of "elephants" are either extinct genera (*Stegolophodon* and *Palaeoloxodon* teeth of uncertain origin) or tapir (Cranbrook, 2000; Cranbrook *et al.*, 2000). The paucity of *E. maximus* fossils in Borneo is in contrast to the presence of Holocene (< 11,000 years) fossils (at Niah, Sarawak and Madai, Sabah) of the Malayan tapir (*Tapirus indicus*) and Javan rhinoceros (*Rhinoceros sondaicus*), both of which are now extinct in Borneo. Holocene *E. maximus* teeth have been found in caves in Sumatra (Medway, 1977) and late Pleistocene and Holocene fossils of *E. maximus* in Java (Van den Bergh *et al.*, 1996), suggesting a late Pleistocene colonization of the Greater Sunda islands by *E. maximus*. However, *E. maximus* fossil and subfossil material is rare over much of its range (Maglio, 1973) and the scarcity of such remains in Borneo may be due to chance (Medway, 1977) or may reflect the paucity of zoo-archaeological studies.

Elephant distribution and numbers in Borneo

The earliest records from which distribution data can be gleaned, date back to the late 19th century (St. John, 1863; Pryer, 1881; Jentink, 1884; Anon, 1886; miscellaneous reports in the British North Borneo Herald during the late 19th to early 20th century). The elephant distribution at that time appears to have been similar to that in 1980 with the exception of the Sandakan Peninsula and extreme south-east Sabah, where plantations excluded elephants during 1955-1980 (Davies & Payne, 1982). Thus, apart from the reduction in species range over the past 20 years due to forest loss in Sabah, the distribution of elephants in Borneo appears to have been rather stable as far back as their distribution can be inferred from historical records.

In 1949, the Conservator of Forests, British North Borneo (H. Keith, quoted in de Silva, 1968) estimated the Sabah elephant population size at 2000 animals. His successor, G. S. Brown commented that Keith considered "the actual number may be only half as much or perhaps twice as many" (Deraniyagala, 1955). Contemporary estimates by foresters and planters ranged from 500 to 5000 (Banks, 1949). Davies & Payne (1982) provided an estimate of between 500 (based on known groups in accessible areas) and 2000 (based on known species distribution and likely average population density). Currently, it is estimated that between 1100 - 1600 wild elephants live in Sabah (Asian Rhino & Elephant Action Strategy (AREAS) project, unpublished data), while a much smaller number occur in the northern part of East Kalimantan, contiguous with the Sabah population.

Possible source populations

Transporting elephants by sailing ship across oceans a few hundred years ago would necessitate their boarding, disembarkation and restraint on board, hence a well trained animal. It would also require the transport of large quantities of food and fresh water. Given the logistic difficulties, geographic proximity makes Sumatra

or Peninsular Malaysia the most likely source of animals introduced to Borneo. However, as commonly believed, if they did originate from animals gifted to the Sultan of Sulu by the East India Company, the source population could also be India. Comparison of the Borneo population to the three putative source populations Sumatra, Peninsular Malaysia and India and in addition, to those of Laos, Cambodia, Thailand, Bangladesh, Bhutan, and Sri Lanka in both mitochondrial and nuclear DNA analysis and additionally Vietnam in the mitochondrial analysis, found it to be unique and not closely related to any of these populations (Fernando *et al.*, 2003). Thus, both mitochondrial and nuclear data suggest elephants are indigenous to Borneo and not introduced by humans (Fernando *et al.*, 2003). In the case of mitochondrial DNA, the evidence supporting a 'natural' origin of Borneo elephants was three fold; the uniqueness of the Borneo haplotype, the degree of divergence from other Asian elephant haplotypes, and congruence with the patterns of distribution and relatedness of other Sunda haplotypes.

Although the mitochondrial genome in general accumulates point mutations much more rapidly than the nuclear genome, and the d-loop of the mitochondrial genome faster than other mitochondrial regions, the rate of evolution of the Asian elephant d-loop is only about 3.5% per million years (Fleisher *et al.*, 2001). The earliest time elephants could have been introduced to Borneo by humans is only a few hundred years ago, which would approximate zero in a time scale relevant to mitochondrial evolution. Thus, if elephants were introduced to Borneo, a haplotype identical to that found in Borneo would be found in the source population. The study by Fernando *et al.*, (2003) sampled almost all extant Asian elephant populations across their range but did not observe the Borneo haplotype anywhere else. Therefore, Borneo elephants could not have originated from any extant population.

Given that the Borneo haplotype was unique, the arguments for an anthropogenic origin of the Borneo population are, 1) Introduction from a source population that has since become extinct or 2) Fixation in Borneo of a very rare haplotype not represented in the range-wide sample. Although the current Asian elephant range is highly fragmented, the extant populations are spread out over a larger part of the historic range. The representative sample analyzed from extant populations in Fernando *et al.*, (2003) is likely to have captured a high proportion of the mitochondrial diversity of the species. The capture probability of a haplotype is directly proportional to its frequency in the population and the size of the sample collected. Therefore, common, rather than rare haplotypes have a greater probability of being 'captured', be it capture of individuals for introduction a few hundred years ago, or collection of samples for study today. If elephants were introduced to Borneo, the founder population would have been only a few individuals and the haplotype/s represented would likely have been the common haplotypes in the

source population. Given the study sample in Fernando *et al.*, (2003), it is unlikely that either an extinct source population in which the Borneo haplotype was common, or the introduction of a rare haplotype not sampled in other populations, provide sufficient explanation for a unique Bornean haplotype.

Since 1980, one of us (J. Payne) has been informed many times by people working in the timber and plantation industries in eastern Sabah that elephants were introduced for logging, and have run wild. This suggests that elephants in these forests are those that were released or escaped the logging camps, and their descendents. Indeed, several Thai or Burmese elephants were brought to British North Borneo (now Sabah) by the Bombay Burmah Trading Company around 1948 for log hauling in Tingkayu, south-eastern Sabah and they were all later returned to Thailand because feeding elephants in the hill dipterocarp forests was too problematic (Q. Phillipps & R. Ibbotson, pers. coms.). Therefore, the elephants in eastern Sabah could not be descended from the logging elephants and the study by Fernando *et al.*, (2003) also supports this. However, it illustrates how an incident within living memory may lead to propagation of a theory in contradiction of historical evidence.

Distribution of elephants in Borneo

As far as can be ascertained from published records, the historic distribution of elephants in Borneo appears to have approximated the current distribution. There is no clear evidence to suggest that elephants were more widespread in Borneo during pre-historic times. Thus, unless fresh evidence is found in the form of sub-fossil or fossil material confirming their pre-historic occurrence in other parts of Borneo, it has to be assumed that their current distribution reflects the past. This limited distribution could be due to ecological or biogeographic factors.

1) Ecological factors: Elephants appear to be largely limited to habitat below 600 m in Borneo and areas of intensive use are below 300 m. Until the widespread commercial logging in the hill and mountain ranges of Borneo started about 30 years ago, the preferred elephant food plants (monocotyledons and pioneer dicotyledonous plants; Olivier, 1978) were very sparsely distributed in these high, predominantly steep regions, and were mainly found along the larger river valleys in the lowlands. The scarcity of suitable food resources in the higher reaches could have limited dispersal and determined elephant distribution. Sukumar (1989) proposed that an Asian elephant needs 75-100 g of sodium daily in order to avoid a deficit. Davies & Payne (1982) and Payne (1992) suggested that availability of sodium strongly influenced the distribution of large mammals, especially elephants and rhinoceros, in Sabah. In Borneo, natural mineral sources such as salt-rich springs and "mud volcanoes", the latter being grey-coloured mineral-rich mud which is forced from underground by methane gas, appear to be more common in the lowlands and are used today

by elephants. Deficiency of minerals in the montane flora and the apparent lack of alternative mineral sources could have influenced elephant distribution.

2) Biogeographic factors: If elephant distribution in Borneo was shaped by the effects of climatic and geologic history, Pleistocene land connections, and geographic barriers to dispersal, we would expect them to similarly affect other taxa, leading to concordant distribution patterns of multiple taxa. Indeed, peculiarities in the distribution of both flora and fauna support the recognition of northeast Borneo as a unique biogeographic unit (MacKinnon *et al.*, 1996). The north-western lowlands are considered much richer floristically than the north-east or south (Ashton, 1972; MacKinnon *et al.*, 1996), and an area concordant with known elephant distribution in Borneo is recognized as the east coast Sabah floristic sub-province (Wong, 1998). This area lies east of a rough arc from Mount Kinabalu along the eastern flank of the Crocker Range southeast through the Sook, Pendawan and Maliau basins to the Tanjung Redeb area of northeast Kalimantan. A number of mammals including two endemic squirrels (*Petaurillus hosei* and *P. emiliae*), two rats (*Chiropodomys major* and a newly discovered species at Danum Valley, Sabah), a mongoose (*Herpestes hosei*) (MacKinnon *et al.*, 1996) and 24 species of bats (Payne *et al.*, 1985) are confined to this region. This is also reflected in the avifauna, with a number of species replacements in Sabah by semispecies or allo-species (black-headed pitta *Pitta ussheri* versus garnet pitta *P. granatina*, white-fronted falconet *Microhierax latifrons* versus black-thighed falconet *M. fringillarius*), several species absences in Sabah where a form that is montane in the rest of Borneo occupies both the montane and the lowland niche of the “missing” Sabah lowland form (grey-breasted spiderhunter *Arachnothera affinis*, black-fronted leafbird *Chloropsis flavocincta*), species absence in Sabah without any replacement form (Hose’s oriole *Oriolus hosei*), and presence in Sabah without any replacement form elsewhere in Borneo (fulvous-chested flycatcher *Rhinomyias olivacea*). The latter species and two woodpeckers, the speckled piculet *Picumnus innominatus* and greater goldenback *Chrysocolaptes lucidus*, are examples of species that are widespread in South and South-east Asia, yet—like the Asian elephant—are confined in Borneo to Sabah in the north-east. These examples are all described in Smythies (1999). Thus, the distribution of elephants could be a consequence of biogeographic factors.

It is possible that resource availability and biogeographic factors, or both led to the limited elephant distribution in Borneo. However, elephants are extreme generalists and are able to survive in a wide range of habitats. Also, in many parts of Asia, elephant range extends well over 1000 m [upto 3200 m in NE India (AREAS unpublished data)]. Therefore, while resource availability may have had some bearing on the distribution of elephants, there does not appear to be a clear correlation, and data on resource availability is insufficient to make a compelling argument. In the same manner, the

referred to biogeographic patterns are based on species distribution, hence afford only very coarse comparisons. Future genetic analysis of other taxa both widespread and limited in distribution to the northeast, and correlation with their ecological affinities and species history on Borneo could better evaluate the relative importance of the two hypotheses. We also encourage detailed morphometric analysis of Borneo elephants, as well as search for sub-fossil and fossil *E. maximus* material in Borneo to further establish the evolutionary history of Asian elephants in Borneo.

Conservation implications

Deraniyagala (1950; 1955) considered the Borneo elephant a distinct subspecies, based on its appearance, the examination of a type skull in the British Museum and a sub-fossil tooth, originally reported to be of an elephant, from a cave in Bau, upper Sarawak, now in the Sarawak Museum. He considered Bornean elephants to be smaller in stature, have straighter more slender tusks and their skull to be shallower dorsally above the rostrum, than Indo-Ceylon (Ceylon = Sri Lanka) elephants (Deraniyagala, 1950; 1955). Subsequent workers have considered them not to be a distinct taxon, but the same as the Indian elephant *E. maximus indicus* (Shoshani & Eisenberg, 1982) or Sumatran elephant *E. maximus sumatrensis* (Medway, 1977), based on the assumption that they originated from stock introduced by humans or that the morphological differences were insufficient to warrant such a distinction.

The difficulty of delineating subspecies has led to the development of subspecific designations that are more definable and relevant to conservation, such as Evolutionarily Significant Units (ESU) and Management Units (MU) (Ryder, 1986; Moritz, 1994), although they too are not without problems (Paetkau, 1999). In the case of the Asian elephant, based on mitochondrial DNA analysis, the Sumatran population has been suggested to represent an ESU (Fleischer *et al.*, 2001). If Borneo elephants were feral descendants of introduced animals, in terms of Asian elephant conservation they would be of lesser importance than as a naturally occurring unique population at the edge of the species range. Conversely, if they were indigenous, they could represent an ESU or MU depending on their level of divergence, and they would need to be managed separately from other Asian elephants especially in *ex-situ* conservation.

Borneo elephants were monophyletic in the mitochondrial phylogenetic analysis and displayed uniqueness in the microsatellite analysis of Fernando *et al.*, (2003). The independent evolutionary trajectory of Borneo elephants from that of other Asian elephants, fulfill the criteria for recognition as a separate ESU (Fernando *et al.*, 2003). Thus, there is good reason to devote continued efforts to maintain wild breeding populations of the Borneo elephant and their *in-situ* conservation should be a priority in Asian elephant conservation plans. In addition, Borneo elephants should

be managed separately in *ex-situ* conservation with the objective of preserving their unique genetic make up and should not be cross bred with animals originating from other Asian elephant populations. Examination of pedigrees of captive bred animals and planned future mating of selected individuals, as well as avoiding further breeding of animals with mixed parentage, would be desirable.

The extent of genetic variability within a population determines its evolutionary potential and its ability to cope with environmental change, disease, and demographic perturbations. Loss of genetic variability can result in lowered individual fitness, impaired adaptability (Frankel & Soule, 1981; Allendorf & Leary, 1986), and inbreeding depression (Ralls *et al.*, 1986; Charlesworth & Charlesworth, 1987). However, some natural populations appear to thrive in spite of greatly reduced genetic variability (Ellegren *et al.*, 1993) and populations that undergo inbreeding for extended periods could purge deleterious recessive genes from their genomes and reduce so-called genetic load (Lande, 1988). Although outbreeding generally has beneficial effects, outbreeding depression can occur through loss of local adaptation or the dissolution of co-adapted gene

complexes (Templeton, 1986).

Borneo elephants display a significantly low level of genetic variability (Fernando *et al.* 2003). A lesser degree of genetic diversity loss in African Addo elephants led to recommendations for introduction of elephants from other populations (Whitehouse & Harley, 2001). However, the loss of diversity in Addo elephants was very recent and human induced. Given the evolutionary history of Borneo elephants, we would advocate caution before any such intervention is considered. Studies of overt indicators of inbreeding depression such as congenital deformities, behavioral changes, lowered fertility, sperm deformities and lowered recruitment would be logical next steps, in the conservation and management of this population. A wider study of the genetic variability of the Borneo elephant, with an extensive geographic sample and analysis of additional nuclear markers such as Major Histocompatibility Complex (MHC) loci, which are directly involved with the immune response, would provide greater insights into their genetic viability. Additionally, studies on the ecology, behavior and social organization of Borneo elephants could provide insights into the adaptation and survival of insular populations of large mammals.

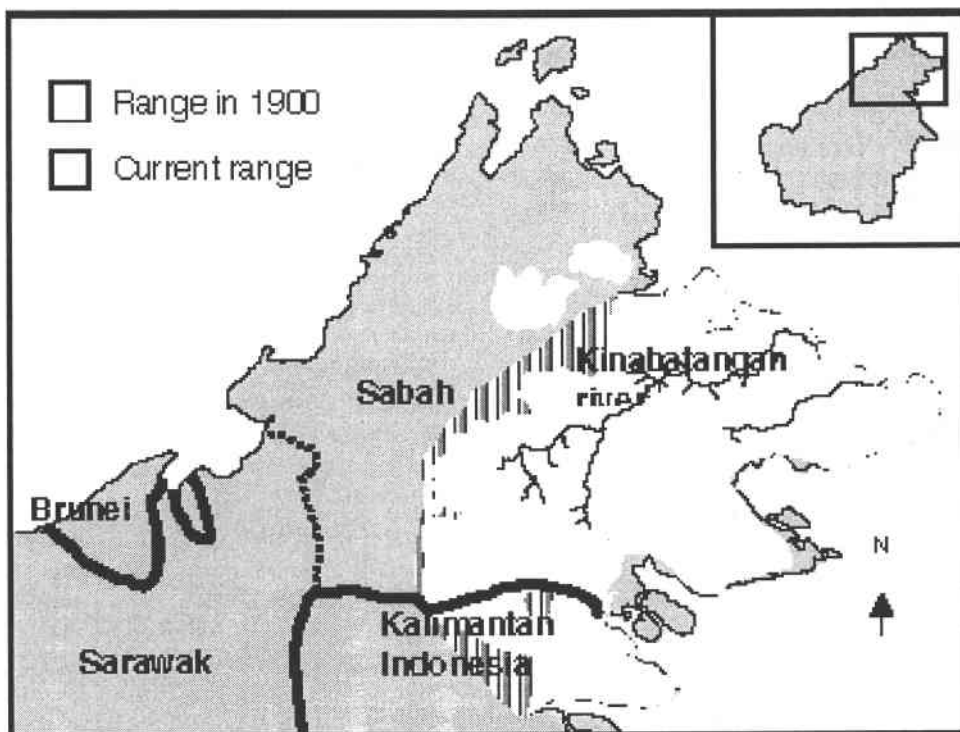


Fig. 1 Map of NE Borneo showing past and present Elephant ranges.

References

- Allendorf, F.W. & Leary, R.F. (1986) Heterozygosity and fitness in natural populations of animals. In *Conservation Biology. The Science of Scarcity and Diversity* (ed. M.E. Soule), pp. 57-76. Sinauer, Sunderland MA.
- Anon (1886) *Colonial and Indian Exhibition, 1886. Handbook of British North Borneo*. W. Clowes, London.
- Andaya, B. (1979) *Perak, the Abode of Grace*. Oxford University Press, Kuala Lumpur.
- Ashton, P.S. (1972) The Quaternary geomorphological history of western Malesia and lowland forest phytogeography. In *The Quaternary Era in Malesia* (eds. P. Ashton & M. Ashton), pp. 35-49. Dept. of Geography, University of Hull, Misc. Ser. No. 13.
- Banks, E. (1931) A popular account of the mammals of Borneo. *J. Malay. Brch. R. Asiatic Soc.*, 9(2): 1-139.
- Banks, E. (1949) *Bornean Mammals*. Kuching Press.
- Charlesworth, D. & Charlesworth, B. (1987) Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics*, 18: 237-268.
- Cranbrook, Earl of (2000) Northern Borneo environments of the past 40,000 years: archaeozoological evidence. *Sarawak Museum Journal*, 55 (76, new series): 61-109.
- Cranbrook, Earl of, Currant, A.P. & Davison, G.W. (2000) Quaternary mammal fossils from Borneo: *Stegodon* and *Hippopotamus*. *Sarawak Museum Journal*, 55 (76, new series): 215-233.
- Dalrymple, A. (1767) *A Plan for Extending the Commerce of this Kingdom and of the East India Company*.
- Davies, G. & Payne, J. (1982) *A Faunal Survey of Sabah*. WWF Malaysia, Kuala Lumpur.
- Deraniyagala, P.E.P. (1950) The elephant in Asia. *Proc. 5th ann. Sess. Ceylon Assoc. Sci.*, (1949) 3: 1-18.
- Deraniyagala, P.E.P. (1955) *Some Extinct Elephants, Their Relatives and the Two Living Species*. Government Press, Ceylon.
- Ellegren, H., Hartmen, G., Johansson, M., & Andersson, L. (1993) Major histocompatibility complex monomorphism and low levels of DNA fingerprinting variability in a reintroduced and rapidly expanding population of beavers. *Proceedings of the National Academy of Science of the USA*, 90: 8150-8153.
- Everett, A.H. (1893) A nominal list of the mammals inhabiting the Borneo group of islands. *Proceedings of the Zoological Society, London*, 1893: 492-496.
- Fernando, P., Vidya, T.N.C., Payne, J., Stuewe, M., Davison, G., Alfred, R.J., Andau, P., Bosi, E., Killbourn, A., & Melnick, D.J. (2003) DNA analysis indicates that Asian elephants are native to Borneo and are therefore a high priority for conservation. *PLoS Biology*, 1: 1-6.
- Fleisher, R.C., Perry, E.A., Muralidharan, K., Stevens, E.E., & Wemmer, C.M. (2001) Phylogeography of the Asian elephant (*Elephas maximus*) based on mitochondrial DNA. *Evolution*, 55: 1882-1892.
- Frankel, O.H. & Soule, M.E. (1981) *Conservation and Evolution*. Cambridge University Press, Cambridge.
- Harrisson, T. & Harrisson, B. (1971) The Prehistory of Sabah. *Sabah Society Journal Monograph*, 4, I-xxiii: 1-272.
- Holloway, J.D. & Hall, R. (1998) SE Asian geology and biogeography: an introduction. In *Biogeography and Geological Evolution of SE Asia* (eds. R. Hall, & J.D. Holloway), pp. 1-23. Backhuys Publishers, Leiden, The Netherlands.
- Hooijer, D.A. (1972) Prehistoric evidence for *Elephas maximus* L. in Borneo. *Nature, London*, 239: 228.
- Hunt, J. (1811) *Some Particulars Relating to Sulo, in the Archipelago of Felicia*. Source not stated, photocopy in the Tun Haji Mohd. Fuad Stephens Research Library, Kota Kinabalu, Sabah, Malaysia.
- Jentink, F.A. (1884) De oliphant en de rhinoceros of Borneo. *Tijdschr. Ned. Aardrijks. Genootsch.*, (2)1: 554-559.
- Lande, R. (1988) Genetics and demography in biological conservation. *Science*, 241: 1455-1460.
- Laufer, B. (1925) *Ivory in China*. Field Museum of Natural History Chicago. Anthropology Leaflet No. 21.
- MacKinnon, K., Hatta, G., Halim, H., & Mangalik, A. (1996) *The Ecology of Kalimantan*. Periplus Editions Ltd., Hong Kong.
- Maglio, V.J. (1973) Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society Philadelphia. New Series*, 63: 1-149.
- Marsden, W. (1811) *The History of Sumatra*. Republished in 1966 by Oxford University Press, Kuala Lumpur.
- Medway, Lord (1977) *Mammals of Borneo*. Monographs of the Malaysian Branch, Royal Asiatic Society No. 7, Kuala Lumpur.
- Moritz, C. (1994) Defining 'evolutionary significant units' for conservation. *Trends in Ecology and Evolution*, 9: 373-375.
- Müller, S. (1839-40) De zoogdieren van den Indischen

Archipel. In *Verhandelingen over denatuurlijke geschiedenis der Nederlandsche overzeesche bezittingen Zoologie (Mammalia)* (ed. C.J. Temminck), pp. 1-57. Leiden.

Olivier, R.C.D. (1978) On the ecology of the Asian elephant. Ph.D. thesis, University of Cambridge, UK.

Paetkau, D. (1999) Using genetics to identify intraspecific conservation units: a critique of current methods. *Conservation Biology*, 13: 1507-1509.

Payne, J. (1992) Rarity and extinctions of large mammals in Malaysian rainforests. In *Proceedings of the International Conference on Conservation of Tropical Biodiversity, "In Harmony with Nature", 12-16 June 1990* (eds. S.K. Yap & S.W. Lee), pp. 310-320. Malayan Nature Society, Kuala Lumpur.

Payne, J., Francis, C., & Phillipps, K. (1985) *A Field Guide to the Mammals of Borneo*. The Sabah Society & WWF Malaysia.

Pryer, W.B. (1881) Animal life in Borneo. *Zoologist*, 5 (3): 393-398.

Ralls, K., Harvey, P.A., & Lyles, A.M. (1986) Inbreeding in natural populations of birds and mammals. In *Conservation Biology. The Science of Scarcity and Diversity* (ed. M.E. Soule), pp. 35-56. Sinauer, Sunderland MA.

Ryder, O.A. (1986) Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology and Evolution*, 1: 9-10.

Shoshani, J. & Eisenberg, J.F. (1982) *Elephas maximus*. *Mammalian Species*, 182, 1-8.

de Silva, G.S. (1968) Elephants of Sabah. *Sabah Soc. J.*, 3: 169-181.

Smythies, B.E. (1999) *The Birds of Borneo*. 4th edition, revised by G.W.H. Davison. Natural History Publications, Kota Kinabalu.

St. John, S. (1863) *Life in the Forests of the Far East. Second Edition*. Smith, Elder, London.

Sukumar, R. (1989) *The Asian Elephant. Ecology and Management*. Cambridge University Press, Cambridge.

Templeton, A.R. (1986) Coadaptation and outbreeding depression. In *Conservation Biology. The Science of Scarcity and Diversity* (ed. M.E. Soule), pp. 105-116. Sinauer, Sunderland MA.

Van Den Bergh, G.D., Sondarr, P.Y., De Vos J., & Aziz, F. (1996) The proboscideans of the South-East Asian islands. In *The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives* (eds. J. Shoshani & P. Tassy), pp. 240-248. Oxford University Press, Oxford, UK.

Whitehouse, A.M. & Harley, E.H. (2001) Post-bottleneck genetic diversity of elephant populations in south Africa, revealed using microsatellite analysis. *Molecular Ecology*, 10: 2139-2149.

Wong, K.M. (1998) Patterns of plant endemism and rarity in Borneo and the Malay Peninsula. In *Rare, Threatened and Endangered Floras of Asia and the Pacific Rim* (eds. C.I. Peng & P.P. Lowry), pp. 139-169.



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