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AN ECOLOGICAL SURVEY OF THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL

PART III: UNGULATE POPULATIONS

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ABSTRACT

Population density and biomass estimates for wild and domestic ungulates in the Royal Karnali-Bardia Wildlife Reserve, Nepal, are presented and compared with values obtained from other reserves in South Asia. Wild ungulate population densities varied in relation to habitat diversity; large herbivores were most numerous where early and intermediate successional stages intergraded with one another and only sparsely distributed in continuous climax sal Shorea robusta *forest. Chital* Axis axis *was the most abundant wild ruminant in the reserve. It and the nilgai* Boselaphus trago-camelus *constituted 88% of the total wild herbivore biomass in the southwestern corner of Karnali-Bardia, where an intensive study was carried out. The biomass of domestic stock utilising the same study area in 1975 was computed to be 15–17 times higher than the levels attained by wild ungulates in April of 1977, nearly two years after the reserve borders had been closed to domestic grazing. Observations during the hot-dry season indicated that both wild and domestic ruminants competed for the same forage species.*

Among the wild ungulates, chital were decidedly the most gregarious, commonly associating in feeding aggregations of over 20 individuals on the open savannahs. Nilgai and wild boar Sus scrofa *formed smaller groups while barking deer* Muntiacus muntjak *and hog deer* Axis porcinus *were primarily solitary. Chital exhibited a peak in rutting activity during the late hot-dry season and a subsequent birth peak in February. Nilgai exhibited a different pattern, breeding in January and calving during the monsoon, when optimum foraging conditions prevailed.*

INTRODUCTION

The Terai zone of southern Nepal, skirting the outermost foothills of the Himalayan chain, was long regarded as one of the premier big game hunting areas of South Asia

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(Symthies, 1942). The alluvial tall grass flood plains and riverine forest tracts associated with the large tributaries of the Ganges system provided extensive habitat for a host of large herbivores and predators. The persistent threat of malaria, precluding large scale agricultural development, effectively preserved wildlife populations and their habitats until quite recently. The control of the malarial vector through an intensive spraying campaign launched in the early 1950s, however, opened up a substantial portion of potentially arable flat land to impoverished hill farmers. In one of the world's most mountainous countries, such a resource quite naturally became the object of desire for an expanding human population struggling to maintain subsistence agriculture under harsh environmental conditions (Eckholm, 1976). As a result, much of the prime jungle habitat was cleared for cultivation. The dramatic decline in wildlife populations witnessed in the last two decades spurred the timely creation of several reserves and one national park in this region. However, because of the remote locations of these sanctuaries, the difficulties of censusing wildlife populations in a monsoonal environment, and the initial emphasis on priorities other than research, the true nature of the wildlife resources in these reserves remained long unknown.

Intensive study in one of these newly gazetted sanctuaries, the Royal Karnali-Bardia Wildlife Reserve, began in June 1975 and continued through May 1977. Located in the southwestern corner of the Terai, Karnali-Bardia was one of three former hunting reserves designated for protection by His Majesty's Government of Nepal and the World Wildlife Fund's 'Operation Tiger' Project. This action preserved one of the largest tiger *Panthera tigris* populations left in the Terai, a relict herd of swamp deer *Cervus duvauceli*, and a small population of gharial crocodile *Ghavialis gangeticus*, all listed as endangered species (IUCN, 1971, 1972). In addition, Karnali-Bardia supported Nepal's largest population of nilgai *Boselaphus tragocamelus*, a large antelope generally associated with xeric habitats of the Indian subcontinent. The most visible wild ungulate in the reserve was the chital *Axis axis*, especially in the savannahs and grasslands bordering on riverine forest associations (Dinerstein, 1979*b*).

The major aim of this study was to gather data on the populations of these two ungulate species, the chital and the nilgai. Research conducted elsewhere on the Indian subcontinent identified them as important prey items in the diets of large predators (Schaller, 1967; Berwick, 1974; Martin, 1978, Muller & Zurcher, 1973). To this end their populations were censused during the latter half of the two-year study.

A second aim was to determine the capacity of climax and subclimax habitats to support wild ungulate biomass. The vegetation of Karnali-Bardia is markedly homogeneous, with approximately 70% of the reserve dominated by several associations of climax sal *Shorea robusta* forest (Dinerstein, 1979). The remaining 30% contained a mixture of habitat types considered to be in early to mid-successional stages of development. Thus the existing composition and distribution of plant communities offered an ideal opportunity to examine any relationships between habitat diversity, plant succession, and wild ungulate biomass.

Nearly all of the newly created wildlife reserves of South Asia have been forced to contend with domestic stock grazing during the last decade. Current (1977) herd sizes around Karnali-Bardia were assessed through a house-to-house survey and later contrasted with densities existing in 1975, before the institution of control measures. The direct and indirect impacts of domestic grazing on habitat conditions for wild ungulates, which are substantial, were discussed previously (Dinerstein, 1979).

Other objectives of this study were to obtain information on the grouping characteristics of wild ungulate populations, age and sex ratios, and lengths and possible peaks in reproductive activity. Several of the South Asian species appear to show a pronounced birth period over certain parts of their range and no detectable pattern in other areas (Schaller, 1967).

Intensive research on South Asia's wild ungulate populations began with Schaller's pioneering study in Kanha National Park, India in 1964. Subsequent studies by Eisenberg & Lockhart (1972) and Berwick (1974) have added considerably to our knowledge about the ecology and behaviour of several of these species. Nevertheless, wildlife research in South Asia still remains in its infancy. Only in Chitawan National Park, Nepal, has a research programme been supported over a span of several years. Hopefully future management policies will allow for expanded research opportunities to augment the important conservation work which has been completed to date.

THE STUDY AREA

A detailed description of the location of the intensive 11·8 km^2 study area, its vegetation, climate, soils, topography, and the past land use in the reserve environs, is available in part one of this series (Dinerstein, 1979*a*). The phenology of the vegetation, and the seasonal food habits, distributions, and movements of wild ungulates in the study area were discussed in the second paper of this series (Dinerstein, 1979*b*). The reader is referred back to these papers for background information.

METHODOLOGY

Three principal methods were chosen to census ungulate populations within the intensive study area: pellet group counts, strip censusing by motor vehicle, and sample area counts from observation platforms. Transects along game trails and water courses were also conducted both in the intensive research area and in other parts of the reserve. The specific techniques of each method as used in Karnali-Bardia are described below.

The pellet group method was employed primarily in habitat types where poor visibility prohibited strip censusing by vehicle. Tall grass flood plain and sal forest habitats were originally selected for this reason. The savannah habitat, where visibility was quite satisfactory during half of the year, was also included in this analysis to compare density figures obtained from this method with results from strip censusing and sample area counts. In addition, establishing plots in these three habitats offered two advantages: first, tall grass flood plain, savannah, and sal forest represented plant associations which differed considerably in physiognomy, and second, each association was made up of vegetation in a different stage of successional development (Dinerstein, 1979*b*). Tall grass flood plain was the earliest seral stage identified, sal forest was considered to be the climax vegetation, while savannah habitat occupied an intermediate position between the two.

It was decided to locate sample plots along permanent transects in the hope that this method would be continued after the completion of this study. Initially, the study area was traced onto graph paper from aerial photographs. The cubes of the graph paper which fell on the perimeter of each habitat to be sampled were numbered. An azimuth was then selected by coin toss to decide on the direction that the transects would follow. It was decided to locate the plots on three parallel transect lines in each of the three habitats. The starting point for the transects were the numbered cubes corresponding to the first three figures read from a random numbers table. The distance between each plot on the transect was randomised between 0·3 and 45·0 m.

Neff (1968) reviewed the benefits and disadvantages of different sizes and shapes for pellet plots. Long and narrow rectangular plots (3·6 m by 21·9 m) were felt to be best suited to the habitat conditions encountered. It was attempted to clear the plots at monthly intervals. A defecation rate of 13 pellet groups per day was tentatively assumed for all cervids in the study area.

The use of this technique is limited to the dry period (November-May) since during the monsoon pellets are moved laterally and break down rapidly. In addition, dung beetle activity increases significantly with the onset of the monsoon rains, which also decreases the accuracy of pellet counts in the wet season. The influx of local thatch grass cutters in early November of 1976 caused changes in habitat utilisation by wild ungulates. This source of disturbance ended by mid-November after the allotted time for cutting had expired. Pellet plots were cleared following the departure of the villagers and censusing begun.

The cervids studied by this method were chital, hog deer, and barking deer. As noted by other researchers (Graf & Nichols, 1966; Eisenberg *et al.* 1970), there is considerable variation exhibited in the shapes of chital pellets. In Karnali-Bardia, depending upon the food source, the shapes ranged from long light brown, near perfect cylinders from droppings containing earth to tear-shaped and elongated pellets composed of succulent vegetation. It was felt that the faeces of barking deer, with their characteristic comma-shaped and small size, could be readily distinguished from those of hog deer and chital. Part of the first year of this study was spent testing this method and collecting pellets for reference. Examination of a number of pellet groups indicated that hog deer droppings were on the average smaller than those of chital and could be separated in the field. Nilgai and sambar densities could not be assessed by this method; nilgai dung in communal piles and sambar were not ordinarily present in the intensive study area.

To minimise some of the more common observer errors associated with this method, several guidelines were established and adhered to throughout the course of monitoring. Before censusing began, the newly located plots were searched thoroughly by a number of workers to ensure the removal of all pellets. The same team sampled all of the plots thereafter. In order to maintain visual acuity, no more than 10 plots per day were examined in dense habitat conditions. Pellet groups with more than half of the total number of pellets inside the plot boundary were tallied.

Strip censusing was initially planned for each of the six habitat types described within the study area. However, visibility considerations and logistical problems limited the application of this method to use only in the open savannah/grasslands during the hot-dry season (April-May) of 1977. The network of roads through this habitat assured adequate coverage. The critical problem inherent in this sampling technique is the accurate determination of strip width. Hirst (1969) used a series of cut-out models of wild ungulates in a South African woodland to quantify the distance at which wild ungulates remained visible from a moving vehicle. Berwick & Jordan (1971) employed a similar method in the Gir Forest Sanctuary, India, another semi-arid woodland environment. In Karnali-Bardia, in place of cut-out models, I substituted the skin of a chital (considered to be an intermediate-sized ungulate among the various species sampled) to demarcate the distance from the observer at which the skin (propped up to resemble a live animal) became obscured by the vegetation. A total of 50 measurements were taken along the 7·0 km strip. With the aid of aerial photographs the disappearance distances were plotted on a graph paper map of the study area and the perceived strip width computed.

In 1977 strip censusing began in the first week of April after two major fires had greatly improved the visibility in the savannahs. Between 6 April and 7 May, nine strip censuses were conducted. By the end of the first week in May, however, the flooding of the Khoraha River severed access to the study area by motor vehicle and curtailed further attempts at strip censusing for the remainder of the year.

The census party consisted of a driver and two observers equipped with 7 × 35 binoculars. Each observer was responsible for counting animals on one side of the motor track. Large feeding aggregations of chital were counted by both observers to compare accuracy and then recounted. Since the ultimate objective of this method was to count as many animals as possible, censusing occurred in the hour around sunset (1800 h Nepal standard time), the period of the day when most ungulates were on their feet, actively feeding, and hence most visible (Dinerstein, 1979*b*).

Dasmann & Taber (1955) successfully censused black tailed deer *Odocoileus* *hemionus* by sample area counts from observation points overlooking chaparral habitat in the California Coast Range. The big game species of the Indian subcontinent have long been hunted from tree platforms, or machans. It soon became apparent that machan sightings would prove the most efficient way to count ungulate groups in open habitats (Fig. 1). Five platforms were located in the

Fig. 1. Tree platforms, or machans, permitting undisturbed viewing of wild ungulates in the open savannah habitat for much of the year.

savannah/grasslands where visibility was found to be greatest. In order to obtain observations when ungulates were most active (i.e., between 1800–2000 h and 0500–0600 h) it was necessary to stay for the whole night on these platforms. Between March 1976 and May 1977 over 140 evenings were spent in the tree hides. Because of insufficient funds to weatherproof the machans against the monsoon, this activity was restricted to the dry period. The procedure followed was to count the number of ungulates visible in areas of determined size from these five machans. From a series of counts over the cool-dry and hot-dry season, a density estimate was obtained. This method appears most applicable to censusing relatively sedentary ungulate populations in open habitat conditions. As described earlier, chital, nilgai, barking deer and hog deer all occupied rather small home ranges (Dinerstein, 1979*b*), thus reducing the bias that would be introduced by census attempting to a highly migratory population with this method. A further five machans were located in the five other habitat types.

Transects were relied upon to census ungulates in other parts of the preserve inaccessible to motor vehicles and unsuitable (in the light of distance and transportation considerations) for machan construction. Pellet transects along the base and on the slopes of the northern Churia ridge were employed to obtain an idea of presence and absence of ungulates. Track counts along the major jeep trails and stream beds provided estimates of relative population densities in different habitats over the seasons.

Data regarding the rutting and birth seasons of the chital were collected systematically from February 1976 until the middle of May 1977. Four indicators were selected and studied to determine the lengths and possible peaks of the rutting and reproductive seasons: antler condition, braying by bucks, sexual activity, and fawn observations.

Antler size classes distinguished by Schaller (1967) were employed to facilitate comparisons between the condition and behaviour of bucks in Karnali-Bardia with Schaller's observations from Kanha National Park, India. Four categories, 0–10 inches (0–25 cm), 11–20 inches (26–50 cm), 21–31 inches (51–75 cm), and greater than 31 inches (75 cm), were recognised. Yearling males possess spike antlers only several inches in length. Prime bucks were almost always in the 75 cm plus size class. Changes in antler condition were tabulated on a monthly basis.

Chital bucks emit a loud hoarse bray during the rut. The number of brays and the time at which they were heard were recorded daily during the study period. When I was forced to leave the study area for short periods of time, and the number of brays was only recorded for a portion of the month, weekly averages were extrapolated to cover the missing period.

Tending of does, chasing, aggressive behaviour, vaginal sniffing by bucks, and attempted and successful copulations comprised the behavioural responses originally chosen as signs of bucks in rutting condition.

The number of fawns observed per 100 does recorded on a monthly basis was also calculated to discern possible reproductive patterns. Furthermore the percentage of heavily pregnant does compared with barren females was used to detect the season and degree of synchrony in birth patterns.

Nilgai, being bovids, do not shed their horns, and unlike chital and swamp deer, emit no conspicuous rutting call. Thus sexual activity and fawn observations were the only criteria available to denote rutting behaviour and periods of parturition, respectively, for this species. The same was true for wild boar.

Two problems occur in attempting to classify large chital groups by sex and age in the dense subtropical vegetation prevalent over most of Karnali-Bardia. The first major difficulty is to ensure that all the members of an aggregation have been counted. The second involves separating yearling from adult females. Almost all of my classifications of groups larger than 15 individuals were made from machans with the aid of binoculars. Observing chital from an elevated platform facilitated correctly identifying all of the individuals in an aggregation. This factor was especially important after the fawning season when young animals might often be obscured from an observer on the ground by low vegetation and/or other members of the group. Machan sightings as opposed to ground observations also simplified classifying bucks into the four antler size categories and distinguishing between yearlings and does. One attribute which I felt helped to separate yearling from adult females was the size of the head and the length of the snout, being larger and longer, respectively, in adults.

Domestic stock constitute potential forage competitors for wild ungulates, so a survey of the domestic stock belonging to the 11 villages that had previously grazed the study area was undertaken on a house-to-house basis. The census was conducted at the end of the two-year study, thereby enabling me to become familiar with a number of the local villagers, grazing conditions on communal lands, and current herd sizes. The actual censusing was performed by reserve game scout Gagan Singh, who had been resident in the area for 12 years, and myself. The livestock at hand and on communal grazing areas were counted to check against inaccuracies. The domestic ungulates were separated into the following categories: cattle (cows, bullocks, calves), buffalo (males, females, calves) goats (adults, kids) and sheep (adults, lambs).

POPULATION DENSITIES AND BIOMASS

Population densities of wild ungulates obtained by three different techniques for selected habitats within the study area are compared in Table 1. Strip census results for chital and nilgai closely approximated sample area count estimates in the open savannah habitat. However, densities obtained through strip counts for hog deer, barking deer, and wild boar were significantly lower than sample area count figures. In the case of swamp deer, there were so few in the study area that it was doubtful if this method produced useful data. Sample area count estimates for hog deer, barking deer, and wild boar appeared to be more representative than strip census results of actual population densities in the open savannah habitat during the hot-dry season of 1977.

A total of 30 pellet group plots were located in each of the three habitats studied: sal forest, tall grass floodplain, and savannah/grassland. Plots in the first two associations were monitored from November 1976 through May 1977; savannah plots were read from November to February only. Density estimates for chital and hog deer from pellet group counts in sal forest and tall grass flood plain compare well with estimates obtained by direct observations along transects. A statistical analysis of preliminary census data revealed that the number of plots needed to obtain

TABLE 1

A COMPARISON BETWEEN STRIP CENSUS RESULTS AND SAMPLE AREA COUNT ESTIMATES FOR SIX WILD UNGULATE SPECIES IN THE SAVANNAH/GRASSLAND HABITAT DURING THE HOT-DRY SEASON OF 1977 AND ESTIMATES FOR WILD UNGULATES IN SAL FOREST AND TALL GRASS FLOOD PLAIN HABITAT FROM NOVEMBER 1976 THROUGH MAY 1977.

(ALL DENSITY ESTIMATES EXPRESSED AS N/km^2)

Species	*Savannah/grassland*		*Sal forest*		*Tall grass flood plain*	
	Strip census (*n* = 9) $\bar{x} \pm SE$	*Sample area count estimate*	*Pellet group*	*Direct count*	*Pellet group*	*Direct count*
Chital	102·3 ± 11·9	97·0	21·1 ± 2·9	15·4	4·0 ± 1·1	5·8
Nilgai	3·2 ± 0·8	3·8				
Wild boar	3·8 ± 0·6	7·7				
Hog deer	0·4 ± 0·3	2·0			7·5 ± 2·8	7·0
Barking deer	0·1 ± 0·7	1·0				

accurate estimates (with $\alpha = 0{\cdot}05$) required the examination of over 100 plots in each of the three habitats. Such a large number of plots did not prove practical to maintain given the dense habitat conditions in the study area and the time constraints placed upon the use of this technique by other research priorities.

If, instead, values obtained by pellet group counts are accepted as indicators of trends in population densities between different habitat types, useful comparisons can be drawn. The most obvious change in population densities of chital occurred in sal forest between mid-April and mid-May of 1977 when densities dropped substantially from the preceding period (i.e., from 24·0 deer/km^2 to 12·2 deer/km^2). This decrease was correlated with a change in plant phenology; during April and May records show that many of the shrub, forb, and graminoid species common to the sal forest habitat were either dormant or leafless (Dinerstein, 1979*b*). In the open savannahs, on the other hand, the re-emergence of new green shoots after a burn in April attracted large numbers of chital. It seems probable that a number of those individuals utilising the sal forest habitat moved the short distance necessary to graze on the new flush in the savannahs.

Density estimates for chital from pellet group counts in the savannahs exceeded values obtained by the other two methods. Part of this discrepancy probably lies in the assumed defecation rate. During the period of monitoring in this habitat, deer were again drawn into the savannahs by the abundance of green forage stimulated by controlled burns. Longhurst (1954) observed a higher daily defecation rate for domestic sheep fed on high quality forage than the standard 13·0 pellet groups per day assumed in most calculations for wildlife work. In order to bring pellet group counts in line with strip census and sample area count data, a rate of 22 pellet groups per day would be required, a not unreasonable figure.

Table 2 presents a summary of population density and biomass estimates for wild

TABLE 2

POPULATION DENSITY AND BIOMASS ESTIMATES OF SIX WILD UNGULATES IN THE INTENSIVE STUDY AREA IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL, APRIL 1977

(INTENSIVE STUDY AREA = 11·8 km²)

Species	*Estimate of numbers*	*Density (N/km^2)*	*Unit weight (kg)*	*Biomass (kg/km^2)*	*% contribution to total wild ungulate biomass*
Chital	350–400	29·7–33·9	M-64; F-57; Yr-45; f-23[a]	1440–1644	54
Nilgai	60±	5·0	M-227; F-181; Yr-114; f-55[b]	956	34
Wild boar	50±	4·2	61·8	260	4
Hog deer	25–50	2·1–4·2	M-48; F-43; Yr-34; f-16	74–148	4
Barking deer	20±	1·7	18[a]	31	1
Swamp deer	6	0·5	159[a]	81	3
Totals	511–586	43·3–49·6		2842–3120	100

[a] from Schaller (1967)
[b] from Berwick & Jordan (1971)

ungulates based upon census data from April 1977. The density and biomass values apply only to the 11·8 km² study area which encompassed the most floristically diverse section of the reserve in addition to being the most attractive habitat for large herbivores. Thus the estimates obtained for this area constitute ecological densities and biomass, i.e., the density and biomass of a species in a particular part of a habitat or habitats which receives maximum use (see Eisenberg & Seidensticker, 1976). A crude estimate averaged over the entire 348 km² sanctuary would reveal that Karnali-Bardia supports much lower levels of wild ungulate biomass than that recorded in the 11·8 km² intensive study area.

Chital were the most numerous of the six wild ungulate species common to the study area, accounting for approximately 68 % of the total wild ungulate population. Nilgai and wild boar comprised 10 % and 9 %, respectively, of the total estimate. Hog deer, barking deer, and swamp deer occurred in lesser numbers.

The estimate of the large herbivore biomass for the study area was put between 2698–2976 kg/km². The two most numerous wild ungulates, chital and nilgai, accounted for 88 % of the total biomass in the study area. The contribution by the remaining four ungulates was small in comparison. In the calculation of biomass values, average weights for chital, swamp deer and barking deer are taken from Schaller (1967). The unit weight for wild boar (61·8 kg) is an average derived by Seidensticker (1976) which agrees closely with an average of estimates for different sex and age classes obtained by R. Taber (pers. comm.) from wild boar in Pakistan. Average weights for female and young nilgai are from Berwick & Jordan (1971). Male nilgai and hog deer average weights are based upon my own estimates.

In certain tropical habitats, arboreal herbivores and frugivores may rival ungulates as the major contributors to the total large mammal biomass (Eisenberg & Thorington, 1973; Eisenberg & McKay, 1974). Populations of the two primate species indigenous to Karnali-Bardia, langur *Presbytis entellus* and rhesus *Macaca* *mulatta* were censused in February and March 1976 by a research team from Johns Hopkins University. The results of this survey are presented in Table 3. Censusing occurred approximately 1½ months before the birth seasons of both species. Langurs were found to be twice as numerous as rhesus in and adjacent to the study area;

TABLE 3

TROOP SIZE, POPULATION DENSITIES, AND BIOMASS ESTIMATES FOR RHESUS AND LANGUR MONKEYS IN AND AROUND THE INTENSIVE STUDY AREA, IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL, FEBRUARY-MARCH, 1976[a]

(INTENSIVE STUDY AREA = 11·8 km^2)

Species	*Troop letter*	*Troop size*	*Density* (N/km^2)	*Sex and age ratios* ♂♂	♀♀	*Juv*	*Infant*	*Average weight* (*kg*)				*Biomass* (kg/km^2)	*% of wild ungulate biomass*
Rhesus	A	2											
	B	25											
	C	20											
	D	1											
	E	1											
	F	7						♂♂	♀♀	Juv	Inf[b]		
	6	56	4·7	39	100	77	31	7·4	6·0	2·1	1·3	20·9	1
Langur	A	12											
	B	1											
	C	5–10											
	D	15											
	E	35–40											
	F	24											
	G	10											
	H	6											
	I	1						♂♂[c]	♀♀	Juv	Inf		
	9	109–119	9·2–10·0	36	100	72	36	21·0	13·6	4·5	2·0	95–103	4
Total		165–175	14·0–14·8									116–124	5

[a] adapted from Teas & Whitesides (1976)
[b] Southwick & Siddiqi, unpublished
[c] Prater (1965) (Male langurs only)

population densities for langur, an arboreal folivore and frugivore, were estimated at 9·2–10·0/km^2 and for rhesus, a more terrestrial feeder, at 4·7/km^2. Total primate biomass for the study area was placed at 116–124 kg/km^2, or 5 % of the wild ungulate biomass estimate. Average weights for rhesus were furnished by C. H. Southwick (pers. comm.), for male langurs taken from Prater (1965), and for female, juvenile, and infant langur monkeys derived from my own estimates.

The relationships between habitat diversity and the densities and distributions of wildlife populations were first discussed by Elton (1927) and Leopold (1933). The edge effect, the ability of interfaces between distinct habitat types to sustain a more abundant and diverse fauna than more homogeneous habitats, was clearly at work in Karnali-Bardia. Figure 2 illustrates the changes in habitat types recorded along a randomly chosen transect line across Khoraha Island, located in the intensive study area. The route followed crossed the boundaries between six different plant associations a total of 17 times in the course of only 2·3 km. In addition, the starting point of the transect lay within 1 km of agriculture and 2 km of sal forest, two habitats not encountered in the transect. This same section of Karnali-Bardia supported what I estimated to be the largest concentration of wild ungulate biomass found anywhere in the reserve.

In contrast, much of the remaining vegetative cover of Karnali-Bardia showed little variation in community structure and composition, being dominated almost entirely by several associations of continuous sal forest. Sambar, barking deer, chital, and wild boar, the wild ungulate species commonly associated with such habitat conditions, did not lend themselves easily to sampling with some of the techniques employed in the intensive study area. Between the nocturnal behaviour of some of these species and poor visibility in the sal forest habitat, sightings were few. Nevertheless, from my search time in this habitat, along with the findings from informal pellet transects and track counts, I estimated the density of sambar in sal forest with a tall grass understory and access to perennial water sources at 3·0–4·0 deer/km^2 during the hot-dry season. I would not imagine sambar densities to exceed 1·0 deer/km^2 further than 3·0 km from a permanent drinking source. A similar distribution pattern was exhibited by chital, barking deer, and wild boar, all of which are limited in habitat selection by high drinking water requirements. Thus one would expect population densities to fluctuate seasonally in the interior sal forests of the reserve between the hot-dry season, when water is scarce, and the monsoon when the availability of drinking water is not a limiting factor in habitat selection.

Apart from the problem of greater access to perennial water resources, the quantity and quality of forage plants for grazing ungulates available on Khoraha Island far exceeded the amount produced by a similarly sized area of sal forest. Thus the greater biomass of wild ungulates observed in the study area compared with the sal forest habitat may be directly attributable to differential forage production. For a deer of the forest edge like the chital, the maximisation of the forest/savannah ecotones provides more food and better habitat than does a continuous forest situation. All of these factors combined, the lack of available surface water, the absence of much diversity in community structure, and the low production of green grass forage in relation to other habitats, account for the low carrying capacity of the sal forest for large terrestrial herbivores.

The results of a survey of domestic ungulates from 11 villages which had previously been grazed in the intensive study area prior to 1975 are presented in Table 4. Cows were more abundant than any other type of stock, followed by male buffalo and bullocks. The low numbers of female buffalo were explained by the expense of maintaining these animals for milk production; few local residents could afford such a luxury. The density of cattle in the study area was 2·5 times higher than that of buffalo.

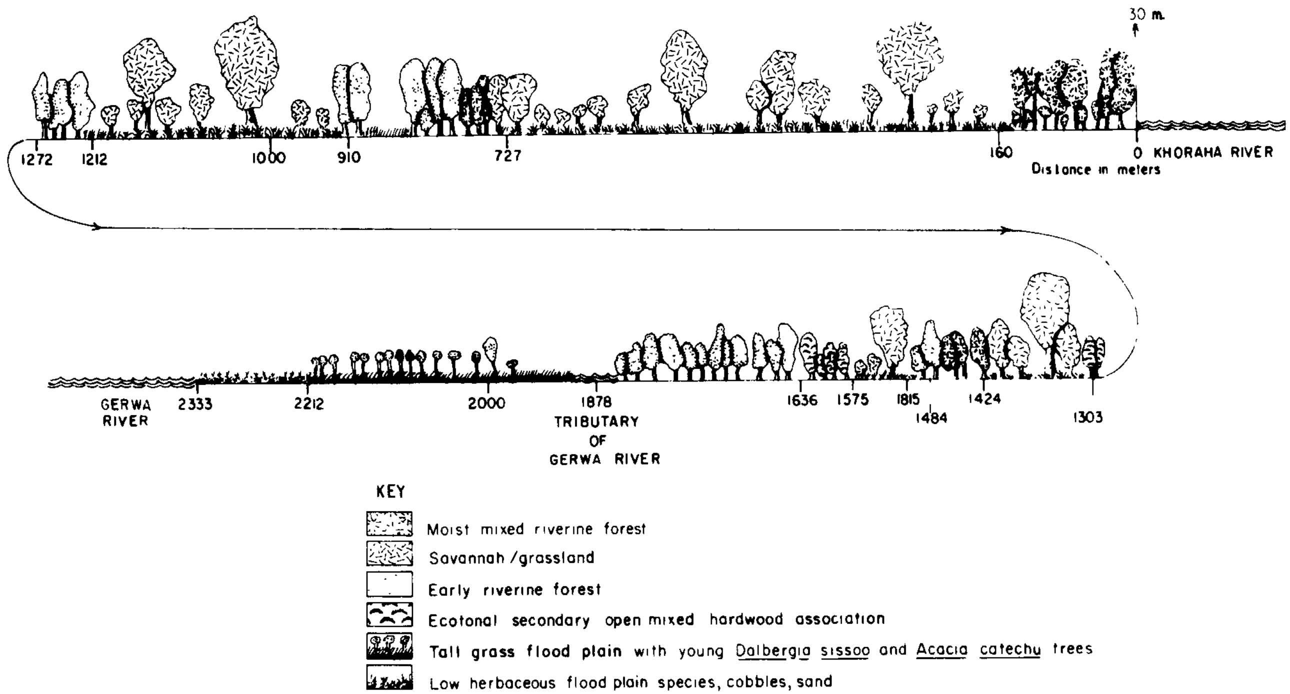

Fig. 2. Changes in plant associations along a transect across Khoraha Island, Royal Karnali-Bardia Wildlife Reserve, April 1976.

TABLE 4

POPULATION DENSITY AND BIOMASS ESTIMATES OF DOMESTIC STOCK WHICH UTILISED THE INTENSIVE STUDY AREA PRIOR TO 1975 IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL

	Total population estimate	*Density* (N/km^2)	*Sex and age ratio* ♂♂	♀♀	*young*	*Average weights used for biomass calculations (kg)*	*Biomass* (kg/km^2)	*% contribution to total biomass*
Cows	863					180	13164	
Bullocks	412					295[a]	10300	
Calves	333					90[a]	2540	
Cattle subtotal	1608	136·3	50	100	39		26004	55
Female buffalo	109					410[a]	3787	
Male buffalo	446					410[a]	15497	
Calves	99					120[a]	1007	
Buffalo subtotal	654	55·4	409	100	98		20391	42
Adult goats	473					20	802	
Kids	256					10	215	
		61·7						2
Adult sheep	216					25	458	
Lambs	88					12	89	
		25·7						1
Total domestic stock	3295						47959	

[a] from Berwick & Jordan (1971)

Approximately 97 % of the domestic ungulate biomass was contributed by cattle and buffalo while sheep and goats accounted for only 3 % of the total figure. In addition, the grazing pressure exerted by these latter two ungulates was significant only along the border of the study area; unlike cattle and buffalo, they were not permitted to wander far from the reserve boundary. Average weights used in the calculation of biomass estimates for bullocks, calves, and buffalo are from Berwick & Jordan (1971). The weights ascribed to cows, goats, and sheep are from my own observations.

It was originally hypothesised that a census of domestic ungulates in 1977 would reveal a decline in population numbers when compared with figures obtained for 1975, the period before grazing control became effective in Karnali-Bardia. Starvation, disease, and the sale of excess animals to pastoralists residing farther away from the reserve were three factors expected to shrink existing herd sizes. Table 5, a comparison of mean stock numbers per household between 1975 and 1977, indicates that little change occurred in domestic population numbers over this two-year interval. The only statistically significant difference observed was the increase in the number of calves between 1975 and 1977. These rather surprising results can be explained by a combination of economic and cultural considerations.

TABLE 5

CHANGES IN MEAN NUMBER OF STOCK ANIMALS PER HOUSEHOLD BETWEEN 1975 AND 1977 FOR THE ELEVEN VILLAGES WHICH PREVIOUSLY GRAZED THE STUDY AREA TOTAL NUMBER OF HOUSEHOLDS IN SURVEY = 229

Animals	*1975* $\bar{x}$/*household*	*1977* $\bar{x}$/*household*	*% change over 2-year interval*	*t-statistic (paired t-test)*[a]
Cows	3·8	4·1	+7	+0·79
Bullocks	1·6	1·3	−19	−1·76
Calves	1·4	1·8	+22	+3·60*
Female buffalo	0·5	0·5	0	—
Male buffalo	1·9	2·0	+1	+1·25
Calves	0·3	0·3	0	—
Adult goats	2·1	2·1	0	—
Kids	1·1	0·9	−18	−2·22
Adult sheep	0·9	0·9	0	—
Lambs	0·4	0·4	0	—

* significant difference
[a] overall $\alpha = 0{\cdot}10$
α for each animal class = 0·01

The vast majority of farmers around the reserve area live at a subsistence level; the possession of at least a pair of draught animals per household is essential for the cultivation of agricultural crops. Thus, for example, no significant change was observed in the numbers of male buffalo and bullocks during the two-year period. If an animal dies, it will be replaced as long as the farmer has the means to purchase another.

The high number of cows and calves is obviously a reflection of the cultural and religious convictions of Hindu farmers which prohibit any effort at population control of this sacred animal. It was also believed that the numbers of goats and sheep did not fluctuate greatly because such animals are raised for consumption during festivals; most families maintain at least one goat and ewe for such occasions. The most dramatic effect, I believe, of the closing of the reserve to domestic grazers is the increased workload for farmers as a result of the need to collect additional fodder for their stock. The possibility remains that benevolent monsoons during the two-year interval has masked to some degree the true dynamics of cattle populations. Counts of domestic cows in subsequent years may indeed show a decline as more and more animals are forced to concentrate on already overstocked communal grazing grounds.

GROUPING CHARACTERISTICS

None of the wild ungulate species present in Karnali-Bardia, with the exception of wild elephant, are reported to remain in long-term, stable social groups (Schaller, 1967; Eisenberg & Lockhart, 1972; McKay, 1973; Martin, 1978). Among the cervids I observed only the temporary association of does with their fawns.

TABLE 6

MONTHLY AND SEASONAL GROUPING PATTERNS OF THE WILD UNGULATES PRESENT IN THE STUDY AREA, ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL

Species	*Month/year*	*Number of groups*	*Group size in %*									*Largest group observed*	*Mean group size*
			1	2	3	4	5	6–10	11–20	21–30	31+		
Chital	March 1976	83	18	13	11	6	8	26	11	1	6	40±	7·5
	April	98	20	19	18	2	7	18	8	8	2	30±	5·7
	May	21	27	5	5		5	10	10	27	10	33	13·2
	July	34	15	15	2	5	5	15	15	15	12	60±	13·2
	August	15	20	13	7	7	13	7	13		20	50±	11·9
	October	33	21	16	3	6	21	12	9	9	3	55	8·4
	November	35	26	14	9	9	20	17		3	3	53	5·5
	December	104	14	12	11	8	6	25	15	3	6	60±	8·5
	January 1977	147	22	10	5	12	8	18	18	5	2	40	7·4
	April	177	20	20	8	5	11	14	7	9	6	91	29·1
	May	80	21	16	11	4	5	21	11	4	4	58	7·7
	Combined data	827	20	14	8	6	10	17	10	8	7		10·7
Nilgai	Combined data from hot-dry season, 1976 and 1977	96	31	24	21	8	5	8	3			11	2·9
Wild boar	March 1976–May 1977	32	50	20	6	3	6	9	6			17	3·1
Barking deer	March 1976–May 1977	31	94	6								2	1·1
Hog deer	March 1976–May 1977	30	48	18	21		3					5	1·7
Swamp deer	March 1976–May 1977	6		16		16	34	34				8	5·2

The application of the word 'herd' to describe groups of chital is a misnomer (Graf & Nichols, 1966; Schaller, 1967). Group composition was observed to change frequently during feeding periods and in flight from potential predators. This apparent lack of group solidarity, however, did not detract from the sociality of this species; on the contrary, chital were the most gregarious of the ungulates in Karnali-Bardia (Table 6), associating in large feeding aggregations of at times up to 100 individuals. The formation of large groups occurred when forage conditions improved in the savannahs during April, May, and December after controlled burns or natural fires had stimulated the re-emergence of the perennial grasses. The large aggregations observed throughout the monsoon were attributed to the predator avoidance strategies of chital in dense habitat conditions. While high quality forage is abundantly distributed during the monsoon, which might cause deer to disperse while feeding, the vegetation itself reaches its maximum height and density at this time, thereby substantially reducing visual recognition of stalking predators. Remaining in large groups facilitates the detection of predators for a species like the chital, where individuals utter warning vocalisations in response to danger, and also lessens the chances of any one individual being taken. In this manner the behaviour of chital in response to dense habitat conditions may override feeding strategies normally employed during a period of optimal forage availability. The smallest average monthly group size, recorded in November, might be attributed to poor grazing conditions in the savannahs but could also be a result of a small sample size. For a more detailed review of predator avoidance and feeding strategies for South Asian ungulates the reader is referred to Eisenberg & Lockhart (1972).

Sex and age ratios for chital are presented in Table 7, with 1 January taken as the arbitrary birthdate for all age categories. Few chital were classified during the monsoon months (i.e., July, August, and October); poor visibility at this time of the year combined with the congregation of chital in large groups precluded accurate

TABLE 7

SEX AND AGE RATIOS FOR CHITAL IN AND AROUND THE STUDY AREA IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL FROM MARCH 1976–MAY 1977

Year	*Month*	*N Individuals classified*	*Males*	*Females*	*Yearlings*	*Fawns*
1976	March	299	37	100	19	8
	April	325	45	100	11	42
	May	106	59	100	11	59
	July	84	65	100	32	74
	August	16	50	100	13	63
	October	65	31	100	25	48
	November	79	35	100	15	48
	December	387	63	100	39	80
1977	January	733	114	100	177	21
	April	1006	67	100	42	67
	May 1–14	278	66	100	41	77

counts. The data accumulated over this period are primarily based on observations of the smallest groups consisting of 1–5 individuals. These are not representative of the population as a whole during the monsoon.

The high number of fawns in December 1976 were all dropped nine months previously. No newborn fawns were observed until January 1977. The high ratio of males and yearlings relative to females in January was attributed to the decreased observability of females just prior to the peak in parturition.

Figure 3 compares the observability of single bucks compared with all-male groups (i.e., two more males) sighted between January and May 1977. Solitary adult

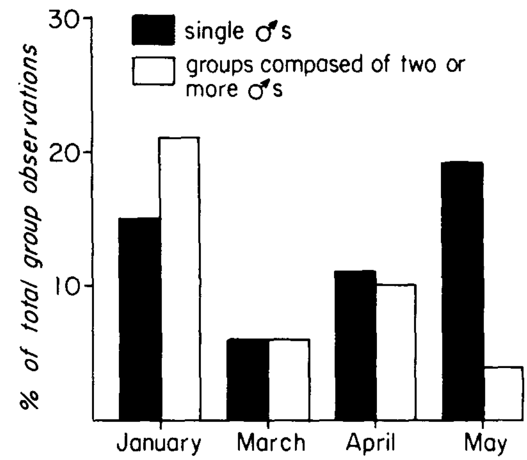

Fig. 3. Observability of solitary adult chital bucks compared with all male groups (i.e. two or more males) for the period leading up to the rut. Pooled data from 1967 and 1977.

males were observed most often in May, during the onset of the rut, when bucks wander widely in search of estrous females (Fig. 4). Normally intolerant of excessive exposure to intense solar radiation, large chital bucks seemed oblivious to the heat during the peak of the rut and would often be seen moving about at midday.

Nilgai occur in groups, usually ranging in size between 1 and 10 individuals (Table 6). The largest group observed was of a breeding herd of 27 grazing in a recently burned grassland (Fig. 5). Sex and age data from the study area indicated that adult males outnumbered adult females by a substantial margin (Table 8). These findings might initially suggest a declining population and perhaps selective mortality of females. However, the five nilgai kills located during the course of the study period were all found to be adult males. Schaller (1967) obtained sex and age ratios for nilgai populations in different parts of India. Average ratios between males and females were in the order of 59:100 in Keoladeo Ghana Sanctuary and 37:100 in Vanbihar Sanctuary. The discrepancy between the observed ratios from other areas and those found in Karnali-Bardia was attributed to behavioural factors which

Fig. 4. During the rut chital bucks will range widely in search of receptive does. May 1976.

TABLE 8

SEX AND AGE RATIOS FOR NILGAI IN AND AROUND THE STUDY AREA IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL AT SEVERAL MONTHLY INTERVALS IN 1976 AND 1977

Year	*Month*	*N Individuals classified*	*Males*	*Females*	*Yearlings*	*Fawns*
1976	April	122	125	100	48	19
1977	January	32	73	100	45	91
	April	74	118	100	44	11
	May	23	250	100	17	17

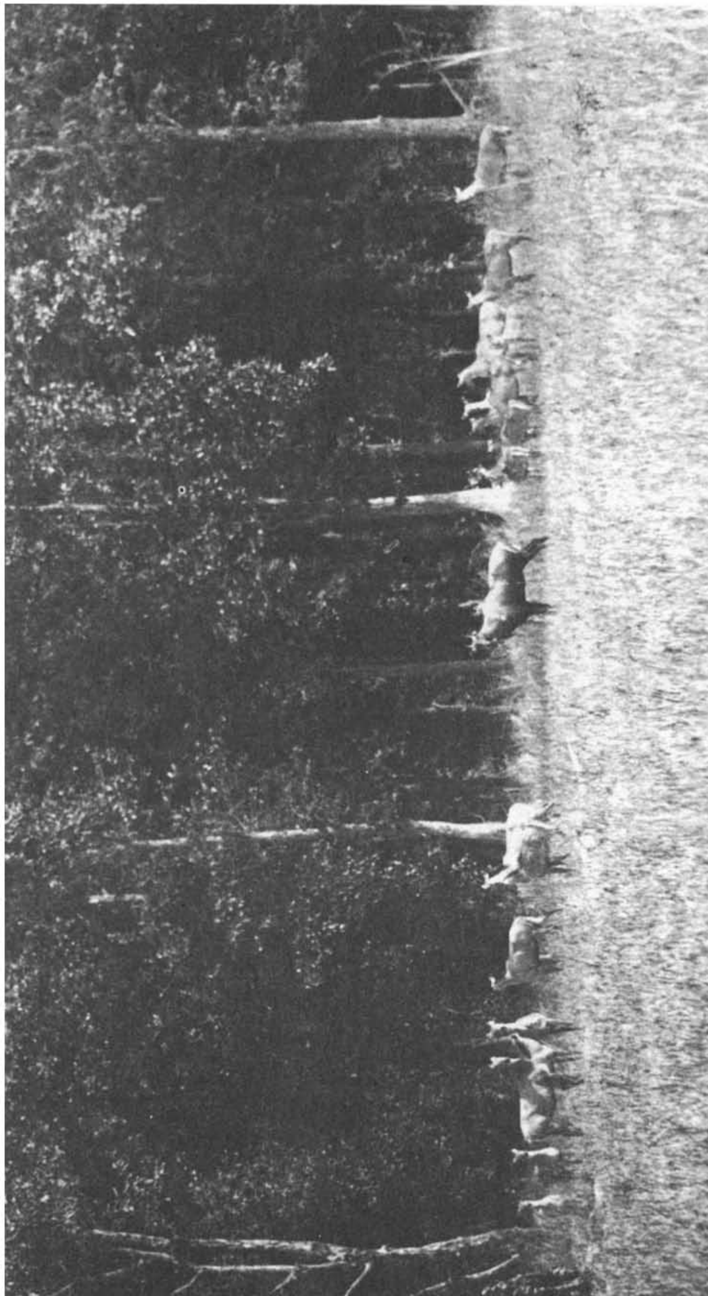

Fig. 5. Nilgai formed large breeding herds in the open grasslands in January. This group of 27 individuals (not all shown) contained only one bull.

introduced a bias in sampling. Nilgai remain in all-male herds for a considerable part of the year; for example, 62 % of the total nilgai observations during the hot-dry season were of such bachelor groups (Table 9). The sightings of a number of these

TABLE 9
POOLED CLASSIFICATIONS OF NILGAI GROUPS FOR THE HOT-DRY SEASONS OF 1976 AND 1977 IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL

N (*groups classified*)	*% of observations*			*Batchelor herds only-% (N = 60)*					
	All male groups	*Mixed groups*	*Female-young groups*	*1♂*	*2♂*	*3♂*	*4♂*	*5♂*	*6–10♂*
95	62	13	24	37	28	20	3	7	5

bachelor groups may have skewed age and sex ratios. The composition of the large breeding herds combined with data collected on peripheral subadult and adult male groups in January provide a more reasonable estimate of the nilgai population in Karnali-Bardia.

Group sizes of the other ungulate species in the study area are also presented in Table 6. Barking deer were the most solitary, followed closely by hog deer. Sounders of wild pig varied widely in size. Swamp deer were observed infrequently; it was thought that by April 1977 only six animals remained in the intensive study area, a female and its yearling and two adult males and females.

ANTLER CONDITION AND REPRODUCTION

It is generally assumed that in the North American wapiti *Cervus canadensis*, the dominant stags (i.e., those with the largest antlers) do most of the breeding (Altmann, 1952). Schaller (1967) believed that in Kanha National Park, India, the chital bucks in the largest antler size class, or approximately one-fourth of the population, probably accounted for over half of all copulations. The largest antlered males of chital introduced in Texas accounted for more than 82 % of all copulations (Fuchs, 1977). If antler condition is a reliable indicator of rutting activity, one would expect a peak in breeding to be associated with the periods at which the greatest percentage of bucks in the largest antler size class had burnished antlers. On the other hand, if a substantial percentage of hard-antlered bucks in the largest size classes are to be found throughout the year, such data would imply the absence of a restricted breeding period.

Table 10 presents the per cent of chital bucks from the intensive study area in hard antler and velvet between March 1976 and May 1977. In 1976, 50 % of all the bucks observed in July were in hard antler in '75 cm +' size class. Not a single buck was observed to be in velvet in this same size class during these two months. In direct contrast, 50 % of all bucks sighted in March were in velvet in the '75 cm +' class and not a single male in hard antler.

TABLE 10

PERCENT OF CHITAL BUCKS IN HARD ANTLER AND VELVET IN FOUR DIFFERENT ANTLER SIZE CLASSES, RECORDED MONTHLY IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL, MARCH 1976–MAY 1977

Year	*Month*	*N Individuals classified*	*Total % hard*	*Total % velvet*	*0–25 cm*		*26–50 cm*		*51–75 cm*		*75 cm*	
					Hard	*Velvet*	*Hard*	*Velvet*	*Hard*	*Velvet*	*Hard*	*Velvet*
1976	March	31	13	87	0	6	0	19	0	0	0	58
	April	47	43	57	0	2	6	28	19	15	17	13
	May	30	83	17	0	10	23	0	10	7	50	0
	July	44	100	0	15	0	6	0	26	0	53	0
	October	16	69	31	ND	25	63	6	6	0	0	0
	November	25	24	76	ND	48	16	20	8	8	0	0
	December	116	38	62	ND	33	26	13	12	13	2	0
1977	January	191	17	83	7	43	11	17	1	18	0	4
	April	184	59	41	1	8	17	20	23	7	17	7
	May 1–14	22	55	45	5	18	9	9	14	14	27	5

ND no data recorded

Findings from October 1976 through January 1977 offer further evidence that the largest chital bucks exhibited a marked synchrony in antler development. None of the males observed in October, November, and January, and only 2 % of all males sighted in December, possessed hard antlers in the '75 cm +' class. Conversely, the percentage of bucks with velvet spikes during these same four months were 25 %, 48 %, 42 %, and 43 %, respectively. The data from Karnali-Bardia differ from the findings from Kanha National Park, India, where a higher percentage of chital bucks was observed in hard antler throughout the year, a pattern more characteristic of deer in tropical habitats (Schaller, 1967).

In addition, I observed a definite sequence in the time of shedding between bucks in the different antler size classes. The largest antlered bucks shed earlier than did the '51–75 cm' class males. In 1976, the first '75 cm +' antler was discovered on 31 July. My observations indicated that most of the '75 cm +' bucks drop their antlers in September and October. The '51–75 cm' bucks drop their antlers before the '26–50 cm' class males do. A number of bucks in this latter size class did not shed their antlers until as late as December and January. Most of the bucks remaining in hard antler between October and January were in this size category.

As reported by Schaller (1967), chital may not shed both antlers on the same day. One 30–51 cm buck with only one antler was observed for two consecutive days in January. Bucks with deformed antlers were recorded on only two occasions. Chital with broken antlers were encountered several times. In each case only one of the antlers had been broken off.

In the Calcutta Zoological Gardens, Schaller (1967) found that for bucks in the '75 cm +' size class a space of $5\frac{1}{2}$ to $6\frac{1}{3}$ months elapsed between the shedding of the old antlers until the cleaning of the new pair. Although bucks in this group require twice as much time to grow a new set of antlers as would a buck in the 26–50 cm class, the largest bucks emerge into hard antler and shed sooner than do the smaller males.

Bucks clean and polish their antlers primarily by rubbing them against tree trunks, saplings, and lianas between 5 cm and 15 cm diameter; *Mallotus philippinensis*, a tree forming clumps of shade at the edge of the savannahs, was heavily used by chital bucks. The heartwood of this tree is of a reddish hue, which may be partly responsible for the rich colours observed on the antlers of several males.

In subtropical habitats, where observability of ungulates during breeding periods is often impeded by the dense vegetation, braying assumes increased importance as a means of detecting sexual activity. In chital, as in other ungulate species where males vocalise prior to breeding, braying probably informs other males and oestrous females that a particular buck is approaching or is in rutting condition. In Kanha National Park, India, Schaller (1967) observed that males in hard antler in the largest antler size class (i.e., 75 cm +) accounted for 96 % of all vocalisations. My own limited observations of braying bucks support Schaller's findings. In addition, I noticed a distinct difference in tone between the calls of the oldest and largest males and the younger bucks. Fully mature males uttered the hoarsest and deepest brays while the brays of younger males were much higher in tone. The data from this rough classification also indicated that the largest males with burnished antlers bray more frequently than do the smaller hard antlered bucks.

Figure 6 shows the number of brays uttered by rutting chital bucks at monthly intervals. During three of the months of the study period (September 1976 and February and March 1977) no observations were made. Where Fig. 6 indicates that braying can be heard to some extent throughout the year, a definite peak occurred in April and May, with braying still heard frequently through August. Braying activity also corresponded with an increased level of agonistic behaviour observed among hard-antlered males and the period when copulation was presumed to be most frequent. In an introduced population of chital in Texas, Russ (1977) found that the monthly distribution of all types of sexual activity correlated quite closely with braying data. After August, braying became less obvious and remained so until January. It was believed, however, that most of the brays recorded in January were uttered by the same buck. During a large portion of the year braying activity was most frequent in the early morning (0500–0700) and early evening (1700–2000) hours. In May, braying could be heard throughout the day.

Twice as many brays were recorded in April 1977 as in April 1976 and perhaps $5\frac{1}{2}$ times as many brays in May 1977 as in May 1976 (the latter figure being based upon extrapolated values). Since the amount of time spent in the study area in April and May 1976 and 1977 did not vary considerably, the dramatic increase in the observed number of brays must be assigned to other factors. The removal of domestic stock

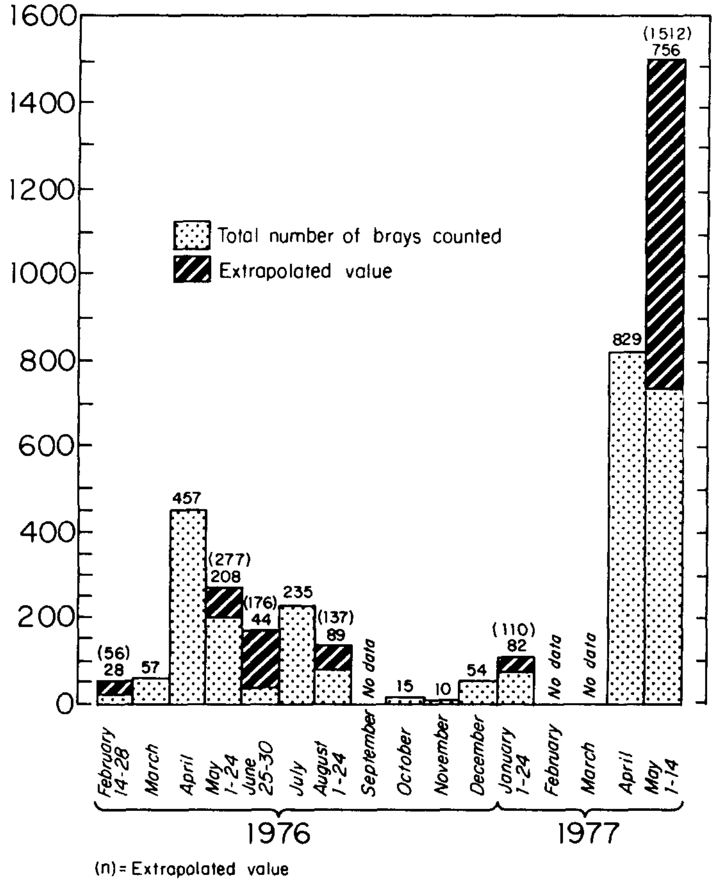

Fig. 6. The total number of brays emitted by chital bucks recorded daily from February 1976 through May 1977, Royal Karnali-Bardia Wildlife Reserve, Nepal.

grazing and poaching pressure beginning in April 1975 has allowed wild ungulates to reclaim in full the most productive habitats in the reserve. Perhaps what is being observed here is (1) the result of a significant increase in the chital population and thus more bucks in rutting condition, (2) an improvement in the overall physical condition of males, and (3) an increase in rutting behaviour associated with the cessation of human disturbance. While the values for the same months in 1976 and 1977 might be different, the general shape of the curve with the peak in April and May has not changed.

Observations of sexual activity proved difficult to obtain in the first year of the study. Past human harassment of deer populations during the rutting period combined with the chital's proclivity for remaining inside forested habitat when many such behavioural interactions occurred were the primary reasons for the meagre amount of data recorded. In 1977, however, signs of sexual activity were more numerous in the open savannah/grassland habitat than they had been in 1976. In general, my observations closely parallel those recorded by Schaller (1967) in Kanha National Park. Bucks in the largest antler size class were observed tending does, chasing, exhibiting flehmen, thrashing, pawing, preaching, and braying far more frequently than bucks with smaller antlers. Tending and chasing were only observed in May, and a single attempted copulation was observed in the same month. No successful copulations were witnessed during the study. It appears likely that chital either mate at night, copulate in dense vegetation, or both. Sparring between the smaller hard-antlered males occurs throughout the year, although this behaviour was most commonly displayed in April and May. The largest antlered bucks rarely joined in such contests although the large chital bucks in Texas do on occasion engage in serious combat (Fuchs, 1977). Presumably visual recognition of antler size leads to dominance ranking, mitigating the need for expending energy in such sparring bouts. Sparring bouts might serve as a form of play between younger males in hard antler during the monsoon.

In deer, the size of the foetus is known to increase substantially during the last three months of pregnancy. Heavily pregnant does were most commonly observed in December and January. The number of new fawn observations recorded between January and April also attests to the existence of a definite birth peak for chital in Karnali-Bardia (see Table 7). The length of time that does hide their fawns is not known, but based upon relative size estimates, I would judge this period to last about one month. Most fawns observed in April were believed to be two months old. Asdell (1964) listed the gestation period for chital at 7·0–7·5 months. Other sources provide values ranging from six months (Prater, 1965) to 8·0–8·5 months (Schaller, 1967). Breeding in the Karnali-Bardia study area probably begins by mid-May and fawning by the first week in January, with the peak of each period most likely occurring one month thereafter. The estimated gestation period of 7·5 months agrees with the results from a study of introduced deer in Hawaii (Graf & Nichols, 1966) and from another introduced population in Texas (Russ, 1977).

One recently born nilgai calf was observed near the end of the hot-dry season of 1976 in late May. However, all of the nilgai calves observed in breeding herds in January 1977 appeared to have been born during the monsoon. Zoo records and reports by other researchers offer conflicting information on the rutting activity of nilgai. Prater (1965) and Asdell (1964) stated that nilgai breed throughout the year. Berwick (1974) in the Gir Forest noticed a peak in breeding in January and February and a birth peak in August and September (monsoon). The evidence obtained by Schaller (1967) from Keoladeo Ghana and Vanbihar sanctuaries in India implies that monsoon births are quite common. In the London Zoo, births were most common in the late spring (Jarvis & Morris, 1962; in Schaller, 1967). Most accounts place the gestation period of nilgai at 8 months and 1 week (Asdell, 1964; Prater, 1965; Berwick, 1974).

Swamp deer bugling was heard in early December. All three adult females observed in mid-April 1977 were pregnant. In Kanha, the peak of the rutting period occurs in the latter part of January (Martin, 1978). The gestation period for the swamp deer has been reported to be between 240–250 days (Asdell, 1964), which would put the peak fawning period around late September.

My observations of wild boar suggest that pigs are able to breed over much of the year. Sounders containing many young piglets were sighted in December, April, May, and October.

Hog deer males were observed to be in velvet during the hot-dry season. Several fawns observed in April were probably born in February. One fawn was sighted in November and believed to have been dropped in October. The literature available denotes a peak in rutting activity between September and October (Prater, 1965). Schaller (1967), in a survey of hog deer populations in several reserves in Uttar Pradesh, India, believed that the rut extended from June through January with a peak in activity during September and October. Brown (1936) reported the gestation period for hog deer to be 8 months, a relatively long interval for such a small deer species.

DISCUSSION

Eisenberg & Seidensticker (1976) compared wild ungulate population densities and biomass estimates obtained from nine different wildlife sanctuaries in South Asia. Biomass was found to be highest in those reserves containing riverine forest intermingled with grassland and savannah habitats, while continuous tropical evergreen forest supported the lowest levels of wild terrestrial herbivores. Furthermore, those associations thought to be in early and intermediate successional states of development sustained more biomass than climax vegetation. This same pattern was observed in Karnali-Bardia.

Looking at the individual species, the ecological densities and biomass levels attained by chital in the Karnali-Bardia intensive study area exceeded estimates reported from other reserves on the Indian subcontinent (Table 11). Density and biomass levels for hog deer, barking deer, and wild boar, however, were less than values obtained in similar habitats such as in Chitawan National Park, Nepal. Swamp deer estimates in Karnali-Bardia were far below levels observed in Kahna, Kaziranga, and Jaldapara wildlife reserves, India. No data were available with which to compare ecological densities and biomass of nilgai.

Wild ungulate biomass in the East African savannahs surpasses the estimates reported for South Asian habitats (Stewart & Zaphiro, 1963; Schaller, 1967;

TABLE 11
COMPARISONS OF ECOLOGICAL DENSITY ESTIMATES FOR SEVERAL WILD UNGULATE SPECIES IN KARNALI-BARDIA WITH DATA FROM OTHER WILDLIFE SANCTUARIES IN SOUTH ASIA

Species	*Location*	*Unit weight (kg)*	*Ecological density (N/km^2)*	*Ecological biomass (kg/km^2)*	*Authority*
Chital	Karnali-Bardia	(see Table 2)	29·7–33·9	1440·0–1644·0	This study
	Wilpattu NP Sri Lanka	45·3	12·0	544·0	Eisenberg & Lockhart (1972)
	Chitawan NP Nepal	54·8	17·3	951·0	Seidensticker (1976)
	Bharatpur, India	45·0	12·3	553·0	Spillet (1967)[a]
	Bandipur, India	45·0	36·0	1620·0	Sharatchandra & Gadgil (1975)
Hog deer	Karnali-Bardia	(see Table 2)	2·1–4·2	74·0–148·0	This study
	Chitawan	31·0	35·0	1085·0	Seidensticker (1976)
Swamp deer	Karnali-Bardia	159·0	0·5	81·0	This study
	Kanha NP, India	189·0	5·2	986·0	Schaller (1967)
Barking deer	Karnali-Bardia	18·0	1·7	31·0	This study
	Wilpattu	13·4	2·3	30·8	Eisenberg & Lockhart (1972)
	Chitawan	14·0	6·7	94·0	Seidensticker (1976)
Wild boar	Karnali-Bardia	61·8	4·2	260·0	This study
	Chitawan	61·8	5·8	360·0	Seidensticker (1976)

[a] = adjusted by Eisenberg & Seidensticker (1976) for comparisons

Berwick, 1974; McKay & Eisenberg, 1974). However, if the contribution by domestic ungulates is included in the total biomass estimate for South Asian reserves, the new combined figure would approximate levels observed in a number of African game parks (Schaller, 1967; Berwick, 1974; Seidensticker, 1976). In the Karnali-Bardia study area, the density of domestic cattle (136/km^2) and buffalo (55/km^2) utilising the study area prior to 1975 yielded a maximum seasonal biomass estimate of 47,959 kg/km^2. This value was 15–17 times higher than the levels reached by wild ungulates in the same section of the reserve in 1977. These figures testify to: (1) the apparently high productivity of the grassland habitats in the Terai zone, and (2) the marked ability of the grasslands in monsoonal environments to withstand heavy grazing pressure in comparison with grasslands of semi-arid regions.

The disparity between wild and domestic ungulate biomass would be of concern to wildlife officials if herbivores were competing directly for the same resources. Competition for forage plants between wild and domestic ruminants has been shown to exist in temperate habitats (Mackie, 1970). Berwick (1974), working in the Gir Forest Sanctuary, India, concluded that competition between wild and domestic herbivores was negligible during the critical hot dry-season (the period when direct conflict for food resources would substantially lower wild ruminant nutrition). Instead, during the hot-dry period, wild ungulates shifted to browsing the nutritious young leaves of trees and shrubs while domestic stock utilised coarse grasses. It appears, however, that this pattern observed in the Gir Forest may be restricted to the more xeric habitats of the Indian subcontinent.

In the moist subtropical deciduous forest habitats so characteristic of the Terai belt, an overlap in the feeding strategies of wild and domestic ruminants was observed. For example, a small grassland known locally as Baithini Phanta was heavily grazed by domestic stock until early 1976 when grazing control became effective. Wild herbivores were seldom observed utilising the same phanta. By April 1977, after nearly a year of adequate protection from domestic animals, groups of chital ranging between 40 and 80 individuals would congregate in the early evenings and late mornings on the phanta; use by wild boar and barking deer also increased. My observations from a machan overlooking the grassland ultimately revealed that both wild and domestic ruminants preferred the same forage species during the hot-dry season (i.e., the shoots of the grasses *Imperata cylindrica*, *Vetiveria zyzanoides*, and *Saccharum spontaneum*). A ruminant like the swamp deer, which is reported to subsist almost entirely on grasses (Martin, 1978), along with hog deer and chital, was probably most severely affected by interference from domestic stock. Competition between cattle and the one-horned rhinoceros *Rhinoceros unicornis* was observed in Chitawan National Park, Nepal (A. Laurie, pers. comm.). In Karnali-Bardia, with the installation of a fenceline and frequent patrolling of the reserve borders by well-trained guards, the impact of domestic grazing has ended. Future censuses of wild ungulate populations will help to establish further the degree of past conflict between wild and domestic herbivores.

Predation has been identified as the key factor in limiting wild ungulate population numbers in two South Asian reserves, the Gir Forest Sanctuary (Berwick, 1974) and Kanha (Schaller, 1967). In Karnali-Bardia, the density of the understory vegetation, the behaviour of the large predators in removing their kills to secluded locations, and abundance of scavengers, hampered the accumulation of adequate data on mortality to assess the role of predation as a possible limiting influence on large herbivore populations. Two sources of error clearly stand out in examining kill records for Terai habitats. First, young animals of the smaller-sized ungulate species are sometimes completely consumed. Second, kills discovered only in open habitats may well distort the role of any one prey item in the diets of tiger and leopard.

Thirty-four of the 35 tiger droppings collected in or adjacent to the study area contained chital hairs, while signs of wild boar were present in only one scat. While such a small sample size prohibits the conclusion that chital was the most important prey item for the tiger, these preliminary results are in line with findings from other tiger sanctuaries of South Asia. Data recorded in 1964, 1972, and 1973 from Kanha National Park, India, listed chital as present in 52·2%, 78·5%, and 77%, respectively, of the droppings analysed (Schaller, 1967; Muller & Zurcher, 1973; Martin, 1978). Of course, differences between the composition and relative abundance of the prey fauna in Karnali-Bardia and Kanha would be reflected in the excrement analysis, but it seems nevertheless that the chital remains the optimal prey item for the tiger wherever the ranges of these two species overlap.

Predation by tigers on domestic cattle and buffalo occurred on 25 occasions during the monsoon of 1975 but diminished considerably after this period when domestic stock were excluded from the reserve (Dinerstein, 1979*b*), The discovery of three sambar, two barking deer, five wild boar, five nilgai, and one porcupine killed by tigers does indicate the presence of other species in the diet of this large carnivore.

In temperate latitudes, the most adaptive reproductive strategy for wild herbivore populations is to restrict parturition to the months of mild weather and plentiful green forage production. Moreover, selection pressure against those individuals deviating from this scheme would rapidly remove those animals from the gene pool. In tropical habitats, where a number of environmental parameters show little seasonal variation and where forage conditions remain favourable throughout the year, the breeding and birth seasons of wild ungulates show no seasonal pattern. However, if tropical deer do show a definite birth season, it may be in response to negative factors. Blouch (1977) attributed the reproductive seasonality of white-tailed deer *Odocoileus virginianus gymnotis* in the llanos region of Colombia to the lethal effects of prolonged heavy rains on fawn survival.

Three of the ungulates studied in Karnali-Bardia, chital, nilgai, and swamp deer, all possessed distinct breeding and birth seasons. Other species, such as sambar, may also be placed in this category, but for the purpose of this discussion only the first three ungulates will be considered.

As described earlier, chital in Karnali-Bardia showed a peak in rutting activity in the late hot-dry season and a birth peak in February. In the Royal Sukla Wildlife Reserve, located approximately 112 km west of Karnali-Bardia, braying activity data indicated that bucks in Sukla Phanta may arrive in rutting condition one month later than in the Karnali-Bardia study area (C. Rice, pers. comm.). Separated by such a short distance and lying at approximately the same latitude and elevation, it is highly doubtful if any significant variation in climatic conditions exists between the two areas. Data from Chitawan National Park, also situated in the Nepalese Terai, offer conflicting evidence, where Seidensticker (1976) noted the absence of a well-defined birth season.

Schaller (1967) pointed out the difficulties of correlating changes in weather conditions, plant phenology, and productivity with periods of parturition and breeding for South Asian ungulates. The data on chital from Karnali-Bardia tend to support this statement. Figure 7 contrasts changes in temperature, precipitation, and forage conditions with the observed reproductive schedule of chital. While a correspondence between an increase in rutting activity with a rise in temperature (and an increase in day length) was observed, the most obvious correlation, between the abundance of green forage and fawning, was not substantiated by the data. It is

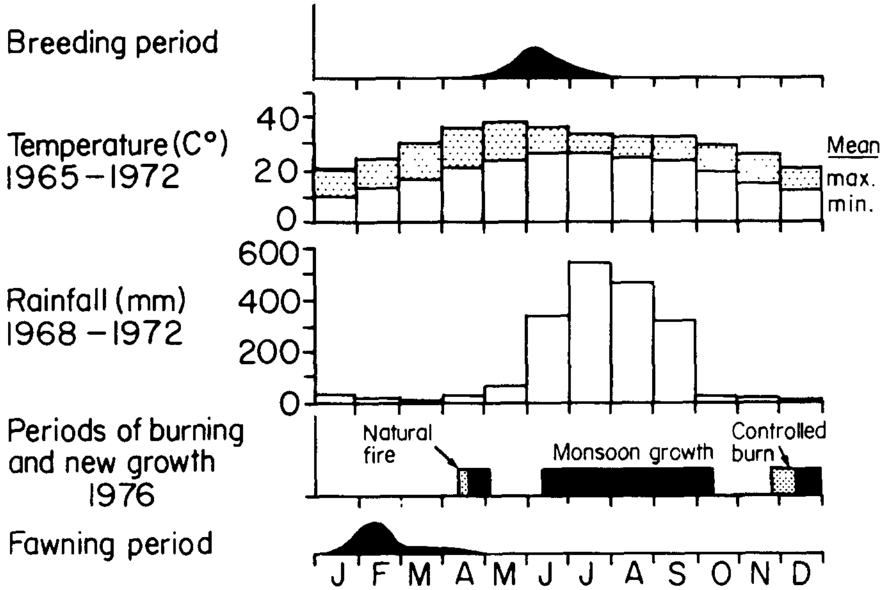

Fig. 7. A comparison of temperature and rainfall regimes, production of green forage and the reproductive schedule of chital in the Royal Karnali-Bardia Wildlife Reserve, Nepal, 1976.

generally thought that wild ungulates must maintain a high level of nutrition prior to parturition and throughout lactation for a successful recruitment of young. At first glance it seems that chital could not have selected a more inappropriate time to drop their fawns, i.e., just prior to the beginning of the long hot-dry season. By December, many of the favoured grazing species have become dormant, and through the peak parturition period, the available plant tissue of most of the remaining graminoid species begins to desiccate under the intense solar radiation of the hot-dry period. Nevertheless, the high survival of fawns in 1976 appeared to indicate that chital may be well adapted to the present environmental regime.

Singling out the availability of green forage as the sole determinant of the timing of parturition may be misleading. For example, if the monsoon rains in Karnali-Bardia have the same effects on chital fawn mortality as do the heavy rains on fawn survival of white-tailed deer in the llanos region of Colombia (Blouch, 1977), chital may reproduce during the hot season to avoid critical temperature stress from the soaking rains during the monsoon and from the low temperatures of the cool-dry season. I doubt that such a parallel exists, however, since both the monsoon rains and the air temperature remain warm throughout the wet season. Complicating the matter even further is the evidence that the congener of the chital, the hog deer *Axis porcinus*, reproduces primarily during the monsoon.

A history of burning periods would certainly help to clarify any possible relationship between range fires, the availability of new green shoots, and seasonal birth peaks. Unfortunately, no such records exist. It seems conceivable that if burning occurred annually over many years time in December and January then the peak in parturition observed in February would be adaptive for a grazer like the chital. Perhaps other less obvious factors are responsible for the pattern observed in Karnali-Bardia.

Nilgai and swamp deer gave birth during the monsoon when optimum foraging conditions prevailed. Rutting activity was apparently confined to the cool-dry season and accompanied by a drop in temperature and decreasing day length. For nilgai, this same pattern was found in free-ranging populations in Texas, where this species was first introduced in 1932 (Fall, 1972). Both species also show considerable variation in breeding and parturition over their respective ranges (Prater, 1965; Schaller, 1967; Berwick, 1974). It seems evident that South Asian ungulates possess the capacity to respond to local environmental conditions which may create significant differences in the timing and lengths of the rutting and birth seasons and that the particular local conditions to which the Karnali-Bardia chital have responded are not yet understood.

Both the observed reproductive schedule of the chital and biomass relationships between the different plant associations in the reserve further support the habitat management strategies suggested in Part II of this series (Dinerstein, 1979*b*). Controlled burns in December and January would dramatically improve grazing conditions at a critical point during the gestation period of the chital. In addition, wild ungulates in Karnali-Bardia reach maximum biomass levels where forest edge borders on savannah/grassland and perennial sources of drinking water. Thus a policy of water hole development and patch cutting could make the dry continuous sal forest habitat more attractive to ungulates on an annual basis. Since the chital has been identified as the single most important prey item in the tiger's diet, management plans should initially focus on the needs of this species. Certainly the benefits from such a programme including the above measures would be shared by the other wild ungulates of the reserve.

The information presented in this three-part series on Karnali-Bardia has been an attempt to document existing conditions in a newly created wildlife reserve in the Nepalese Terai. In the first paper it was shown that, barring human interference, the trend of the vegetation is towards continuous climax forest; man's activities, most prominently forest clearing, grazing of domestic stock, and fire, maintain the existence of subclimax habitats. The second paper illustrated the habitat utilisation patterns of wild ungulates in subclimax compared with climax associations, demonstrating the need for the maintenance of a diversity of habitat conditions. The present paper reveals that these early and mid-successional associations supported far more wild ungulate biomass than did the less attractive climax vegetation.

It is hoped that future research in the Terai will more fully elucidate the ecology of subclimax plant communities. These grassland and riverine forest habitats not only support the highest levels of wild ungulate biomass, they are also the favoured habitats of four endangered species: the swamp deer, the one-horned rhinoceros, the asiatic buffalo, and the tiger. Until the results of a long-term study on changes in plant composition, community distribution, and productivity are available, recommendations for the management of these habitats can only be viewed at best as tentative. The ecological data generated from such a study would enable wildlife officials better to understand the more subtle inter-relationships which exist between wild ungulates, predators, and habitat conditions in monsoonal environments.

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