

BIOGEOGRAPHIC HISTORY OF THE JAVAN LEOPARD *PANTHERA PARDUS* BASED ON A CRANIOMETRIC ANALYSIS

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The leopard, *Panthera pardus*, occurs on Java, Indonesia, but is absent from Sumatra and Borneo, the islands that lie between Java and the rest of the leopard's geographic range. Recent molecular research has suggested that Javan leopards are a distinct taxon that split off from other Asian leopards hundreds of thousands of years ago, which raises the question of how the species arrived on Java but apparently bypassed Borneo and Sumatra. I have further investigated this issue by linking the results of a morphometric analysis of 121 leopard skulls to my palaeoenvironmental reconstructions for the region. The results suggest that the Javan leopard is craniometrically distinct from leopards from the rest of Asia. I hypothesize that in the Middle Pleistocene (about 800×10^3 years ago) leopards migrated to Java from South Asia across a land bridge that bypassed Sumatra and Borneo. During the last glacial maximum, when Java, Borneo, and Sumatra were connected, leopards could not survive on either Borneo or Sumatra because of the islands' relatively low ungulate biomass and competition from other large carnivores that were better adapted to tropical evergreen forest habitat.

Key words: cat, craniometrics, felid, fossil, morphometrics, phylogeny, Pleistocene, skull, Southeast Asia

The leopard, *Panthera pardus* Linnaeus, 1758, has the widest distribution of the wild cats, with populations in much of Sub-Saharan Africa, the Middle East, and most of Asia. Its most southeastern representative occurs on the Indonesian island of Java. Several authors have suggested that Javan leopards are not native to the island, but were probably introduced from India (e.g., Bergmans and van Bree 1986; Whitten et al. 1996). This was based on the assumption that no fossils of the species have been reliably reported from the island; also the leopard's Southeast Asian distribution is disjunct, with populations on Java and the Malay peninsula, but not on Sumatra and Borneo (Fig. 1). Apparently contradicting the hypothesis that humans introduced leopards to Java, Hemmer and Schütt (1973) and Brongersma (1935) reported Middle–Late Pleistocene fossil remains of leopard from several localities on the island.

Molecular analyses by Miththapala et al. (1995) and Uphyrkina et al. (2001) suggested that the Javan leopard is a distinct taxon that split off from its nearest relatives as early as the Middle or Middle-Late Pleistocene (about $800\text{--}300 \times 10^3$ years ago) and that might be the sister group to all the other

Asian leopards. Both Miththapala et al. (1995) and Uphyrkina et al. (2001) found strong statistical support for the basal position of African leopards in the leopard's phylogenetic tree and for the sister group position of Javan leopards to all other Asian leopards. Africa and Java are at the 2 extremes of the leopard's geographic distribution, and the basal position of these taxa in the leopard's phylogeny suggest an unusual evolutionary history. Uphyrkina et al. (2001) therefore concluded that the Javan leopard is highly distinctive for evolutionary reasons that remained uncertain.

In this research I investigated the differences between leopards from Java and from other parts of Asia using craniometric analysis to ascertain whether Javan leopards are morphologically distinct from others. Also, I have attempted to explain the disjunct distribution pattern of Southeast Asian leopards, and the underlying evolutionary history. This research is part of more extensive Ph.D. research that investigates mammalian distribution patterns in Southeast Asia by reconstructing past climates and topography from available palaeoenvironmental data and combining them with phylogenetic analysis.

MATERIALS AND METHODS

I measured 16 skull characters on 121 skulls of mature specimens of *P. pardus* (Appendix I): greatest length (GL); basal length (BPL); condylobasal length (CBL); zygomatic width (ZW); width across

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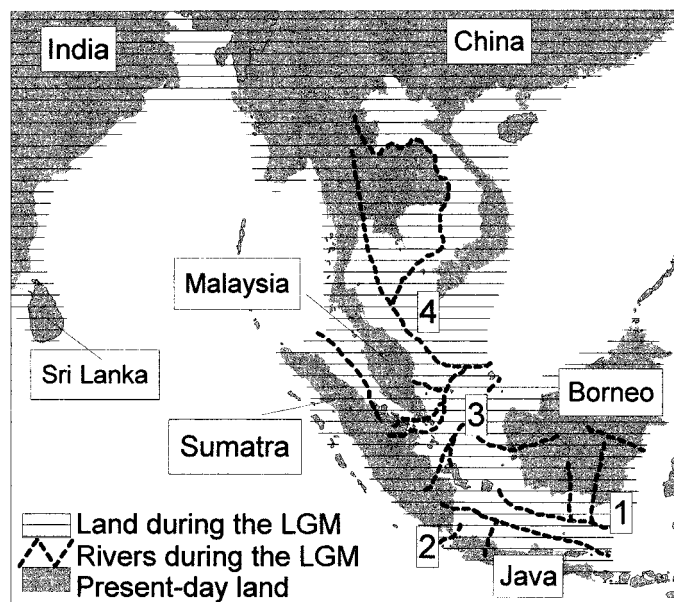


FIG. 1.—Location diagram of main areas mentioned in the text; also showing the approximate land area during the last glacial maximum and the main river courses: 1 = North Siam River; 2 = Molengraaff River; 3 = Sunda Strait River; 4 = Java Sea rivers. LGM = last glacial maximum (after Meijaard 2003; Meijaard and Groves 2004).

upper canines (BC); interorbital width (IO); infraorbital width (InfO); postorbital width (PO); occipital breadth (OB); occipital height from basion (OHB); occipital height from opisthion (OHO); mandible length (ML); mandible height (MH); lower toothrow length including canine (LTR); greatest diameter of auditory bullae (GDB); and least diameter of auditory bullae (LDB). All measurements were taken to an accuracy of 0.1 mm with a pair of Vernier calipers (precision 0.05 mm). Age classes were determined as follows: adult = m3 erupted and basilar suture fused; between young adult and adult = m3 erupted and basilar suture fusing; young adult = m3 erupted and basilar suture open; and juveniles = m3 not erupted. I analyzed the measurements using SPSS 11.0 software (SPSS Inc., Chicago). First, I determined whether there was a significant difference between males and females; second, whether there were significant differences between age classes. Subsequently, I investigated the morphological variation between and within the Asian subspecies using principal component and discriminant analyses.

RESULTS

An analysis of variance (ANOVA) revealed that, for all variables but postorbital width, there were significant differences ($P < 0.001$) between males and females (see Appendices II and III for means and standard deviations). The 2 sexes were therefore treated separately in most subsequent analyses. There were also significant differences ($P < 0.05$) for greatest length, basal length, condylobasal length, zygomatic width, occipital height from basion, occipital height from opisthion, and mandible height between the 3 age classes of mature male leopards, and for greatest length, basal length, condylobasal length, zygomatic width, interorbital width, mandible length, and mandible height in mature females. I analyzed sexes in-

dependently, but initially lumped the age classes unless this was clearly masking the amount of geographic variation.

A principal component analysis of the Asian male leopards formed 2 clusters of specimens, 1 with all Javan skulls and another cluster with all other skulls. The same analysis for females indicated more structure with two clusters, 1 with specimens from Java, Malaysia, and Indochina, and a 2nd mixed group of specimens from Central China, India, Nepal and Kashmir, with the Sri Lankan specimens apparently a subset of the 2nd group (Fig. 2A). The correlation values between the 1st component in the component matrix, which represented 73% of the total variance, and the variables, ranged between 0.84 and 0.97 for all variables, except for postorbital width ($r = 0.36$) and least diameter of auditory bullae ($r = 0.41$). This indicates that the Javan specimens are primarily separated from the others by their smaller size. The Malaysia-Indochina specimens are primarily differentiated by the 2nd component, which appears to be correlated with high values of postorbital width and least diameter of auditory bullae. The remaining specimens from Sri Lanka, China, India, Nepal, and Kashmir showed little differentiation among each other, but were different from the Javan, Malaysian, and Indochinese ones. Based on this outcome I initially divided the specimens into 4 groups for conducting discriminant analyses: Java; Malaysia and Indochina; Sri Lanka; and China, India, Nepal, and Kashmir.

A discriminant analysis of all South, East, and Southeast Asian specimens (both sexes, all ages), assuming equal prior probabilities for all groups, created a group of 32 specimens from Java that did not overlap with other groups; 4 Javan specimens overlapped with the other Asian groups, but not with Sri Lankan specimens (Fig. 2B). Of these 4 Javan specimens, 2 had a higher posterior probability of belonging to the group consisting of Malayan and Indochinese specimens. When I allowed the observed group sizes in my sample to determine the probabilities of group membership, all Javan specimens had the highest posterior probability for belonging to the Javan group, meaning that none of them was more likely to belong to any of the other groups. In that analysis, 1 of the 9 Malaysia-Indochina specimens had a higher posterior probability of belonging to the group of Javan specimens, and 2 specimens were more likely to belong to the group consisting of specimens from China, India, Nepal, and Kashmir. Two of the 31 specimens from China, India, Nepal, and Kashmir had a low posterior probability ($P = 0.29$) of belonging to the Javan group, 2 others showed a higher statistical affinity with the Malaysia-Indochina group, and 3 specimens associated with the Sri Lanka group. The Sri Lankan group was well separated with 18 of the 20 specimens having the highest posterior probability of belonging to that group; 2 were more likely to belong to the group of specimens from China, India, Nepal, and Kashmir.

The above results suggest that Javan leopards are morphologically distinct from other Asian leopards, whereas the remaining Asian leopards separate into 2 or 3 geographic groups. To further investigate the statistical separation between the Asian leopards, I analyzed the skulls within sex classes. A discriminant analysis split the female specimens into a Javan

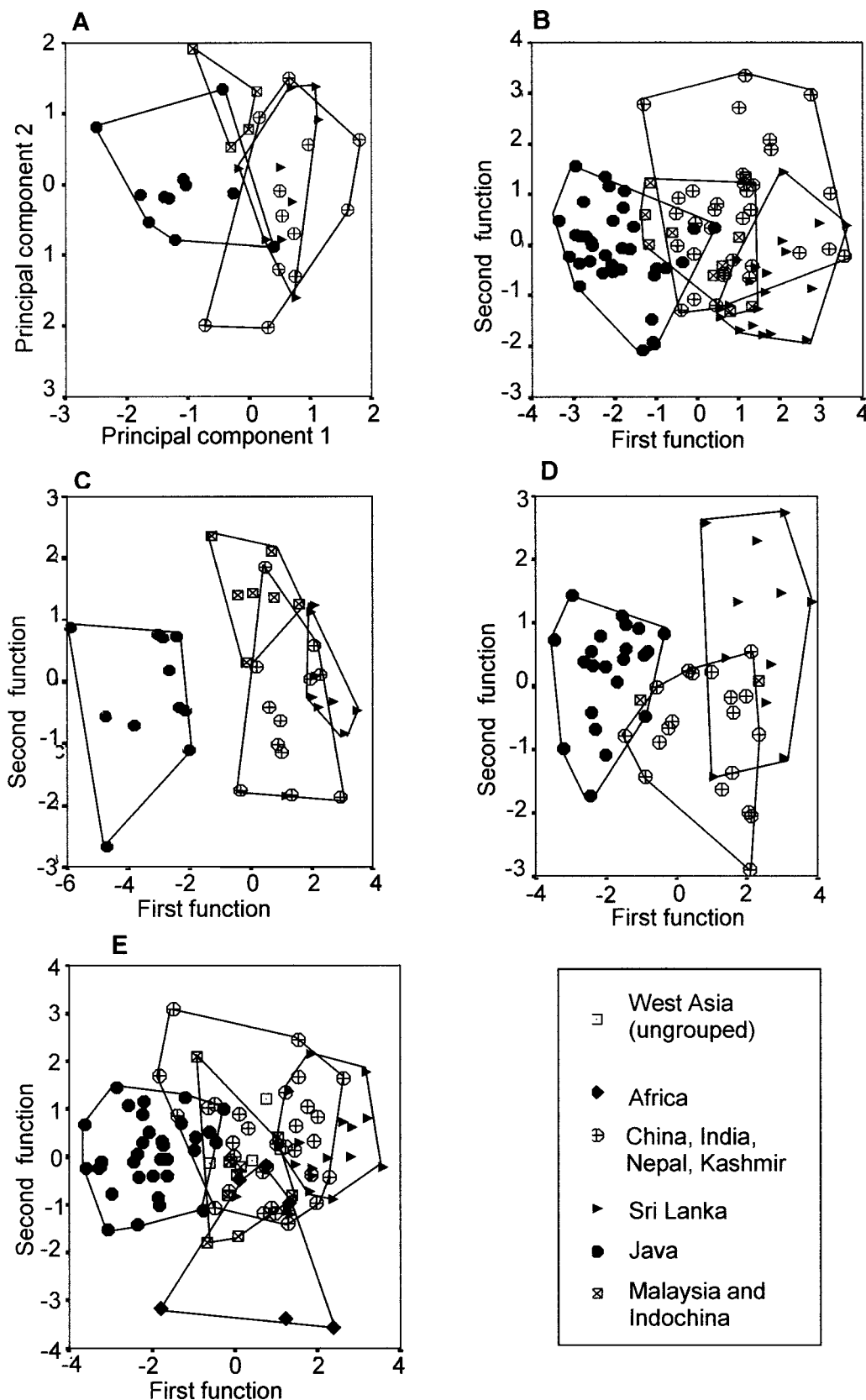


FIG. 2.—Analysis of leopard skulls by geographic areas, shown as A) principal component analysis for skulls of female Asian leopards, B) discriminant analysis for skulls of Asian leopards, C) discriminant analysis for skulls of all female leopards from Asia, D) discriminant analysis for skulls of all male leopards from Asia, and E) discriminant analysis of all leopard skulls (Asia and Africa).

group and a mixed group consisting of all other Asian specimens (Fig. 2C). The structure matrix shows that the Javan group is primarily differentiated by low values of the 1st function, which represented 89% of the total variance. This correlates with relatively low values of Javan skulls for mandible length, greatest diameter of auditory bullae, zygomatic width, occipital height from basion, width across upper canines, and lower toothrow length including canine. The groups containing Malaysia and Indochina specimens were also well separated from the others, with all specimens having the highest posterior probability of belonging to that group. The groups from Sri Lanka and China, India, Nepal, and Kashmir were less well separated: 2 of 9 Sri Lankan specimens had a higher posterior probability of belonging to the China, India, Nepal, and Kashmir group; 4 of 12 China, India, Nepal, and Kashmir specimens had a higher posterior probability of belonging to the Sri Lanka group; and 1 of the China, India, Nepal, and Kashmir specimens was more likely to belong to the Malaysia-Indochina group.

In a discriminant analysis of male skulls, all Javan specimens had the highest posterior probability of belonging to the Javan group (Fig. 2D). Because there were only 2 male specimens from Malaysia and Indochina, these were entered as unknowns; one of these (a specimen from Selangor, Malaysia) was predicted to belong to the Javan group, the other (from Laos) to the Sri Lankan group. Sri Lankan specimens overlapped partly with those in the China, India, Nepal, and Kashmir group, with 1 of the 11 specimens having a higher posterior probability of belonging to that mainland group. Two of the 19 specimens in the China, India, Nepal, and Kashmir group were more likely to belong to the Javan group, whereas 2 others were more likely to belong to the Sri Lanka group. The positive loadings of function 1 indicate that the differences between the Java specimens and the others were primarily size related, although not so much in the overall skull size, but rather in the size and shape of specific parts (mostly auditory bullae, occipital condyles, and mandible).

To investigate how skulls from Central and Southeast Asia differed from those from Africa and West Asia, I added male and female specimens from the latter two groups to the analysis (Fig. 2E). Overall, 72% of the originally grouped cases ($n = 100$) were correctly classified as belonging to their respective groups. The classification accuracy was highest for the Javan specimens, of which 88% ($n = 29$) were correctly classified as belonging to the Javan group; the second highest accuracy was for the Sri Lankan group with 80% of the specimens classified correctly. The African and West Asian specimens appeared to be differentiated from Central and Southeast Asian specimens because of the low values of Function 2; this function was positively correlated primarily with infraorbital width, occipital height from basion, zygomatic width, and mandible length.

DISCUSSION

Craniometrics and taxonomy.—In the discriminant analysis of adult male and adult female leopards, the Javan specimens separated from the others as a distinct group (Figs. 2C and 2D), although this distinctness was less pronounced in the principal component analysis. This indicates that the Javan leopard is

craniomorphologically different from other leopard populations. The distinctness of the Javan leopard is supported by molecular data from Miththapala et al. (1995) and Uphyrkina et al. (2001). The first study, using allozymes, mitochondrial DNA restriction sites, and feline-specific minisatellites, found evidence for the phylogenetic distinction of six geographically isolated groups of leopards: (1) Africa, (2) Central Asia, (3) India, (4) Sri Lanka, (5) Java, and (6) East Asia. The study by Uphyrkina et al. (2001) using mitochondrial DNA sequences (727 bp of *NADH5* and control region) identified 9 distinct groups, which they proposed as revised subspecies of *P. pardus*. These groups coincided with those found by Miththapala et al. (1995), with Indian leopards clustering with Sri Lankan individuals (83% bootstrap support), and the 3 East Asian subspecies forming a monophyletic lineage with high statistical support (99%); the Javan subspecies was found to be a sister species to all other South and East Asian leopards, although sample size of this subspecies was small.

The pelage characteristics of the Javan leopard also suggest that it is distinct from its geographically nearest relative on the Thai-Malay Peninsula (Chasen 1940; Pocock 1930) and *P. p. delacouri* from Indochina (Pocock 1930; Weigel 1961). Hemmer (1967) indicated that the size and density of the rosettes of the Javan leopard were more like those of African leopards than of other Asian leopards.

The slight differentiation based on craniometrics of *P. p. kotiya*, the Sri Lankan leopard, from the Asian mainland leopards is concordant with the molecular findings by Miththapala et al. (1995), who reported that *P. p. kotiya* is different from, but closely related to, *P. p. fusca* (their subspecies from the Indian subcontinent).

The skulls from Malaysia and Indochina, although few in number, appear to group with skulls from China, India, Nepal, and Kashmir (Figs. 2B, 2C, and 2E), rather than with the geographically nearer Javan specimens, although there were some exceptions to this. Additional specimens from Malaysia and Indochina are required to test whether a much larger sample would lead to more variation in the data and more overlap with any of the other geographic groups. Further research could also indicate whether Malaysian leopards are morphologically more closely related to those from mainland Asia or from Java, an important factor in the leopard's biogeographic history (see below).

The fact that the craniometric analysis did not differentiate the African from the Asian skulls, as would be expected from the molecular data, might be caused by the low number of specimens from Africa. Also, the African specimens originated from geographically distant locations (including Zanzibar, Sinai, Ethiopia, Somalia, Angola, and Southwest Africa) and the considerable morphological variation among these specimens (see high standard deviations in Appendix II and III for African and also West Asian specimens) would have led to lower discriminant resolution. I expect that if more African and West Asian skulls are added to the sample the group will separate more distinctly from the Asian skulls.

Having discussed the morphological variation in leopards, the question arises what implications this could have for the

taxonomy of *P. pardus*. This is an important question because taxonomic changes could have wide-ranging consequences for the conservation biology and management of the species. For instance, captive breeding program managers need to know how taxa are related to each other to maintain maximum genetic diversity, or governments need to specify units to be protected under law. In the present paper, the question is whether the Javan leopard is so distinct that it could be elevated to species level. Using a phylogenetic species concept (Cracraft 1997; Cracraft et al. 1998), this would require that 100% of the Javan leopard specimens of at least 1 age or sex class can be distinguished from equivalent categories from all other geographic groups.

Miththapala et al. (1995) concluded that the Javan leopard was distinct from other Asian leopards, based on high bootstrap support (99%), but they retained the trinomial, because, quoting from Avise and Ball (1990), “they have extrinsic barriers of reproduction,” being isolated on an island. The craniometrical and phylogenetic characters of the Javan leopard appear to support the distinctness of this taxon. I believe, however, that the case for specific distinctness of the Javan leopard is not yet convincing enough, especially because there is a lack of specimens from Malaysia and Indochina. More craniometric and genetic study is therefore required to determine whether there is overlap or whether Javan leopards are diagnostically distinct from all other leopards.

Biogeography.—One of the unexplained mammalian mysteries is how the leopard ended up on Java when it is absent from Sumatra and Borneo. There are also no reliably identified fossils of leopards from either Sumatra or Borneo, although Late Pleistocene fossils of many other species have been found on these islands. At present, shallow seas separate Java, Sumatra, Borneo, and the Malay Peninsula, but these areas were connected by land during periods of low sea level in the Pleistocene (Molengraaff and Weber 1920; Tjia 1970; Voris 2000). If it is assumed that leopards migrated to Java some time during the Pleistocene, then how could they have bypassed Sumatra and Borneo, and if they did not, why did they become extinct on these two islands? Below I put forward a hypothesis on how this could have happened.

The oldest African leopard remains were found in southern Africa and dated at 3.5×10^6 years old (Turner and Anton 1997). Hemmer and Schütt (1973) reported leopard fossils from the Pinjor Stage in the Upper Siwaliks of India dated at about 2×10^6 years ago, which seems to be nearly contemporaneous with appearances of leopards as fossils in Yunnan Province, southern China at about 1.7×10^6 years ago (Pan 1993). In Vietnam and Cambodia, leopard fossils have been found at several sites, dated between 475 and 80×10^3 years ago (see Olson and Ciochon 1990). According to Hemmer and Schütt (1973), fossils of leopards in Java date back to the Middle Pleistocene, whereas von Koenigswald (1933) considered fossil bones tentatively identified as leopard to belong to the Ngangdong Fauna (Middle–Late Pleistocene). Hemmer and Schütt (1973) suggested that Pleistocene leopards on Java were more similar to leopards that occurred in Pakistan during the Early–Middle Pleistocene (about $2\text{--}0.8 \times 10^6$ years

ago) than to present-day subspecies of continental Asia. From these palaeontological findings I tentatively conclude that the leopard migrated from Africa to Asia in the Early Pleistocene and from South Asia to Java some time during the Middle or Middle–Late Pleistocene.

The migration scenario that follows from the fossil record is confirmed by molecular data. Miththapala et al. (1995) estimated the divergence of the Javan leopard from the ancestral taxa of the Malaysian and Asian leopards at about 800×10^3 years ago. Uphyrkina et al. (2001) suggested a later date; their small sample size for Javan leopards precluded an estimate of their divergence time, although their data suggested that this happened between 830×10^3 and 169×10^3 years ago. These molecular phylogenies suggest that divergence of Javan leopards from its mainland relatives followed dispersal from Africa during the Middle Pleistocene.

It remains unclear by which way leopards migrated from the Asian mainland to Java. Migration could have followed a land bridge between Peninsular Malaysia and Java, as hypothesized by Meijaard (2003). What is clear is that during the Middle–Late Pleistocene (about $800\text{--}20 \times 10^3$ years ago) there were several periods of lower sea level, some of which could have exposed at least parts of the Sunda Shelf (the present-day shallow sea area between Malaya, Borneo, Sumatra, and Java), potentially allowing leopards to migrate from Java back into Borneo, Sumatra, and mainland Asia. The entire Sunda Shelf became exposed during the last glacial maximum (e.g., Beaufort 1926; Molengraaff and Weber 1920; Tjia 1980; Verstappen 1975, 1980). The question is why the Javan leopard did not use the land connections to disperse to Sumatra and Borneo.

To investigate why leopards do not occur on Borneo and Sumatra an ecological assessment is required of the leopard and its potential habitat on Java, Sumatra, and Borneo. Modern Asian leopards have a varied diet, but show a preference for small-to-medium-sized ungulates (Nowell and Jackson 1996), and they better tolerate open, drier habitat than tigers (*Panthera tigris*—Santiapillai and Ramono 1992). But how well can leopards tolerate tropical rainforest conditions, especially in competition with tigers and clouded leopards (*Neofelis nebulosa*)? Where tigers and leopards coexist, the former can displace the latter both temporally and spatially; the extent to which this occurs depends on the magnitude of prey biomass, especially the biomass of ungulates in smaller size classes, and the density of the vegetation (Seidensticker 1976). This is supported by Santiapillai and Ramono’s (1992) finding that Javan leopard numbers increased after the extinction of the Javan tiger, and Schaller (1967) reported that leopards were few in areas where tigers occur. In several areas where large predators occur, only those with high ungulate biomass contain tiger and leopard (and in one area also clouded leopard; Table 1). Below a biomass of about 900 kg/km^2 only 1 large predator seems able to survive. Taman Negara, a tropical evergreen forest area in Peninsular Malaysia, seems to be the exception to this trend, because there the 3 large cat species co-occur even though prey biomass was estimated to be quite low (Kawanishi 2002).

TABLE 1.—Estimates of ungulate biomass and presence of big cat species in several areas in South and Southeast Asia.

Area ^a	Ungulate biomass (kg/km ²)	Large cats present	Main vegetation	Source
India				
Gir WS	3,292	Leopard, lion	Forest with tree savanna and scrub	Khan et al. 1996
Nagarhole	3,000 ^b	Tiger, leopard	Deciduous forest	Karanth and Sunquist 1995
Kaziranga NP	2,858	Tiger, leopard	Alluvial forest and tall grass	Eisenberg and Seidensticker 1976
Kanha NP	1,708	Tiger, leopard	Mostly forest	Eisenberg and Seidensticker 1976
Jaldapara WS	984	Tiger, leopard	Alluvial forest and tall grass	Eisenberg and Seidensticker 1976
Sri Lanka				
Gal Oya NP	886	Leopard	Forest, savanna, grass	Eisenberg and Seidensticker 1976
Wilpattu NP	766	Leopard	Forest, savanna, grass	Eisenberg and Seidensticker 1976
Nepal				
Chitwan NP	1,790	Tiger, leopard	Mixed forest and open areas	Eisenberg and Seidensticker 1976
Thailand				
Huai Kha Kaeng WS	901–1,985	Tiger, leopard, clouded leopard	Deciduous and evergreen forest	Srikosamatarata 1993
Malaysia				
Taman Negara NP	200–400	Tiger, leopard, clouded leopard	Tropical evergreen forest	Kawanishi 2002
Java				
Baluran NP	1,015 ^c	Leopard (tiger is extinct)	Deciduous forest and grasslands	Hoogerwerf 1970
Ujung Kulon NP	492 ^c	Leopard (tiger is extinct)	Mostly forest, some grass	Hoogerwerf 1970
Borneo				
Ulu Segama	550 ^{b,d}	Clouded leopard	Tropical evergreen forest	M. J. Heydon in litt.
Kayan-Mentarang NP	107 ^b	Clouded leopard	Hill dipterocarp forest	C. Yeager in litt.
Sumatra				
Bukit Barisan NP	631 ^{b,e}	Tiger, clouded leopard	Tropical evergreen forest	O'Brien et al. 2003

^a NP = National Park, WS = Wildlife Sanctuary.

^b Estimated from densities and weights given in source.

^c Biomass estimated with Hoogerwerf's estimate of total number of each species multiplied by average body weights and divided by area of the park.

^d Pigs not included because their density fluctuates considerably; biomass estimate therefore is a minimum.

^e Estimated biomass for tapir (20 kg/km²—Whitten et al. 2000) added to estimated ungulate biomass.

The data in Table 1 are not conclusive; assessing ungulate biomass is difficult and the estimates in Table 1 were derived by a variety of methods. Still, they tentatively suggest that in the tropical, evergreen rainforests of Borneo and Sumatra, prey densities might have been too low (or might have fluctuated too much, as for bearded pigs, *Sus barbatus*—Caldecott et al. 1993) to sustain more than one large cat species. The low estimates for ungulate biomass in Asian tropical rainforests are similar to those from various vegetation types in Africa with much lower estimates in rainforest than in riverine forest and savanna or savanna woodland (reviewed by Plumptre and Harris 1995). Because Sumatra's volcanic soils generally sustain a higher biomass than the less fertile Borneo (MacKinnon et al. 1996), the former might have provided sufficient resources for two species, the tiger and the clouded leopard, and the dhole (*Cuon alpinus*) would have provided further competition for the leopard (see Karanth and Sunquist 1995); Borneo probably only provided enough resources for the clouded leopard. The partly arboreal clouded leopard is well adapted to stalking prey in rainforest (Rabinowitz et al. 1987). On Java, vegetation structure has generally been more open than on Borneo and Sumatra, with grassy areas and

deciduous forest as well as tropical rainforest, and throughout the Pleistocene and Holocene there was an abundance of ungulate species (e.g. Medway 1971); this has allowed leopards, tigers, and clouded leopards to co-exist (clouded leopards became extinct here in the Holocene, and tigers in the 1970s). Although ungulate biomass estimates for Peninsular Malaysia (where tiger, leopard, and clouded leopard occur) were reported to be low, folivore monkey densities were 5–10 times higher than in Sabah, Borneo (Payne, 1990); Payne suggested this was primarily caused by lower soil fertility in Sabah and thought that this could explain the absence of tigers and leopards from Borneo. Seidensticker (1986) similarly speculated that leopards and tigers are absent from Borneo due to a deficiency of large ungulate prey, and leopards from Sumatra by an abundance of other felids. Wong (2002) concluded that the absence of large carnivores from Borneo is a consequence of the low density of prey species, which in turn is related to the ecological effects of mass fruiting cycles of the dominant tree species of Dipterocarpaceae and the structure of the forest itself.

Finally, in addition to the ecological barriers that might have prevented leopards from dispersing into Sumatra and Borneo,

there were also considerable physical barriers that could have stopped or delayed the dispersal of leopards. The landmasses of Java and Borneo were separated by two large rivers that flowed along the length of the present Java Sea (near 1 in Fig. 1), whereas Sumatra and Java were similarly separated by a river in the present Sunda Strait (near 2 in Fig. 1), and Malaya and Borneo were separated by the very large Molengraaff (near 3 in Fig. 1) and Siam (near 4 in Fig. 1) rivers on the northern Sunda Shelf.

In conclusion, I hypothesize that Javan leopards arrived on the island of Java during the Middle Pleistocene, and since then little or no gene flow has occurred between leopards on Java and those in other parts of Asia. In light of its distinctiveness, and its status on the IUCN's Red List of Threatened Species as Endangered (<http://www.redlist.org>, accessed 10 October 2002), I urge conservation authorities to give renewed conservation attention to the Javan leopard. A Java-wide survey would be an important first step towards achieving this goal.

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APPENDIX I

Specimens examined.—Specimens were measured in the following museums: Zoological Museum Cibinong (formerly known as Museum Bogoriense), Indonesia (ZMC); Zoological Reference Collection, Singapore (ZRC); National Museum of Natural History, Leiden, The Netherlands (NMNH); The Field Museum, Chicago, Illinois, USA (FMNH); Natural History Museum of Los Angeles County, California, USA (LACM); and the Natural History Museum, London, United Kingdom (BMNH). In addition, 1 skull was measured in the Baluran National Park, East Java.

Africa: BMNH 19.9.30.2 (Zanzibar Island); BMNH 31.9.27.1; BMNH 4.5.9.35 (Somaliland); BMNH 29.12.23.2 (Sinai); BMNH 35.9.1.130 (SW Africa); FMNH 1446 (Ethiopia).

Burma and Thailand: BMNH 29.6.1.17; BMNH 29.9.1.9; LACM #8216; ZRC 4.1083.

China: BMNH 2.6.10.5; BMNH 10.5.2.9; BMNH 67.1.8.2; FMNH 33469.

East Asia: BMNH 95.10.19.1 (Amur Bay).

India: BMNH 115 k; BMNH 25.1.3.2; BMNH 25.6.13.1; BMNH 26.10.8.19; BMNH 26.10.8.22; BMNH 27.2.14.23; BMNH 29.6.1.15; BMNH 29.6.1.10; BMNH 29.9.26.1; BMNH 29.9.26.2; BMNH 30.1.4.4; BMNH 31.1.10.4; BMNH 31.1.10.5; BMNH 31.9.21.3; BMNH 32.8.24.3; BMNH 34.4.11.1; BMNH 34.8.17.5; BMNH 34.8.17.6; BMNH 61.453; FMNH 27443; FMNH 34872; FMNH 91259; ZMC 6862.

Indochina: BMNH 28.7.1.31 (Annam); FMNH 31792; FMNH 31793 (Laos).

Java: Baluran 961; BMNH 1938.11.30.16; BMNH 9.1.5.596; NMNH 940; NMNH 4702; NMNH 4705; NMNH 23097; NMNH 33834; NMNH 33835; NMNH 33837; NMNH 33838; NMNH 33840; NMNH 38665; ZMC 69; ZMC 115; ZMC 174; ZMC 521; ZMC 1618; ZMC 1684; ZMC 3193; ZMC 3374; ZMC 3790; ZMC 6838; ZMC 6839; ZMC 6840; ZMC 6841; ZMC 6844; ZMC 6845; ZMC 6846; ZMC 6847; ZMC 6849; ZMC 6850; ZMC 6852; ZMC 6853; ZMC 6856; ZMC 6860; ZMC 8314; ZMC 12848.

Malaysia: ZRC 4.1085; ZRC 4.1087; ZRC 4.1088; ZRC 4.1089; ZRC 4.1090.

Nepal: BMNH 115 a; BMNH 41.12.4.1; BMNH 45.1.8.24; BMNH 45.1.8.29; NMNH "cat. Jentink 1887."

Sri Lanka: BMNH 1937.7.30.1; BMNH 26.6.1.8; BMNH 31.1.2.12; BMNH 31.1.2.13; BMNH 31.1.2.15; BMNH 31.1.2.16; BMNH 31.1.2.19; BMNH 31.1.2.21; BMNH 31.1.2.22; BMNH 31.1.2.23; BMNH 31.1.2.25; BMNH 36.1.22.7; BMNH 46.197; BMNH 46.219; BMNH 46.219; BMNH 54.649; BMNH 75.2277; FMNH 99534; FMNH 99535; FMNH 99536; FMNH 99538.

West Asia: BMNH 34.8.12.1 (Baluchistan); BMNH 55.1182 (South Persia); BMNH 55.428 (Yemen); BMNH 91.10.7.8; BMNH 91.10.7.177 (Sind); FMNH 57956 (Iran); FMNH 60626 (Afghanistan).

APPENDIX II

Skull measurements (in mm) for male leopards for all age classes (in mm). Abbreviations for skull variables are given in methods section of text.

	Malaya and Indochina			Java			Sri Lanka			China, India, Nepal, and Kashmir			Africa		
	\bar{X}	<i>n</i>	<i>SD</i>	\bar{X}	<i>n</i>	<i>SD</i>	\bar{X}	<i>n</i>	<i>SD</i>	\bar{X}	<i>n</i>	<i>SD</i>	\bar{X}	<i>n</i>	<i>SD</i>
GL	220.3	3	10.1	203	24	14	226.9	12	21.8	225	24	18.8	207.7	4	20.4
BPL	184.7	3	8.8	169.4	24	10.3	193.1	12	15.8	190	22	16.2	175.9	3	19.3
CBL	197.2	3	7.4	181.1	24	10.7	202.4	11	21.4	203.7	21	15.7	191.2	4	16.6
ZW	141.3	3	8.7	131.2	24	8	146.5	12	14.6	144.8	23	14.5	131.6	4	15.2
BC	59	3	4.2	53.3	24	2.9	56.6	12	9.7	56.9	24	4.4	52	4	3.9
IO	39.5	3	3	36	24	2.4	40.2	12	4.4	40.3	24	4.5	34.6	4	3.4
Info	59.1	3	1.8	53.1	24	2.3	58.8	12	5.2	59.2	24	5	52.7	4	4.1
PO	42	3	2.7	40.2	24	1.9	43.8	12	2.6	42.9	24	2.9	41	4	2.6
OB	80.5	2	14.6	64.8	22	3.5	79.1	11	13.4	71.8	20	6.4	68.1	3	3.8
OHB	62.8	3	4.8	59.7	24	4.3	63.4	12	5.4	63.6	22	6	56.4	3	5.7
OHO	41.4	3	3.3	40.4	23	3.3	43.9	12	4.9	44.2	21	5.8	35.9	3	4.8
ML	144.4	3	6.7	132	24	8.8	150.1	12	13.3	147.9	22	11.3	138.4	4	13.2
MH	68.6	3	3	61.3	24	5.1	69	12	8.9	70.5	22	8.3	61.8	4	6.6
LTR	78.5	3	1.9	72.6	24	3.7	79.3	12	6.5	79.3	23	4.4	77.1	4	5.3
GDB	32.4	3	2	28.3	24	1.8	32.4	12	2.2	32.2	22	2.2	30.7	3	1.2
LDB	20	3	2.1	18.4	24	1.1	18.6	12	1.5	18.9	22	1.6	18.2	3	1.4

APPENDIX III

Skull measurements (in mm) for female leopards for all age classes (in mm). Abbreviations for skull variables are given in methods section of text.

	Malaya and Indochina			Java			Sri Lanka			China, India, Nepal, and Kashmir			Africa			West Asia		
	\bar{X}	<i>n</i>	<i>SD</i>	\bar{X}	<i>n</i>	<i>SD</i>	\bar{X}	<i>n</i>	<i>SD</i>	\bar{X}	<i>n</i>	<i>SD</i>	\bar{X}	<i>n</i>	<i>SD</i>	\bar{X}	<i>n</i>	<i>SD</i>
GL	184	9	9	170	13	10	194	9	5	195	13	9	183	3	15	193	5	19.6
BPL	154	8	7	144	13	9.2	166	9	4	165	13	7.2	154	3	14	165	5	16
CBL	166	7	8	155	13	9.5	178	9	5	177	13	7.6	166	3	14	175	5	16.8
ZW	120	9	6	110	12	6.7	127	9	4	127	13	5.3	114	3	19	124	5	13
BC	49.6	9	2	46.2	12	3.1	49.9	9	1	49.7	14	1.4	44.9	3	7.9	48.2	5	5.8
IO	33.2	9	2	31.3	13	2.7	34.3	9	2	35.4	13	3.1	33.3	3	5.2	38.1	5	4.3
Info	50.3	8	2	47.3	13	2.5	51.7	9	2	52.6	14	1.8	47.4	3	5.7	53.7	5	3.8
PO	41.8	9	2	40.5	13	1.5	42.2	9	2	41.1	12	2.5	38.3	3	7.2	42.9	5	3.6
OB	63.5	9	5	59	13	6.3	66.1	9	7	66	13	8	62.4	2	11	68.5	5	13.7
OHB	51.6	8	3	50	13	2.9	54.2	9	2	55	13	3	50.2	3	5.6	54.4	5	6.4
OHO	32.2	7	3	31.9	13	2.2	36.2	9	2	36.8	13	2.9	33.2	3	3.6	35.7	5	4
ML	123	8	6	110	12	8	131	9	3	130	13	5.8	118	3	14	129	5	15.2
MH	57.1	9	5	49.7	12	4.7	57.4	9	2	59.2	14	3.6	53.6	3	8.1	55.7	5	7.2
LTR	68.6	9	3	62.8	12	3.8	70.6	9	2	70.4	14	3.9	66.6	3	5.9	70.4	5	7.7
GDB	28.6	9	2	25.7	12	1.4	30.3	9	1	28.9	13	1.7	29.3	3	4.3	28.8	5	2.4
LDB	18.1	8	1	16.2	12	0.8	16.8	9	1	16.6	13	1.6	18.4	3	2.6	16.3	5	1.1