CHAPTER 7: SOLVING MAMMALIAN RIDDLES

The literature of science is filled with answers found when the questions propounded had an entirely different direction and end.

The log from the Sea of Cortez
Steinbeck

The Leopard

I developed a hypothesis to explain the absence of Panthera pardus from Sumatra and Borneo (see Meijaard in press, Appendix 4). It appears that leopards first migrated to Java from the Malay Peninsula using the Middle Pleistocene land bridge. After this land bridge broke up, Javan leopards became isolated on the island leading to considerable morphological and genetic divergence from the mainland Asian leopards. The reason why leopards did not invade Borneo and Sumatra when Java became once more connected to those areas is probably a combination of low prey species density (especially on Borneo) and competition from other large carnivores (especially on Sumatra). I showed that there appears to be a positive correlation between prey biomass and the number of sympatric large carnivores. Java with its more open habitat and rich volcanic soils probably supported (and still does) a much higher prey biomass than Borneo and Sumatra so that leopards survived on that island.

Tiger

The tiger’s absence from Borneo (but see Meijaard 1999a) is probably caused by a similar factor as the leopard’s absence from that island, although proof for this is lacking. The data in Table 5 (Appendix 4) appear to indicate that tigers do not occur below a prey biomass of about 750 kg/km². The data for Ujung Kulon and Taman Negara, however, suggest that tigers and leopards can still co-exist below these biomass estimates. Clearly more accurate data on predator absence/presence and density and prey biomass (including all potential prey species assessed by a standard methodology) are needed before really meaningful conclusions can be drawn. There is a chance that tigers did occur on Borneo during the Late Pleistocene (Hooijer 1963a) and there are several reports of very recent occurrence of tigers as well (e.g., Witkamp 1932, and see other references in Meijaard (1999a)). Because of the drier conditions during the LGM and the more open vegetation with increased presence of grasses, ungulate density in Borneo during the LGM may have been higher than now. Possibly tigers did occur on Borneo but disappeared during the Holocene because of a decrease in prey biomass brought about partly by climatic warming and possible hunting by people. Unless new fossils are found this matter will remain speculative.
The Proboscis Monkey

It is interesting to note that among the 217 primate remains that have been identified at the West Mouth of Niah Cave in Sarawak, not a single Proboscis Monkey has been identified (Harrison 1996), and, in fact, *Nasalis* is completely missing from the fossil record in Borneo or elsewhere (Hooijer 1962a; Harrison 2000). This absence of fossils may be partly related to the species’ present rarity or even absence from most of coastal Sarawak (see Meijaard & Nijman 2000), although the species is still common in Sabah from where there are also no fossil records. Interestingly, there are also no subspecies of *Nasalis larvatus*, which suggests that dispersal across Borneo occurred relatively recently, or that the species’ dispersal is not hampered by geographic barriers that exist for other primates that did differentiate subspecifically. Groves (2001b) discussed the phylogenetic position of *Nasalis* (including *Simias*); *Nasalis* may either be sistergroup to all other Colobinae, or this group initially split into an Asian and African group before *Nasalis* differentiated from the other Asian colobines. Also, the position of *Nasalis* in the Asian group remains unclear, it could either be the first branch in the Asian group (Collura et al. 1996), or it assorts with *Rhinopithecus* and *Pygathrix* (Zhang & Ryder 1998). Whichever the case, *Nasalis* appears to be a relatively old species that differentiated from other colobines several Mya (see Chapter 4). *Nasalis* and the apparently closely related *Simias concolor* from the Mentawai Islands appear to be surviving remnants of a species or species group that used to be much more widely distributed, presumably in Central Sundaland, during the Late Miocene-Pliocene.

It is unclear why, during the LGM, *Nasalis* did not manage to disperse into Sumatra or Java where suitable mangrove habitats occurred (see Chapter 3). One possible explanation would be that the species did not yet occur on what is now Borneo during the LGM, or that it was restricted to a small part of Borneo, which would explain the absence of fossil material from either Late Pleistocene or Holocene deposits in northwest and north Borneo. But the question then remains to which area the species was restricted and, more importantly, why it was restricted, and also how it was released and managed to disperse across Borneo. A likely candidate seems to be an island offshore Borneo where *Nasalis* survived while elsewhere on Borneo it went extinct.
Presently, *Nasalis* only occurs on the following offshore islands: Bruit, an island just west of Sarawak, and basically part of a river delta; Jambongan, an island just off the east coast of Sabah; Tarakan, an island close to north East Kalimantan; and Laut, a large island off the south-east coast of Borneo (Meijaard 2003). The latter seems to be the only candidate for a hypothesized Miocene–Pleistocene refuge for *Nasalis*, because the other islands are relatively small and appear to be of recent origin. According to van Bemmelen (1970, p. 351), Laut Island was emergent, probably as a large island, during the Tertiary. At that time it was surrounded by the depositional basins of Southeast and East Borneo and western Sulawesi. The Quaternary rise of the Meratus-Samarinda Range from the Tertiary Basin of SE Borneo would presumably have narrowed the gap that existed between the Laut Island area and mainland Borneo. During the LGM when Laut became connected to the rest of Borneo, *Nasalis* could have dispersed into Borneo.

This hypothesis, far-fetched as it may seem at first sight, apparently fits the data better than any alternative theories. The isolation of *Simias* on the Mentawais and *Nasalis* on the large Pulau Laut could have been the result of centrifugal evolution where older species are displaced by newcomers (macaques or colobines) and only survive in places where they are not outcompeted by these newcomers. The idea may be tested, if Pliocene fossils of *Nasalis* are ever found on Pulau Laut. Other data that would support this hypothesis is evidence for a Early–Middle Pliocene separation between *Simias* and *Nasalis*, and low levels of intra-specific genetic variation within *Nasalis*, which would indicate that the species only recently spread out over Borneo. Also if Pulau Laut played an important role as an island refuge then I would expect that also other species were isolated there. The challenge is to identify these other species with similar phylogenetic and biogeographic patterns as *Nasalis*.

**Orang-utan**

The main riddle regarding Orang-utan evolution and biogeography is how the Sumatran and Bornean forms can be genetically so different, considering that they should have been able to exchange genetic information during the times that land existed between Borneo and Sumatra. Based on the information in Chapter 4.2 I
propose the following evolutionary model for Orang-utans, which seems most parsimonious in light of the available data:

1. During the Early–Middle Pleistocene the mainland Asian Orang-utan separated from the Bornean population, possibly at the time when Borneo first became an island (although this could also have happened considerably earlier). This resulted in a population on Borneo, on the Asian mainland (possibly consisting of several species, see Schwartz et al. 1995), and possibly on Sumatra (the one which gave rise to *P. dipoisi*).

2. During the Middle Pleistocene, Orang-utans migrated from the Asian mainland to Java, following the Java Sea landbridge. At the height of the Middle Pleistocene glacial (ca. 0.8 Mya), the Bornean Orang-utan became separated into several isolated populations, probably in the few areas where lowland rainforest remained. Considering that the climatic conditions on the Asian mainland would have been more severe than those in Borneo, it is likely that the mainland Asian Orang-utans were also isolated in small pockets of suitable habitat.

3. During the Middle–Late Pleistocene, *P. dipoisi* became extinct after the Toba explosion, making room for a new arrival from the Asian mainland, *P.p. palaeosumatrensis*. The data by Muir et al. (2000) suggests that *P. dipoisi* hybridised with this new species, and that there were possibly further genetic contributions from the Bornean and Javan populations to those in Sumatra.

4. During the Late Pleistocene–Holocene, the colder and drier climatic conditions on the Asian mainland led to the demise of mainland Asian populations, while similarly the populations on Java became extinct. Jablonski and Whitford (1999) suggested that the Orang-utan’s extinction in mainland Asia is the result of its reliance on regular supplies of high-energy food, long gestation period, and very long interbirth intervals. This made it impossible for the species to survive in areas without predictable environments that supplied year-round easily digested, energy-rich foods.
**Banteng**

In Chapter 6.3. I hypothesized that Banteng were probably introduced from Java to the Asian mainland and that the Banteng is native to Borneo. This would provide a sufficient answer to the mammalian riddle regarding this species, i.e. why is the species absent from Sumatra. Further testing is needed to provide evidence.

**Tragulus javanicus on Java**

My research on mouse-deer has not resulted in sufficient information to explain the absence of *T. napu* from Java. Even though this species is more closely tied to tropical wet evergreen forest than *T. javanicus*, such habitats must have been available on Java during the LGM (as shown by the continued existence of many rainforest-dependent species); clearly *T. napu* did not use the opportunity to establish itself on Java. The fossil record is not of much help. Fossil of both species have been reported from various areas, but considering that it is difficult and sometimes impossible to assign even present-day cranial and dental material to either species, identification of fossil *Tragulus* finds should be taken with a grain of salt.

In Chapter 6.4 I pointed out that populations of *T. napu* from Borneo, Sumatra, and the Malay Peninsula group together quite tightly in a craniometric comparison, which would suggest that there have either been high levels of gene flow within that region. If *T. napu* managed to migrate between Borneo and Sumatra, one would expect that some animals also managed to reach Java; as far as I know this did not happen. A possible explanation may be that there are subtle differences in the ecology of species from the *T. napu* and *T. javanicus/kanchil* groups, which might preclude the presence of the former on Java. Although at a macro-level the species occur sympatrically, very often only one or the other is common. For instance, *T. napu* is absent from Tasek Bera, Peninsular Malaysia, but *T. javanicus* is often encountered (Syakirah et al. 2000), while around the Iwan and Kat Rivers in the mountains of East Kalimantan, *T. napu* was often seen, but not *T. javanicus*, which was, however, very common in other areas (Wulfraat & Samsu 2000). The species therefore appear to be ecologically separated to a higher extent than indicated in the general ecological text books on SE Asian species. Possibly their specific ecological niches provide an explanation for the absence of *T. napu* from Java, but the data are lacking to support this.
Chapter 7. Solving mammalian riddles

Elephants

The alleged introduction of elephants to Borneo is based on its restricted distribution on the island, with most of the populations occurring in Sabah and a few in the north of East Kalimantan Province. Van Balen (1914), without referring to primary sources, reported that in the early 1800s, the Oost-Indische Compagnie sent several elephants as a present to the Sultan of Sulu (in the Philippines). As the sultan feared that these elephants would destroy the vegetation on his tiny island, these animals were later released near Cape Usang in present-day Sabah. This story was quoted by several other authors (e.g. Müller 1839-1844; Banks 1931; Medway 1977; Payne et al. 1985). Furthermore, Corvanich (1995 in Ambu et al. 2003) reported that as late as the mid-1960s a number of tame timber elephants from Thailand were sent to the east coast of Sabah to assist in the logging industry. It seems therefore clear that elephants were introduced to Borneo. Medway (1977), however, pointed out that trained elephants were already observed in Brunei in 1521, while the existence of Late Pleistocene–Holocene elephant remains provide further evidence that the species has been present on Borneo for much longer than just the last couple of centuries. It therefore seems that elephants are indigenous to Borneo, which is supported by Deraniyagala’s (1955) finding that it is by far the smallest elephant subspecies, with distinct craniometric features, while Hubback (1942) claimed that the Bornean elephant has much straighter tusks than any other subspecies. This leaves the question why the species is restricted to the northern part of the island.

Martin (1884, in van Bemmelen 1970, p. 298) described a molar of Elephas sumatranus (= maximus) from the upper Pleistocene in Bangka Island. If identified correctly, this means that elephants probably extended from Sumatra to Bangka during the LGM, and they could from there easily have reached Borneo. This concurs with Payne’s (1990) hypothesis that elephants were widespread on Borneo during the LGM but that they were wiped out as sea levels rose during the Holocene. Only the east Sabah population survived because of an adequate array of salt licks. The latter part of this hypothesis seems unconvincing. Salt licks occur throughout Kalimantan (pers. obs.), although probably not in fresh water and peat swamps. Furthermore, other

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4 A recent paper by Fernando et al. (2003) confirmed that Bornean Elephants were a distinct evolutionary units that had been isolated since the Middle Pleistocene.
species like Orangutans and Sumatran Rhinoceros, whose densities have also been linked to the availability of mineral soils, occurred throughout Borneo, which suggests that either they are not limited by the availability of minerals or that these minerals are available in many places. However, exact data on the density of mineral licks in Borneo are unavailable and the issue remains unresolved.

Finally, elephants, probably *Elephas maximus*, only recently became extinct on Java. According to Dammerman (1934), they persisted until at least 1 Kya, although this does not prove that elephants are native to Java, as they could have been introduced by Hindu traders. Late Pleistocene finds from West Java, however, do proof that *E. maximus* was native to the island and probably arrived there with the Punung Fauna some 70 Kya (van den Bergh, 1999). Interestingly, elephants were drawn on a 17th century map of West Java (see Egon 1989), and they were described as locally common on Java in the 17th century (Prevost (Abt) 1755); the same source also mentions trade in ivory (it used the Dutch word ‘elpenbeen’, whereas rhino horn is referred to as ‘hoorn’). Extinction through over-hunting seems to be a likely explanation for their disappearance from Java.

*Sus barbatus, S. verrucosus, and S. scrofa*

The absence of *Sus scrofa* from Borneo is remarkable, because this species occurs in almost all other parts of the Eurasian continent. In Peninsular Malaysia and Sumatra it co-exists with *S. barbatus* and on Java with *S. verrucosus*. It does appear, however, that in those areas *S. scrofa* outcompetes the other two species, especially now that the extent of suitable habitat is declining and competition between pig species is on the increase. *S. scrofa* arrived on Java in the late Middle Pleistocene, presumably from Sumatra (where I think most members of the Punung Fauna originated). Theroretically, *S. scrofa* would therefore have been able to reach Borneo during the LGM, either from Malaya, Sumatra, or Java. Apparently, this did not happen, as there is neither fossil nor recent evidence for the presence of *S. scrofa* on Borneo. *S. scrofa* occurs in a wide range of vegetation types, and it is unlikely that an ecological barrier existed between Borneo and the other three areas that prevented the species from
reaching Borneo. Pigs also swim well and it is unlikely that their dispersal was prevented by river barriers.

If *S. scrofa* did occur on Borneo (without leaving any traces) the only possible explanation for their disappearance from the island is that they were wiped out by disease. This is not quite satisfactory either. Diseases have affected the pigs of Borneo, for instance when in 1871, 1872, and 1878 rinderpest killed large numbers of wild pigs in Central Kalimantan (Knapen 1997). Another epidemic was reported by Nieuwenhuis (1907, Vol. I, 196), who mentioned that during his first journey through central Borneo in 1894 pigs were rare, because both the wild and domestic population had been killed off by an epidemic in central Borneo in 1888 and 1889. Feuilletau-de Bruyn (1933) further reports that in 1906, ’very many bearded pigs’ succumbed to a contagious disease in the Tabalung area (north-east Ulu Sungai, S. Kalimantan). Still, considering that *S. scrofa* and *S. barbatus* are closely related it is unlikely that only one species was affected by disease, although it is possible that both species were affected but only one died out completely.

A possible explanation lies in the geology of Borneo and the related low fertility of its soils. Whereas *S. barbatus* is perfectly adapted to the highly fluctuating food availability inherent to Bornean dipterocarp forests and to non-edge habitats, *S. scrofa* is adapted to more productive ‘edge’ habitats (Caldecott 1991). It is possible that such edge habitats almost completely disappeared during the Holocene climatic optimum and *S. scrofa* might have been outcompeted by *S. barbatus*. Until more data become available on the comparative ecology of *scrofa* and *barbatus* this explanation remains hypothetical, especially because Sumatra has a similar vegetation to Borneo, but here *S. scrofa* survived.