Seidensticker '86

# LARGE CARNIVORES AND THE CONSEQUENCES OF HABITAT INSULARIZATION: ECOLOGY AND CONSERVATION OF TIGERS IN INDONESIA AND BANGLADESH

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ABSTRACT:

The tiger (*Panthera tigris*) emerged from the 1969 IUCN meeting in New Delhi as a focal animal in international conservation efforts. A decade later populations of 4 subspecies (*P. t. tigris, P. t. corbetti, P. t. altaica/-longipilis, P. t. sumatrae*) seem relatively secure but populations of the other forms (*P. t. virgata, P. t. amoyensis, P. t. sondaica, P. t. balica*) are deplete or extinct.

Conditions that led to the extirpation of tigers in Bali and Java and the survival of tigers in Sumatra and the Bangladesh Sundarbans are examined. The extirpation of tigers on Bali and Java was attributed to extensive habitat fragmentation and the insularization of small habitat blocks and reserves ($<500$ km$^2$), widespread loss of critical ungulate prey through disease, and direct mortality by man. Large tiger populations survived in the large, remote blocks of contiguous habitat in Bangladesh (6000 km$^2$) and Sumatra (where some blocks exceed 30,000 km$^2$). Inbreeding coefficients $>0$ in captive tiger populations reduce survivorship of young and reduce fertility. The importance of maintaining an adequate effective population size is asserted for wild tiger populations. Initiatives to include wildlife management and conservation of natural areas within programs for economic advancement in Bali, Java, Sumatra, and Bangladesh are outlined.

Key words: Bali, Bangladesh, conservation, habitat, Indonesia, insularization, Java, *Panthera tigris*, regional planning and conservation, Sundarbans, Sumatra, tiger.

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Legal protection and the establishment of protected areas have been cornerstones in conservation programs to check declines and restore threatened and endangered large vertebrates. These steps are accomplished only through tremendous effort by conservationists. Hence, Holloway's (1978) report to the Survival Service Commission's Deer Working Group was deeply disturbing:

> An analysis of population trends compared with the protected status of mammals that are threatened with extinction throughout their world range, however, shows that although nearly 90% of these taxa have complete or partial protection by law and over 50% of them occur in one or more protected areas, at least half of the total population of these species and subspecies are still considered to be decreasing. A more detailed examination of these data demonstrates no marked improvement in population trends with increased protective effort, as measured by categories of protection that the species have been granted (p. 393).

Holloway's analysis suggested that a threshold or plateau in system performance had been reached in spite of increased protective efforts. I have graphically depicted my interpretation of this finding in Fig. 1. An increase in performance beyond the plateau would be obtained by increasing population size of the target species, establishing additional secure populations, and ensuring genetic diversity is maintained through adequate effective population size for each management area. Protective efforts are one component in the complexity of the conservation system. Other components that increase complexity are management initiatives such as habitat improvement, securing and protecting larger reserves, protecting essential habitats outside reserves, and incorporating protection and habitat requirements for target species within land management systems surrounding reserves.

Holloway's estimates indicate about half of the world's threatened and endangered mammals are beyond reach of increased protective efforts alone. Restoration of these or even a subset of these will require what Terborgh and Winter (1980) have called "corrective and preventative management" which they suggest "will have to become bywords of the conservation movement world around." They refer specifically to management actions that must be taken to ensure that benign neglect does not allow dangerous imbalances to occur within reserves or ecosystems that have been preserved. This view is too restricted. The idea of "corrective and preventative management" is part of increasing the complexity of the conservation system (Fig. 1) in general and needs to be applied in a larger conservation context to include: 1) species

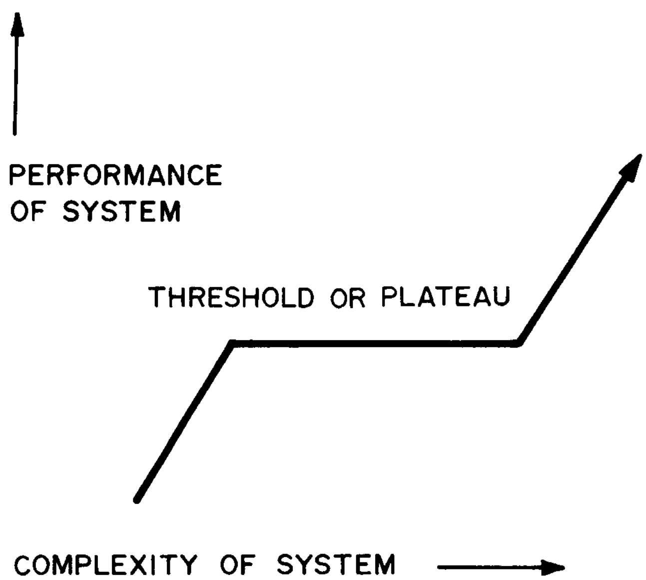



Figure 1. Performance and complexity of the conservation system: improving performance equals improvement in population trends, factors that ensure the security of taxonomic forms, and ecosystem integrity; system complexities can be external and/or internal and include added degrees of protection and increased attention by the system to technological, socio-economic and biological constraints to management.

that occur outside strict nature preserves (see Giles, 1978, for definitions of the different classes of protected areas), and 2) range sensitive species that cannot be contained in strict preserves given a region's economic realities. Institutionalizing the idea of "corrective and preventative management" requires asking how specific measures required for a particular species will be determined. How these can be included within local and national administrative and cultural/political systems. How a particular management action or set of management actions, once decided upon, will be financed. In this paper I report on efforts to address these questions in conserving tigers in South and Southeast Asia.

Concern for the tiger's survival in India and throughout its range was roundly expressed at the 1969 New Delhi (India) meeting of the International Union for the Conservation of Nature and Natural Resources (IUCN) by a consensus of very senior conservationists (S. Ali, Z. Futehally, J. C. Daniel, G. Mountfort, S. D. Ripley). Subsequently in 1972, IUCN and its sister organization, the World Wildlife Fund, initiated "Operation Tiger" or "Save the Tiger" to raise funds, to generate international public support, and encourage national governments within the tiger's range to undertake their own action programs (Mountfort 1981).

Through the 1970's this combined international and national thrust became a focus to conserve Asian wildlife in general. The Government of India launched a program that was partially independent of established administrative structures (IBWL 1972, Saharia 1982). However, most countries within the tiger's range worked with established administrative services to initiate programs that included all or part of the following elements: national policy declarations; moratoriums on tiger hunting; new protective legislation for wildlife in general; upgrading and/or expanding existing reserves; establishing new reserves; strengthening administrative support through increased allocations for staff, staff training, equipment and facilities; undertaking outreach projects to inform administrators in other services, politicians, and the public of the plight of wildlife in general and the tiger specifically; surveys to determine distribution and abundance; basic research on tiger habitat, population structure and dynamics; becoming a party to the International Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES); and joining international captive breeding efforts or at least listing captive tigers in international registers such as the *International Zoo Yearbook* (IZY) and the *International Tiger Studbook.* Table 1 shows that an impressive effort was made throughout Asia. No conservation program or combination of programs in the past compares with this in extent and magnitude.

By 1979 when representatives from most countries involved met in New Delhi at the International Symposium on the Tiger, wild populations of 4 subspecies—*P. t. tigris, P. t. corbetti, P. t. altaica/-longipilis,* and *P. t. sumatrae* (Fig. 2)—were declared relatively secure as long as the newly established conservation measures were maintained (Jackson 1979). Four subspecies—*P.*

Table 1. Actions taken to conserve tigers and other wildlife in selected Asian countries since 1969.

| | India | Nepal | Bangladesh | Thailand | Indonesia | China |
|---|---|---|---|---|---|---|
| Moratorium on tiger hunting | + | + | + | + | + | ? |
| Protective legislation for wildlife and habitats | + | + | + | B | BP | BP |
| Upgrading and/or expanding existing reserves/parks | + | + | + | + | + | + |
| Establishing new reserves | + | 0 | 0 | + | + | + |
| Wildlife habitat needs included in forest management | 0 | 0 | 0 | 0 | 0 | ? |
| Increase staff & facilities | + | + | P | + | + | ? |
| Outreach programs | + | + | P | + | + | + |
| Surveys to determine tiger distribution and abundance | + | + | + | 0 | + | + |
| Basic research on tiger habitat needs | + | + | + | 0 | + | ? |
| Basic research on tiger population behavior and dynamics | + | + | 0 | 0 | 0 | ? |
| Party to CITES | 1976 | 1975 | 1982 | 0 | 1979 | 1981 |

Notes: + = considerable action; 0 = little or no action; P = planned action; B = in place before 1969; ? = not known to me; Date = date the country became a party to the Convention.
Sources: Blower et al. 1977; Goodland 1981; IBWL 1972; Library of Congress 1979*a*, 1979*b*, 1980*a*, 1980*b*; McNeely 1975; Mountfort 1981; Seidensticker and Hai 1983; Saharia 1982

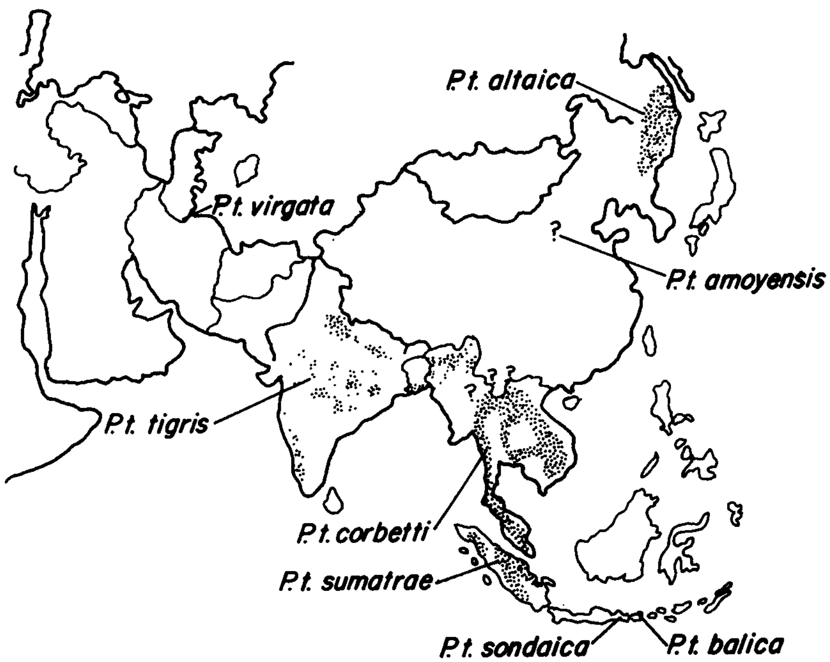



Figure 2. Distribution of *Panthera tigris* ca. 1975: *P. t. virgata*, extinct (Joslin, person. commun.); *P. t. tigris* (Sankhala 1979); *P. t. corbetti* (Lekugal and McNeely 1977); *P. t. amoyensis*, a few (Lu and Shen, this volume); *P. t. altaica* (Matjushkin et al. 1977, 1978; Lu and Shen, this volume); *P. t. sumatrae* (this report), *P. t. sondaica* and *P. t. balica*, extinct (this report).

*t. virgata, P. t. amoyensis, P. t. sondaica,* and *P. t balica*—were deplete or extinct. Joslin (pers. commun.) reported on the status of the Caspian tiger (*P. t. virgata*) and Lu and Shen (this volume) reported on the decline of the central Chinese tiger (*P. t. amoyensis*).

Between 1976-1978 my colleague Ir. Suyono and I undertook field surveys for *P. t. balica, P. t. sondaica* and *P. t. sumatrae,* tiger subspecies found respectively on the Indonesian islands of Bali, Java, and Sumatra (Fig. 2, 3*a*). I was invited in 1978 and again in 1980 to visit the Sundarbans Forest on the Ganges delta. With M. A. Hai, I assisted in planning wildlife conservation as part of forest management practices in the Bangladesh coastal zone. These surveys and planning exercises form the basis of this report which is directed towards identifying factors which led to the extirpation of 2 tiger subspecies and the survival of 2 others. My focus is on the Sunda or island tigers. The Sundarbans has long been isolated from any adjoining forest tract, and its tiger population is also an insular one; albeit, this island is fundamentally different from the others. My aim in this paper is to identify ways and means to further the management of tigers and all South and Southeast Asian wildlife.

I acknowledge my heavy intellectual debt to John Eisenberg for impressing upon me the value of understanding historic and phylogentic inertia and its constraints on any evolving system and to Clifford Geertz for his many insights into the sociology of the regions where I have worked. The World Wildlife Fund and the Governments of Indonesia and Bangladesh encouraged and funded the surveys upon which this report is based. The National Geographic Society supported my work in Bangladesh in 1980. The National Zoological Park, Smithsonian Institution, supported this work from its inception. I thank my colleagues and friends in Indonesia, Bangladesh, Gland, and at the National Zoological Park for their encouragement and assistance in an undertaking that has spanned 8 years.

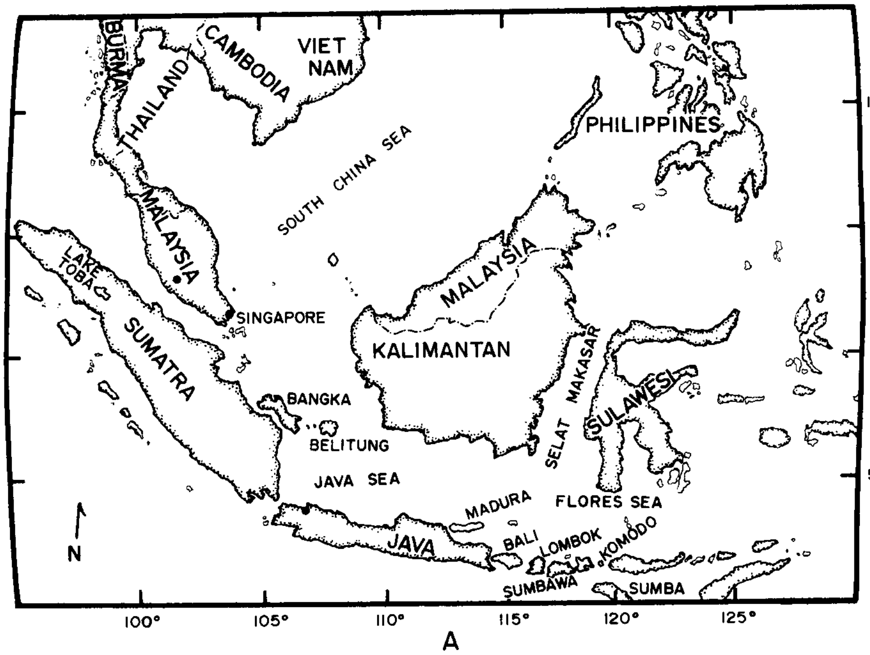
## TIGER SUBSPECIES AND CAPTIVE POPULATIONS OF SUNDA TIGERS

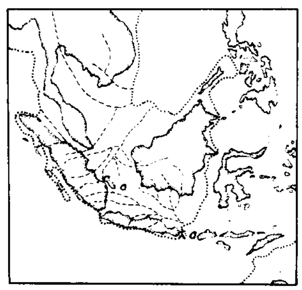
The tigers in the Sundarbans are the subcontinent subspecies *Panthera tigris tigris* (Linnaeus 1758). Mazak (1976, 1981) confirmed earlier taxonomists and assured us that tigers found on the islands of Bali, Java, and Sumatra are valid subspecies: *P. t. sumatrae* (Pocock 1929) on Sumatra, *P. t. sondaica* (Temminck 1844) on Java, and *P. t. balica* (Schwarz 1912) on Bali (Fig. 3*a*). Table 2 and Figure 4 summarize the diagnostic cranial and coat differences and Mazak's data on size.

It has often been reported that the island subspecies are notably smaller than those found on the mainland with *balica* the smallest form (Pocock 1908; Sody 1933*a*, Hooijer 1947). I was impressed by this size difference after viewing living tigers from Sumatra, Nepal, India, and Bangladesh. To the great credit of his industry and dedication, Mazak (1981) has ferreted out hard data (Table 2); *balica* is the smallest form based on the 8 specimens that have survived in museums (Mazak et al. 1978). There is little difference between *sumatrae* and *sondaica* and both are smaller than *tigris.* The diameter of the tracks of *sondaica* and *sumatrae* on similar surfaces, however, are larger than I have seen for *tigris* in Bangladesh, India, or Nepal. Hoogerwerf (1970) also noted the large size of *sondaica* tracks.

The earliest known fossil tigers come from the lower Pleistocene Trinil deposits of central Java (Hemmer 1971, 1979; De Vos et al. 1982). These first tigers were as large as or larger than any of the tiger subspecies alive today. The series of tiger fossils available from the Java deposits shows considerable variation in size over time (Hooijer 1947, 1949; Hemmer 1971). Hooijer and Hemmer have associated this variation in size with fragmentation and rejoining of populations but they did not identify causal factor(s). Fossils of leopards *Panthera pardus* from Java are few, but they also show a marked variation in size with the largest individuals from the mid-Pleistocene (Hemmer and Schutt 1973).

Mazak (1981) attributed the small size of the Island tigers to Bergmann's rule "and can be explained from the viewpoint of thermoregulation." A decade earlier McNab (1971) examined this "rule" from an ecological perspective and concluded that body size in hunters is mainly determined by the frequency distribution of the size of prey available and the presence of species that use



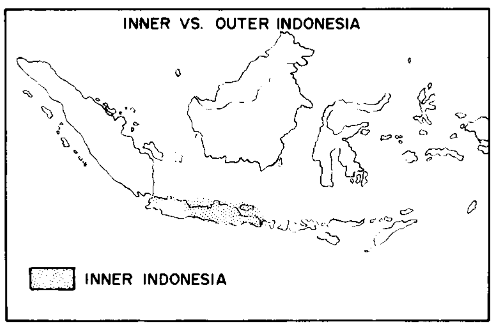




Figure 3. Southeast Asia: A) Islands and mainland areas with place names. Kalimantan, Brunei, and East Malaysia form the Island of Borneo. The Isthmus of Kra is at the southern tip of Burma. B) The Sunda Shelf is indicated by the dotted line and the dashed line indicates the old Sunda river systems (after Verstappen 1975). C) The location of outer and inner Indonesia (from Geertz 1963*a*).

Table 2. Characteristics of *Panthera tigris tigris, P. t. sumatrae, P. t. sondaica, P. t. balica.*

| | *tigris* | | *sumatrae* | | *sondaica* | | *balica* | |
|---|---|---|---|---|---|---|---|---|
| | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ |
| Adult size: wt. (kg) | 180-258 | 100-160 | 100-140 | 75-110 | 100-141 | 75-115 | 90-100 | 65-80 |
| Total length (mm) ("between pegs") | 2700-3100 | 2400-2650 | 2200-2550 | 2150-2300 | 2480 | — | 2200-2300 | 1900-2100 |
| Greatest length of skull (mm) | 329-378 | 275-311 | 295-335 | 263-294 | 306-349 | 270-292 | 295-298 | 263-269 |
| Ground coat color | lighter | | notably darker | | darker, richer | | darker, richer | |
| Color of underside | clean white | | dirty white | | a lighter shade | | a lighter shade | |
| of forelegs and throat | sharply defined | | unclearly defined ground color | | of same general ground color | | of same general ground color | |
| Stripes | fewer, widely spaced | | numerous, closely spaced, may have spots at ends | | numerous, very closely spaced may have spots at ends | | | |
| Occipital plane (see Fig. 4) | broad | | broad | | narrow | | narrow | |
| Bullae | normal | | normal | | normal | | somewhat flatter | |
| Nasals (see Fig. 4) | short and wide | | short and wide | | long and narrow | | long and narrow | |

Sources: Sody 1933a, Mazak 1981.

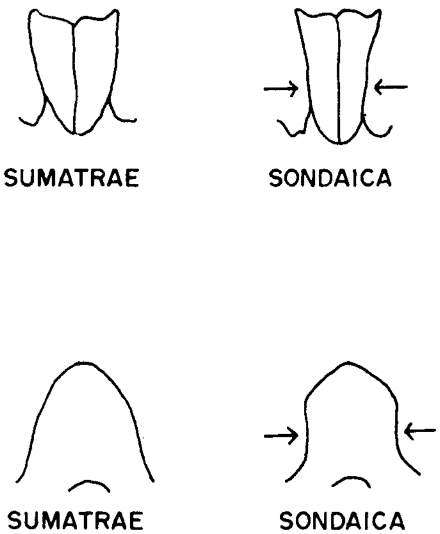



Figure 4. Diagnostic characteristics of the skulls of *Panthera tigris sumatrae* and *P. t. sondaica:* nasal bones, top; occipital region, bottom (after Hemmer 1969).

the same food resources. With no competitors and rusa (*C. timorensis*), the smallest *Cervus,* as its major prey, we find on Bali tigers with the smallest body form. With a more diverse prey base and competitors on Java and Sumatra, we see a larger body size but one well below the largest tigers from mainland Asia that feed on the largest *Cervidae* and *Bos.*

Pender and Barkham (1978) analyzed the breeding records of rare species reported in the *IZY* over the 15 years that such data had been collected. Their analysis of the data indicated that *P. t. altica, P. t. tigris* and *P. t. sumatrae* were self sustaining captive populations. There are no records or memory of Bali tigers ever being in a zoological collection (B. Galstuan, long-term director of the Jakarta Zoo, pers. commun.). Small numbers of Javan tigers are listed in some of the *IZY* summaries. P. Leyhausen (per. commun.) has cautioned that these were probably *P. t. sumatrae* and an examination of the Budapest Zoo "Javan" tiger confirmed it was the Sumatran form (Kutunidisz and Mazak, per. commun.). Documentation concerning the origins of these "Javan" tigers is not sufficient to include them in the *International Tiger Studbook* (Seifert and Muller 1980). B. Galstaun (per. commun.) told me that *P. t. sondaica* were common in Indonesian collections before World War II. During the war, these zoos and their collections were disbanded. Following the war when zoo collections were reestablished, Javan tigers were very rare in the wild and it was much easier to acquire Sumatran tigers which is the subspecies in Indonesian collections today.

Ballou and Seidensticker (1983) have undertaken a genetic and demographic analysis of the captive Sumatran tiger population. We found the deleterious effects of inbreeding (inbreeding coefficients $>0$) included increased juvenile mortality and reduced fertility. This also has been reported in other small inbred populations by Ralls and her colleagues (Ralls et al. 1979, Ballou and Ralls 1982). Seal and Foose (1983) obtained similar results for captive Siberian tigers in North American collections. There has been a fragmentation of the captive Sumatran tiger population into 2 genetic lines. One of those lines, that with the highest average inbreeding coefficient (0.41), in clearly on the way to extinction. The hypothesis that these results are the result of "outbreeding depression" (Shields 1982) has been tested with this and other data sets from mammals in zoological collections and rejected (Tempelton, Ralls, and Ballou, per. commun.). The number of lethal equivalent genes in any individual in the captive Sumatran tiger population has been calculated to be 5-10 (Ballou, per. commun.).

The problem of inbreeding depression is taken very seriously in the management of captive populations in zoological parks (AAZPA 1982). These results also define a critical condition for the management of tiger populations in small reserves or any tiger population where the effective population size ($N_e$) is less than several hundred (Foose and Seal, this volume).

## ZOOGEOGRAPHY OF SUNDERLAND AND TIGER HABITATS

The extent and fragmentation of exposed land area on the Sunda Shelf during the Pleistocene were associated with marked shifts in climate and punctuated with intense volcanic activity. During Pleistocene glacial maxima, the exposed shelf (Sundaland, Fig. 3*b*) had a land area of about 2.2 million $km^2$ (Eudey 1980). For comparison, India has a land area of 3.3 million $km^2$. There is a general concensus that 120,000 yr BP water levels were 5-8m above present levels (Verstappen 1975, Chappell and Thom 1977). (All my intensive study sites were then submerged.) The most recent regressive phase was about 18-12,000 yr BP at the Pleistocene-Holocene interface. Water levels may have been as low as −85m for much of the preceding 12,000 years (Biswas 1971, Verstappen 1975). Since then sea levels have remained about what they are today, and tiger populations on the Malay Peninsula, Sumatra and Java have been isolated from each other for the last 6,000 years.

Groves (unpublished rep.) has concluded that the Malay Peninsula and Sumatra form one zoogeographic unit as do Borneo/Bangka, Java/Bali, and Burma/Thailand. His analysis of relationships among island and mainland mammal assemblages indicates that in the late Pleistocene all of Sundaland was separated from the mainland by water at the Isthmus of Kra. The barriers formed by the great Sunda River system (Fig. 3*b*) and the distribution of rain forest refugia resulted in endemics and subspecies typical of these zoogeographic units. The tectonically active Sunda Shelf has been tilting so that the western and southern edges have been rising with a regression of the sea from west to east. The rising sea first separated the major zoogeographic units, followed by the further isolation of the islands we have today (Fig. 3*a*).

The first tigers were part of the Trinil assemblage that included *Hystrix* (*-Acanthion*), *Felis* (*-Prionailurus*), *Mececyon* (a canid), *Stegodon, Rhinoceros, Mun-*

*tiacus, Axis, Duboisia, Biobos (Bos), Bubalus, Sus, Presbytis (-Trachypithecus), Macaca,* and *Meganthropus (Homo).* Another Pleistocene assemblage found at Jetis/Kedung Brubus also includes *Manis, Lutra, Hyaena, Tapirus, Hippopotamus, Elephas, Cervus (-Rusa), Epileptobos* (DeVos et al. 1982, DeVos and Sondaar 1982). A listing of the recent assemblage of mammals for Java would include *Panthera, Hystrix, Felis, Cuon, Rhinoceros, Muntiacus, Bos, Bubalus, Cervus, Tragulus, Presbytis, Macaca,* and *Homo.* By including *Pongo, Elephas, Tapirus* and *Neofelis* and removing *Bos* and *Panthera parus* the same assemblage typifies the large mammal fauna of Sumatra today. In Bali and the Sundarbans, the tiger is sympatric with *Muntiacus, Cervus* or *Axis, Sus,* and *Felis* (Table 3). An inspection of these assemblages indicates that the tiger coevolved as the largest predator in a community of large ungulates. The essential component of any assemblage of which the tiger is part is cervids. Suids are also frequently found with tigers but appear to be much less important as food (Schaller 1967, Seidensticker 1976, McDougal 1977, Sunquist 1981).

During the last glacial period and 3-4 times before, the climate of Sundaland was continental and characterized by lower temperatures, much lower precipitation and a distinct dry season (Verstappen 1975, CLIMAP 1976). The vegetation mosaic during these periods of expanded land area would have been cores of rain forest refugia nested in vast expanses of monsoon forest and tree savanna. Rivers, in many places associated with large reed beds, converged as wide swamps in the low areas between the major islands. In picturing tiger habitat on the Sunda Shelf at that time, we should think of the Ganges system 200 years ago rather than today's Bornean and Sumatran rain forest habitat. Today, monsoon forests and tree savannas within the Sunda tigers' historic range are found only in east Java, west Bali, and the northern tip of Sumatra. The principal vegetation types in the Greater Sunda Islands are the various tropical rain forest formations (Ashton 1971, Whitmore, 1975).

The predominance of a single monsoon rainfall pattern with a tendency towards forest types that are seasonally dry and partially deciduous probably resulted in reduced ungulate diversity in South Asia when compared with East Africa (Eisenberg 1981). The extant large ungulates, banteng (*Bos javanicus*), gaur (*Bos garus*), water buffalo, (*Bubalus bubalis*), swamp deer (*Cervus duvauceli*), and the extinct Schomburgk's deer (*C. schombergki*) are predominately grazers. In South Asia the *Cervidae* emerged as the important radiation with extensive adaptation to both grazing and browsing niches (Eisenberg and Seidensticker 1976). The tiger, the largest cat, is their primary predator.

Hooijer (1975) noted that before the last rise in sea level the species pool of large mammals from which present island distributions had to draw was widespread over the Sunda Shelf. Table 3 shows that the Borneo/Bangko zoogeographic unit is relatively impoverished when it comes to large mammals. One and perhaps both *Cervus* species, probably *Elephas,* and *Bos* were introduced rather recently by man (Medway 1977, Wharton 1968). Lacking an abundant and/or diverse large ungulate prey base, the absence of tigers and leopards from Borneo is not surprising.

Table 3. Distribution of felids, canids and ungulates in the Greater Sunda Islands, Malay Peninsula, Thailand, and the Ganges Delta.

| | Sundarbans Forest Division[1] | Ganges Delta | Thailand | Malay Peninsula | Sumatra | Java | Bali | Borneo |
|---|---|---|---|---|---|---|---|---|
| Area ($km^2$) | 6,000 | 80,000 | 510,000 | 155,400[2] | 473,600 | 127,000 | 5,500 | 743,200 |
| Felidae | | | | | | | | |
| *Panthera tigris* | + | E | + | + | +[4] | E? | E | F[3,4] |
| *P. pardus* | 0 | E? | + | + | F[5] | + | 0[6] | 0 |
| *Neofelis nebulosa* | 0 | 0 | + | + | + | F | 0 | + |
| *Felis marmorata* | 0 | 0 | + | + | + | 0 | 0 | + |
| *F. teminicki* (inc. *badia*) | 0 | 0 | + | + | + | 0 | 0 | + |
| *F. planiceps* | 0 | 0 | 0 | + | + | 0 | 0 | + |
| *F. bengalensis* | + | + | + | + | + | + | + | + |
| *F. viverrina* | + | + | + | 0 | + | + | 0 | 0 |
| *F. chaus* | + | + | + | 0 | 0 | F | 0 | 0 |
| Canidae | | | | | | | | |
| *Vulpes bengalensis* | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 |
| *Canis aureus* | 0 | + | + | 0 | 0 | 0 | 0 | 0 |
| *Cuon alpinus* | 0 | 0 | + | + | + | + | 0 | 0 |
| Elephantidae | | | | | | | | |
| *Elephas maximus* | 0 | 0 | + | + | + | F | 0 | F/I? |
| Tapiridae | | | | | | | | |
| *Tapirus indicus* | 0 | 0 | + | + | + | F | 0 | F |
| Rhinocerotidae | | | | | | | | |
| *Dicerorhinus sumatrensis* | 0 | 0 | + | + | + | 0 | 0 | + |
| *Rhinoceros sondaicus* | E | E | E | E | E | + | 0 | F |
| Suidae | | | | | | | | |
| *Sus barbatus* | 0 | 0 | 0 | + | + | 0 | 0 | + |
| *S. verracosus* | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 |
| *S. scrofa* | + | D | + | + | + | + | D/Fr | 0 |
| Tragulidae | | | | | | | | |
| *Tragulus javanicus* | 0 | 0 | + | + | + | + | 0 | + |
| *T. napu* | 0 | 0 | + | + | + | 0 | 0 | + |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Cervidae | | | | | | | | |
| *Muntiacus muntjak* (inc. *feae*) | + | E? | + | + | + | + | + | +[7] |
| *Axis axis* | + | E | 0 | 0 | 0 | 0 | 0 | 0 |
| *A. procinus* | 0 | E | + | 0 | 0 | 0 | 0 | 0 |
| *Cervus unicolor* | 0 | E | + | + | + | 0 | 0 | I? |
| *C. timorensis* | 0 | 0 | 0 | 0 | 0 | + | + | I |
| *C. eldi* | 0 | 0 | E | 0 | 0 | F | 0 | 0 |
| *C. schomburgki* | 0 | 0 | E | 0 | 0 | 0 | 0 | 0 |
| *C. duvauceli* | E | E | 0 | 0 | 0 | 0 | 0 | 0 |
| Bovidae | | | | | | | | |
| *Bos javanicus* | 0 | 0 | + | 0 | F | +/D | E/D | +/I? |
| *B. gaurus* | 0 | 0 | + | + | 0 | 0 | 0 | 0 |
| *Bubalus bubalis* | E | E/D | +/D | D | D/Fr | D/Fr | D | D/Fr |
| *Capricornis sumatraensis* | 0 | 0 | + | + | + | 0 | 0 | 0 |

Notes: + = present; 0 = absent; E = recent extinction; F = fossil; ? = status uncertain but may occur; D = domestic form present; Fr = feral; I = introduced by man.
[1] Distance between Malay Peninsula/Borneo: 510 km; Malay Peninsula/Sumatra: 65 km; Borneo/Sumatra: 410 km; Sumatra/Java: 26 km; Java/Bali: 2.5 km.
[2] Area south of the Isthmus of Kra. The area was an island for varying periods during the Pleistocene.
[3] There is a report and a photograph of a tiger said to have been taken in the upper S. Belagan but this has not been authenticated. My own view is that where tigers occur, they are obvious. Many good observers have spent too much time on Borneo for tigers to go unnoticed if they did or do occur there.
[4] U.S. Navy personnel went tiger hunting on Bangka in 1854; their temporary disappearance caused some concern that they had been eaten (Gould 1961). There are no known specimens in any museum. Chasen (1940) reports that tigers have reportedly been sighted on islands in the Reau Archipelago including Bintin (= Bintang), Panjait Layer and Setoko (I have been unable to locate the latter two islands on any current or older map.).
[5] There are reports (of questionable reliability) of leopards occurring in Sumatra but no specimens were ever obtained (Sody 1949). There are fossils (Hooijer 1975). I observed no signs of leopards on Sumatra during my survey. Comments on the occurrence of tigers in Borneo are applicable here for leopards.
[6] Sody (1933*b*) comments specifically that leopards do not occur on Bali. I saw no evidence that they did between 1976-1978 (Seidensticker 1978). Recent reports of leopards may indicate that a leopard has been released there.
[7] *M. atherodes* also occur on Borneo (C. Groves, pers. commun.)
Source: Chasen (1940), Hooijer (1975), Gould (1961), Groves (pers. commun.), Hendrichs (1975), Honacki et al. (1982), Hoogerwerf (1970), Lekagul and McNeely (1977), Medway (1971, 1977, 1978), Raven (1935), Seidensticker (1978). Sody (1933*b*, 1949).

In a felid guild, tigers are dominant to leopards. As the social subordinate, the leopard is found in habitats from which the tiger is absent or it exists with a decreased niche breadth (Seidensticker 1976). In Javan high rain forests and secondary forest habitats today, leopards feed heavily on primates; where tigers are absent, as in Sri Lanka, leopards mostly ignore primates and feed on cervids and juvenile *Sus* (Seidensticker 1983). Data (Table 3) suggest that a tight packing of felids, including clouded leopard (*Neofelis neublosa*), marbled cat (*Felis marmorata*), and Asian golden cat (*F. temmincki*) which are sympatric over a rather large geographical area in closed tropical rain forest habitat, effectively monopolize the arboreal and terrestrial food resource space at lower end of the size spectrum. These felids occur in Borneo and the leopard does not. The tiger is present and feeds on the larger cervids and suids in Sumatra and this felid triad also occurs there, and the leopard does not. I hypothesize that leopards were "squeezed out". Much of Thailand/Burma where there are extensive tracts of monsoon forest and tree savannah, and the *marmorata-nebulosa-temmincki* triad does not occur and compete in feeding at the smaller end of the resource space, is good leopard habitat. This triad does not occur in the Java/Bali zoogeographic unit which is also under a stronger monsoon influence than Sumatra. Habitat and landscape apparently were sufficiently diverse on Java and the island is large enough to provide refugia for leopards. With the tiger gone from Java today, leopards have expanded their range into rain forest where 30 years ago they did not occur (Hoogerwerf 1970). Leopards do not occur with tigers in the Sundarbans mangrove forest. In the past they did occur on the northern forest fringe where the tiger had been excluded (Curtis 1933). Bali apparently is too small to support both species. I postulate that leopards have expanded their numbers in the Malay Peninsula since man killed tigers in large numbers and cut large areas of high rain forest.

The wet tropical forest vegetation types which dominate the Greater Sunda Islands are not good tiger habitat as we have come to know good tiger habitat in the *dun* valleys in the upper tributaries of the Ganges at the base of the Himalayas (Seidensticker 1976, McDougal 1977, Sunquist 1981), the monsoon forest and meadows of central India (Schaller 1967), and the extensive mangrove forest at the edge of the Ganges Delta (Hendrichs 1975). Tigers are thinly distributed through most of the Sumatran forest formations (pers. obs., Borner 1978, Van Strien 1978) but they never obtain the densities we have observed in Nepal or India (Table 4). Tiger density and home range size are strongly and positively correlated with biomass of larger cervid prey (Seidensticker and Suyono 1980, Sunquist 1981), and this essential prey biomass is strongly positively correlated with the extent of forest/grassland edge available (Eisenberg and Seidensticker 1976). This, of course, is Leopold's (1933) "law of interspersion." Where we might expect crude biomass of essential ungulate prey for tigers to reach 1300 $kg/km^2$ in good habitats in the Nepal terai, our estimates for South Asian rain forests do not exceed 500 $kg/km^2$ and the actual amount is probably lower (Eisenberg and Seidensticker

Table 4. Synopsis of land-use changes and decline of natural vegetation in Java, 1815-1975

| | |
|---|---|
| 1815 | 5 million people; 12% of the Island under cultivation; mostly sawah, some maize on dry fields. |
| 1833 | 7 million people; establishment of the "culture system" by the Netherlands East Indies Company with policy for the use of sawah lands for growing sugar and indigo and dry fields for growing perennial cash crops; 100 million coffee trees established. |
| 1850 | 9.6 million people; great expansion in the irrigation system, spread of cassava as a dry-field food crop; 600 million coffee trees had been established. |
| 1885 | 20 million people; official policy to increase food production using dry-field crops; sawah expanded through large scale irrigation improvement; beginning of the Corporate Plantation System resulting in increased sawah under sugar production (1:1 rice to sugar). |
| 1900-1915 | 28 million people; rice production could no longer keep step with increasing population; 150% increase in dry-field land under cultivation. |
| 1915-1928 | 10% increase in sawah; 26% increase in dry-field area. |
| 1928-1938 | New sawah and dry-field increased less than 3 and 5%, respectively, indicating all cultivable lands were essentially under production in one form or another; population was about 46 million; 23% of the Island remained under forest cover. |
| World War II | Widespread deforestation without replanting. |
| 1950-1970 | Conversion of many remaining forest tracts to plantations of teak (*Tectona grandis*) especially in east Java; total production (teak and *Agathis*) forests on Java was 1.8 million ha. |
| 1975 | 85 million people; less than 8% of the Island is under natural forest cover. |

Source: Biro Pusat Stastik (1977); Bailey and Bailey (1960); Geertz (1963*a*); Keyfitz (1965).

1976, Seidensticker 1983, Table 5). The very large ungulates—elephant (*Elephas maximus*), tapir (*Tapirus indicus*), and Sumatran rhino (*Dicerorhinus sumatrensis*)—only occur at low densities in rain forest. Young of these species are only occasionally taken by tigers and do not warrant inclusion in estimations of available tiger prey biomass (Seidensticker 1976, McDougal 1977, Sunquist 1981).

## LANDFORM, LAND USE, AND TIGER DISTRIBUTION

In July, 1978, I interviewed a man in Bali who told me that one evening a month earlier as he approached his temple he saw a "harimau loreng" (striped, big cat = tiger) drinking from a spring flowing from the base of a giant *Ficus* that shaded that holy place. No one could or should try to convince this man that the Bali tiger has been extinct for perhaps a quarter of a century. I relate the story because it points to the problem of investigating the process of extinction when the animal is the cultural phenomenon that tigers are throughout their range and beyond.

Java and the Ganges Delta are two of the world's most populated regions. Java and its satellite island of Madura with an area of 132,187 km$^2$ support

84 million people; Bangladesh with 143,998 km$^2$, 79 million; Bali with 5,561 km$^2$, 2.2 million; and Sumatra with 473,606 km$^2$, 19 million. That's 643, 548, 400 and 40 person/km$^2$, respectively, for areas that until recently all sustained tiger populations (statistics are based on standardized 1975 census figures in Biro Pusat Statistics 1977, Bangladesh Bureau of Statistics 1978). Viable populations of tigers, a concept I discuss below, still occur in Bangladesh and Sumatra. Crude density estimates of people (number of people/country or major geographic area) are not useful as direct indicators of the conservation status of this range-senitive, large carnivore or to identify the issues to be addressed in improving the conservation system. The intensity of human land-use as influenced by landform, the history of agriculture development, and resource export practices in a region are far more important in predicting the status of this species. These factors frame the options which are available in any future course of conservation action.

*Bali.*—Fig. 5 shows landform and land-use, the development of the transportation net, and the known collection localities for Bali tigers. The rich volcanic slopes with their superb drainage and climate made irrigation both technically possible and seasonally stable in Bali. On palm-fringed terraces up to 700 m, especially on the southern slopes of the volcanoes, the Balinese culture and political system developed around intensive wet-rice agriculture (Fig. 5*b*). The relatively barren and/or unproductive southern peninsula and the western end of the Island were largely ignored. The Island's transportation network was strongly influenced by the grain of major gorges and spurs; east-west (lengthwise) communication and transportation are much more difficult and were, thus, less important than north-south or crosswise transportation (Geertz 1963*b*, 1980). With this deterrent, and with major political and agricultural activities centered on the Island's southern side, much of the early inter-island trade simply went by to Java. When plantation and small holder agriculture for export did become established in the late 1800's, development focused on the northern slopes of the volcanoes and the narrow alluvial strip around the Island. The Dutch did not establish colonial control until about 1910. Old maps show that roads were even longer in coming. Bridges spanning the north-south gorges are frequently destroyed by the Island's earthquakes. The collection sites of the last Bali tigers were largely beyond the end of the road system as it existed in the 1930's (Van Den Brink 1981). A complete road loop of the Island was only recently completed (Fig. 5*c*).

Most of the 8 Bali tiger specimens entered the world's museums in the 1930's (Mazak et al. 1978), and all but one came from western Bali. Dutch tourist literature (Dreesen 1937) describes tiger hunting in western Bali during the 1930's. Sody (1933*a*) reports on the famous Dutch hunters', A. and B. Ledeboer, large tiger kill from the Island during the 1920's and early 1930's. W. Meijer's translation of de Voogt (1937) provides a brief description of conditions in the area where these tigers were collected, based on a tour of duty there as a forest officer from 1933-1936: ". . . the whole western part of

Bali should be preserved as a nature reserve. Gilimanuk is an ideal spot for a field biological station. Various magnificent objects for study are close by: coral sea-gardens, mangroves, dunes, savannah, water birds, deer (*Cervus timorensis* and *Muntiacus muntiac*), tigers, and farther towards the south east hornbills, lutung (*Presbytis cristata*) and kera (*Macaca fascicularis*). In the mangrove occurs also *Osbornia octodonta* a tree unknown in Java."

There are reports that tigers existed in Bali until the 1950's, but no specimens reached museums from that period. The 20,000 ha Bali Barat Game Reserve was established in West Bali in 1941. In the 1960's and 1970's much of this and adjacent forest lands were planted in forest plantations (Seidensticker 1978), but I doubt that this had any influence on the Bali tiger's demise. It had already been extirpated. I suspect that most Bali tigers were eliminated from the Island by the end of World War II. It is possible that stragglers reported in the 1950's were immigrants swimming the 2 km Bali Straits from Java. Tigers in the Sunderbans swim much larger tidal rivers (Hendrichs 1975). However, there are no specimens from this period to confirm this. The final passing of the Bali tiger came about half a century after Schwarz first described it to science in 1912.

*Java.*—Fig. 3*c* shows what Geertz (1963*a*) called "outer and inner Indonesia". This typology draws a distinction between intensive, wet-rice cultivation (sawah) of the densely populated inner Indonesian islands and the diverse, multicrop, dry-field cultivation (swidden) of the less populated outer islands. Each system provides its own opportunities and limitations to wildlife conservation. Distinct cultural-political systems have developed around each agricultural system. Each has an entirely different potential for adaptation to the cultivation of cash crops for market economies. A swidden agricultural system might reach carrying capacities of up to 50 people/km$^2$; wet-rice agriculture in some areas of Java supports up to 2000 people/km$^2$ (Geertz 1963*a*). The ecological support system of swidden agriculture breaks down through overpopulation if it is used too frequently or too intensively. The system shifts to "lalang" (*Imperta cylindrica*) or something equally unproductive. Sawah productivity depends upon the quality of the water control system: more labor working to increase the efficiency of the rice terrace or the ancillary water works results in increased productivity.

When Raffles surveyed Java during the short tenure of the British (1815), "the quantity of land cultivation to the land still in a state of nature was estimated as 1 to 7 (in Keyfitz 1965)," and the population was about 5 million. The overwhelming features of Java's landscape are the more than 30 active volcano cones (Fig. 6*a*). Unlike India or China where wet-rice is grown on flat, river flood plain, sawah developed in Java in the rich alluvial basins surrounded by volcanoes or unirrigable limestone hills. The alluvial plains that comprise about 1/2 of the Island were malaria-infested and posed technical irrigation problems. These alluvial plains and the limestones and other thin-soil areas were largely ignored for cultivation until the mid-1800's. From

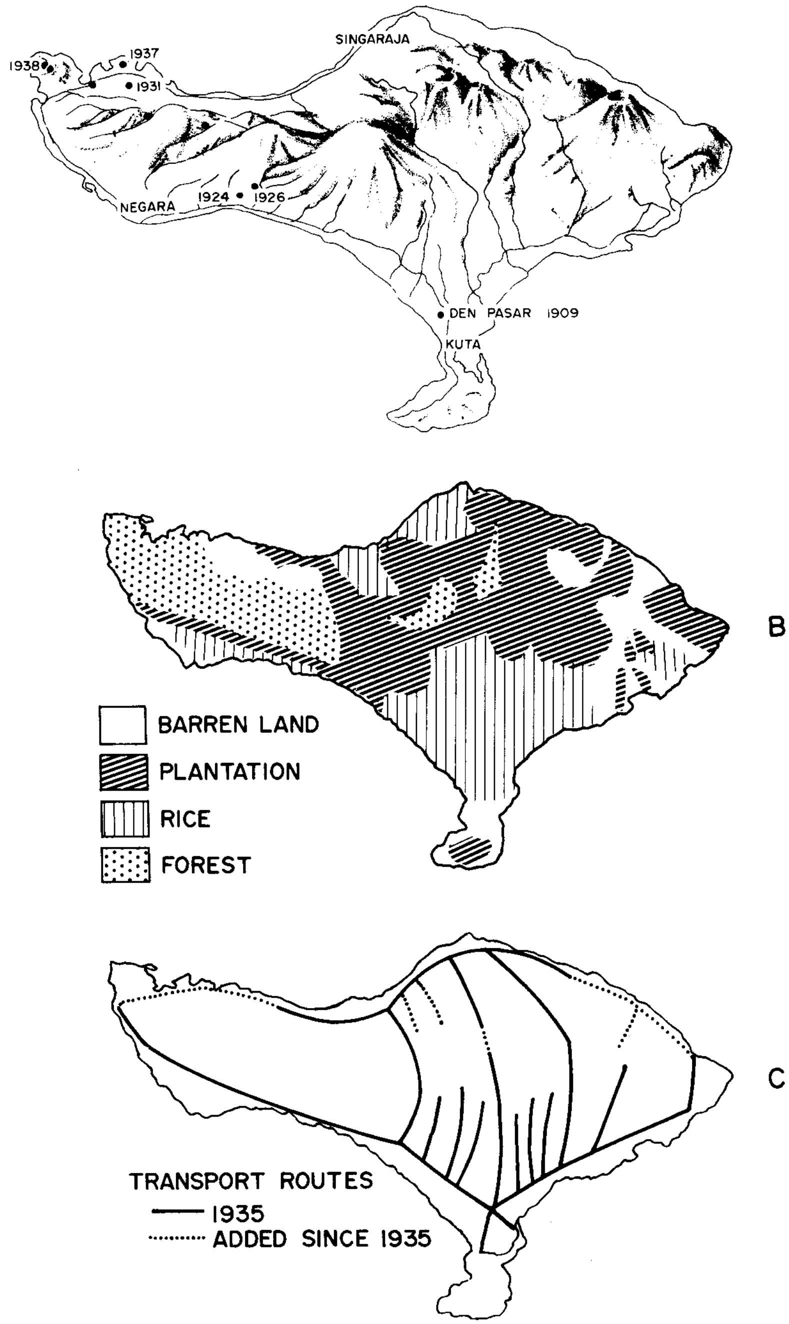



Figure 5. Island of Bali, Indonesia: A) Shown are landforms, major cities and the dates and locations where specimens of *Panthera tigris balica* were collected and known to occur. B) Land-use on Bali ca. 1970 (after Ditdjen Agraria 1971). C) The major roads on the Island in 1935 when the most *P. t. balica* were collected and major roads today.

that time on, the Netherlands East Indies Company efficiently and systematically brought all remaining cultivable lands in Java under production (Geertz 1963*a;* Table 4).

Tigers and other wildlife declined, as forested areas, alluvial plains, and river basins were converted for use in agriculture. Fig. 6*c* presents data on the pattern of the constriction in tiger distribution. This was obtained from many sources, primarily by Treep (1973), and was modified as information became available while I worked in Indonesia during the late 1970's. In 1850, tigers were still widespread. Harper (1945) reports they were considered bothersome then. By 1940, they had been eliminated from all but the most inaccessible Island reaches. Much of the extensive monsoon forest area where tigers had lived in East Java was converted to teak plantations which as wildlife habitat is depauperate (pers. obs., Bell 1979). (These plantations do provide habitat for the warty pig, *Sus verrucosus,* Blough et al. 1983).

In the 1920's and 30's a system of reserves was established on Java (Hoogerwerf 1970, Blower et al. 1977). By the mid-1960's the tiger survived in only three of these: Ujung Kulon (Schenkel and Schenkel-Hulliger 1969, Hoogerwerf 1970), Leuweng Sancang (Galstaun, pers. commun.) and Baluran (Pfeffer, 1965). Tigers did not survive in these reserves after the mid-1960's when major civil unrest rocked the Island and the reserves were sometimes used as sanctuaries by armed groups. During this period, too, disease reduced the rusa population (Galstaun, pers. commun.). For example, rusa only survived on the scattered islands off the Ujung Kulon coast and I found that it is from these that the reserve is being repopulated.

By 1970 tigers could only be found in a rugged area on the southeast coast known as Meru-Betiri. This was established as a game reserve in 1972. Fig. 7 shows many of the environmental features that provided the setting for the tigers' survival outside a protected area in spite of land-use and population pressure. The major features included: 1) The presence of an insular rain forest nested in predominantly monsoon vegetation. These forest patches are created by increased rainfall on the east side of large East Javan volcanoes which catch the monsoon driven clouds. 2) The southeast coast of Java does not have the rich soils from Raung volcanic ash that cover areas to the north. The soils are derived from old andesite formations and are infertile. 3) The area is sharply incised and generally unsuitable even for swidden agriculture. 4) Large scale plantation agriculture only came to this and much of the surrounding areas after World War II. In the headwater basins and vallies of the rivers that originate on the slopes and ancillary ridges of Gunung Betiri, the tiger managed to survive.

Most of the areas below 1000 m surrounding the Reserve indicated as forest in Fig. 7 are planted in teak, coffee and rubber trees. The 500 km$^2$ area that was declared a reserve in 1972 contains as complete a range of vegetation types as can be found anywhere in Java, but essential tiger habitat, the lower alluvial river flood plains, had been established in plantations within the

Table 5. Densities reported for tigers in different habitats[1].

| Location (size, $km^2$) time; source | Habitat type | Est. crude ungulate prey biomass ($kg/km^2$) seasonal/daily movement | Major ungulate prey | Crude density $km^2$/individual *Panthera tigris* |
|---|---|---|---|---|
| *Sundarbans Forest,* Bangladesh (6000), 1975; Hendrichs (1975) | Mangrove forest; tidal pulse-stable system | 1250; local, daily, with tides | *Sus scrofa*<br>*Axis axis* | est. 12 |
| *Chitwan National Park,* Nepal (544) 1976; McDougal (1977) Seidensticker (1976) Sunquist 1981 | Hills; monsoon forest, riverine plain with forest and tall grass; monsoon dry season, lowland flooding | 1340; local, seasonal with flooding | *Sus scrofa*<br>*Muntiacus muntjak*<br>*Axis Axis*<br>*Axis porcinus*<br>*Cervus unicolor* | 19 |
| *Kanha National Park,* India (320) 1964; Schaller (1967) | Hills; monsoon forest and meadows; monsoon dry season | 740 (wild), 2400-2500 with domestic stock; monsoon local seasonal movement | *Sus scrofa*<br>*Muntiacus muntjak*<br>*Axis axis*<br>*Cervus unicolor*<br>*Cervus duvauceli*<br>*Tetracerus quadricornis*<br>*Boselaphus tragocamelus*<br>*Antilope cervicapra*<br>*Bos guarus* | 19 |
| *Ujung Kulon National Park* Java, Indonesia (300) 1930's: Hoogerwerf (1970) | Hills, sea coast; rain forest with meadows, ever wet | 380; little | *Sus scrofa*<br>*Sus verrucosus*<br>*Tragulus javanicus*<br>*Muntiacus muntjak*<br>*Cervus timorensis*<br>*Bos javanicus* | 75-100 |
| *Meru-Betiri National Park* Java, Indonesia (500) 1976: Seidensticker and Suyono (1980) | Mountainous, sea coast; rain forest plantation edge | 200 (est.); little | *Sus scrofa*<br>*Sus verrucosus?*<br>*Tragulus javanicus*<br>*Muntiacus muntjak*<br>*Bos javanicus* | 170 |

| | | | | |
|---|---|---|---|---|
| *Gunung Leuser National Park*<br>Sumatra, Indonesia<br>(4,400)<br>1972-1975: Borner (1978) | Mountainous;<br>continuous rain forest | low (est. < 400)<br>scattered<br>little seasonal movement | *Sus barbatus*<br>*Muntiacus muntjak*<br>*Cervus unicolor*<br>*Tragulus javanicus*<br>*Tragulus napu*<br>*Capricornis sumatraensis* | est. 90 |
| *Lazouski Reserve*<br>(11,600)<br>1973-1977; Matjushkin et al. (1977, 1978) | Mountainous, sea coast<br>Conifer/broad-leaf forest, river bottoms; snow, severe winters | very low; scattered<br>concentration in winter | *Sus scrofa*<br>*Cervus elephas*<br>*Cervus nippon*<br>*Capreolus capreolus*<br>*Nemorhaedus goral* | 100-170 |
| *Sikhote-Alin Reserve*<br>(31,000)<br>1970-72; Matjushkin et al. (1977, 1978) | Mountainous; conifer/broadleaf; river bottoms; snow, severe winters | very low; scattered, seasons with snow conditions | *Sus scrofa*<br>*Cervus elephas*<br>*Cervus nippon*<br>*Capreolus capreolus*<br>*Alces alces* | 250-500 |

Notes:
Nomenclature follows Honacki et al. (1982).
Tigers do not readily cross large open land areas (Seidensticker 1976) and this appears to be a major deterrent to dispersal (Smith, in prep.). Hendrichs (1975) found that tigers would swim wide tidal rivers in the Sundarbans.

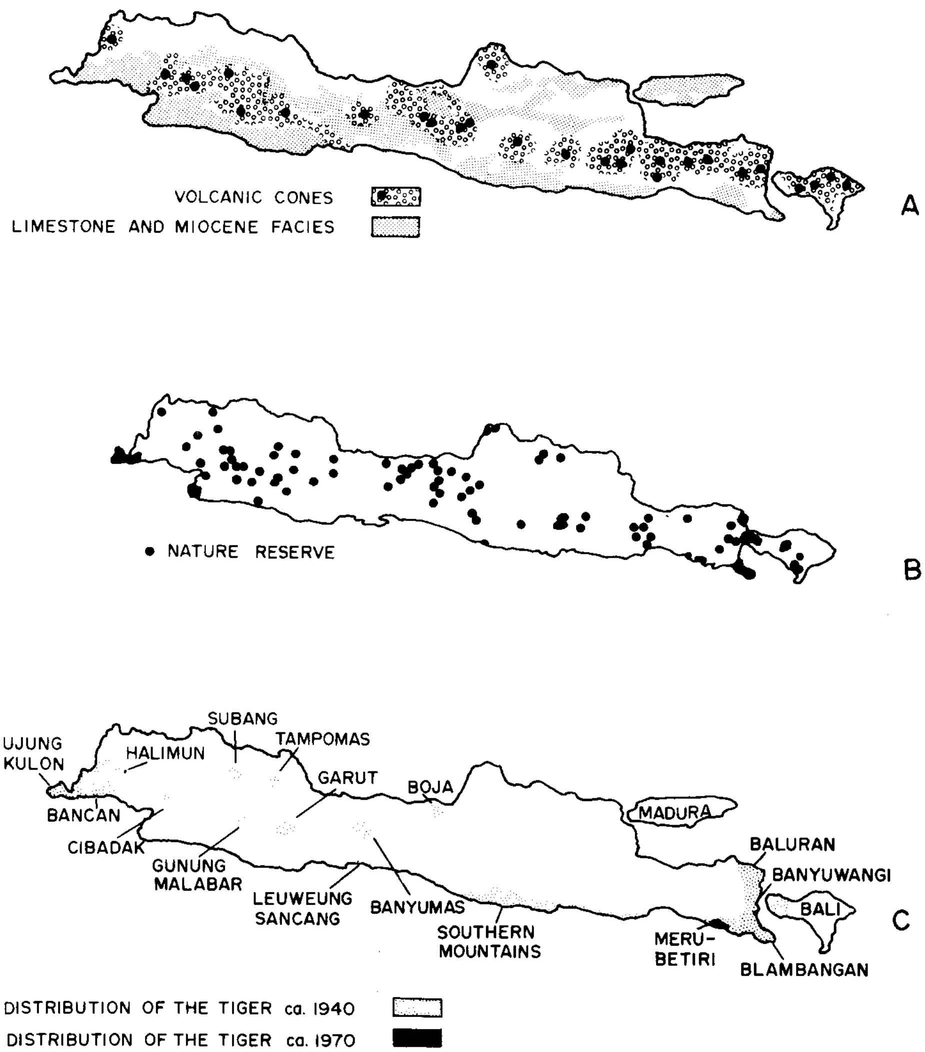



Figure 6. Island of Java, Indonesia: A) Landforms of Java showing volcanic cones, limestone and miocene facies and alluvial plains and basins. B) The system of nature reserves was established on Java mostly during the 1920's and 1930's (Blower et al. 1977) C) Decline of *Panthera tigris sondaica:* in 1830, the tiger was distributed over most of Java; by 1940, it was found only in a few remote forest areas and reserves; by 1970, it lived only in the areas in and around Gunung Betiri (after Seidensticker and Suyono 1980).

reserve. By 1976, 7000 people lived there. There were a few banteng using the forest/plantation edge but there were no rusa. Those populations apparently had been decimated through disease. In 1976 there were at least 3 tigers living in Meru-Betiri (Seidensticker and Suyono 1980). The Government of Indonesia pursued a policy of preservation and restoration, but recent attempts by competent observers have failed to find any sign that the tiger has survived (Blouch, pers. commun.).

*Sumatra.*—Sumatra, the world's sixth largest island, bisected by the equator, and for the most part without any distinct dry period, supports a range of tropical forest formations (Whitmore 1975) on a diverse geomorphological base (Fig. 8*a*). On the eastern side, including about one-half the land area, are alluvial plains and fans, piedmont, and peneplains. Towards the center are scattered island-like folded mountains that rise above the plain and are distinct from the Bukit Barisan (Mountains) that extend for 1600 km down the entire west side. This western spine, rising to 3800 m, is composed of block mountains with a great graben, the Semangko or Sumatra Fault, with more than 10 active volcanoes scattered along its length. The west coast is a narrow alluvial strip pinched in by towering mountain flanks (Katili and Hehuwat 1967, Verstappen 1973).

The Island's eastern edge, at the seaface on the Strait of Malacca, is a narrow strip of mangrove forest. Behind beach ridges, mangroves blend into brackish water swamp forest, and this into extensive peat swamp forest (Dries-

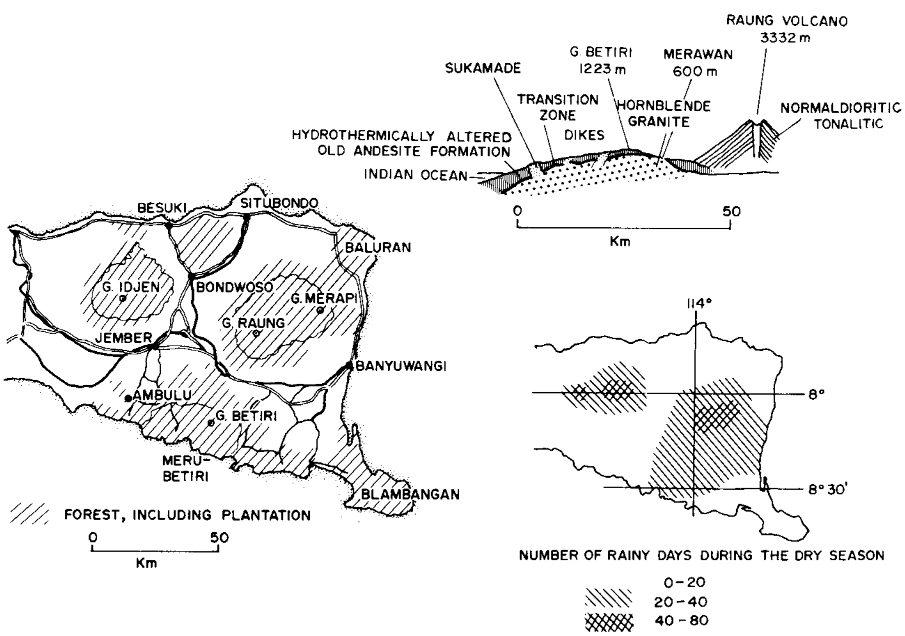



Figure 7. Landforms and land-use in East Java (from Seidensticker and Suyono 1980): The main lines of commerce and the forest areas are indicated. Almost all natural forest below 1000 m has been converted to plantations of teak, coffee, and rubber. Meru-Betiri National Park is on the old andecite formation and not part of the Raung Volcano complex. Monsoons from the southwest drive clouds against the big volcanoes which results in increased rainfall and a reduced dry season. In areas influenced by this, rain forest islands occur surrounded by the predominantly monsoon vegetation of eastern Java.

sen and Soepraptohardjo 1974). These comparatively unproductive forest types (Janzen 1974) occupy the entire coastal plain. Silt-laden rivers of "white-water" originating in the mountains form levies and lance through the swamps emptying directly into the Strait rather than through distributaries into the swamps. The swamps are distinct ecological systems. Their primary input is rain water; their output is tannin-laced, black-water rivers (air hitum) that drain into the white-water rivers or directly into the Strait.

Squeezed between the steep flanks of the Bukit Barisan on the west and the swamps on the east is classical lowland evergreen rain forest growing on the narrow alluvial fans, piedmont, and the peneplains. The mountains support lower and upper mountain rain forest. The west coast is a long, narrow sandy beach, fringed with palms and mangroves in sheltered bays and divided by impassable alluvial swamps where the major mountain drainage systems enter the Indian Ocean. Tigers only occur at low to moderate densities in these habitats (Table 5).

The history of land-use in Sumatra can be roughly partitioned into 3 phases: 1) Agricultural production confined primarily to growing of foodstuffs for domestic consumption with limited production for trade predominated until the latter part of the 1800's. 2) Since the late 1800's, there has been a rapid expansion of agricultural production for export crops as this continues. 3) There has been rapid expansion of materials production (timber and oil) from World War II to the present.

The wide distribution of poor soils and the ever-wet climate contained the extent of forest conversion until after World War II. Large expanses of the Island including the eastern swamp and the mountain flanks, are not suited for swidden or large scale sawah development. Many of the young volcanoes produced acidic rather than basic ejecta resulting in a poor soils over much of the island (Fig. 8*a*) (Geertz 1963*a*, Diessen and Soepraptohardjo 1974). Sawah systems did develop along much of the Sumatra Fault and in the Padang Highlands, behind some of the levies along the major rivers, and in a few areas along the coast in the north, west and southeast (Terra 1958). Sumatra typifies "outer Indonesia" and the majority of agricultural development was and is *ladang* (temporary fields) and swidden both independent of sawah or closely associated with it.

There are no early estimates of the population for Sumatra as there are for Java, but by 1930 when Java's population was estimated to be 42 million, there were only an estimated 6 million people living in Sumatra (Loeb 1972).

In the early 1800's, the British established ports at Benkulu, Padang, and Sibolga and established strong ties with the "pepper ports" along the east coast. Agricultural production for export only really "took-off" after J. Niehaus moved to Deli (Medan) from East Java in 1863 and established a tobacco industry that soon expanded to dominate world markets. Sumatra surpassed Java in export earnings by 1900 (Geertz 1963*a*). Export agriculture developed using swidden to grow annuals such as tobacco and to establish perennials. Much of this was and remains in the hands of small holders, although some

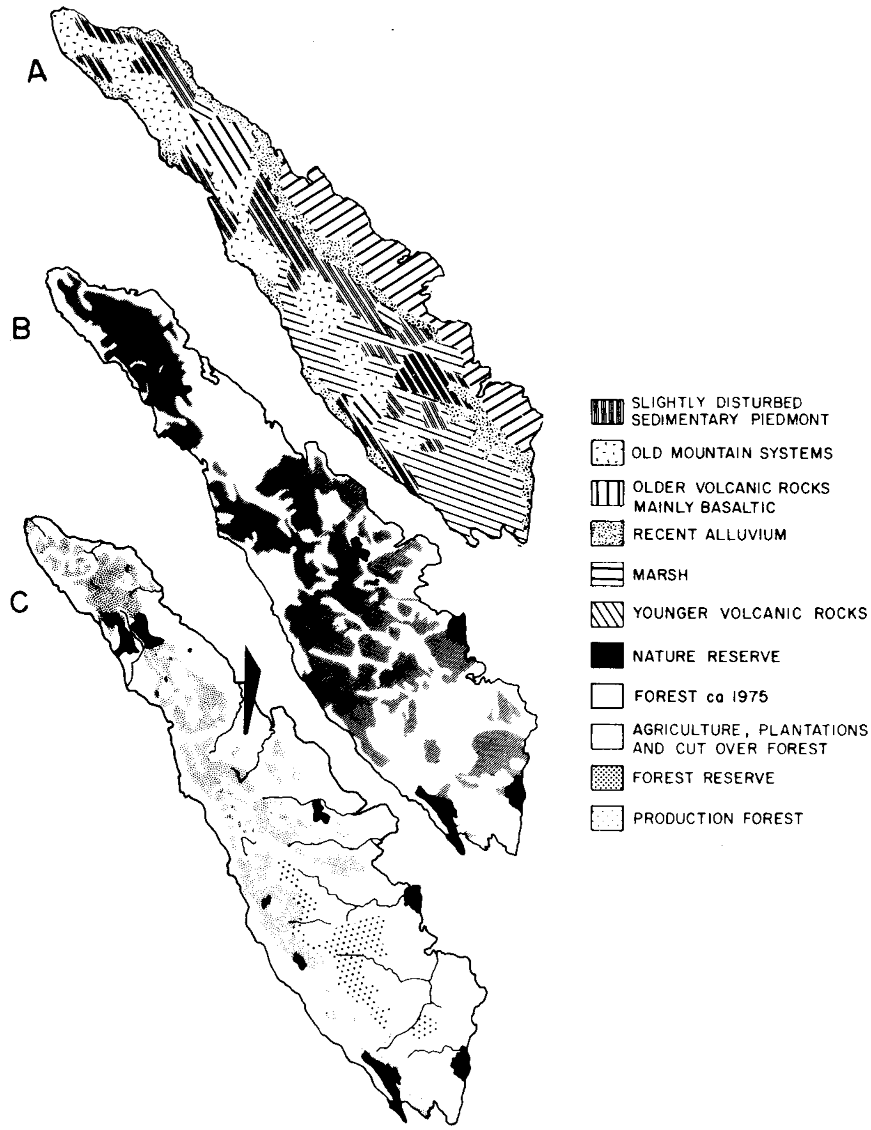



Figure 8. The Island of Sumatra, Indonesia: A) The landforms of the islands showing the western mountain spine, the Bukit Barisan, and the broad eastern lowlands. B) The areas of exploitable timber remaining on Sumatra ca. 1975. C) The planned forest estate including both production and protection forest. The reserve system (1975) is indicated. The production forest will be established as plantations of pines and other exotic species (Direktorat Jenderal Kehutanan 1978). The arrow locates the Rocan-Barumun study site.

huge plantations were established during the first decades of this century. In 1906 the first rubber plants (*Havea braziliensis*) were introduced to the East Coast. By 1940, Sumatra produced one third of the world's rubber. There were parallel increases in the swidden lands developed for coffee, tea, oil, palm, and others (Thee 1977, Pelzer 1978).

Following World War II, a newly independent Indonesia looked to the outer islands to produce export earnings. The central Sumatran oil fields were put into production, and these were joined by new fields in the north and south so that by 1975 the Island was producing more than one million barrels/day (Hooper 1972, Anon. 1977). In the 1960's, forestry production was greatly expanded. The great rivers provided a ready-made transport system and access to millions of cubic meters of timber. Fig. 8*b* shows the distribution of forest (ca. 1975) judged to be exploitable by the Forest Department. Fig. 8*c* shows the planned forest reserves and production forest for Sumatra in the year 2000. Production forests indicated in Fig. 8*c* are planned plantations. Clearly, the process of fragmentation and reduction of the great tropical forests of Sumatra is well underway.

Indonesia's Department of Nature Conservation (a branch of Forestry) realized that the swamps and lowlands, resistant to development and peopleing in the past, were undergoing rapid change as a result of forestry and oil operations. The Department expressed a desire to establish a major new lowland reserve. The Director General (now Minister) of Forestry gave his approval if a suitable area free of working timber concessions could be found. Borner (1978) spent most of 2 years on a World Wildlife Fund project surveying Sumatra for Sumatran rhino and other large mammals and came to regard a large tract, about 1 million ha, between the Barumun and Rokan rivers and extending from the Bukit Barisan to the Strait as the best possibility (Fig. 8*c*). Ir. Suyono and I spent much of 1977 surveying this vast area to determine established land-use, planned development, and to assess if problems in establishing control and providing protection for a reserve could be overcome.

Extending from the Malacca Strait to the piedmont, the area includes an impressive range of tropical forest formations including: mangrove, brackish water forest, peat swamp forest, freshwater swamp forest, and lowland evergreen rain forest. About half the area is peat swamp. The tiger occurred at low density over most of the region along with a small population of Sumatran rhino, tapir, and scattered small groups of elephants. The survival of the large mammals in this area was tied to the *pematangs* (sand hills) and the lightly folded alluvial ridges and fingers that extended from the foothills to the swamps; the peat-swamp was inferior or unsuitable large mammal habitat. On these higher areas, man was the principle disturbing agent.

Rain forests do not support a high carrying capacity of large ungulates (Eisenberg and Seidensticker 1976). In South Asian rain forests, carrying capacity is further reduced for ungulates through the forest's domination by the mast fruiting Dipterocarpaceae (Janzen 1974). The small muntjac (*Mun-*

*tiacus muntjak*) and mouse deer (*Tragulus javanicus, T. napu*) are thinly distributed in the forest. Wild swine (*Sus barbatus*) are migratory and with sambar (*C. unicolor*) concentrate near *ladang* farms and others areas of secondary growth. *Imperata* grasslands that have become established on overworked swidden and ladang are not good habitat for any grazers (Eussen and Wirjahardja 1973).

We estimated the human population of the area to be more than 50,000. Large areas bordering the rivers had been converted to rubber small holdings. Resource extraction activities in the region were well advanced. The central Sumatran oil field extends into and may prove to underlie the entire survey area. Timber concessions completely blanketed the area. The commercially profitable areas above the swamp, which are the vital areas for the conservation of the large mammals, are under timber production and/or were being farmed. The most efficient operations were extracting as much as 9,000 $m^3$ of hard woods of the genus *Shorea* per month, most of which was exported. At least 15 saw mills drew their timber supply from this area.

Shifting cultivators were responding in a classical manner to the expanding road network needed for oil and timber extraction. Human habitation in the past was restricted primarily to the banks of the major rivers flowing from the Bukit Barisan and piedmont. The forest was viewed as a common property resource with no precedent for long-term land tenure. While the extraction of resources is regulated through concessions granted by the central and provincial governments, the orderly disposition of land for farming in newly developed areas has been problematic. The result in most areas is a spreading wedge of new and old ladang along the roads. In many cases the result seems irreversible, at least in the near future. We found large fields of *Imperta cylindrica* burned regularly to provide food, albeit of low quality (Eussen and Wirjahardja 1973), for free ranging domestic water buffalo.

These findings essentially halted our hope of establishing a new major reserve in Sumatra's lowland. The conservation of Sumatran tigers in protected areas would have to make do with the existing reserve system (Fig. 8), and by expanding these where possible. Mountain rain forests are not particularly good tiger habitat. For example, Van Strien (1978) estimated the tiger population for all of the Gunung Leuser reserve group (about 1 million ha), which is Indonesia's biggest and best rain forest reserve (now national park), to be between 20 and 100 individuals. Clearly, most of the remaining Sumatran tigers will have to be protected through some mechanism other than reserved lands. Tigers occur over large areas of Sumatra, inhabiting second growth forest, the edge of *Imperata* grasslands, and along the edges of the fields of the shifting cultivators, feeding on the deer and swine that live there. Efforts to conserve tigers must focus in these areas.

*Sundarbans.*—The Ganges, Brahmapurtra and Meghna Rivers join in Bangladesh and form a 10,000 $km^2$ delta, the largest in the world. Table 3 lists the assemblage of large mammals that once lived in the forest and grasslands. Few areas in the world could have matched the standing crop biomass of ungulates (Eisenberg and Seidensticker 1976) living there. Today the only remaining large block of forest lies at the delta's edge (Rashid 1977, Gitting and Akonda 1982).

At the edge of the delta is the world's largest mangrove forest, the Sundarbans (Fig. 9). This is an open, dynamic, resilient, heterogenous ecological system (Seidensticker and Hai 1983). The 6,000 km$^2$ of waterways and the forest that form Sundarbans Forest Division lies at the interface and is the sum of happenings in 2 huge ecological systems—the Ganges/Brahmaputra watersheds and the Bay of Bengal. The tides, floods, and intense and frequent cyclonic storms, make it a dynamic pulse-stable system (Odum 1971) which is constantly changing and renewing. As such, it is resilient to disturbance from within the forest and waterways, but sensitive to those from the outside, particularly to changes in the flow of fresh water. Variations in the flow of

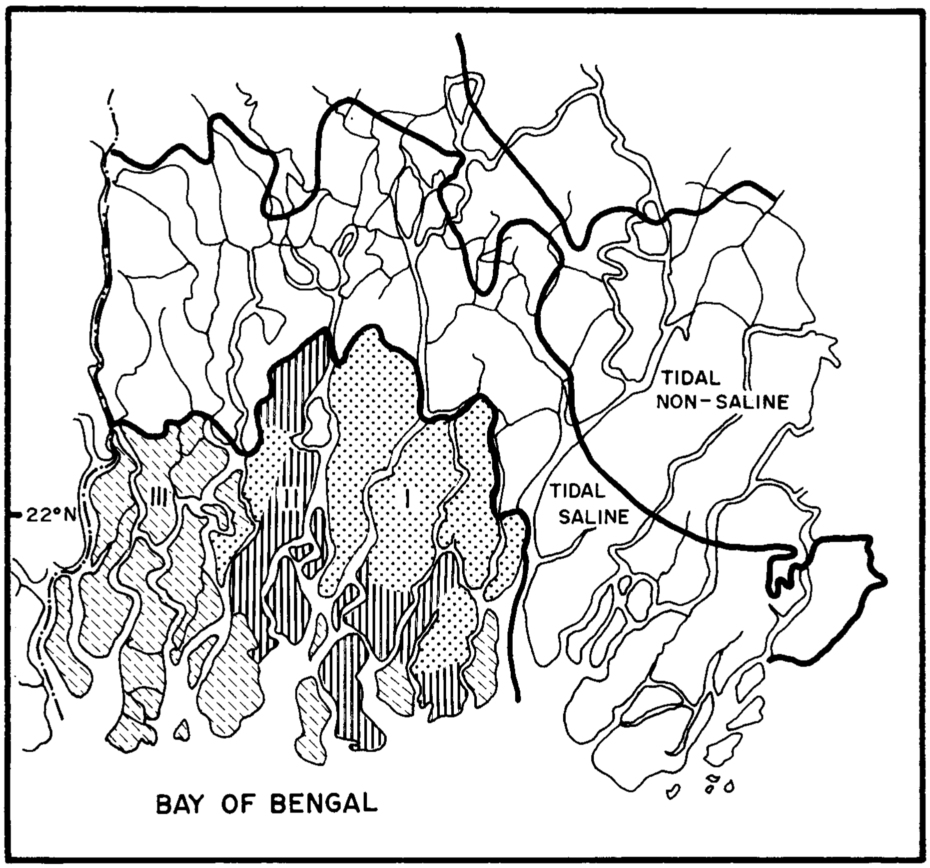



Figure 9. The southern region of Bangladesh showing the zones of tidal influence and the Sundarbans Forest Division. The forest can be divided into three classes based on productivity (I is highest) which is dependent on the flow of fresh water from the Ganges and Brahmaputra distributaries (from Seidensticker and Hai 1983).

fresh water and the tides are compartmentalized by the distributaries of the Ganges and tidal rivers and productivity of the system is thus compartmentalized (Hendrichs 1975) (Fig. 9).

Curtis (1933) and Choudhury (1968) outlined two centuries of change on the lower delta. Seidensticker and Hai (1983) summarized this in the *Sundarbans Wildlife Management Plan.* For purposes here, it should be noted that 200 years ago the region's chief consumable resource was its undeveloped land. In the eighteenth century the forest were about double its present size. Forest clearing was encouraged. In 1828 the British Government assumed propriety rights. Regulated clearing and cultivation went on until about 1875. It was during this development phase that a decline in the diversity of large mammals occurred as their habitat went under the axe and plow. The switch from land transformation to forest utilization in the 1870's occurred when the population of Bangladesh was under 22 million people (Rashid 1977); in 1931, when the first management effort was to increase the number of mangrove species in production, the population was 36 million; in 1960, the starting date of the current working plan (Choudhury 1968), it was 55 million; today, it is more than 80 million; at the present rate of increase, the population will be 100 million by the early 1990's. In the next few years, therefore, there will be as many people added to the population as were present in Bangladesh when the curves of supply and demand for timber and other products of the Sunderbans crossed and it was deemed necessary in support of economic development to switch from land transformation to the management of forest utilization.

The process of forest management has been a series of incremental acts to bring more food, fiber, and material into production. This has been done with care and control. A substantial increase in production of these goods has resulted without apparent damage to the system. The demand for products will continue to rise.

Clearly, the management system that has developed over the century with the Sundarbans under the control of the Forest Department has been to seek ways to increase forest output within the constraints of sustained yield philosophy. There has been no concurrent development of management mechanisms to maintain *optimal ecosystem function.* The major strength of the management system has been that an entire coastal region was placed under the control of one governmental unit. The Department has been able to control forest use. Analysis and common sense indicate that the future development of the management system will necessarily have to reflect the natural functions and dynamic rhythms of the ecosystem if the full component of values is to be maintained.

Table 3 lists species that were known to live on the delta and those that occur today in the Sundarbans Forest Division. Some large mammals have not survived forest conversion: Javan rhino (*Rhinoceros sondaicus*), hog deer (*Axis porcinus*), swamp deer (*Cervus duvauceli*), and water buffalo (*Bubalus bubalis*). These were primarily delta species unsuited for living in a mangrove swamp.

There have been some recent invaders into the mangrove forest from the newly converted adjacent lands; jungle cat (*Felis chaus*), jackel (*Canis aurens*), bengal fox (*Vulpes bengalensis*) (Mukherjee 1975). Through it all, tigers and axis deer (*Axis axis*) have survived, and perhaps thrived (Hendrichs 1975, Seidensticker and Hai 1983). Hendrichs and the Forest Department estimate there are over 300 tigers living in the Sundarbans Forest Division (Table 5). I found tigers everywhere in the forest, and I have no reason to doubt this estimate. Hendrichs and local *shikaris* emphasize that tigers frequently swim even big tidal rivers. Any tiger that ventures out of the forest is killed (Bangladesh Forest Department, pers. commun.). The Sundarbans Forest Division produces fiber and food that are essential to the economy of Bangladesh. It is also one of the largest effective wildlife refuges in South Asia.

## MAINTAINING TIGER POPULATIONS

Tigers survived under very different institutional, socio-economic and environmental conditions in the Sundarbans and Sumatra, but they did not survive in Java and Bali where they had been protected by law and reserves that had been established in the 1930's and early '40's in what was tiger habitat. This is an important result of this survey because it suggests how the conservation system can be adapted to improve performance (Fig. 1). 1) Conservation initiatives to ensure the long-term survival of tiger populations should be tailored to the conditions of the specific environment. 2) There is great risk that tigers will eventually disappear from any small, isolated reserve either through stochastic processes or the effects of inbreeding depression.

The reserves where the last Javan tigers were found are small ($<500$ km$^2$) and isolated, but in the 1930's when most were established, they were nested in expanses of forest that still covered about 25% of the Island (Table 4). During the next 2 decades there was widespread fragmentation of the forest and the reserves were insularized. Where tigers did manage to hang on was in the largest, diverse, and most remote blocks of contiguous habitat on the Island: Gunung Betiri and associated river systems, Ujung Kulon-Halimun, and the Southern Mountains (Fig. 6). It shouldn't be surprising that it was the environmental conditions rather than the establishment of a reserve which were important. For example, the Meru-Betiri area was made a reserve only in the early 1970's, and the evidence is strong that tigers survived in the Halimun area after it was fragmented from the Ujung Kulon Peninsula and tigers disappeared from that reserve. Much of the Southern Mountains were deforested or turned into plantations of teak and others species. The final *coup de grace* to tigers in these small areas can be attributed to stochastic processes or the human condition, depending upon your point of view: 1) uncontrolled fragmentation of the forest during the social disruption of World War II and the events following, 2) widespread loss of critical ungulate prey populations through disease, 3) the civil unrest of the 1960's which resulted in more dead tigers killed by armed groups seeking the sanctuary provided by the reserves. There really is not much a wildlife manager or anyone could do about this class of problem.

Tiger populations in the 6000 $km^2$ Sundarbans and in large contiguous tracts of habitat in Sumatra (some tracts exceed 30,000 $km^2$) survived the conditions of the last 40 years where those in Java and Bali did not. They could not have survived the extirpation of essential ungulate prey. With the axis deer the dominate prey species for Sundarbans tigers, this is potentially the more vulnerable population to a threat of the loss of prey through disease transferred from domestic to wild ungulates, but there is little contact between livestock because cattle (*Bos indicus*) and dometic water buffalo do poorly in this brackish water environment.

The analysis of data now available from captive populations of 2 tiger subspecies (Ballou and Seidensticker 1983; Seal and Foose 1983) show it is unwise to ignore effective population size ($N_e$) in any conservation initiative for wild tiger population management. An $N_e$ of > 100 is the basis for planning the management of captive tiger populations (Foose and Seal, this volume), and this is a reasonable number upon which to base the management of wild tiger populations. There are few data on the structure and dynamics of wild tiger populations. Based on those which are available for tigers and other big cats, roughly 25-50% of crude tiger density should be used in calculating $N_e$. If the crude tiger density is 1 tiger/50 $km^2$, it will require 25,000-50,000 $km^2$ of that habitat to support the $N_e$ = 250 for that population. The summary of crude density data in Table 5 can be used to make this calculations in different environs where tigers are found.

An attractive technology to reduce the risk of inbreeding to tigers living in smaller reserves is artificial insemination (AI) of several resident females with the semen of males from other populations in accord with a planned schedule. Much research has been done with AI in tigers with virtually no success or success with cats in general (U. Seal and M. Bush, per. commun.). We also know there would be great risk from territorial residents to any translocated tigers used in efforts to optimize $N_e$ (Seidensticker et al. 1976, Sunquist 1981). Any project to attempt this would have to create a place in the resident social structure for the translocated animal.

The wildlife manager has but one way to optimize $N_e$ for wild tiger populations: adequate contiguous habitat. Another dimension to the structure of essential habitat is that patches that support essential ungulate prey at densities sufficient for a female tiger to rear cubs must be generously dispersed through that area. Conditions in the Sundarbans and in Sumatra are such that $N_e$ is high. Land-use and forest harvest practices now are such that the second condition, the adequate distribution of prey in sufficient density for tigers to rear young, is also met in both regions. A fundamental difference between Sumatra and the Sundarbans is administrative control of access to forest areas and the implication this has for keeping rates of mortality in tiger populations at sustainable levels.

A major attractive feature of the concept of designated "tiger reserves" in the conservation system is that it greatly facilitates the focusing of purpose and land-use objectives. This focuses manpower and training efforts and this facilitates control of access to the area and its resources. When managers control access with the support of the general public they can bring man-induced mortality rates for a target species under a strong measure of control. Tiger populations in the Sundarbans benefit from the *defacto* protection the area provides because access to the extraction of resources is under strong administrative control. The point where it became economically more important to control access and harvest resources at a sustainable rate rather than clear new land areas in southern Bangladesh was reached a century ago. Fig. 9 shows that economic planners calculate that they do not expect to reach this stage in land-use ratio in Sumatra until about the turn of the century. With the expansion of the transportation net which must be developed for logging and other resource extraction activities, control of access and thus, control of any minor resource, such as wildlife, is confounded.

A major socio-economic component in the tiger conservation program initiated after the 1969 IUCN meeting was to render the tiger a non-commodity in any physical sense as far as that was possible. The fact that there is a high, cross-cultural metaphysical interest in the tiger made it possible to transcend functional rationales usually invoked in endangered species preservation campaigns (Raven et al. 1971; Myers 1976, 1979). Judging from the broad response shown in Table 1, what was initially a fund raising slogan, "Save the Tiger" (Mountfort 1981), quickly became a metaphoric assertion for conserving Asian wildlife in general. As a metaphor, "Save the Tiger" has very specific performance implications (Fernandez 1971), and quick action was called for. Name recognition facilitated the quick acceptance of the tiger's plight world wide making it socially acceptable to place a moratorium on hunting which in turn set the stage for the enactment of new, stronger national legislation to protect wildlife and the negotiation and ratification of CITES. These interdependent actions have effectively maintained the tiger in a non-commercial status and greatly reduced trade.

There has been some leakage through trade in tiger parts used in traditional medicine (McNeely and Wachtel 1981). Some skins are still in international trade through non-member CITES countries such as Singapore (per. obs.). There has been some illegal trade of skins within some countries (Borner 1978). Some animals are necessarily removed as problem animals. This leakage from tiger populations is not trivial in my estimation, but there is no way to know how this relates to sustainable mortality rates in the tiger populations affected. But certainly what was a massive hemorrhage from man induced mortality in tiger populations has been greatly reduced.

The non-commercial status of the tiger will continue to be an essential condition for its conservation for the reasons Clark (1973) has emphasized, and this is particularly true in Sumatra as land-use practices change large areas of wet tropical forest into a man-dominated landscape. Whether the face of Sumatra resembles that depicted in Fig. 9 or some slightly different protection-conservation-utilization land-use ratio, the improvement in the conservation system for any species-orientated or general conservation initiatives will have to adapt to and become a part of improving the economic conditions of the region. Specific planning proposals for the conservation of tigers and the other regions addressed in this report are discussed in the next section.

## LINKING WILDLIFE MANAGEMENT AND ECONOMIC DEVELOPMENT

The 4 regions for which case studies have been presented lie along a continuum of increasing complexity in terms of increasing the performance of the conservation system (Fig. 1): Sundarbans, Meru-Betiri, Bali Barat, and Sumatra. Seidensticker and Hai (1983), Seidensticker and Suyono (1980), and Seidensticker (1978) have listed the principles upon which conservation plans for the first 3 areas can be based and these are listed here in outline form. Sumatra is big and complex and I have general suggestions on how planning for wildlife management in a context of economic development can proceed there.

*Sundarbans.*—The 6000 $km^2$ of waterways and forest that form the Sundarbans Forest Division is valuable and provides food, fiber, and building materials that are of critical importance to the southern region and the economy of all Bangladesh. The forest is a buffer against storms and a major nursery area for many of the fisheries in the Bay of Bengal. It is not possible to buy a replacement for the goods and services this area provides the people of Bangladesh.

The Sundarbans is a well managed forest that can accommodate heavy use without despoliation. Uncontrolled use inevitably is destructive, but the Sundarbans has a century long history of careful husbandry. To meet ever-rising needs, the forest management system has limited access and continues to bring additional forest products into production on a sustained yield basis.

The Sundarbans is a magnificent wildlife refuge. Wildlife populations have flourished under forest management practices in the past. The area is the largest contiguous tiger habitat on the Subcontinent. Additional wildlife management needs can be met by increasing the Forest Department's capacity to control the access and activities of forest users and by including wildlife management expertise within the forest management system decision making process. The capability to do this can only evolve under a deliberate policy over time. In the very productive, pulse-stable ecosystem of the Sundarbans with its 20-year cutting cycle and forestry operations widely dispersed over the forest, wildlife management and forestry management activities could have a synergistic effect towards achieving a management goal of *best achievable ecosystem function* (Seidensticker and Hai 1983). In that context, an increased investment in wildlife management certainly can be cost effective.

*Meru-Betiri.*—We based the comprehensive management plan for Meru-Betiri on 7 propositions (Seidensticker and Suyono 1980):

— Meru-Betiri is beautiful and valuable.
— Meru-Betiri is vulnerable.
— Uncontrolled exploitation and disruption are inevitably destructive to the area.
— Observation of conservation principles can avert destruction and ensure enhancement.
— Protection and management can only be achieved through an ecosystem approach.
— Survival of the Reserve is dependent on a clear formulation of policy and on the people employed.
— The power of public opinion can decide the fate of Meru-Betiri Reserve and the last Javan tigers.

The key issue for securing long-term protection for this reserve, even if the tiger had little chance to survive by 1976, was through what planners in Indonesia call "critical land areas" (Goodland 1981). Meru-Betiri is essentially an island surrounded and disrupted by shifting cultivation and plantations. Physiographic position and topographic ruggedness once served to inhibit development of the area but steep slopes increase its vulnerability to erosion and poor soils decrease its resilience to man's disruptive influences. Agriculture and forestry operations already exceed land capabilities in this region of Java (FAO 1974). The welfare of 500,000 people and the economy dependent on the watershed protection provided by the reserve were threatened unless the reserve was maintained and any activity that would alter the structure and function of the reserve curtailed. Conserving Meru-Betiri was an exercise in bringing a critical land area under strong management control.

In the original management plan, we did not include a proposition that expressly stated the need to include the Reserve and surrounding forest areas in all regional economic planning, but this was accomplished at the national level through the efforts of the Indonesian Minister for Environment and Development. The elements of the plan were implemented by Presidental Decree in 1976. The Reserve was declared as one of Indonesia's first national parks in 1982.

*Bali Barat.*—Surrounded on three sides by water, the principal threats to the Bali Barat Reserve came not from Bali, for there was an excellent guard staff, but from the sea. The Bali Barat Reserve forests were being removed to provide firewood to make lime from the coral near Java. The lime provided building materials for industry on Java. If conservation action was to proceed on Bali, it was this part of the chain that had to be dealt with. Although Bali Barat had been in nature reserve status since 1941, that status had essentially served to make it a commons, rather than to provide protection. If any portion of the Reserve was to remain intact, action would have to be taken at the regional level to turn the Reserve from a commons into a central, positive feature in Bali's economy.

The following steps were suggested (Seidensticker 1978): 1) declare the Reserve and all adjacent forest a national park (about 80,000 ha), 2) develop a program to bring some of the tourist flow that already exists on Bali into this park (about ½ million visitors each year or about ½ of all Indonesia's tourists), 3) use deforested lands at the edge of the park, to develop plantations for firewood and for the Balinese wood carving industry, 4) integrate existing plantation into the natural forest and 5) establish an intensive management program for the endangered, endemic Rothschild's mynah or Jalak Bali (*Leucopasar rothschildi*).

There was resistance to the idea of establishing the area as a national park primarily because it does not compare to the magnificence of the rain forests of Gunung Leuser in Sumatra. Some thought this would detract from the national park concept. I argued that national park status is essential to create the focus and to act as a catalyst in the process of change. Man has been a part of the Bali landscape for thousands of years. Forests and habitats will take time to heal from overuse just as they have taken time in areas such as the United States' Shenandoah National Park. Non-consumptive use of the area, such as tourism, is important in generating income, and a real value of the expanded boundaries of the park is in protecting the watersheds thereby insuring the health of local agricultural systems. This is Bali, not East Africa, or North America, or a rain forest in Sumatra. This is Bali, and to be effective, conservation action must be carefully tailored for Bali. Bali Barat National Park was declared in 1982.

*Sumatra.*—The focus of Sumatra's economy is on the export of raw materials and agricultural products. Any improvement on or even moderate expansion of the current reserve system must in some way accommodate this.

As I view Sumatra, there are 2 opportunities to improve wildlife management on the Island in the context of economic development. The protection of wildlife can be included in the protection of critical land areas. Two obvious areas can be included in this classification: 1) the slopes of the Bukit Barisan where they are subject to earthquakes (and this includes most undeveloped areas), and 2) the mangrove and brackish-water swamp forest on the Island's eastern fringe. The soils in this latter region are mostly unsuitable for agricultural development, and this is the nursery area for many of the fisheries in the Strait of Malacca (Hanson and Koesoebiono 1979). With adequate protection these would become extensive and magnificient wildlife refuges on Sumatra. These physiographic regions will support tigers only at very low densities, but these are potentially such large areas with opportunities for many connecting corridors to other forests that the effective population size for tigers would be large.

Tigers occur and will continue to reach their greatest densities where populations of essential prey concentrate. This is through the center of the Island on the alluvial plains, the peneplains, and on the alluvial fingers that extend into the swamps where there are now ladang, swidden, oil fields, timber concessions, and plantations of rubber and oil palm. The survival of the Sumatran tiger is tied to the management of wildlife populations in these areas. The issue of who owns the wildlife and regulates its use outside of reserves is critically linked to the tiger's survival. It is illegal to kill a tiger in Sumatra, but people do and will continue to do so as long as it remains possible to sell a skin. Some have suggested permit hunting of tigers as a means to bring harvest under some measure of regulation, but for reasons outlined above, and without a strong control system in place, this would create more problems than it would solve. Establishing the ways and means to regulate the harvest of other wildlife such as deer, wild swine, and particularly primates, provides an opportunity to establish a system of control throughout the Island that can be based, in time, on sustainable harvest data. This system can also function to protect sensitive and threatened wildlife species that in many cases must live at least part of their lives outside established reserves. In a recent reorganization, the Indonesian Department of Nature Conservation was given forest protection responsibility. A broad, cost-effective wildlife management capability can evolve within that framework.

The momentum of land-use change is well underway and will continue in Sumatra. Conservation opportunities lie in recognizing the fundamental patterns of this change and developing the wildlife conservation systems accordingly. Indeed, careful study of the interplay between tiger distribution and the patterns of land-use in two of the world's most densely peopled countries has a broad significance as an example of the conditions with which any policy and program must come to grips to bring conservation initiatives into the process of economic modernization.

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