AN ECOLOGICAL SURVEY OF THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL. PART II: HABITAT/ANIMAL INTERACTIONS

ERIC DINERSTEIN†

College of Forest Resources, University of Washington, Seattle, Washington 98195, USA

ABSTRACT

The habitat utilisation by ungulates in a newly created tiger sanctuary of the southwestern Nepalese Terai is analysed. While most of the Royal Karnali-Bardia Wildlife Reserve is covered by a rather homogeneous belt of moist subtropical deciduous forest, one section of the reserve supported a wide variety of habitat types. In this area, flood plain, savannah, and several riverine forest associations intergraded with stands of the dominant Shorea robusta *forest. Free-living mammals responded to this ecological heterogeneity, permitting an analysis of habitat preferences by the following species: chital* Axis axis, *nilgai* Boselaphus tragocamelus, *hog deer* Axis porcinus, *barking deer* Muntiacus muntjak, *swamp deer* Cervus duvauceli, *sambar* Cervus unicolor, *and two primate species, common langur* Presbytis entellus, *and rhesus monkeys* Macaca mulatta. *Differences in feeding and anti-predator strategies offered a degree of ecological separation between most of the ungulates studied. Changes in plant distribution and phenology affected ungulate food habits, energy budgets, movements, and seasonal distribution. A special feeding relationship between certain ungulates and langur and rhesus monkeys was observed. The sambar, an ungulate capable of exploiting a feeding niche in continuous climax forest, appears to be best adapted to the habitat types which dominate most of Karnali-Bardia, while only 30% of the reserve could be considered prime habitat for the chital, the most abundant grazing ungulate in the reserve. Proposals to improve habitat conditions for grazing ungulates through an experimental programme integrating controlled burns, water hole development, and the creation of openings in continuous climax forest are examined.*

---

† Present address: Institute for Environmental Studies, 230 Engineering Annex, Fm-12, University of Washington, Seattle, Washington 98195, USA.

Biol. Conserv. 0006-3207/79/0016-0265/$02·25 © Applied Science Publishers Ltd, England, 1979
Printed in Great Britain

INTRODUCTION

South Asian ungulate populations have dwindled dramatically in the years following the Second World War. The major factors responsible for this decline appear to have been habitat destruction through forest clearing for cultivation, grazing competition from domestic stock, disease, the proliferation of firearms, weakening of police power, and timber exploitation. Development of programmes of restoration require data on ungulate ecology and the vegetation resource base. However, a survey of the literature available on the species of this region reveals a scarcity of basic ecological information concerning their life histories, population dynamics, and habitat utilisation. Unfortunately, wildlife research in South Asia has not received the same priority as it has in North America, Europe, and East Africa (Eisenberg & Seidensticker, 1976). It is only rather recently that a growing concern for the endangered wildlife of the subcontinent has underlined the need for more intensive research on all species as a prerequisite for the development of sound conservation policies.

The Royal Karnali-Bardia Wildlife Reserve, situated in southwestern Nepal, proved well suited for a study of the interactions between the various wildlife species and habitat types common to the Terai zone of South Asia. Protected since the last decade as a Royal hunting reserve, Karnali-Bardia remains rich in the diversity of its mammalian fauna (Table 1) and also its avifauna, to which 207 bird species have been recorded to date (details to be published later).

Within the reserve an area of 11·8 km^2 was selected for intensive study in June 1975. It exhibited practically the whole range of habitat types found in the reserve, including surface water during the hot season. Lack of water poses severe difficulties for ungulates in the interior sal forests of Karnali-Bardia. In the first eight months of the two-year study (June 1975–June 1977), I sampled all of the major habitat types encountered in the study area by vegetational analysis and with the aid of aerial photographs mapped their distributions (Dinerstein, 1979). For the purpose of this paper the generic names of the six habitat types identified in the first paper will be employed in lieu of their original taxonomic designation. The changes are summarised below:

Shorea robusta–Buchanania latifolia forest = sal forest
Dalbergia sissoo–Acacia catechu forest = early riverine forest
Ficus glomerata–Mallotus philippinensis-Eugenia jambolana forest = moist mixed riverine forest
Bombax savannah/grassland = savannah/grassland
Ecotonal secondary open mixed hardwood forest = same
Saccharum spontaneum–Tamarix flood plain = tall grass flood plain

Seasonal utilisation of these habitat types by the larger herbivores of the reserve was investigated, with particular emphasis on the relation between plant phenology and use by wildlife in this typically monsoonal environment.

TABLE 1
MAMMALS RECORDED FOR THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL (THIS STUDY)

English name	*Scientific name*
Rhesus macaque	*Macaca mulatta*
Common langur	*Presbytis entellus*
Tiger	*Panthera tigris*
Leopard	*Panthera pardus*
Jungle cat	*Felis chaus*
Large Indian civet	*Viverra zibetha*
Small Indian civet	*Viverricula indica*
Common mongoose	*Herpestes edwardsi*
Striped hyaena	*Hyaena hyaena*
Indian fox	*Vulpes bengalensis*
Jackal	*Canis aureus*
Indian wild dog	*Cuon alpinus*
Sloth bear	*Melursus ursinus*
Smooth Indian otter	*Lutra perspicillata*
Common yellow bat	*Scotophilus heathi*
Short-nosed fruit bat	*Cynopterus sphinx*
Indian pipistrelle	*Pipistrellus coromandra*
Large flying squirrel	*Petaurista petaurista*
Five-striped palm squirrel	*Funambulus pennanti*
Indian porcupine	*Hystrix indica*
House rat	*Rattus rattus*
Indian hare	*Lepus nigricollis*
Indian elephant	*Elephas maximus*
Gangetic dolphin	*Platanista gangetica*
Goral	*Nemorhaedus goral*
Nilgai or blue bull	*Boselaphus tragocamelus*
Sambar	*Cervus unicolor*
Bharasingha or swamp deer	*Cervus duvauceli*
Chital or spotted deer	*Axis axis*
Hog deer	*Axis porcinus*
Barking deer	*Muntiacus muntjak*
Wild boar	*Sus scrofa*

The ultimate aim of the study, in conservation terms, was to achieve an improved status of the tiger *Panthera tigris*, for which these large herbivores comprise a vital food source. Plans for the management of ungulate populations to provide more prey for the tiger will be best developed in harmony with local ecological conditions, which strongly affect local plant phenology and productivity. A principal aim was to identify the major interactions between the existing habitat types and the endangered fauna of the Nepalese Terai, and to suggest managerial strategies for wildlife conservation.

METHODS

The density of the understory vegetation in Karnali-Bardia creates formidable difficulties in observing ungulates during at least half of the year. This situation is compounded by the behaviour of the ungulate species studied since many are either nocturnal or crepuscular. It was soon discovered that the most efficient method of observing ungulates directly was from a series of tree platforms, or machans. During the two years of the study, I spent over 140 nights in 10 different machans in order to observe ungulates in the early evening and early morning hours, the periods when visibility was best. For each sighting, the following data were recorded: time of day, weather conditions, species observed, group size, group composition, behaviour (e.g. resting, drinking, feeding, etc.), distance from observer, habitat type, distance to the edge of the next closest habitat type, distance to water and the border with agriculture, and the duration of the observation.

When ungulates were observed at the interface of two distinct vegetation types, the use of edge habitat was denoted and later calculated as a percentage of the total sightings. Machan observations also allowed the possibility of observing undetected the grazing and browsing behaviour of ungulates and the browsing behaviour of langur and rhesus monkeys. These observations provided a major source of data on seasonal plant use by animal species. Herbaceous and graminoid species selected by ungulates were checked on the ground for signs of feeding after each machan observation.

Indirect methods of determining habitat utilisation under such conditions were also employed. The standard plot method developed by Eisenberg *et al.* (1970) in Sri Lanka served as one index of habitat used by wild ungulates. The presence of large herbivores as indicated by the number of faecal piles on a series of plots in three major habitat types was monitored from November 1976 through May 1977. The use of this technique is limited to the dry period (November through 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 probably decreases the accuracy of pellet counts at this time of the year. The ungulate species studied by this method were hog deer *Axis porcinus*, chital *Axis axis*, barking deer *Muntiacus muntjak*, swamp deer *Cervus duvauceli*, and wild boar *Sus scrofa*. Track counts, strip censuses, and transects were also employed to obtain both quantitative and qualitative information on habitat utilisation, and track counts, transects, and direct observations to assess trends in habitat preference in the other parts of the reserve.

In order accurately to determine the relationship between plant phenology and habitat preference, it was first necessary to identify the most ecologically important plant species in the reserve. For those species which were difficult to separate in the field (e.g. *Cyperus* spp.), I compiled a notebook containing drawings of previously identified specimens at the Herbarium of the Department of Medicinal Plants, Kathmandu. Particular attention was paid to vegetative characteristics in order to facilitate the recognition of species without their flowering parts. In the first week of January 1976, transects totalling over 7 km in length were established through the six major habitat types distinguished within the study area. Phenological changes observed along these transects were recorded weekly until January 1977, that is, new leaves emerging, mature leaf, leaves falling, leaves absent, flowering, and fruiting of trees, climbers and shrubs. The phenology of grasses and sedges was described by three different conditions: emerging (which included the length of time the plant still remained green), flowering, and dormancy. Herbaceous plants were described in a similar manner. The criterion for determining if a change in phenology had occurred was that the condition of 25% of any species encountered along the transect had shifted from one phenological category to another over the course of the week.

Since the food habits of ungulates and primates were to be studied on a seasonal basis, it was necessary to demarcate the three seasons of the year in as straightforward a manner as possible (see Dinerstein, 1979).

True sunrise and sunset for the days of the year selected in constructing the activity graphs for chital and nilgai were derived from the Smithsonian Meteorological Tables (List, 1963). A latitude of 30° N was chosen as the closest approximation to the location of the study area.

HABITAT UTILISATION

Wild ungulate groups observed in the six major habitat types of the study area are shown in Table 2. The habitat types are arranged from left to right in terms of successional pattern. A comparatively similar amount of time was spent in each habitat type relative to its proportional distribution over the study area. The one exception to this was in the ecotonal secondary open mixed hardwood forest which was visited less frequently during the monsoon. A few cautions should be mentioned before inferring trends in habit use from direct counts. First, observability varied by habitat and season. For example, monsoon observations in those habitats

TABLE 2

NUMBER OF ENCOUNTERS OF WILD UNGULATES IN THE MAJOR VEGETATION TYPES IN THE STUDY AREA, ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL, MARCH 1976–MAY 1977

Species	*Tall grass flood plain*		*Early riverine forest*		*Moist mixed riverine forest*		*Savannah/ grassland*		*Ecotonal secondary open mixed hardwood forest*		*Sal forest*	
	T	N	T	N	T	N	T	N	T	N	T	N
Chital	38	10	226	24	651	137	5532	642	130	26	361	28
Nilgai	25	3	21	7	28	15	307	87	27	9	55	16
Wild boar	0	0	8	2	12	7	71	20	2	2	3	1
Barking deer	0	0	0	0	7	7	6	6	7	7	13	11
Hog deer	17	9	1	1	0	0	21	13	9	5	6	2
Swamp deer	0	0	7	1	5	1	19	4	0	0	0	0

T = total number observed.
N = number of groups observed.

characterised by a tall grass understory were limited by the height and density of the vegetation. Second, the results in Table 2 are probably biased against the most nocturnal species, such as wild boar. Third, the results do not include the presence of wild ungulates in croplands, a subject which will, however, be treated elsewhere in this paper. Although direct observations alone provide only a crude estimate of habitat use, the most obvious patterns will be discussed below.

Chital were distributed over all of the habitat types but were encountered most frequently in the savannah/grassland community (Fig. 1). They probably utilised the tall grass flood plain to a greater extent than indicated in Table 2, since sightings were minimised by poor visibility. Track counts along the flood plains offer considerable support to this claim.

Nilgai, like chital, favoured the savannah/grassland habitat over the other associations, particularly during the hot-dry season, when 86 % of the observations were made in this habitat type.

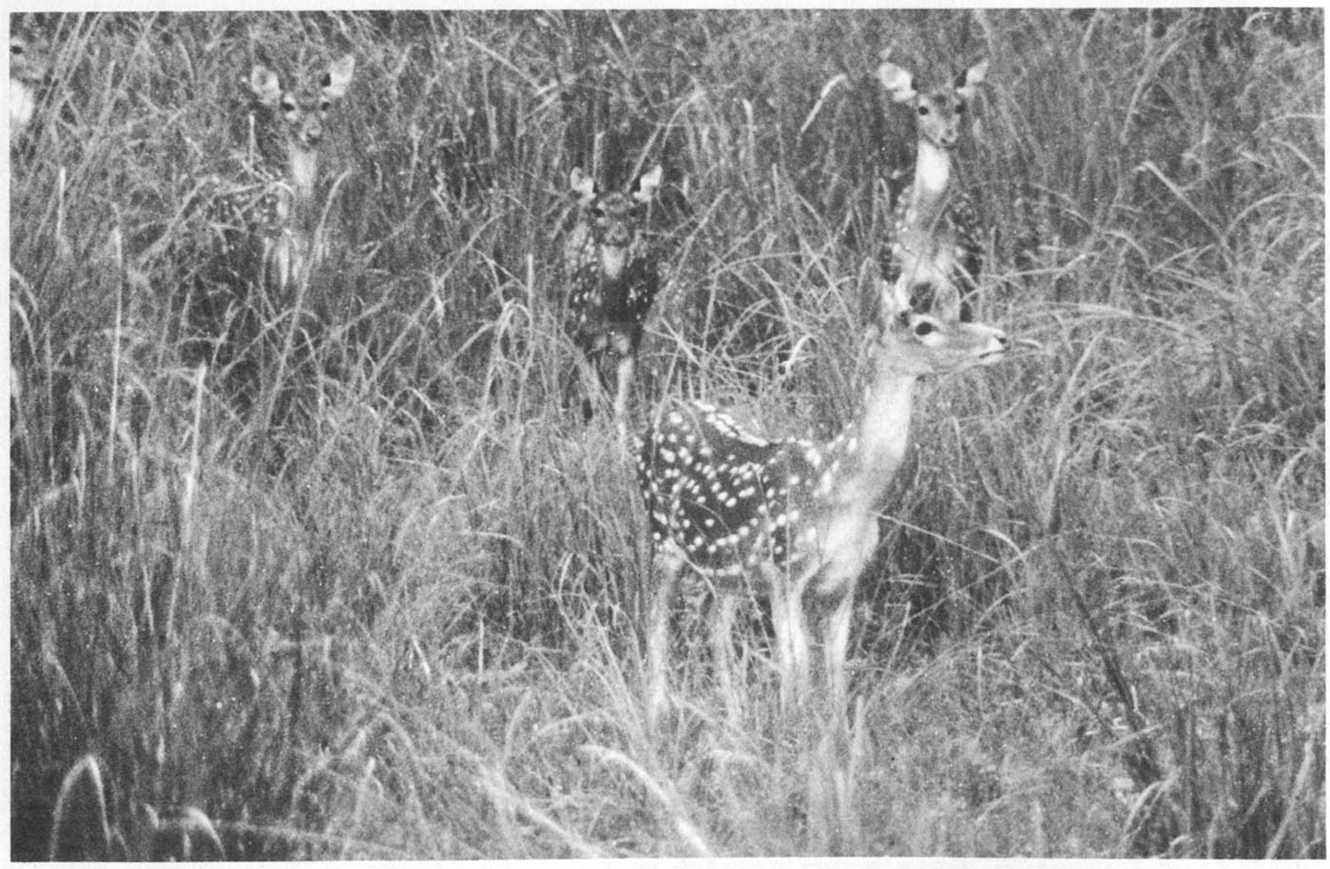
Barking deer were encountered most frequently in sal forest and were not observed in either the tall grass flood plain vegetation nor in early riverine forest.

Hog deer were most commonly observed in the tall grass flood plain and savannah/grassland habitats. From direct observations it appeared that hog deer and barking deer exhibited less seasonal variation in habitat selection than the other ungulates described above.

During the course of the study, the few remaining groups of swamp deer of Karnali-Bardia were encountered only in the hot-dry seasons of 1976 and 1977. The use of open savannah/grassland habitat at this time of year in Karnali-Bardia corresponds with the seasonal preference of swamp deer in reserves supporting much larger populations (Schaller, 1967; Spillett, 1967; Krishnan, 1972; Singh, 1973; Martin, 1978).

The wild elephant population (5–6 individuals) was not resident in the reserve. Its migrations appeared to coincide with the ripening of the paddy crop late in the monsoon period (September), although stray bulls did occasionally pass through the study area during the hot-dry season. Tracks, droppings, and signs of feeding indicated that elephants remained primarily in the sal forests of the reserve during the day and came out into the fields at night to graze on the rice crop.

Habitat utilisation by wild ungulates as determined by the number of faecal piles per hectare is presented in Table 3 (method adapted from Eisenberg & Lockhart (1972)). Tall grass flood plain, savannah/grassland, and sal forest habitats were specifically chosen as representative of the three major physiognomic classes of vegetation in the study area, and plots were located in each type. They also typified associations which were considered to be early, middle, and late successional stages. Use by nilgai and sambar could not be assessed by this method; nilgai dung in communal piles while sambar were ordinarily not present in the intensive study area. The pellets of chital, hog deer, and barking deer were separated by size and characteristic shapes (Dinerstein, 1980).



ig. 1 July 1976. A chital doe stands alert in the tall grass of the open savannah habitat. The dense monsoon growth often obscures the visual detection of potential predators.

TABLE 3

HABITAT UTILISATION BY WILD UNGULATES IN THREE HABITAT TYPES AS INDICATED BY THE NUMBER OF FAECAL PILES PER HECTARE IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL, DECEMBER 1976–MAY 1977

Species	*Tall grass flood plain*	*Savannah grassland*[a]	*Sal forest*
Chital	2	174	16
Hog deer	5	0	0
Wild boar	0	2	3

[a] Monitored December–February only.

Although the pellets of the Indian hare were not counted, the frequency with which they were found combined with direct observations suggested that hares were numerous in the flood plain vegetation and to a lesser degree in the savannah grassland habitat. While chital favoured savannah over the forested and flood plain associations, hog deer were recorded only in the flood plain plots. This same separation in habitat preference between hog deer and chital was observed by Seidensticker (1976) in the Royal Chitawan National Park, Nepal. Wild boar were poorly represented in all three of the habitats sampled, perhaps explained by the preference of pigs for croplands, early riverine forest, and moist mixed riverine forest where signs of their activity (e.g. diggings) were numerous.

The interaction of a number of environmental variables creates seasonal patterns of habitat utilisation by wild ungulate populations. The effects of the abiotic and biotic factors on the vegetation of Karnali-Bardia have already been discussed (Dinerstein, 1979). These same modifying factors also affect the seasonal movements and distributions of the reserve's ungulate populations, not only through their effects on the vegetation, but also directly. The most obvious abiotic factors include (1) high daytime temperatures during the hot-dry season, (2) the limited availability of surface water in forested habitats in the same period of the year, and (3) the total amount of precipitation during the monsoon. Fire and the overgrazing of domestic stock were originally identified as the two most important biotic factors. With the advent of grazing control in 1975, however, only fire remained as a significant parameter to consider.

The high temperatures recorded from March through June caused most ungulates to retire under cover during the middle of the day. The activity curve for chital during the hot-dry season clearly illustrates this point (Fig. 2). Two peaks were observed; one just after sunrise and one at sunset, with little movement occurring in the intervening hours. Under such conditions the importance of shady forest edge bordering on the open savannahs becomes paramount. Clumps of trees, such as *Mallotus philippinensis*, with low spreading crowns create small islands of shade near the edge of the savannahs and were sought out by ungulates at midday (Fig. 3). The activity curve for chital in the cool-dry season in this same savannah habitat, however, showed a somewhat different pattern (Fig. 4): they remained out longer in the late morning and noon hours when solar radiation was less intense than in the hot-dry season.

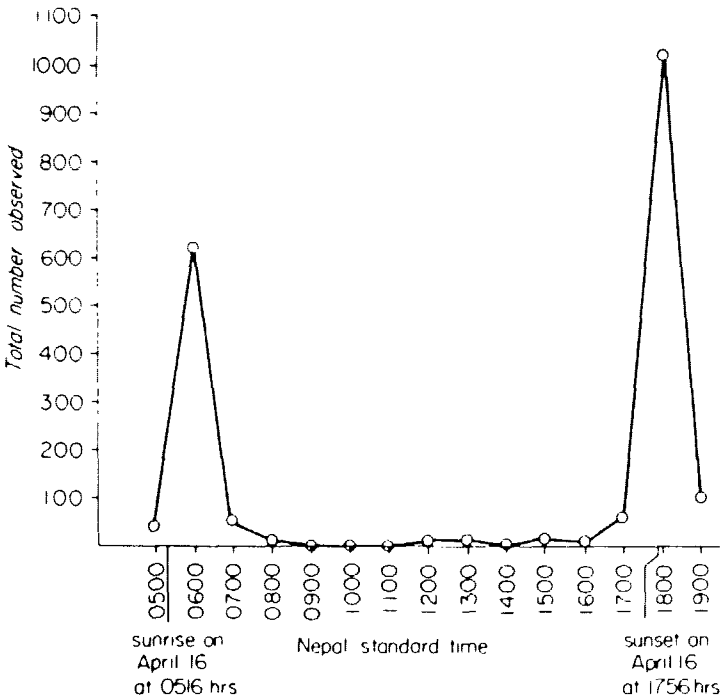


Fig 2 Activity pattern of chital during part of the hot season (1 April–15 May, 1977) based primarily upon machan observations

Fig 3 The low umbrella-shaped crowns of *Mallotus philippinensis* provide much needed shade for certain ungulate species during the heat of the day

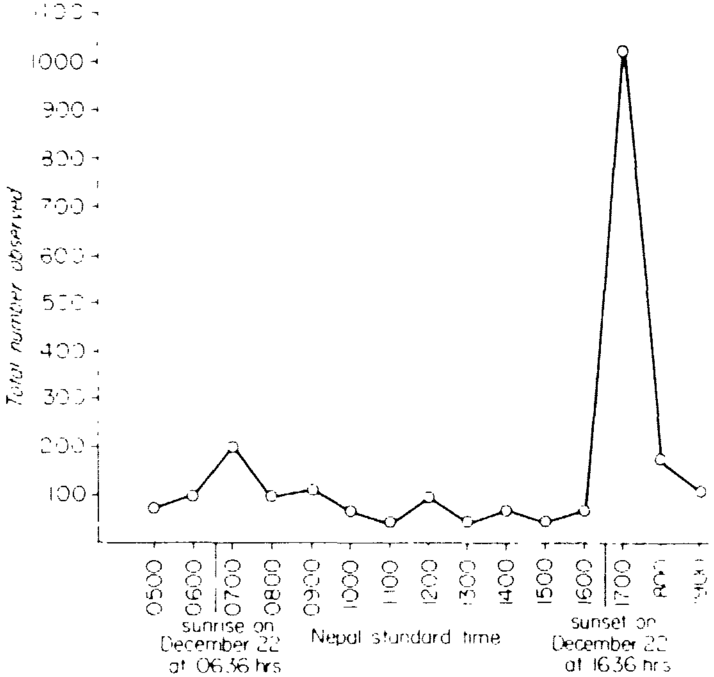


Fig. 4. Activity pattern of chital during the cool season (15 October 1976–25 January 1977) based primarily upon machan observations.

During the hot-dry season there was a more pronounced peak of chital observations in the evening than in the morning (Fig. 2). Since I spent the night in the same machan from which I had recorded the morning observations, this removed the possibility that the chital which would normally be out in the savannahs were scared off by an observer approaching the machan in the dawn hours. Thus chital must either be feeding to a greater extent in forested habitat at sunrise or else resting under dense cover after feeding during the night.

Nilgai and blackbuck (the latter locally extinct but surviving as a small relict population in a protected area outside the reserve) seem to be more tolerant to direct sunlight than some of the other ungulates studied (Fig. 5). Both species were observed out longer in the open sun during the hot-dry season than chital, barking deer, hog deer, or sambar. The thermoregulatory mechanisms of nilgai have not been studied, but since they do not wallow as do some other bovids, it seems probable that, being large-bodied, like the camel, the eland, and the oryx, they are able to store heat to some degree as an adaptation to temperature stress (Schmidt-Nielsen *et al.*, 1957; Taylor, 1969).

The availability of surface water limits the distribution and movements of

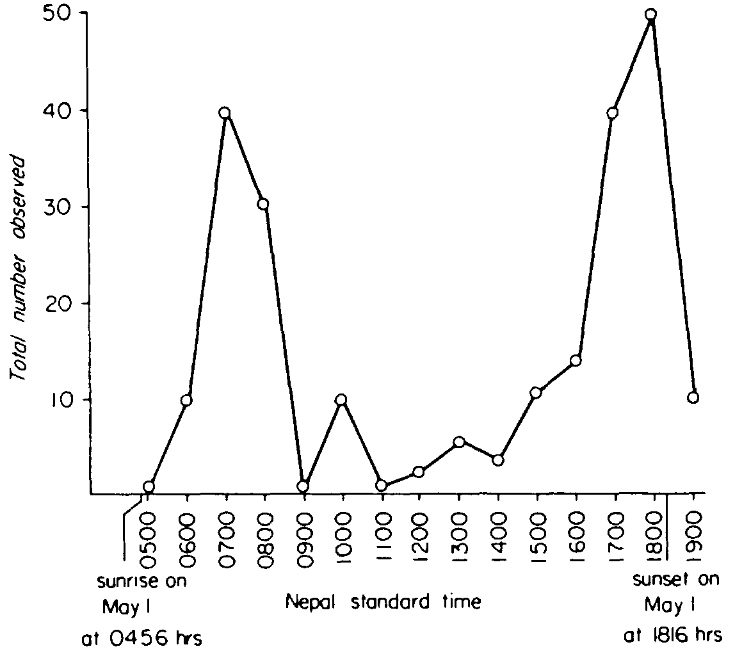


Fig. 5. Activity pattern of nilgai during the hot season (combined data from February–June 1976 and 1 April–15 May, 1977) based primarily upon machan observations.

ungulates and their predators in Karnali-Bardia during the hot-dry season. Almost all of the ungulate species encountered, as well as tiger and leopard, need to drink at least once a day at this time of the year (Schaller, 1967). Chital were found only at very low densities beyond a distance of 2 km from water. For barking deer and hog deer this distance was even smaller. It is primarily this factor that makes sal forest (which covers about 70 % of the reserve) marginal habitat for chital from November through May. McKay & Eisenberg (1974) also noticed the propensity of chital to concentrate around permanent water holes during the hot-dry season in Sri Lanka.

Since most of the precipitation occurs during the four-month monsoon period, the relative amount of soil moisture has a direct impact on the phenology of the vegetation. Heavy pre-monsoon rains as early as May stimulate new growth in graminoid species. The lush growth of vegetation associated with the monsoon provides abundant grazing and browse for ungulates. In addition, the rains create standing water in many depressions in the sal forest, thus alleviating the problem of water scarcity during the dry season. A curve correlating the number of observations of chital in the sal forest habitat over the year would be roughly proportional to the annual distribution of rainfall.

The effects of fire on the habitat utilisation of the wild cattle of South Asia have been described by Wharton (1968). In Karnali-Bardia, annual fires induce the re-emergence of perennial grasses at a time when grazing conditions would otherwise be least favourable for ungulates (i.e. February through May). Hot fires burn out the dense understory vegetation in most of the habitat types, reducing cover but also favouring the detection of potential predators. Shoot growth of the perennial species of the grasslands is greatly accelerated by precipitation shortly after the fires. In 1976, a lag time of only 12 days was observed between the last day of the burns and the appearance of the first new shoots.

PLANT PHENOLOGY

Investigations into the relationship between the seasonal quality and abundance of important forage plants and the movements and distributions of ungulates have clarified patterns of habitat utilisation in East African grasslands (Bell, 1971). The work by Berwick (1974) in the Gir Forest Sanctuary, Gujarat, India, and most recently by Martin (1978) in Kanha National Park, India, are the only similar studies conducted on the Indian subcontinent. However, while the moist subtropical deciduous forests of Karnali-Bardia are affected by the same climatic factors as the Gir Forest and Kanha National Park, there remain substantial differences in vegetation between the three areas. The present study thus provides initial documentation of plant phenology in relation to habitat utilisation for those reserves scattered along the base of the outermost ranges of the Himalayas.

The phenology of the important tree, climbing, shrub, herbaceous, and graminoid species was recorded on a weekly basis during 1976. Figures 6 to 11 summarise these weekly observations. A detailed listing of the phenology of each species will be published later.

Among the 43 tree species studied, 50% flower during the hot-dry season. Fruiting, in contrast, is divided more or less equally between the cool and hot seasons but occurs to some degree during the early monsoon as well (Fig. 6). The actual abundance of fruit is, however, probably highest in and around the months of December and May, since Fig. 6 (which does not differentiate between the contribution of the common and less common trees) includes at least 10 species whose production does not add appreciably to the total fruiting biomass. Most trees are deciduous; 86% drop their leaves during the cool-dry season and come into new leaf in the hot-dry season (Fig. 7). A number of important exceptions do occur: *Ficus glomerata* fruits up to eight months of the year, and so includes all the seasons; *Scheichera trijuga* fruits during the hot-dry season in alternate years; *Shorea robusta* (sal) drops its leaves at the same time that new ones are emerging.

The evergreen species in the tree layer include *Aegle marmelos*, *Alstonia scholaris*, *Eugenia jambolana* and *Streblus asper*.

In the shrub layer, nearly 80% of the species become deciduous by the end of the

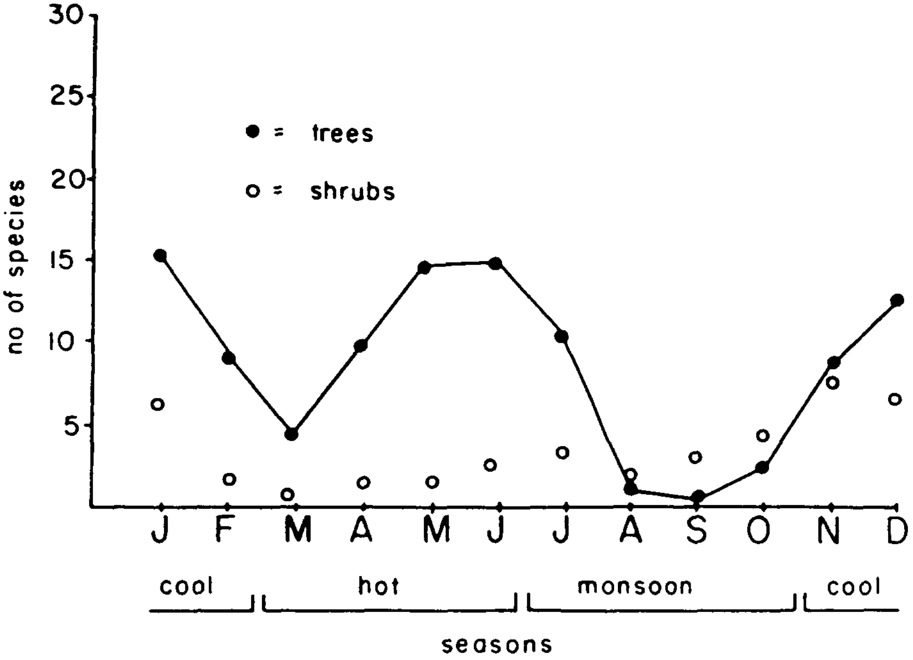


Fig. 6. Fruiting seasons for the major tree and shrub species in the study area.

cool-dry season and produce new leaves at the end of the hot-dry season (Fig. 8). It is primarily this dense shrub layer in the forested habitats which reduces visibility through the monsoon and into the cool-dry season. As in the tree layer, the fruiting of shrub species occurs throughout the year (see Fig. 6).

Herbaceous plants seemed to respond to the increased precipitation during the monsoon and were less conspicuous at other times of the year (Fig. 9).

In light of the heavy crop damage attributed to wild ungulates in Karnali-Bardia (this study) and in Royal Chitawan National Park, Nepal (A. Laurie, pers. comm.), I have included the phenology of the economically important plants cultivated around the study area (Fig. 10). From April to June the fields lie fallow, since local farmers raise only one crop of rice per year.

The phenology of grasses and sedges (Fig. 11), illustrates the critical roles played by both soil moisture and fire in controlling the abundance of new growth in Karnali-Bardia. Eighty per cent of the graminoid species studied dry up during the cool-dry season and remain dormant until the following monsoon. The second week of June in 1976 seemed to be the demarcation point at which the onset of the rains caused a significant change in the phenology of the graminoid vegetation.

The effects of burning stimulated new growth in the dominant perennial species of the savannahs and grasslands as observed in the months of April and November.

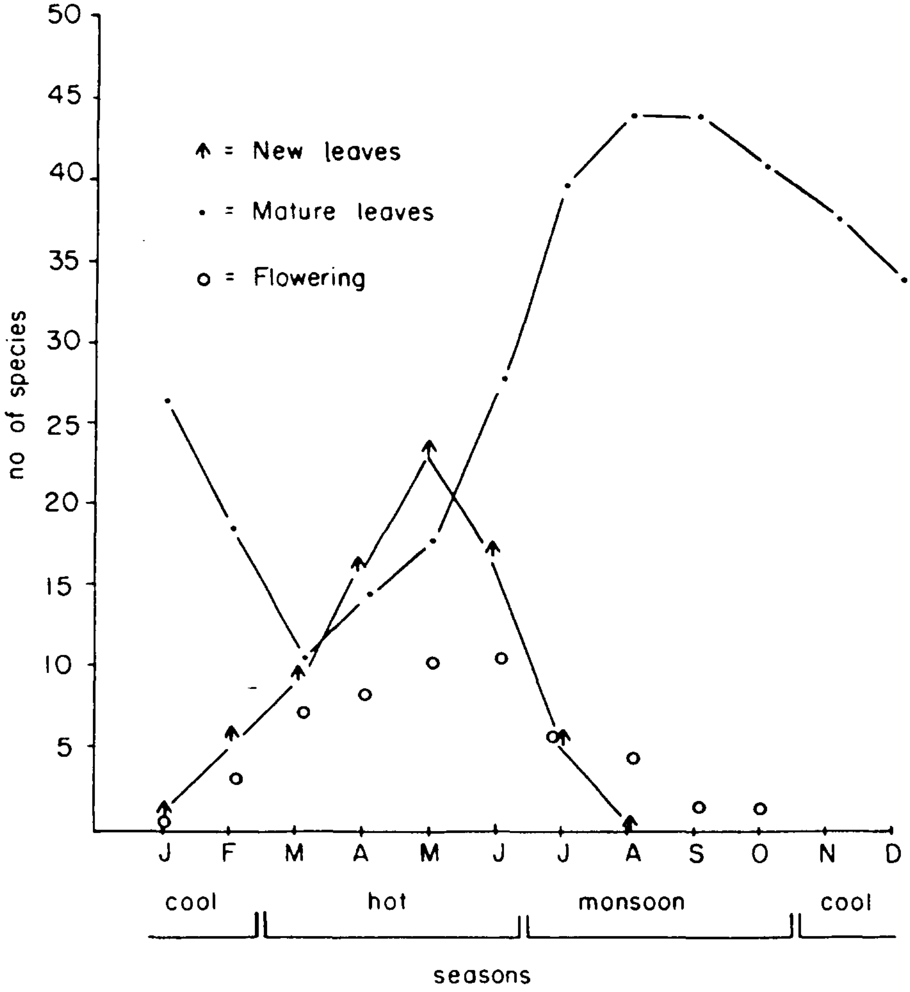


Fig. 7. The phenology of the major tree species in the study area illustrating the number of species in new leaf, mature leaf, and flowering over the year.

Fires are liable to occur from late November until June with the likelihood of such an event increasing as the hot-dry season progresses. Some of the most important grazing species for ungulates (e.g. the grasses *Imperata cylindrica*, *Vetiveria zyzanoides*, *Saccharum spontaneum*, *Erianthus ravennae*, and *Desmostachia bipinnata*) are adapted to an annual burning regime (Dinerstein, 1979).

Given the environmental conditions and the phenological patterns described above, changes in forage quality over the seasons would be expected. The early monsoon period (i.e. July–August) is marked by a resurgence of the natural

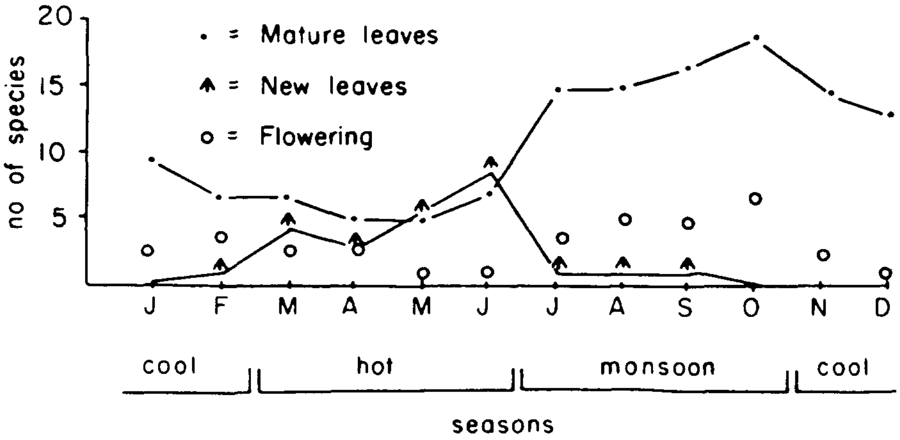


Fig. 8. The phenology of the major shrub species in the study area illustrating the number of species in new leaf, mature leaf, and flowering over the year.

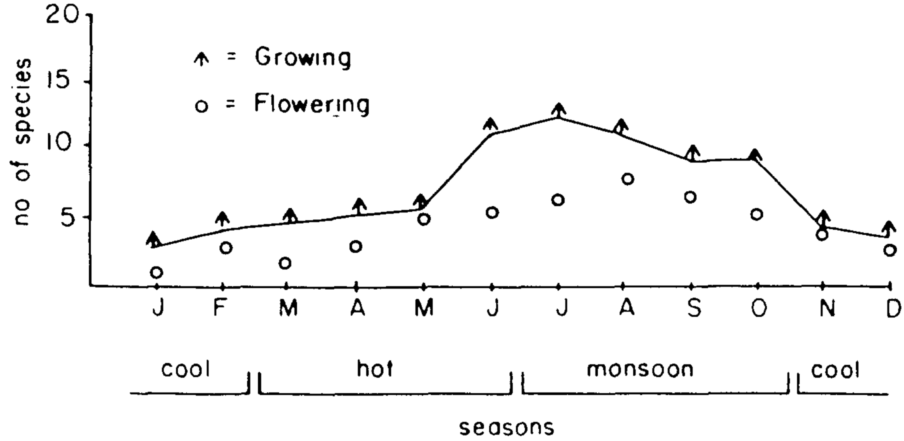


Fig. 9. The phenology of the major herbaceous plants in the study area illustrating periods of growth and flowering over the year.

vegetation, creating optimum foraging conditions for both grazing and browsing ungulates. As the cool-dry season progresses, however, the quality of the available browse and grazing species decreases as a number of plants become dormant. If controlled burns occur in December, forage conditions for wild ruminants improve in the savannah/grasslands. With the coming of the hot-dry season, the nutritional level of many browse plants increases dramatically when those species come into leaf (Berwick, 1974). The most commonly utilised grass species, however, decrease

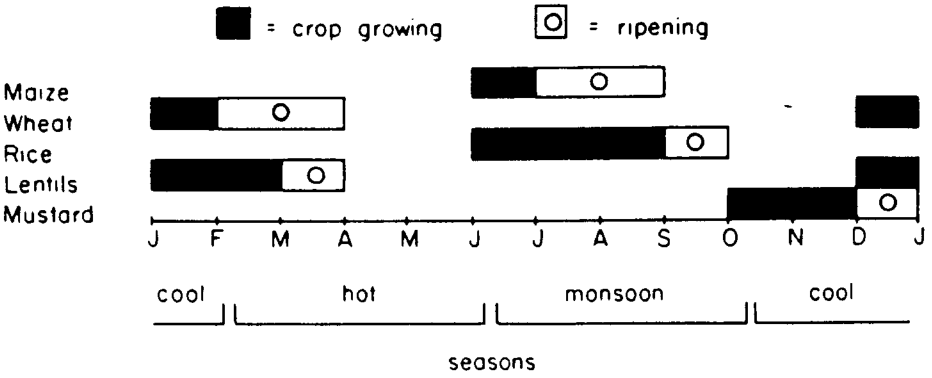


Fig. 10. The phenology of the most important crops cultivated around the study area.

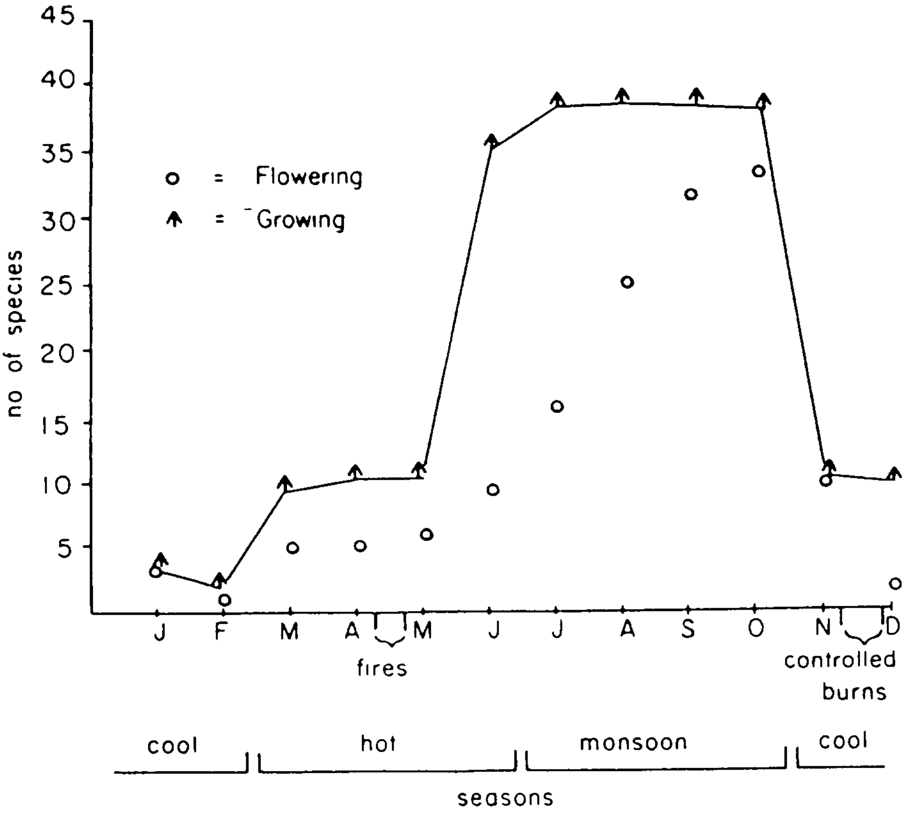


Fig. 11. The phenology of the major grasses and sedges in the study area illustrating periods of growth and flowering over the year.

significantly in food value during the hot-dry season (e.g. mid-February through May) unless mitigated by controlled burns or natural fires which usually clear out the understory by mid-April. If no burning occurs, most of the graminoid vegetation will remain in this unpalatable state until the pre-monsoon rains in May allow for the emergence of more nutritious shoots.

FOOD HABITS

The food habits of wild ungulates were discerned primarily through direct observations from machans and along transects within each habitat type. The food habits of primates were also included when it was discovered that ungulates and primates favoured many of the same species. The abundance of any item selected and its relative availability to the ungulate or primate choosing it were also considered.

Although the data presented in Table 4 indicate that chital are willing browsers, utilising a wide variety of tree and shrub species, the bulk of their diet is composed of

TABLE 4

SEASONAL FOOD HABITS OF THE CHITAL IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL, 1976–77

Species utilised	*Part selected*	*Hot-dry season (mid Feb.-June)*			*Monsoon (June-mid Oct.)*			*Cool-dry season (mid Oct.-mid Feb.)*		
		(*u*)	(*a*)	(*pr*)	(*u*)	(*a*)	(*pr*)	(*u*)	(*a*)	(*pr*)
Trees:										
Acacia catechu	seedlings				1	1	1	1	1	1
Acacia catechu	fruits							3	2	1·5
Adina cordifolia	leaves							4	1	4
Adina cordifolia	fruits							1	1	1
Aegle marmelos	seedlings	4	1	4	4	1	4	4	1	4
Alstonia scholaris	seedlings	2	1	2	2	1	2	2	1	2
Antidesma diandrum	seedlings							3	1	3
Bassia latifolia	flowers	3	2	1·5						
Bassia latifolia	leaves							1	1	1
Bauhinia malabarica	leaves	2	1	2	2	1	2			
Bauhinia racemosa	fruits	1	1	1						
Bombax ceiba	leaves	2	1	2						
Bombax ceiba	flowers	4	2	2						
Cordia sp.	fruits	1	1	1						
Dalbergia sissoo	fruits							2	2	1
Ehretia laevis	seedlings							1	1	1
Emblica officinalis	seedlings + fruits							3	1	3
Eugenia jambolana	leaves	1	2	0·5						
Eugenia jambolana	fruits	4	2	2						
Ficus benghalensis	fruits	3	1	3						
Ficus cunia	leaves	2	1	2						
Ficus glomerata	leaves	2	1	2				2	1	2
Ficus glomerata	fruits	4	3	1·3	4	3	1·3	4	1	4
Ficus religiosa	fruits	2	1	2						

TABLE 4—*contd.*

Species utilised	*Part selected*	*Hot-dry season (mid Feb.–June)*			*Monsoon (June–mid Oct.)*			*Cool-dry season (mid Oct.–mid Feb.)*		
		(*u*)	(*a*)	(*pr*)	(*u*)	(*a*)	(*pr*)	(*u*)	(*a*)	(*pr*)
Gardenia turgida	seedlings							2	1	2
Holoptelia integrifolia	seedlings	4	2	2	4	2	2	4	2	2
Holoptelia integrifolia	leaves	3	1	3	3	1	3	3	1	3
Mallotus philippinensis	flowers							2	3	0·6
Mallotus philippinensis	leaves	1	3	0·3						
Mitragyna parvifolia	leaves				3	1	3	3	1	3
Randia dumetorum	seedlings	3	2	1·5	3	2	1·5	3	2	1·5
Randia dumetorum	leaves	3	1	3	3	1	3	3	1	3
Schleichera trijuga	fruits				3	1	3			
Semecarpus anacardium	fruits							2	1	2
Shorea robusta	leaves	1	3	0·3						
Streblus asper	seedlings	4	2	2	4	2	2	4	2	2
Terminalia belerica	fruits							1	1	1
Terminalia tomentosa	seedlings							3	3	1
Zyziphus sp.	fruits							1	1	1
Climbers and lianas:										
Bridelia retusa	leaves							3	1	3
Calamus tenuis	leaves	3	2	1·5	3	2	1·5	3	2	1·5
Dioscorea bulbifera	leaves							1	1	1
Ichnocarpus frutescens	leaves							3	1	3
Milletia auriculata	seedlings							2	2	1
Smilax prolifera	leaves				2	1	2	2	1	2
Spathalobus roxburghii	seedlings							1	2	0·5
Shrubs:										
Asparagus racemosus	leaves							2	1	2
Cannabis sativa	leaves							1	1	1
Clerodendron infortunatum	leaves							1	2	0·5
Leea robusta	fruits				1	2	0·5			
Moghania bracteata	leaves							1	2	0·5
Moghania strobilifera	leaves							1	2	0·5
Phoenix acaulis	leaves	2	2	1				2	2	1
Pogostemon plectranthoides	leaves							1	2	0·5
Sida rhombifolia	leaves							4	2	2
Thespesia lampas	leaves							3	2	1·5
Thespesia lampas	fruits							3	2	1·5
Zyziphus mauritiana	leaves							2	3	0·6
Zyziphus mauritiana	fruits							2	3	0·6
Forbs:										
Crotolaria albida	leaves + stems							4	2	2
Elopantus scaber	leaves + stems							2	2	1
Euphorbia acaulis	leaves							2	1	2
Rungia parviflora	leaves + stems							4	1	4
Scoparia dulcis	leaves + stems							2	1	2
Grasses and sedges:										
Arundo donax	shoots				2	2	1	1	2	0·5
Cynodon dactylon	shoots	4	3	1·3	4	3	1·3	4	3	1·3
Cyperus brevifolius	shoots				2	2	1			
Cyperus cyperoides	shoots				2	2	1			
Cyperus difformis	shoots				1	2	0·5			
Cyperus globosus	shoots				1	2	0·5			

TABLE 4—*contd.*

Species utilised	*Part selected*	*Hot-dry season (mid Feb.- June)*			*Monsoon (June- mid Oct.)*			*Cool-dry season (mid Oct.- mid Feb.)*		
		(*u*)	(*a*)	(*pr*)	(*u*)	(*a*)	(*pr*)	(*u*)	(*a*)	(*pr*)
Cyperus iria	shoots				1	1	1			
Cyperus kyllingia	shoots				1	2	0·5			
Cyperus rotundus	shoots				2	2	1			
Dactyloctenium aegyptium	shoots				2	2	1			
Desmostachia bipinnata	shoots	4	2	2	1	2	0·5			
Digitaria sp.	shoots				1	2	0·5			
Echinochloa sp.	shoots				2	2	1			
Eragrostis coerctata	shoots				2	2	1			
Eragrostis unioloides	shoots				2	2	1			
Erianthus ravennae	shoots	4	3	1·3	1	3	0·3	1	3	0·3
Fimbristylis dichotoma	shoots				2	3	0·6			
Imperata cylindrica	shoots	4	3	1·3	4	3	1·3	1	3	0·3
Panicum sp.	shoots				1	2	0·5			
Paspalum distichum	shoots				1	2	0·5			
Polypogon monospeliensis	shoots				2	2	1			
Pseudopogonotherum contortum	shoots				2	2	1	1	1	0·5
Saccharum spontaneum	shoots	4	3	1·3	4	3	1·3	1	3	0·3
Setaria sp.	shoots				2	1	2			
Sporobolus diander	shoots				2	2	1			
Vetiveria zyzanoides	shoots	4	2	2	4	2	2	1	2	0·5

(u) = use: 1 = observed only once
2 = selected only two or three times
3 = occasionally selected
4 = frequently selected

(a) = availability: 1 = scarce
2 = common
3 = abundant

(pr) = preference $= \frac{\text{use}}{\text{availability}}$

grasses and sedges. In 12 rumen samples examined between January and September by Schaller (1967) from chital in Kanha National Park, India, grasses and sedges averaged 96% of the total volume and never fell below 90%. The attraction of adequate grazing conditions explains the high concentrations of chital on the open grasslands and savannahs after a major burn has stimulated new growth. Controlled burns occurred in the intensive study area in December 1976 and 'natural fires' in April 1976, and March and April 1977. At these times of year the new flush of grasses becomes the most sought-after forage available. From direct observations it appears that the shoots of *Imperata cylindrica*, and to a lesser degree *Saccharum spontaneum*, *Cynodon dactylon* and *Vetiveria zyzanoides*, comprise the bulk of the diets of Karnali-Bardia's grazing ungulates during the hot-dry season and the monsoon. This contradicts in part the findings of McKay & Eisenberg (1974) from Sri Lanka where *Imperata cylindrica* was avoided by chital. It is important to mention that in Karnali-Bardia and elsewhere in the Terai, *Imperata cylindrica* and a number of other tall coarse grasses become much less palatable once growth has progressed beyond the shoot stage. With the abundance of grass growth during the monsoon, chital face little difficulty in meeting their grazing needs. Browse appears to play only an incidental role in their diets during this season.

It is my belief that browse is selected more consistently by chital in the cool-dry season, when many of their favoured grazing species have become dormant and less nutritious. In the savannah, grassland habitat, chital readily browsed the dried fallen leaves of *Randia dumetorum*, *Adina cordifolia* and *Holoptelia integrifolia* before they grazed the older stems of *Imperata*. The flowers of *Bombax ceiba* and the fruits of *Acacia catechu* were readily consumed by chital as well as other ungulates during this season. It also appears that chital selected a wider variety of plants in sal forest during the early part of the cool-dry season (late October - November) than in any other habitat at any other time of the year. Species which were heavily browsed included *Emblica officinalis* seedlings and fruits, *Crotolaria albida*, *Terminalia tomentosa* seedlings, *Randia dumetorum* seedlings, *Sida rhombifolia*, *Elopantus scaber*, *Thespesia lampas*, *Urena lobata* and *Rungia parviflora*. Schaller (1967) attributed the same observed pattern in Kanha to the diminished food value of the grass species utilised prior to the end of the rains.

The fruits of *Ficus glomerata* are highly favoured by both ungulates and monkeys (Tables 4, 5, and 6). It was in the moist mixed riverine forest, where this plant species is dominant, that a special feeding relationship between primates and ungulates was observed to exist. Differences between the foraging strategies of langur and rhesus troops in Karnali-Bardia were evident; langurs are almost exclusively arboreal feeders while rhesus are more terrestrial as shown by the inclusion of ground insects and spiders in their diets. While both species are highly frugivorous, the langur has become an important folivore through the evolution of a ruminant-like digestive system (Bauchop & Martucci, 1968).

The presence of a large monkey population in Karnali-Bardia benefits wild ungulates in several ways. Most important, the feeding behaviour of the two primate species provides a supplement to the diets of wild ruminants. Browse and fruits which would be unavailable to ungulates or available only at a later date (i.e. when ripe fruits fall on their own) are knocked or dropped to the ground by the monkeys' feeding habits. Langurs will actually consume only a partial amount of what they initially pick. Schaller (1967) observed how chital would wait beneath langurs for leaves and fruits from four different tree species in Kanha. In Karnali-Bardia, I have observed that this relationship extends to at least 20 and perhaps as many as 24 food items (Table 6). The frequency of observations of ungulates waiting beneath feeding langur and rhesus troops points to the increased importance which additional fruit and browse may hold at certain periods of the year. Sightings of this nature were most notable in January with both monkeys, deer, nilgai, and wild boar feeding on *Bombax ceiba* flowers and in April, when these species feed on the fruits of *Ficus glomerata*. Other times and food species for which this relationship was readily observable were in November with *Acacia catechu* and *Dalbergia sissoo* fruits, and in July for the fruits of *Eugenia jambolana* and *Schleichera trijuga*.

The monkey troops observed tended to be mobile at times over short distances within the intensive study area (e.g. 1–2 km). Their feeding behaviour described

TABLE 5

SEASONAL FOOD HABITS OF THE NILGAI IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL, 1976–77

Species utilised	*Part selected*	*Hot-dry season (mid Feb.–June)*			*Monsoon (June–mid Oct.)*			*Cool-dry season (mid Oct.–mid Feb.)*		
		(*u*)	(*a*)	(*pr*)	(*u*)	(*a*)	(*pr*)	(*u*)	(*a*)	(*pr*)
Trees:										
Acacia catechu	seedlings				2	2	1	2	2	1
Acacia catechu	fruits							3	3	1
Adina cordifolia	leaves				2	1	2	2	1	2
Aegle marmelos	leaves				4	2	2	4	2	2
Bassia latifolia	flowers	3	2	1·5						
Bassia latifolia	leaves							1	2	0·5
Bauhinia malabarica	leaves	3	2	1·5	3	2	1·5			
Bauhinia racemosa	leaves	4	2	2						
Bombax ceiba	flowers	4	2	2						
Casearia tomentosa	leaves	4	3	1·3	3	3	1			
Dalbergia sissoo	leaves + fruits							2	3	0·5
Ehretia laevis	leaves							1	2	0·5
Emblica officinalis	fruits							4	1	4
Eugenia jambolana	fruits				3	3	1			
Ficus benghalensis	fruits	4	1	4						
Ficus glomerata	fruits	4	3	1·3	4	3	1·3			
Ficus religiosa	fruits	4	1	4						
Gardenia turgida	leaves							1	1	1
Holoptelia integrifolia	leaves	3	1	3	3	1	3	3	1	3
Mitragyna parvifolia	leaves	3	1	3	3	1	3			
Randia dumetorum	leaves	4	2	2	4	2	2	4	2	2
Randia dumetorum	fruits							4	2	2
Schleichera trijuga	fruits				3	1	3			
Semecarpus anacardium	fruits							2	1	2
Streblus asper	leaves	4	2	2	4	2	2	4	2	2
Terminalia tomentosa	seedlings							1	3	0·3
Zyziphus sp.	fruits							1	1	1
Climbers and lianas:										
Calamus tenuis	leaves	2	2	1	2	2	1	2	2	1
Smilax prolifera	leaves				3	1	3			
Shrubs:										
Leea robusta	fruits				1	3	0·3			
Moghania bracteata	leaves							2	2	1
Sida rhombifolia	leaves							4	2	2
Thespesia lampas	leaves + fruits							4	2	2
Urena lobata	leaves							4	1	4
Zyziphus mauritiana	leaves	4	3	1·3	4	3	1·3	4	3	1·3
Zyziphus mauritiana	fruits							4	3	1·3
Forbs:										
Crotolaria albida	leaves + stems							4	2	2
Euphorbia acaulis	leaves + stems							2	1	2
Rungia parviflora	leaves + stems							2	1	2
Grasses and sedges:										
Cynodon dactylon	shoots	2	3	0·6	4	3	1·3			
Desmostachia bipinnata	shoots	2	2	1						
Erianthus ravennae	shoots	2	2	1						
Imperata cylindrica	shoots	4	3	1·3	4	3	1·3			
Saccharum spontaneum	shoots	4	3	1·3						
Vetiveria zyzanoides	shoots	2	2	1						

(u) = use: 1 = observed only once
2 = selected only two or three times
3 = occasionally selected
4 = frequently selected

(a) = availability: 1 = scarce
2 = common
3 = abundant

(pr) = preference $= \frac{\text{use}}{\text{availability}}$

TABLE 6

FOOD SPECIES MADE AVAILABLE TO UNGULATES BY LANGUR AND RHESUS MONKEYS IN THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL

Species browsed	*Part browsed*	*Season of the year when ungulates were observed under trees where monkeys were feeding on this species*
Acacia catechu	fruits	Cool-dry season
Albizzia lebbek	fruits	Cool-dry season
Bombax ceiba	flowers	Cool-dry season
Dalbergia sissoo	fruits	Cool-dry season
Emblica officinalis	fruits	Cool-dry season
Bassia latifolia	flowers	Hot-dry season
Bauhinia racemosa	fruits	Hot-dry season
Bombax ceiba	fruits	Hot-dry season
Ficus benghalensis	fruits	Hot-dry season
Ficus glomerata	fruits	Hot-dry season
Garuga pinnata	fruits	Hot-dry season
Shorea robusta	leaves	Hot-dry season
Bombax ceiba	leaves	Monsoon
Eugenia jambolana	fruits	Monsoon
Ficus glomerata	young leaves	Monsoon
Holoptelia integrifolia	leaves	Monsoon
Mallotus philippinensis	flowers	Monsoon
Schleichera trijuga	fruits	Monsoon
Terminalia tomentosa	leaves	Monsoon
Probably utilised by ungulates:		
Semecarpus anacardium	fruits	Cool-dry season
Bauhinia vahlii	fruits	Hot-dry season
Cordia sp.	fruits	Hot-dry season
Dalbergia sissoo	young leaves	Hot-dry season
Spathalobus roxburghii	fruits	Hot-dry season
Streblus asper	fruits	Hot-dry season

above does not appear to alter whether or not ungulates are waiting beneath them. Thus as long as ungulates move through the same home ranges as the monkeys, they are able to take advantage of what had been dropped several hours or days beforehand. By bounding through the upper canopy layer, langurs will sometimes knock down additional fruits from the trees. The fact that fruit is present in abundance at periods when other forage plants are low in food value makes this relationship especially significant for ruminant nutrition.

Monkeys high in the trees detect predators more quickly than do the ungulates beneath them. Therefore primates may serve as sentinels to browsing ungulates. In riverine forest, where visibility remains poor throughout the year because of the dense understory vegetation, the warning calls issued by monkeys may serve to extend the margin of safety for ungulates that would normally exercise much more caution in entering and remaining to feed in such a habitat. On the ground, monkeys and ungulates associate quite freely, especially in the savannah/grasslands and along river beds. Mixed groups were often observed licking the dried salt off the surface of rocks along the banks of the Khoraha River. In such a situation it may be that the roles are reversed, with chital warning monkeys first of the presence of predators.

Cloud cover, monsoon rains and pre-monsoon storms and cool weather affected the feeding behaviour of chital. Deer remained out longer in the open grasslands and savannahs on cloudy days and on cool mornings in December and January, when radiation stress is presumably negligible. On 12 occasions while waiting out monsoon rainstorms from machans I noticed chital moving away from the forest edge to graze in the open grasslands. A similar behavioural response was noted in Wilpattu National Park, Sri Lanka (J. Eisenberg, pers. comm.).

Nilgai are more closely associated with croplands than are any of the other ungulates indigenous to Karnali-Bardia. This is demonstrated by the role that cultivated plants, such as rice, mustard and lentils, play in their diets, especially from October through January. Nilgai in Karnali-Bardia and in other areas outside the reserve were never encountered more than 4 km from the border with cultivation.

Apart from a shared attraction to agricultural crops, nilgai and chital differ considerably in their feeding habits (Table 5). While the nilgai does graze, the bulk of its natural diet seems to be composed of browse plants. The feeding strategy of the nilgai adheres to the Jarman-Bell Principle (Jarman, 1974, cited in Geist, 1974; Bell, 1971) which associates ungulate body size with the relative digestibility of forage selected. A large-bodied ruminant like the nilgai would require less nutritious forage (i.e. a higher fibre protein ratio) than would the smaller ungulates such as the barking deer, hog deer, and chital. Nilgai, quite naturally, are also attracted to new grazing and browse; in the hot-dry season, the readily available new leaves of a number of tree species common to the savannahs and the nutritious shoots of recently burned perennial grasses drew nilgai into this habitat (Fig. 12). Trees which were heavily browsed included *Randia dumetorum*, *Casearia tomentosa*, *Bauhinia racemosa* and the shrub *Zyziphus mauritiana*. The rapid accumulation of pellets at many new nilgai dung piles along with the increased number of direct observations in this habitat support the view that use increased in April and May. Since nilgai are reported to favour more open habitats than some of the other herbivores (Prater, 1965), it seemed contradictory that in Karnali-Bardia the dense early riverine forest was heavily utilised in the cool-dry season. The explanation appears to be that the abundance of browse species (most notably the leaves and fruits of *Zyziphus mauritiana* and *Acacia catechu*, and the leaves of *Streblus asper*) which are available in this habitat attract the nilgai.

Nilgai are much larger than either chital, hog deer, or barking deer, and therefore more browse is accessible to them. Chital bucks were observed on a number of occasions to rear up on their hind legs to reach the lowest branches of certain trees (e.g. *Adina cordifolia* and *Ficus glomerata*) but in general browse above 1·5 m appears to be essentially unobtainable. Hog deer and barking deer are even more restricted than chital in this regard.

Sambar were conspicuously absent from the intensive study area and generally

Fig. 12. A nilgai bull browses the young leaves of *Casearia tomentosa*, a common tree in the savannah habitat. May 1976

uncommon along the southern border of Karnali-Bardia, the same places where nilgai were frequently sighted. Conversely, amidst continuous sal forest near Dhanwa Tal (located 6·5 km from agriculture), sambar were common while nilgai were absent or present only in very low numbers. Competition for browse plants may be partly responsible for a separation in the distribution of these two large herbivores. Nevertheless, with the sambar's known preference for grasses and sedges from June through October (Schaller, 1967), it seems odd that the savannahs and riverine forest habitats of the study area were not occupied to graze the lush forage provided by the monsoon rains. Poaching can probably be discounted as a factor in the removal of the sambar population from the study area, in that their nocturnal behaviour and acute hearing would make them difficult targets for villagers equipped with outmoded firearms accurate only at close range.

The sambar's ability to adapt to a feeding strategy in dense continuous climax forest confers upon it selective advantage over the other ungulates of Karnali-

Bardia. In mature sal forest associations, sal often becomes a co-dominant with asna *Terminalia tomentosa*. In this situation, the prolific shrub growth which characterises this layer is replaced by a tall grass understory. Some of the species composing this stratum, namely *Themeda triandra*, *Saccharum spontaneum*, *Erianthus ravennae* and *Dendrocalamus strictus*, have been identified as important forage plants for the sambar (Schaller, 1967). This association probably supports higher densities of sambar than does sal forest with a predominantly shrub understory. My own observations agree with past hunters' accounts that sambar, while thinly distributed across the south-facing Churia ridge, are most common where climax sal forest borders major water courses such as along the Babai River gorge and the northern stretches of the Gerwa River below Chisapani.

Wild boar prefer a number of the same fruits as do nilgai and chital including those of *Ficus glomerata*, *Schleichera trijuga*, *Aegle marmelos* and *Emblica officinalis*. The morphological adaptation for rooting, however, creates a major separation in boar-feeding strategies from those of the other ungulates. Diggings in almost all of the forest associations in the study area were frequently observed. Wild boar require a more nutritious diet (i.e. more digestible forage and more quality food per body weight per day) than some of the larger ruminants, thus explaining the attraction of cultivated plants for this omnivore. Although predation on the young of other mammals was not observed, the consumption of carrion by wild boar has been documented elsewhere (Eisenberg & Lockhart, 1972).

Hog deer and chital prefer some of the same grazing plants, but a definite ecological separation does exist between these two congeneric species. The predator avoidance and feeding strategies of the hog deer restrict its distribution primarily to the dense tall grass flood plain habitat and its diet to the few grazing species which are found there. Hog deer favour the stems of *Cynodon dactylon*, a prostrate grass, and the shoots of several tall grass species such as *Saccharum spontaneum*, *Erianthus ravennae*, and *Imperata cylindrica*.

The anti-predator and foraging strategies of the chital have allowed it greater flexibility in habitat selection than the hog deer. The larger of the two species of *Axis* deer, the chital relies on speed to escape the stalking predators of the subcontinent. It is gregarious, associating in large herds on the open grasslands and savannahs, and has evolved an effective system of warning vocalisations in response to the detection of predators. Living, or at least feeding, in large aggregations minimises the risk to any one member of the herd of being eaten and maximises the feeding efficiency of the group, since a solitary animal would be required to exhibit far more caution in foraging under similar circumstances. The hog deer, on the other hand, is a shorter, stockier, slower deer than the chital; it therefore must rely on remaining inconspicuous as its strategy in escaping predators. These relationships are similar to those reported for a variety of ungulates by Eisenberg & Lockhart (1972) and Geist (1974).

The barking deer, being similar in stature to the hog deer, exhibits some of the same anti-predator strategies; it tends to be inconspicuous, nocturnal, but is even more solitary in its behaviour. Another important difference is that barking deer prefers riverine forest and sal forest habitats as escape cover over the tall grass flood plain community. They are so secretive that it proved difficult to obtain more than cursory observations on their feeding preferences. From the limited number of sightings in Karnali-Bardia it would appear that some of the most important grasses (e.g. *Imperata cylindrica* and *Cynodon dactylon*) and the fallen fruits of trees (including *Ficus glomerata*, *Schleichera trijuga* and *Eugenia jambolana*) are important in the diet of this species. According to the Jarman-Bell Principle, the barking deer as the smallest ruminant found in Karnali-Bardia would be expected to seek out more nutritious forage than the other bovid and cervid species.

Swamp deer, like chital, were attracted by the new shoots of *Imperata cylindrica* in the savannahs during the hot-dry season. The food habits of this species at other times of the year in Karnali-Bardia are unknown. Martin (1978), however, found that the diet of the swamp deer was composed almost entirely of grasses in all seasons.

From my own observations and discussions with local farmers it became clear that crop depredation by wild ungulates along the southern border of Karnali-Bardia is most severe during the cool-dry season. In October, farmers must keep continuous evening vigils from makeshift machans constructed over their rice paddies to prevent considerable damage by wild boar, nilgai, and chital. Migratory wild elephant pose a similar threat over a 16-km span of the southern boundary. Most of the damage occurs in fields within 1 km from the reserve border, and local deterrent measures, such as noisemakers, shouts, and flashlights, do little to frighten away wild ungulates. The problem continues in November when the mustard crop emerges; nilgai and chital are especially fond of the young plants. Lentils and wheat, two crops which are sown in the cool season, are also placed in jeopardy by the depredation of nilgai, boar, and chital. Finally, if ungulates are able either to penetrate or jump the makeshift thorn fences erected by local villagers to protect vegetable gardens, these plants will be consumed as well, especially beans, tomatoes, and radishes.

Until 1975 the damage caused by wild ungulates was partially offset by the opportunities for villagers to poach the chital, wild boar, and black-buck entering their fields (nilgai, however, considered by the local Tharu farmers to be too closely related to the holy cow, were not shot). Now with anti-poaching regulations strictly enforced such a compensation no longer exists. Wild ungulates are increasing along the southern border of Karnali-Bardia at the obvious expense of local farmers. It is highly doubtful if crop depredation will decrease in the coming years unless better methods are employed to deter such behaviour. Certainly high fences (over 2 m) combined with wide deep ditches would offer more protection from wild ungulates than do current measures.

The optimum strategy for grazing ungulates in subtropical habitats would be one in which the distance from cover to the feeding areas is minimal, where water is close by, and where an animal could quickly satisfy its daily feeding requirements on nutritious vegetation. Such a situation did indeed exist for populations of several ungulate species along the southern border of the reserve, where water was always available and cropland near. During the periods when the major agricultural crops were ripening, nilgai, chital, and wild boar would shelter in the forests adjacent to the edge of the fields. Every evening at about 2000 h (i.e. approximately 2 h after darkness) wild ungulates began to enter the croplands. The actual distances travelled between sources of food, water and cover were small. If wild ruminants are allowed undisturbed access to the fields for the 10 months of the year when crops are cultivated, there is little incentive for them to spend much time grazing or browsing in the other 'natural' habitats, where food may be less attractive and presence of tigers more probable.

In Karnali-Bardia, several of the ungulates studied fed on browse plants which are known to produce toxic secondary compounds. The Apocynaceae, Euphorbiaceae, and the Anacardiaceae, three families well represented in the forest flora of this region, all contain species which synthesise such substances yet are still readily sought out by wild ruminants. Aromatic species such as *Eugenia jambolana* and *Aegle marmelos* and species with milky juice such as *Bassia latifolia*, *Bassia butyracea*, *Streblus asper*, *Euphorbia acaulis*, *Semecarpus anacardium*, *Alstonia scholaris*, *Holarrhena antidysentrica*, *Ichnocarpus frutescens* and *Ficus* spp. are highly favoured by browsers. The strategies of herbivores with regard to food plants containing toxic chemicals have been reviewed by Freeland and Janzen (1974). Browsing ungulates must possess a gut flora specialised enough to detoxify tannins, phenolics, and other secondary compounds which have evolved through natural selection as a defence mechanism against leaf predation. One method of minimising the consequences of ingesting plant material containing such secondary compounds is to limit the amount of any one species consumed. Another strategy involves browsing only the new leaves of toxic plants, which are generally lower in such chemicals and higher in nutritive value than older growth (Longhurst *et al.*, 1968). When the leaves mature, the concentration of toxic compounds in certain plants rise with a concomitant decrease in protein content (Feeny, 1970). Exploiting this ability to neutralise the effects of secondary compounds may enable ungulates to increase the amount of minerals and trace elements in their diets. Some of the lactiferous plants favoured by chital in Bandipur Sanctuary, India (e.g. *Callotropis* sp.) were found to be high in calcium and phosphorus (Sharatchandra & Gadgil, 1975).

In conclusion, observations thus far indicate that for grazing ungulates, plants are most highly selected in the early stages of growth and that the daily diet, when it contained browse, included a variety of species. Browsers concentrated more heavily on a fewer number of species and included the new shoots of perennial grasses when available. In instances when both grazing and browsing ungulates were allowed undisturbed access to croplands, the daily intake of cultivated species was higher than the percentage contributed by 'natural' forage plants.

MOVEMENTS

The need for adequate grazing conditions is often cited as a major cause of migrations in caribou (Miller, 1974), wildebeest (Talbot & Talbot, 1963), zebra (Bell, 1971) and other large ungulates. The daily and seasonal movements for many of the wild ruminants in South Asian subtropical environments, however, are determined to a large degree by the availability of adequate drinking water. The cervid species of Karnali-Bardia lack the physiological adaptations which desert dwelling bovids have evolved to cope with temperature stress and water loss; therefore they must remain close to riverine habitats during the hot-dry season in lieu of exploiting the extensive but arid belt of sal forest which covers much of the reserve.

Between areas where water sources were perennial and a diversity of habitat types existed, certain responses on the part of ungulates and primates to food availability were observed. Under the above conditions, ungulate movements adhered to a pattern of seasonal concentrations and dispersals over rather short distances. With the exception of elephant and perhaps sambar, most of the ungulates in Karnali-Bardia tended to remain restricted to relatively small seasonal home ranges. A few recognisable chital bucks occupied a seasonal range of mixed savannah and forested habitat no more than 1 km^2 in area. Several easily identified nilgai bulls were recorded to have moved between two savannah areas over 4·8 km apart from one another during the course of the cool-dry season of 1976, but in general this species seemed to occupy smaller home ranges than would normally be expected for an animal of its size. From my observations it appeared that hog deer and barking deer were even more sedentary, each individual probably utilising an area smaller than 1 km^2 for most of the year. Nevertheless, a movement over 1 km within the study area usually implies crossing from at least one habitat type into another. When regarded in this manner short movements on the part of ungulates and primates take on a new significance. For those habitats which contain perennial drinking water, a summary of the most obvious concentrations of wildlife and the time of year in which they occurred is listed below:

1. The concentration of chital on the recently burned grasslands and savannahs after the re-emergence of new growth in December, January, April, and May.
2. The movement of nilgai into the savannahs during the hot season to browse the new leaves of several tree species.

3. The concentration of ungulates along the southern perimeter of the reserve in response to the planting and/or ripening of cultivated crops from late September through March.
4. The congregations of langur and rhesus monkeys in various tree species when feeding on flowers, fruits, and new leaves (e.g. *Bombax ceiba* in January for flowers and April for fruits, *Ficus glomerata* in April and May for fruits, *Acacia catechu* in October for fruits, *Dalbergia sissoo* in March for new leaves, *Schleichera trijuga* and *Eugenia jambolana* in July for fruits).

The only significant dispersal observed was believed to be a result of the improvement of habitat conditions in the dry sal forest during the monsoon. The increased availability of drinking water at this time allowed chital to seek out more palatable forage when some of the preferred grasses in the savannah habitat had become coarse and relatively less attractive. Group sizes of chital in sal forest at this season were much smaller than those of the large feeding aggregations observed in the savannahs in April and May (Dinerstein, 1980).

HABITAT UTILISATION BY OTHER LARGE MAMMALS

One of the initial objectives of this study was to attempt to differentiate the tigers utilising the study area through statistical analysis of pug mark measurements. This project was eventually abandoned when it was realised that the time required to obtain an adequate sample size for a meaningful pug mark analysis cut too heavily into the time allotted for other research priorities. However, the presence or absence of pug marks in the various habitat types did offer a crude estimate of tiger movements and habitat preference over the seasons. Inherent in the above statement is the assumption that the frequency of pug marks along roads and game trails is a reasonable indicator of habitat utilisation. Studies by Schaller (1967), Singh (1973) and Seidensticker (1976) have called attention to the habitual presence of prints along game tracks. On the basis of the frequency of pug mark observations, it appeared that the early riverine forest and the savannah/grassland habitat were preferred over sal forest during the cool and hot seasons of the year. The number of pug marks observed along the flood plains of the Gerwa River pointed to the importance of riparian habitat for this species during the hot-dry season. This is partly a reflection of the daily water requirements of the tiger. As mentioned above, surface water in the dry sal forests becomes scarce in the hot season and tigers must drink daily (Singh, 1973). In addition, the major prey species of the tiger in Karnali-Bardia, the chital, is most numerous in the open savannah habitat, being present in sal forest only at much lower densities throughout most of the year (Dinerstein, 1980). Tigers were observed more frequently in the savannah habitat during the hot-dry season than at any other time of the year. This could partly be explained by the increased visibility in this habitat type after the fires, but could also be a consequence of the concentration of large herds of chital in a relatively small area during the hot season.

One other point worth mentioning about tiger activity is the predation on domestic cattle in communal grazing areas outside the reserve borders during the monsoon of 1975. At least 20 buffaloes and cows were taken by tigers within a three-month period. During the monsoon of 1976, however, only a few domestic stock were killed by tigers. This decrease might be attributed to the increased protection of the most productive wildlife habitat from human intrusion and the consequent greater use by wild ungulates and predators alike.

In the Royal Chitawan National Park, Nepal, Seidensticker (1976) attempted to clarify differences in habitat use between radio-collared tigers and leopards. The leopard was able to exist in the same general areas as the tiger through a specialisation in the use of habitat subtypes, by altering movements and by the selection of a wider variety of prey items to minimise competition.

The abundance of prey species in Chitawan may have allowed the observed overlap in the home ranges of the two predators. In the Karnali-Bardia study area, where prey was less abundant, leopards were rarely observed and pug marks and droppings were also seldom encountered. The meagre amount of data collected on the leopard prohibits drawing any conclusions about niche relationships between the large cats of Karnali-Bardia.

Habitat utilisation by the other large mammals of the reserve will be briefly mentioned. Sloth bear *Melursis ursinus* was observed only once in the study area. Tracks and droppings indicated that this species exists in very low densities in sal forest during the monsoon and in riverine forest during the hot-dry season. The low numbers present in sal forest were rather surprising considering the abundance of termite mounds which harbour an important source of food for this omnivore (Laurie & Seidensticker, 1976). Jackals *Canis aureus* were common in all of the habitat types identified, but were observed most frequently in the savannahs and grasslands (Fig. 13). One sighting of a pack of wild dogs *Cuon alpinus* was recorded in sal forest at the base of the Churia hills (G. Singh, pers. comm.). A deserted wild dog den was discovered by P. Wegge near the northern border of the reserve above the Babai River Gorge. The pug marks of the nocturnal jungle cat *Felis chaus* were frequently encountered along roads in the savannah habitat. The smooth Indian otter *Lutra perspicillata* was common along the Gerwa and Khoraha Rivers. Gangetic dolphins *Platanista gangetica* were occasionally observed in the Gerwa River near Manao. Goral *Nemorhaedus goral* were found along the northern border of the reserve on the steepest exposed ridges of the Churia range and near Chisapani at the base of the Karnali River Gorge (R. Whittaker, pers. comm.). In general goral inhabited the least accessible terrain available. This species may be more common farther up the Karnali River Gorge where steep slopes are more prevalent (C. MacDougal, pers. comm.).

Fig. 13. A jackal emerges from the forest edge after a monsoon storm, July 1976.

PLANT SUCCESSION, HABITAT UTILISATION, AND MANAGEMENT IMPLICATIONS

In the first paper of this series, various factors which altered the composition and distribution of the different habitat types encountered in Karnali-Bardia were discussed (Dinerstein, 1979). In addition, a model of successional change based upon the interactions of these variables with the vegetation was proposed. Now, with a study of habitat utilisation by the larger mammals of Karnali-Bardia, the relative proportion of preferred habitat to the total land area of the reserve takes on an increased significance (Table 7). Hog deer and Indian hare were most prevalent in flood plain habitat, the earliest successional stage identified. Blackbuck, a herbivore once common in Karnali-Bardia, and swamp deer preferred the savannahs and grasslands, habitats which characterise early to mid-successional stages of development. Chital and nilgai were found most frequently in middle successional habitat types. The sambar, along with langur and rhesus, favoured forested habitat, which categorises them as climax species. Wild boar and elephant appeared to utilise habitat types in all stages of successional development. The correspondence between habitat use by ungulates in Karnali-Bardia and the successional stage represented by each habitat type closely paralleled the findings of Eisenberg & Lockhart (1972) in Wilpattu National Park, Sri Lanka.

TABLE 7

THE RELATIONSHIP BETWEEN HABITAT PREFERENCE AND SUCCESSION, AND PERCENT AREA OF SUITABLE HABITAT FOR SOME OF THE LARGER MAMMALS OF THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL

Species	*Habitat type(s) preferred*	*Successional stage of habitat type(s) preferred*	*Percent of total area of the reserve in that stage of development*
Hog deer	Tall grass flood plain	Early	Less than 10
Indian hare	Tall grass flood plain	Early	Less than 10
Blackbuck[a]	Open grassland	Early-middle	10
Swamp deer	Open grassland	Early-middle	10
Chital	Savannah; riverine forest[b]	Middle	30
Nilgai	Savannah; riverine forest	Middle	30
Wild boar	Savannah; riverine forest, sal forest	Middle to late	90
Elephant	All utilised	Early to late	100
Barking deer	Riverine forest; sal forest	Middle to late	90
Langur monkey	Riverine forest; sal forest	Middle to late	90
Rhesus monkey	Riverine forest; sal forest	Middle to late	90
Goral	Steep hill sal forest; exposed ridges	Late	10
Sambar	Sal forest	Late	70

[a] Blackbuck became locally extinct about 1973 but still survive as a relict herd in a sanctuary 30 km from Karnali-Bardia.

[b] Riverine forest in this instance includes both the early riverine forest and the moist mixed riverine forest.

The management implications of the information in Table 7 are worth noting. Two of the three most abundant ungulates, chital and nilgai, preferred subclimax habitats which occupy less than 30% of the total reserve area. Hog deer, more than any other ungulate studied, are limited by the scarcity of their most preferred habitat type, tall grass flood plain. Clearly the distribution of the habitat types in Karnali-Bardia favour an ungulate such as the sambar which is adapted to a feeding niche in continuous climax forest.

In Dinerstein (1979) it was established that flooding, burning and forest clearing were the primary factors involved in creating and maintaining habitats determined to be in early and intermediate stages of successional development. Flooding, however, is an unpredictable factor, even though it may eventually become the most significant environmental variable in the Terai in the next few decades. Thus, at present, burning and patch cutting combined with water resource development remain the only viable alternatives in manipulating habitat conditions in Karnali-Bardia.

Since the trend of undisturbed plant communities is towards climax, and the greatest need is for subclimax, habitat improvement plans would allow for controlled burning. The burning of forest tracts and rangelands by the local aboriginal Tharu people has been an annual husbandry practice which dates back perhaps centuries. No records are available detailing the periods when burns took place, but from my talks with older residents of the area, fires appeared to be most prevalent between February and May, frequently occurring after the thatch grass harvest. Fires were lit without any effort to control them. However, controlled burning would help to regulate, for the benefit of wild herbivores, a phenomenon which has long been an important element in the Terai ecosystem.

Unless portions of grassland are burned, grazing conditions begin to deteriorate by February. Managers should attempt to create a mosaic pattern of new growth interspersed with tall grass cover. Repeated extensive burns in this habitat are known to favour the spread of *Imperata cylindrica* to the exclusion of other perennials. An effort must be made to determine and maintain diversity in the grassland composition through experiments with patch burning at widely spaced intervals, avoiding fires in short grass and sedge communities, and other considerations identified by a research programme.

The development of water holes would make a greater part of the total reserve area potentially usable by ungulates. This effort has already begun with the deepening of the existing water hole at Khodaha Tal. Other forest uses which should be integrated with a habitat management plan are grass harvesting and irrigation canal construction by local villagers.

Chital, nilgai, and barking deer all take advantage of edge forest when available; in the moist mixed riverine forest nearly half (47 %) of the total observations for the first two species were recorded at the interface with savannah/grassland vegetation. In fact, chital reach their highest densities in the reserve at the boundary between savannah and riverine forest habitat (Dinerstein, 1980).

The possibility of creating more edge and savannah habitat through timber management should be carefully examined. Small sections of sal forest along the Gerwa River could initially be cleared. Increased use by ungulates could be monitored by machan observations and pellet accumulation on permanently located plots.

With open grassland at a premium in Karnali-Bardia, the relocation of the two remaining villages inside the reserve (Chisapani and Amraini) would be a logical move, and should be expedited as soon as sufficient funds are available to remunerate farmers for the lands to be purchased. The cultivated fields in both areas would become valuable habitat amidst rather continuous sal forest.

The precarious position occupied by two locally threatened species, elephant and swamp deer, deserves particular attention. The small migratory elephant herd which occasionally frequents the reserve poses a difficult problem in conservation. Elephants can potentially cause heavy localised damage to the rice crop in the area. Traditional forest corridors utilised by elephant have been disrupted by clearing for cultivation and settlements. Given their low numbers, low reproductive rate, and depredating feeding habits, prospects for preserving this herd appear dim.

The low numbers of swamp deer represent another concern for wildlife officials; the Karnali-Bardia study area population appeared to decline from 15 individuals observed in 1976 to only 6 deer in 1977. Their seasonal movements and habitat preferences within the reserve still remain a mystery during eight months of the year. Since swamp deer are reported to be almost exclusively grazers, it would seem that forage conditions in the grasslands of Karnali-Bardia would not be limiting population size. Other factors, such as disease, might be responsible for the decline witnessed over the last few years. Swamp deer utilise wallows during the rutting season in Kanha and no known wallows existed in the study area in Karnali-Bardia. Whether or not streambeds serve as a suitable substitute is unknown. More intensive efforts must be made to locate these animals in the monsoon and cool seasons.

Taking into account the economic, political, and logistical problems inherent in creating and managing a wildlife reserve in South Asia, the Royal Karnali-Bardia Wildlife Reserve has achieved remarkable progress in the protection of its wildlife resources in only two years. Habitat management measures, such as controlled burns, have dramatically improved forage conditions in the savannahs, grasslands, and riverine forests at critical times of the year for wild ruminants. Ungulates have responded in kind by increased use of the most valuable habitat types within the reserve. Further development of managerial strategies must be based on an understanding of the functional relationships between habitat conditions, ungulate populations, and the dynamics of those populations. The third paper in this series will contribute toward this by offering population density and biomass estimates and examining the herd characteristics of the wild ungulates in Karnali-Bardia (Dinerstein, 1980).

ACKNOWLEDGEMENTS

I would like to thank the National Parks and Wildlife Conservation Office of His Majesty's Government of Nepal for the kind support they extended during the course of my study. Chief Wildlife Officer Shah, H. Mishra, P. B. S. Pradhan, and

S. Dhungel were most helpful in this regard. F. Poppleton, P. Wegge, E. Balson, and M. Bolton of the FAO Wildlife Project in Nepal offered assistance when possible. V. Miedema from Peace Corps/Nepal and the Smithonsian/Peace Corps Environmental Program provided moral and some financial support. In Karnali-Bardia I would personally like to thank Warden K. M. Shrestha and his staff for help with logistics and living arrangements. Game Scout G. Singh deserves special acknowledgement for his good humour, friendship, and tireless effort on behalf of the study. M. Gnawali was a gracious host and companion. The original manuscript was read by J. Eisenberg and S. Berwick. The final draft was criticised by R. D. Taber, W. Hatheway, and C. Driver. Finally I wish to thank Bharat Kholi for managing to cross the Babai River in the monsoon flood.

REFERENCES

Bauchop, T. & Martucci, R. W. (1968). Ruminant-like digestion of the langur monkey. *Science, N.Y.*, **161**, 698–9.

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. *Scient. Am.*, **225**, 86–93.

Berwick, S. H. (1974). *The community of wild ruminants in the Gir forest ecosystem, India.* Ph.D. dissertation, Yale University.

Dinerstein, E. (1979). An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal, Part I: Vegetation, modifying factors, and successional relationships. *Biol. Conserv.*, **15**, 127–50.

Dinerstein, E. (1980). An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal, Part III. *Biol. Conserv.*, **17**, in press.

Eisenberg, J. F. & Lockhart, M. (1972). An ecological reconaissance of Wilpattu National Park, Ceylon. *Smithson. Contr. Zool.*, **101**, 1–118.

Eisenberg, J. F., Santiapallai, C. & Lockhart, M. (1970). The censusing of animal populations by indirect methods. *Ceylon Journal of Science, Biological Science*, **8**, 53–62.

Eisenberg, J. F. & Seidensticker, J. (1976). Ungulates in Southern Asia: A consideration of biomass estimates for selected habitats. *Biol. Conserv.*, **10**, 293–308.

Feeny, P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, **51**, 566–81.

Freeland, W. & Janzen, D. H. (1974). Strategies in herbivory by mammals: The role of plant secondary compounds. *Am. Nat.*, **108**, 269–89.

Geist, V. (1974). On the relationships of social evolution and ecology in ungulates. *Am. Zool.*, **14**, 205–20.

Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, **48**, 215–67.

Krishnan, M. (1972). An ecological survey of the larger mammals of penninsular India. *J. Bombay nat. Hist. Soc.*, **69**, 469–501.

Laurie, A. & Seidensticker, J. (1976). Behavioural ecology of the sloth bear. *J. Zool., Lond.*, **182**, 187–204.

List, R. J. (1963). *Smithsonian meteorological tables.* Washington, DC, Smithsonian Institution.

Longhurst, W. H. *et al.* (1968). A basis for the palatability of deer forage plants. *N. Am. Wildl. Nat. Resour. Conf.*, 33rd, 181–92.

Martin, C. (1978). Status and ecology of the barasingha (*Cervus duvauceli branderi*) in Kanha National Park, India. *J. Bombay nat. Hist. Soc.*, **74**, 61–132.

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, 708–21. IUCN Publication, New Ser. No. 39.

Miller, D. R. (1974). Seasonal changes in the feeding behaviour of barren ground caribou on the taiga winter range. In *The behaviour of ungulates and its relation to management*, ed. by V. Geist and F. Walther, 744–55. IUCN Publication, New Ser. No. 41.

Prater, S. H. (1965). *The book of Indian animals*. Bombay, Bombay Natural Society and Prince of Wales Museum of Western India.

Schaller, G. B. (1967). *The deer and the tiger*. Chicago, University of Chicago Press.

Schmidt-Nielsen, K. *et al.* (1957). Body temperature of the camel and its relation to water economy. *Am. J. Physiol.*, **188**, 103–12.

Seidensticker, J. (1976). On the ecological separation between tigers and leopards. *Biotropica*. **8**, 225–34.

Sharatchandra, H. C. & Gadgil, M. (1975). A year of Bandipur. *J. Bombay nat. Hist. Soc.*, **72**, 623–47.

Singh, A. (1973). *Tiger haven*. London, Macmillan.

Spillett, J. J. (1967). A report on the wildlife surveys in northern India and southern Nepal. *J. Bombay nat. Hist. Soc.*, **63**, 492–628.

Talbot, L. M. & Talbot, M. (1963). The wildebeest in western Masailand. *Wildl. Monogr.*, No. 12.

Taylor, C. R. (1969). The eland and the oryx. *Scient. Am.*, **220**, 88–98.

Wharton, C. (1968). Man, fire and wild cattle in Southeast Asia. *Proc. Tall Timbers Fire Ecology Conf.*, **8**, 107–67.