UNGULATES IN SOUTHERN ASIA: A CONSIDERATION OF BIOMASS ESTIMATES FOR SELECTED HABITATS

JOHN F. EISENBERG & JOHN SEIDENSTICKER

National Zoological Park, Smithsonian Institution, Washington, DC, USA

ABSTRACT

The study of ungulate populations in south Asia has lagged behind comparable efforts in Africa. The need for intensive study of Asian wildlife communities is critical. The existing data concerning the numbers and habitat needs of selected mammalian herbivores in south Asia are reviewed. It is concluded that special attention must be given to those species of ungulates which appear to exploit early to mid-succession vegetation stages. These species are especially vulnerable to decline in small parks and reserves where vegetational succession can move rapidly to a climax condition. The ungulate fauna of south Asia is unique and generalisations based on studies in Africa are not necessarily applicable to the subcontinent. The Cervidae emerge as an important radiation in Asia with extensive adaptation to browsing niches.

INTRODUCTION

Although the analysis of ungulate populations from an ecological and behavioural standpoint has enjoyed excellent progress in Africa, the same cannot be said for Asian species. This has occurred because of a multiplicity of factors including difficulties in funding, the politics of research in Asia, as well as the relatively small number of scientists engaged in long-term research projects.

In this paper, we examine the structure and other characteristics of the habitat in a series of national parks and wildlife sanctuaries in India, Nepal, Sri Lanka, and Indonesia (Java) for which census data on wild ungulates are available. Second, we discuss the diversity and abundance of the wild ungulates found living in these habitats. Then we explore the factors possibly underlying trends in habitat utilisation and compare these with the excellent data available for the convergently evolved African ungulate communities. Finally, we relate the significance of these

trends to the preservation and management of ungulate populations in Asian parks and sanctuaries.

We hope this review will stimulate new approaches to ecological research in the national parks of tropical Asia.

HABITAT TYPES

We are primarily concerned in this review with trends in ungulate communities in the Indian subcontinent because the most complete census data available for tropical Asia are from this region. Census data are available for most broad habitat categories with the important exception of tropical evergreen forest. To secure a broad basis for comparisons, we have converted the density values from Hoogerwerf (1970) into biomass estimates. This allows us to include the tropical evergreen forest habitat in Udjung Kulon, Java, as one extreme vegetation class. At the other extreme of habitat types, we have the semi-arid eastern region of the Gir Wildlife Sanctuary reported on by Berwick (1974) and the Bharatpur Wildlife Sanctuary of Rajastan studies by Spillett (1967b). These habitats are characterised by scrub and seasonal grass growth. The Bharatpur Wildlife Sanctuary could be classed as a semi-desert area, but contains a central swamp area resulting from a local drainage pattern.

Figure 1 locates the study areas on an outline map of southern Asia and clarifies the climate patterns by means of climate diagrams adapted from Walter (1973). As can be seen from inspecting Fig. 1, Udjung Kulon is almost continually supplied with rainfall although a brief dry season occurs in July and August. Western Gir and Kanha are similar to one another in climate profile with a single rainy season from May through August. Chitawan shows a similar pattern of rainfall but the period of heavy rains averages some seven weeks longer. The Sri Lanka habitats tend to show two rainfall peaks but each peak is shorter than the single rainy season peak shown by the north Indian study areas.

Soil productivity is difficult to estimate from a comparison of such disparate studies. It should be pointed out that Chitawan experiences annual flooding with substantial deposition of alluvial soils (Seidensticker, 1976). Kaziranga in Assam and Jaldapara in West Bengal show some alluvial deposition and substantial flooding (Spillett, 1967a, c). The productivity of the soil in the western portion of Wilpattu National Park is, however, very low (Eisenberg & Lockhart, 1972).

The vegetative cover type varies in conjunction with drainage, potential productivity of the soil, and climate. For those habitats where we have good data, we can arrange the study areas along a gradient from dense tropical evergreen forests to alluvial plains with grasses exceeding 2 m in height and on through monsoon forests with moderate rainfall to semi-arid areas such as Gir (Fig. 2). The degree of forest cover has a strong influence on the ungalate biomass attainable for a given area. In general the highest ungulate biomasses are attained where forest and meadow or

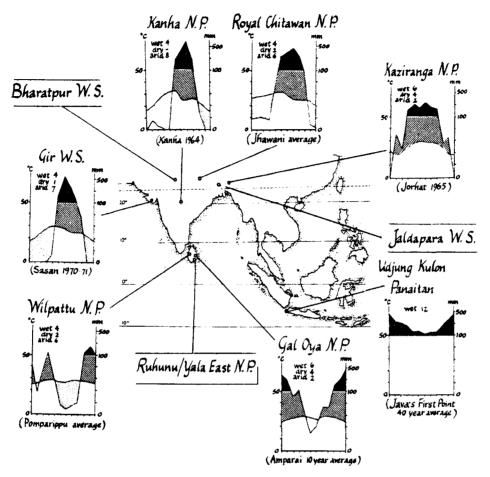


Fig. 1. Climate profiles for south Asian national parks. Black areas under curves indicate precipitation level, probably exceeds the absorption capacity of the soil. Dotted areas on graphs indicate drought periods. These climate diagrams have been constructed according to Walter (1973). Data for Sri Lanka adapted from Mueller-Dombois (1968) and McKay (1973); for Java, Hoogerwerf (1970); for Nepal, HMG (1968); for India, Berwick (1974), Schaller (1967), and US Department of Commerce World Weather Records.

alluvial plain interdigitate to create a maximum interdispersion of cover types (Eisenberg & Lockhart, 1972). This observation is an extension of Leopold's 'edge effect' (Leopold, 1933). This principle is also outlined by Wharton (1968) in his discussion of the distribution of wild cattle (Bos, Bubalus) in southeast Asia, where an almost symbiotic relationship between wild cattle and land clearing in southeast Asia is demonstrable. In order to synopsise the vegetation forms and their various proportions, Fig. 2 offers numerical data concerning the relative proportion of different cover types for those study areas where data are available.

					*	*	1			miline dille.	
Park or Sanctuary	rotal area km²	General vegetation classification	36	short grass (1)	tree salams and grass (2)	tree sarana discontinuous andgrass scrub andgrass (2) (3)	dense scrub (4)	forest (5)	alluvial tal forest gras (6)	重要]	ungulate Biomass
Gir W.S. (qujarat, India)	1166	Dry, semi-deciduous forose and evergreen Krub with savama.		1	25	•	51	3		1	Kg/km²
Gal Oya N.P. (Sri Lanha)	250	Dry, some decidences forest and evergreen scrub with savanna		6	*	1	١	45	ŧ	1	*
Ruhunu Yala N.P. (Sri Lanka.)	1200	Dry, somi deciduous forest and overgreen scrub	(1)	85	1	21	>50	23		ı	~٠
Wilpattu N.P. (Sri Lanka.)	98	Dry, sensi-deciduous forest and evergreen scrub		47		ı	3.2	16		•	<u>\$</u>
Kanha N.P. (Madhya Radesh, India)	3.5	Moist, semi-deciduous forest with meadow.		8)		ŧ	8		t	3011
Royal Chitawan N.P. (Nepal)	545	Moist, semi-deciduous forest/gallery forest and alluvial plain.	(Z)	1	1	1	•	92	8	 }	1760
Jaldapara W.S. (W. Benzal, India)	9	gallery forest and alluvial plain		•	1	t	1	1	\$6	1	***************************************
Kaziranga N.P. (Assam, India)	430	Gallery forest and alluvial plain.	(T)	1	ŧ		,	1	20	80	2853
Udjung Kulon Panaitan (Java, Indonesia)	30	Tropical evergreen forest with meadow.)	02		l l	&		ŧ	492

Fig. 2. Relationship of vegetation types and wild ungulate biomass levels. The relative proportions of different cover types are indicated diagrammatically and with actual percentage figures. For ungulate biomass data, see Appendix A. Data adapted from the following sources; Gir (S. H. Berwick, pers. comn.); Gal Oya (McKay, 1973); Ruhunu (Mueller-Dombois & Fernando, 1969); Wilpattu (Mueller-Dombois & Fernando 1970); Kanha (Schaller, 1967, and Kurt, 1973); Chitawan (Seidensticker, unpublished); Kaziranga (J. J. Spillett, pers. comm.); Jaldapara (Seidensticker, unpublished); Udjung Kulon (Hoogerwerf, 1970).

CENSUS DATA

Biomass data for ungulate populations in Asian habitats were calculated by Berwick (1974), Schaller (1967), Eisenberg & Lockhart (1972), McKay (1973) and Seidensticker (1976). Census data without biomass conversions include the data from Spillett (1967a, b, c) and Hoogerwerf (1970). With the census data from Spillett and Hoogerwerf, we have taken average weights (corrected for age and sex classes) and converted numerical densities into crude biomass estimates. Similar calculations were performed for single species in the data reported by Martin (1973), Barrette (1975) and Meier et al. (1973).

We realise that there are numerous pitfalls associated with ungulate censusing especially in forested habitats where indirect methods of estimation may have to be resorted to, and the results from a variety of authors employing different techniques will invariably introduce sampling errors. The methods for obtaining numerical estimates in Sri Lanka and Nepal are carefully outlined by Eisenberg & Lockhart (1972) and Seidensticker (1976).

To help compensate for one common source of error in recording densities, we have included, where possible, two classes of numerical density and biomass measurement, i.e., the 'ecological' and the 'crude'. In practice, an 'ecological' estimate of density is an estimate corrected for habitat differences within a non-homogeneous habitat. If, for example, the habitat within the study area is one-tenth forested and the species uses only the forested habitat, then the ecological density is reported for that one-tenth part of the habitat suitable for the species x. On the other hand, crude density or crude biomass estimates takes the average density of species x over the entire sample space as the value. A clear separation of ecological values for density or biomass from 'crude' estimates is useful and illuminating. Ecological densities do not vary so much when individual ungulate species are compared but variations in density are often pronounced when crude densities are compared over a range of habitat types.

Appendix A presents the summarised data so determined for 19 species of terrestrial, mammalian herbivores from 10 Asian habitats. The penultimate column of Appendix A portrays the percent contribution to biomass for the species in the designated study area. This is a revealing calculation for it shows that in areas of comparable habitat a species has a remarkably uniform position in the ecosystem in terms of its percentage contribution to biomass. Indeed, this echoes the results of McKay & Eisenberg (1974), which pointed out that almost invariably only 3 to 5 species contribute 80% or more to all herbivore biomass in the ecosystem. The major contributions to biomass levels are almost always the largest species which often have the lowest numerical density.

HABITAT RELATIONSHIPS

The terrestrial herbivore species show marked habitat preferences. For example, the

hare (Lepus nigricollis) typically prefers arid to semi-arid habitats supporting low shrubs and moderate grass cover. In the family Bovidae, the gazelle (Gazella gazella), the four-horned antelope (Tetracerus quadricornis), the blue buck (Boselaphus tragocamelus) and the black buck (Antilope cervicapra) reach their greatest biomasses in the drier habitats supporting moderate grass growth and scrub (see Table 1). In the Cervidae, the axis deer (Axis axis) favours a dry deciduous habitat with scrub (see Table 2). The bovines, such as Bubalus and Bos, prefer moist habitats, but the area must include grassland for grazing. Either alluvial plains and grasses or extensive clearings in part maintained through the activities of man must be present (see Wharton, 1968).

TABLE 1
CRUDE BIOMASS ESTIMATES (KG.KM²) FOR THE BOVIDAE, EXCLUSIVE OF DOMESTIC LIVESTOCK IN INDIA.
INDONESIA (JAVA) AND SRI LANKA

	Dry thorn forest and steppe	Dry semi- deciduous forest with scrub	Moist deciduous forest	Gallery forest and alluvial plain	Tropical evergreen forest with meadows
Gazella gazella					
Gir (east)	2.4		_		
Tetracerus quadricornis					
Gir (east and west)	-	9.3	_		
Kanha	_		5⋅7		_
Boselaphus tragocamelus					
Bharatpur	829-0		_		
Gir (east and west)		166-3			
Kanha		_	11.5	_	
Antilope cervicapra					
Bharatpur	51.8		_	_	_
Kanha	_	_	< 2.0	*******	_
Bubalus bubalis					
Wilpattu	_	81-6	_		
Gal Oya		307-3			
Kaziranga				299-2	
Bos gaurus					
Kanha	_	_	381.9		-
Jaldapara			_	59-1	
Bos banteng					
Udjung Kulon					236.6

Some species seem to be little affected by the gross characteristics of the habitat. The sambar (*Cervus unicolor*) appears in fair numbers over a wide range of habitat types, as does the elephant (*Elephas maximus*), although extremely axid habitats will not support elephants. Rhinoceros (*Rhinoceros unicornis*) appears to be confined to moist habitats supporting semi-evergreen to evergreen forest almost always in association with alluvial plains and tall grass (see Table 3).

The degree of forest cover profoundly affects the biomass of larger mammals which can be supported. As a generalisation, when proceeding from a dry thorn forest to a moist deciduous forest, the mammalian biomass increases as one moves

along an increase in rainfall gradient as shown in Table 4. If the forest cover becomes continuous and there is very little grassland area, then the forest will tend to support a very low density of terrestrial herbivores so that, at the extreme wet end of our imaginary vegetation gradient, the biomass of terrestrial herbivores will decline again. This phenomenon has been discussed by Eisenberg & McKay (1974) with respect to data from Africa.

TABLE 2
CRUDE BIOMASS ESTIMATES (KG-KM²) FOR THE CERVIDAE IN INDIA. NEPAL SRI LANKA, AND INDONESIA (JAVA)

			Deciduous	to semi-eve	ergreen fores	t
	Dry thorn forest and steppe	Dry semi- deciduous forest with scrub	Moist semi- deciduous forest	Inter- mediate	Gallery forest and alluvial plain	Tropical evergreen forest with meadows
Axis axis						
Bharatpur	553-0				_	_
Gal Oya		29.7			_	
Gir	_	172-0	_		_	_
Wilpattu		262-0	_	_		_
Kanha	_	_	143.6	_	_	_
Chitawan	_	_	· - ·	557-9	_	
Jaldapara	_	_	_		4.5	
Axis porcinus						
Bharatpur	21.7	_	_	-	_	_
Chitawan			_	171.2	_	
Jaldapara	_		_		139-0	
Kaziranga	_	_	_	_	96-1	-
Cervus unicolor					,,,,	
Bharatpur	94.5	_	_	-	_	•
Gal Oya		68.0	_		_	_
Gir	_	33-1		_	_	
Wilpattu	_	157-9	_	_	_	
Kanha	_	_	135-1	~	_	~
Chitawan	_	_		443.0		~
Kaziranga	_	-	_	-	37.0	
Jaldapara	_	_	_	_	60.8	-
Cervus duvauceli					000	
Kanha	~	_	37.8	_	_	_
Jaldapara	_	_	_	_	16-1	-
Kaziranga	_		-		79.5	
Cervus timorensis						
Udjung Kulon	_	_			-	130-5
Muntiacus muntjak						
Wilpattu		5-4-20-1	_	_	_	
Kanha	-		7-1	_		-
Chitawan	-	_		46.2	_	_
Kaziranga	_	_	_		1-3	
Jaldapara	_	_	_		17.9	-
Udjung Kulon		_	_	_		7.02

The uniformity of rainfall has a certain effect; that is, within limits the absolute amount of rain is not as important as how evenly the rain is distributed throughout the annual cycle. Whereas Gal Oya in Sri Lanka receives considerably less rain than

TABLE 3
CRUDE BIGMASS ESTIMATES (KG/KM²) FOR ELEPHAS AND RHINOCEROS IN INDIA, NEPAL, SRI LANKA, AND INDONESIA (JAVA)

			Deciduous t	o semi-ever	green forest	
	Dry thorn forest and steppe	Dry semi- deciduous forest with scrub	Moist semi- deciduous forest	Inter- mediate	Gallery forest and alluvial plain	Tropical evergreen forest with meadows
Elephas maximus						
Wilpattu		217	_			
Gal [°] Ova		416				
Kaziranga				_	1484*	_
Rhinoceros unicornis						
Chitawan	_			451-2		
Jaldapara					549	
Kaziranga	-		-		858	
Rhinoceros sondiacus						
Udjung Kulon			_	_	-	119-7

^{*} Probably represents ecological density.

TABLE 4
CRUDE BIOMASS ESTIMATES (KG-KM²) FOR UNGULATES IN INDIA, INDONESIA (JAVA), NEPAL, SRI LANKA, AND VENEZUELA

			Deciduous to	semi-everg	reen Joresi		
•	Dry thorn forest and steppe	Dry semi- deciduous forest and evergreen scrub	Moist semi- deciduous forest with meadows	Inter- mediate	Gallery forest and aliuviul plain	Tropical evergreen Jorest with meadows	Authority
Vild mammalian biomass:							
Bharatpur (Rajastan, India) Gir	1617	_		-	-		Spillett, 1967b
(Gujarat, India)	-	383	_	-	-	-	Berwick, 1974
Wilcattu (Sri Lanka)		765	_	-			Eisenberg & Lockhart, 1972
Gal Oya							-
(Sri Lanka) Canha		886		-		_	McKay, 1973
(Madhya Pradesh, India)		_	1708				Schaller, 1967
Chitawan (Nepal)		_	-	1790			Seidensticker, 1976
aidapara (West Bengal, India)	_	_		_	984	_	Spillett, 1967c
Kaziranga					2858		Spillett, 1967a
(Assam. India) Juliung Kulon		_	~		2030		•
(Ĵava, Indonesia)	_		-	-	_	492	Hoogerwerf, 1970
Domestic ungulate biomass:							
Gir (Gujarat, India)		6171	_	_	_	_	Berwick, 1974
Kanha			47.70				Cabullar 1047
(Madhya Pradesh, India) Chitawan			4678	_			Schaller, 1967
(Nepal)	_	-	_	28076*	_		Seidensticker, 1976
Guarico (Venezuela)		-	_		28288*	_	Eisenberg, unpublished.

Maximum density.

Kanha Park in India, the rainfall in Gal Oya is much more evenly spread than is the case in Kanha (see Fig. 1). In fact, there are two rainfall peaks, which to an extent evens out distribution of precipitation. As indicated in Fig. 1, all rainfall cannot be absorbed by the ground and must contribute to runoff beyond a certain point (Walter, 1973).

Seasonal flooding can contribute to the formation of gallery forest and alluvial plains. The fertility of the soil in these alluvial plains can be recharged on an annual basis and the productivity of grasses may be vastly increased through such a process. Of course, the seasonal flooding will reduce the effective carrying capacity temporarily for an area and the terrestrial herbivores must have methods of retreating away from the flood line only to re-occupy the plain when flood waters recede. Such is the case in western Chitawan and Kaziranga. These two areas, however, support the highest ungulate densities (Table 4).

Where livestock is included in a terrestrial herbivore census, the biomass levels are appreciably increased. The dry deciduous forest and thorn forest of the Gir support over 6,171 kg/km² of combined wildlife and livestock (Table 4). This is far in excess of comparable carrying capacities with no livestock in Sri Lanka and in the Gir. It would appear that livestock severely stress pasture and artificially high densities can be reached. The same may well be said of the situation in Chitawan where livestock densities exceed 28,000 kg/km². This high density of livestock definitely reflects the superior carrying capacities of the alluvial plains at the base of the Himalayan foothills; however, it would be fair to say that this carrying capacity is artificially raised to seven times its normal value.

COMMUNITY STRUCTURE

The diversity of terrestrial herbivore species in tropical Asia varies considerably according to the structure of the habitat. Chitawan in Nepal, with its alluvial plains and interdispersion of various habitat subtypes, appears to support a typical terrestrial herbivore fauna, with rhinoceros, wild swine (Sus scrofa), muntjac (Muntiacus muntjak), axis deer, hog deer (Axis porcinus) and sambar. At the present time, elephant are not to be found in Chitawan, but had occurred previously (Seidensticker, 1976). Schaller (1967) in his study at Kanha has portrayed a typical peninsular India ungulate fauna with gaur (Bos gaurus), blue buck, four-horned antelope, barasingha (Cervus duvauceli) sambar, axis, and muntjac. In Schaller's study area, both the elephant and rhinoceros were absent. The more arid areas of India show higher densities of black buck, blue buck, and, in extremely arid areas, gazelles. In arid habitats members of the tribe Bovini, including Bubalus and Bos, disappear from the fauna as do Elephas and Rhinoceros.

Although browsing ungulates may contribute significantly to mammalian

biomass in habitats dominated by scrub vegetation, it would appear that mixed browsers and grazers or grazers contribute overall the greatest percentage to terrestrial mammalian biomass in any given habitat. This means that grass and the interdispersion of resources, namely grass, shrubs and scrub as well as low stature trees, will create the optimum habitat for utilisation by a diverse terrestrial mammalian herbivore community.

Wild ungulate biomasses in Asia can reach levels which approximate those reported for East Africa yet fall short of the maximum values (McKay & Eisenberg, 1974). In part this appears to result from the fact that primary grazing herbivores are noticeably absent from the ungulate faunas of the wetter areas of india. Sri Lanka and Java. In the semi-arid zones. Antilope and Gazella do considerable grazing, but only axis deer, Bubalus and barasingha seem to be the predominant grazers in the subcontinent. The wild cattle do graze to appreciable extents, but as pointed out previously these species are early to late successional forms and have been strongly influenced by the cultivation patterns of early man (Wharton, 1968). If the natural climax condition of monsoon India and southeast Asia is to tend toward a forest climax, then grazing ungulates may not have evolved to an appreciable extent and browsers (i.e. Cervidae) were favoured. The arid-adapted bovids (Taurotragus, Gazella and Antilope) are, of course, an exception.

The heterogeneous nature of the savanna vegetation in East Africa (Pienaar, 1963) and the predominance of specialised grazing species has not only promoted a high species diversity, but also allows for extremely high biomass levels obtained by the grazers (Talbot & Talbot, 1963; De Vos, 1969; Hirst, 1975). Even in areas of high ungulate diversity in East Africa, the major percentage of the biomass is contributed by 4 to 5 grazing species (McKay & Eisenberg, 1974). The introduction of grazing ungulates as domestic stock in India has resulted in extremely elevated ungulate biomass levels (see Table 4). While the pastures are often severely stressed, the data suggest that cleared land in India can support significant grazing herbivore numbers for a limited period of time. This is especially true for alluvial areas where considerable nutrients are deposited with spring flooding. An analogous situation exists in northern Venezuela where naturally occurring endemic ungulates show a very reduced diversity, a situation that pertains throughout South America (Eisenberg & McKay, 1974). Whereas the browsing white-tailed deer (Odocoileus virginianus) can reach crude biomass levels of 300 kg/km², the grazing caviomorph rodent (Hvdrochoerus) can maintain a low biomass of 270 kg/km² during the summer flooding to 6.240 kg/km² during the spring (March-May) dry season (Ojasti, 1973). Domestic livestock on the same range can reach peak levels of 28,288 kg/km² on stressed pasture (see Table 4).

In summary then, the carrying capacities of wild ungulates in Asia are probably somewhat different from those established for East Africa. The ungulate communities of the arid biomes (Rajastan) are typified by low biomass levels. The

ungulates of northern peninsular India are typified by browsers or partial browsers and can attain moderate biomass levels. *Elephas*, which is a mixed grazer and browser (McKay, 1973), can be a significant contributor to ungulate biomass levels, but is limited to areas where it can have access to permanent water. *Rhinoceros unicornis* is apparently adapted to alluvial habitats where, in the absence of *Elephas*, it can contribute the highest percentage to wild ungulate biomass levels (Seidensticker, 1976: Laurie, in prep.).

CONSERVATION CONSIDERATIONS

The specific habitat requirements for each ungulate species must be accurately determined for a variety of habitat types. Our review points out a few significant trends and correlations, but considering the high rate of habitat destruction in Asia, the need for accurate censusing and field studies in India and southeast Asia is of the highest priority. Only with such information can parks and sanctuaries be managed and proper management is a necessary concomitant of protection.

Extinction through random events even in strictly preserved habitats is a high risk when the protected areas are cut off from possible outside emigration (Willis, 1974). National parks as isolated habitat patches tend to 'behave' as if they were islands. Assuming that the park retains vegetational diversity and succession does not proceed in such uniform fashion as to induce extinction of early successional species through habitat loss, then extinctions can still occur at a predictable rate (Terborgh, 1974). The rate of extinction is proportional to the land area so that, if a park is only $10 \, \mathrm{km^2}$, then the coefficient of extinction for mammals is 9×10^{-6} and for a park of $100 \, \mathrm{km^2}$ the value is 3.9×10^{-6} (Eisenberg, unpublished, based on Terborgh, 1974). Thus in $100 \, \mathrm{years}$ a park of $10 \, \mathrm{km^2}$ with 90 mammalian species would tend to lose seven species through 'natural accidents.' If, however, the vegetation is unmanaged and succession proceeds to a climax condition, then at least 12 species or $13\,^{\circ}_{0}$ could be lost (Eisenberg, unpublished).

We argue here then for a two-pronged approach to wildlife conservation in Asia. First the habitat needs of the mammalian species resident in national parks must be adequately assessed with full recognition of the necessity for maintaining (even by cutting) a vegetational diversity requisite to the discrete needs of the populations in question (Eisenberg & Lockhart, 1972; Seidensticker, 1976). Second, the parks must be of sufficient size to permit not only adequate movement of the larger grazing species (McKay & Eisenberg, 1974), but also to reduce the possibility of random extinctions. This is especially critical for the larger ungulates, such as *Elephas*, and the large predator complement of the mammalian fauna which act as regulators of surplus ungulate production through their predation pressure (Schaller, 1967; Berwick, 1974; Seidensticker, 1976).

ACKNOWLEDGEMENTS

We thank the Smithsonian Foreign Currency Program, World Wildlife Fund, Fauna Preservation Society, and 'Save the Tiger Fund' of the National Zoological Park-Smithsonian Institution for financial support for our own research on Asian ungulates. We are indebted to our colleagues who have shared their ideas and unpublished information with us, particularly Drs J. J. Spillett and S. H. Berwick. Mrs W. Holden prepared the manuscript for publication; Tomi made the line drawings. J. Seidensticker gratefully acknowledges the assistance of Dr T. H. Reed, Director, and the Office of Zoological Research during his stay at the National Zoological Park, Smithsonian Institution, Washington, DC (USA).

REFERENCES

- BARRETTE, C. (1975). Social behaviour of nuntjacs. Ph. D. dissertation, University of Calgary, Alberta. BERWICK, S. H. (1974). The community of wild ruminants in the Gir Forest ecosystem, India. Ph. D. dissertation, Yale University.
- DE Vos. A. (1969). Ecological conditions affecting the production of wild herbivorous mammals on grasslands. In Advances in ecological research, ed. by J. Crass, 137-83. New York, Academic Press.
 EISENBERG, J. F. & LOCKHART, M. (1972). An ecological reconnaissance of Wilpattu National Park, Cevlon. Snithson. Contr. Zool., 101, 1-118.
- EISENBERG, J. F. & McKAY, G. M. (1974). Comparison of ungulate adaptations in the New World and Old World tropical forests with special reference to Ceylon and the rainforests of Central America. In *The behaviour of ungulates and its relation to management*, ed. by V. Geist and F. Walther, 585-602, IUCN Publication, New Ser. No. 24.
- HIRST, S. M. (1975). Ungulate-habitat relationships in a South African woodland/savanna ecosystem. Wildl. Monogr., 44, 1-60.
- HIS MAJESTY'S GOVERNMENT, NEPAL (1968). Soil survey of Chitawan Division. Ministry of Forests, Forest Resources Survey Pubs., No. 5, 1-126.
- HOOGERWERF, A. (1970). Udjung Kulon, the land of the last Javan rhinoceros. Leiden, Netherlands, E. J. Brill.
- KURT, F. (1973). Zoologisch-ökologische Exkursion in den Kanha-Nationalpark (Indien), 1972. Vjschr. naturf. Ges. Zürich, 118, 1-152.
- KURT, F. (1974). Remarks on the social structure and ecology of the Ceylon elephant in the Yala National Park. In *The behaviour of ungulates and its relation to management*, ed. by V. Geist and F. Walther. IUCN Publication, New Ser. No. 24.
- LEOPOLD, A. (1933). Game management. New York. Charles Scribner's Sons.
- MARTIN, C. (1973). Die Barasingha-Population des Kanha-Nationalparkes. Vjschr. naturf. Ges. Zürich, 118, 97-106.
- McKAY, G. M. (1973). Behaviour and ecology of the Asiatic elephant in southeastern Ceylon. Smithson. Contr. Zool., 125, 1-113.
- MCKAY, G. M. & EISENBERG, J. F. (1974). Movement patterns and habitat utilization of ungulates in Ceylon. In *The behaviour of ungulates and its relation to management*, ed. by V. Geist and F. Walther. 1UCN Publication No. 24.
- Meier, E., Anderegg, R., Kleiber, H., Leimbacher, R., Sommer, E. & Welti, W. (1973). Zum Sozialverhalten der Sasin oder Hirschziegen-antilope. Vjschr. naturf. Ges. Zürich, 118, 107-28.
- MUELLER-DOMBOIS, D. (1968). Ecogeographic analysis of a climate map of Ceylon with particular reference to vegetation. Ceylon Forester, 8, 39-58, map.
- MUELLER-DOMBOIS, D. & FERNANDO, K. S. (1969). Vegetation map of Ruhunu National Park. Colombo. Survey Department of Ceylon.
- MUELLER-DOMBOIS, D. & FERNANDO, K. S. (1970). Vegetation map of Wilpattu National Park. Colombo, Survey Department of Ceylon.
- OJASTI, J. (1973). Estudio biologico del chigiire o capibara. Caracas. Fundo Nacional de Investigaciones Agropecuarias.

- PIENAAR, U. DE V. (1963). The large mammals of the Kruger National Park—their distribution and present-day status. Koedoe, 6, 1-37.
- SCHALLER, G. B. (1967). The deer and the tiger. Chicago, University of Chicago Press.
- SEIDENSTICKER, J. (1976). Ungulate populations in Chitawan Valley, Nepal. Biol. Conserv., 10, 183-210.
- SPILLETT, J. J. (1967a). A report on wild life surveys in North India and Southern Nepal: The Kaziranga Wild Life Sanctuary, Assam. J. Bombay nat. Hist. Soc., 63, 494-533.
- SPILLETT, J. J. (1967b). A report on wild life surveys in North India and Southern Nepal: The large mammals of the Keoladeo Ghana Sanctuary, Rajasthan. J. Bombay nat. Hist. Soc., 63, 602-7.
- SPILLETT, J. J. (1967c). A report on wild life surveys in North India and Southern Nepal: The Jaldapara Wild Life Sanctuary, West Bengal. J. Bombay nat. Hist. Soc., 63, 534-56.
- TALBOT, L. M. & TALBOT, M. H. (1963). The wildebeest in Western Masailand, East Africa. Wildl. Monogr., 12, 1-88.
- TERBORGH, J. (1974). Preservation of natural diversity: The problem of extinction prone species.
- BioScience, 24, 715-21.

 WALTER, H. (1973). Vegetation of the earth in relation to climate and the eco-physiological conditions. London. English Universities Press Ltd and New York, Springer-Verlag.
- WHARTON, C. (1968). Man, fire and wild cattle in Southeastern Asia. Proc. Tall Timbers Fire Ecology Conf., 8, 107-67.
- WILLIS, E. O. (1974). Populations and local extinction of birds on Barro Colorado Island, Panama. Ecol. Monogr., 44, 153-69
- World weather records 1951-60, 3 (1966). Washington, DC, US Department of Commerce.

Appendix A follows

APPENDIX A

Taxon and area	Unit weight (kg)	Ecological density No./km²	Crude density No. /km²	Evological biomass kg/km²	Crude biomass kg/km²	button* to crude	Authority for density estimates
LAGOMORPHA Leporidae Lepus nigricoliis Wilpattu Gal Oya	3-13	30-172	4.7	94-540	14.9	2.2	Eisenberg & Lockhart, 1972 McKay, 1973
PROBOSCIDAE Elephus maximus Wilpattu Gal Oya Kaziranga Ruhunu/Yala	1810 1810 1810 1810	0-1 8-0	0-12 0-23	1810 1484 1810	217-0 416-3	28 47 1	Eisenberg & Lockhart, 1972 McKay, 1973 Spillett, 1967 <i>a</i> Kurt, 1974
PERISSODACTYLA Rhinoveros unicornis Chitawan Jaldapara Kaziranga Rhinoveros sundiacus Udjung Kulon	1410 1100 1100	11.2	0.32 0.50 0.85 0.12	15792	451-2 550-0 935-0 119-7	26 26 24 32 32	Seidensticker, 1976 Spillett, 1967 <i>c</i> Spillett, 1967 <i>a</i> Hoogerwerf, 1970
ARTIODACTYLA Suidae Sus scrofa Wilpattu Kaziranga	27.4 24·3	0.7	0 4-0 4-0	19.2	8-1 7-9	- -	Eisenberg & Lockhart, 1972 Spillett. 1967a
Kanha Gal Oya Chitawan Jadapara Bharatpur	25.8 29.0 61.8 26.6 27.1	2.8	0.5 0.5 1.1 2.1	360.0	12.9 14.5 68.3 37.3 57.0		Schaller, 1967 McKay, 1973 Seidensticker, 1976 Spillett, 1967c Spillett, 1967b
rragulidae Tragulus meminna Wilpattu Cervidae	3.2	3:1	9.0	8.6	6-1	~	Eisenberg & Lockhart, 1972

Kanha 189-0 5.2 0.2 980-0 37.8 2 Schallett, 1907; Martin, 1973 Kalatanga 159-0 0.5 79-5 3 Spillett, 1967 Bovidac 0-1 161-0 0-1 57 Spillett, 1967 Revidence in squadricornis 19-0 0-3 5.7 <1 Schallert, 1967 Gir Gir 9-3 2 Bcwick, 1974 Gir Gir 9-3 2 Bcwick, 1974 Kanha 115-0 0-6 9-3 2 Kanha 115-0 0-6 9-3 43 Berwick, 1974 Gir 184-8 0-9 166-3 43 Berwick, 1974 Gir 184-8 0-9 6- 9-3 43 Berwick, 1974 Gir 184-8 4-6
15.5
1940
159-0
161-0 161-1 161-1 2 1940 184-2 184-2 186-3 1
1940 1957 1958 1958 1959
19.0
19-0
19.0
15.5
15.0
1150
115-0
0.9 166.3 43 4.6 829.0 51
4.6 829.0 51
4.6 829.0 51

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APPENDIX A continued

			APP.	APPENDIX A centinued	ntinued		
Taxon and area	Unit weight (kg)	Ecological density No./km²	Criale density Na./km²	Evological biomass kg/km²	Crude tronass kg/km²	bution* to crude biomass	Authority for density esomates
ntilope cerreapra				1			
Canha	13.7	4.8	-0×	1.601	< 2.0	-	Schaller, 1967; Meier et al., 1973
Bharatpur	22.5	1	2.3		8-15	.~.	Spillett, 1967h
zetla gazetla							•
	0.71	i	ci O		÷:		Berwick, 1974
balus bubatis							
Wilpattu	272-0	5.1	6.3	0.80+	9.18	10	Eisenberg & Lockhart, 1972
Kaziranga	272.0	4	Ξ		299.2	2	Spillett, 1967a
ial Oya	279.0	!	Ξ	:	307-3	35	McKay, 1973
s ganerus							
aldapara	991.0	:	-		59-1	9	Spillett, 1967c
Kanha	545.0		10.7		6-188	55	Schaller, 1967
as nameng Udjung Kulon	263-0	:	6·0		236-6	*	Hoogerwerf, 1970

Note: Biomass estimates sometimes vary because investigators have used different weight estimates and/or their calculations have been adjusted with respect to use and sex classes at the time of censusing. Slight discrepancies in totals result from rounding errors.

* Exclusive of domestic stock.