

## Behavioural ecology of the Greater one-horned rhinoceros (*Rhinoceros unicornis*)

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(With 3 plates and 11 figures in the text)

In the Chitawan Valley of Nepal there were estimated to be between 270 and 310 Greater one-horned or Indian rhinoceroses (*Rhinoceros unicornis* L.). Population densities reached 4.85 rhinos/km<sup>2</sup> in the favoured areas of high diversity of early successional vegetation types on the valley floor. The overall population composition was 32.3% adult females, 19.9% adult males, 21.2% sub-adults and 26.6% calves. Females first calved at a mean age of 7.1 years and the median intercalving interval was 2.8 years. Causes of death included poaching, tiger predation on calves and fighting among males. The population was increasing.

Rhinos fed from 183 species of plants belonging to 57 botanical families but grass (50 species) made up between 70 and 89% of their diet according to the season. Considerable seasonal variations in food availability resulted in movements of rhinos between vegetation types. Rhinos' ranges were smallest in the areas of greatest vegetational diversity.

Rhinos rarely formed groups. The most common type consisted of sub-adults—mainly males. Ten auditory displays were distinguished and visual displays, although less striking, included baring the lower incisor tusks. Scents were carried in the dung, the urine and the pedal scent glands. Squirt urination and foot-dragging displays were performed by breeding males only.

There was some degree of range exclusivity among breeding males but no true territoriality. Poor visibility and the relatively unpredictable distribution of resources in time and space have perhaps selected against a territorial mating system. Relationships between ecology and social organization are discussed with reference to other rhino species.

Threats to the continued survival of the Indian rhino include poaching, agricultural encroachment and erosion. In order to spread the risk of a catastrophe, reintroductions of rhinos to other protected areas are proposed.

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### Introduction

The rhinoceroses (Perissodactyla: Rhinocerotidae) are of special interest in the study of the relative influences of phylogeny, ecology, morphology and nutritional energetics on ungulate social organization (Owen-Smith, 1975). The Greater one-horned or Indian rhinoceros (*Rhinoceros unicornis*) is the second largest of the five extant species and was once widespread on the Indian sub-continent. Now, as a result of habitat destruction and hunting for the much valued horn, there are fewer than 1500 individuals, restricted almost entirely to eight small protected areas in Assam, West Bengal and southern Nepal (Laurie, 1979).

Adult male Indian rhinos weigh up to 2100 kg and stand up to 186 cm at the shoulder. Adult females reach weights of about 1600 kg and heights of 160 cm. Both sexes have a single nasal horn, normally between 15 and 45 cm long. Lower incisor tusks are present in both sexes, reaching lengths of up to 20 cm in males, and the molars and premolars are hypsodont, or high crowned, with a complex enamel pattern. The prehensile upper lip is used to gather tall grasses and shrubs but the tip can be folded under and opposed against the lower lip for cropping short grasses. Two folds of skin encircle the body: one behind the forelegs and one in front of the hindlegs. There are deep skin folds around the neck, most marked in adult males, and the skin of the rump is also folded and studded with tubercles. There is a pedal scent gland on each foot with a distensible orifice just above the posterior margin of the sole pad (Cave, 1962).

There are many historical records, hunters' tales, anatomical treatises and accounts of the Indian rhino in captivity but this paper reports the first prolonged field study of the species. The main aim of the study was to collect information on numbers, distribution, population dynamics, diet, movements and behaviour which would be useful in making plans for conservation. The collected data allowed investigation of the relationships between ecology and social organization, consideration of the ways in which individual differences in behaviour might affect reproductive success and comparisons with the ecology and behaviour of other rhinoceros species.

### Study area

The Chitawan Valley of southern Nepal is a synclinal basin within the Siwalik Range, closed to the south by the Dauney, Someswar and Churia Hills and backed to the north by the Mahabharat Range. The study was carried out between December 1972 and June 1976 in the lower part of the valley, on the combined flood plain of the Rapti, Reu and Naryani Rivers and mainly within the 907 km<sup>2</sup> Royal Chitawan National Park (Figs 1 and 2). The main study area, at Sauraha, is shown in Fig. 3.

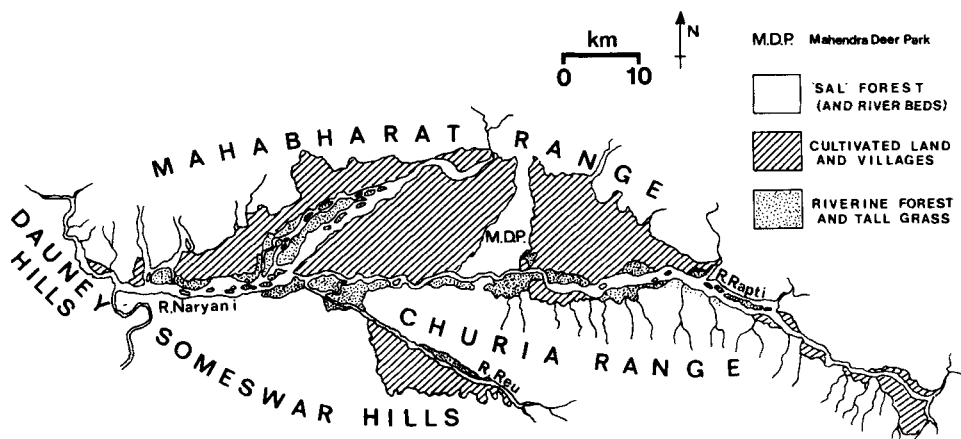


FIG. 1. A map of the Chitawan Valley, Nepal showing the distribution of the major vegetation types.

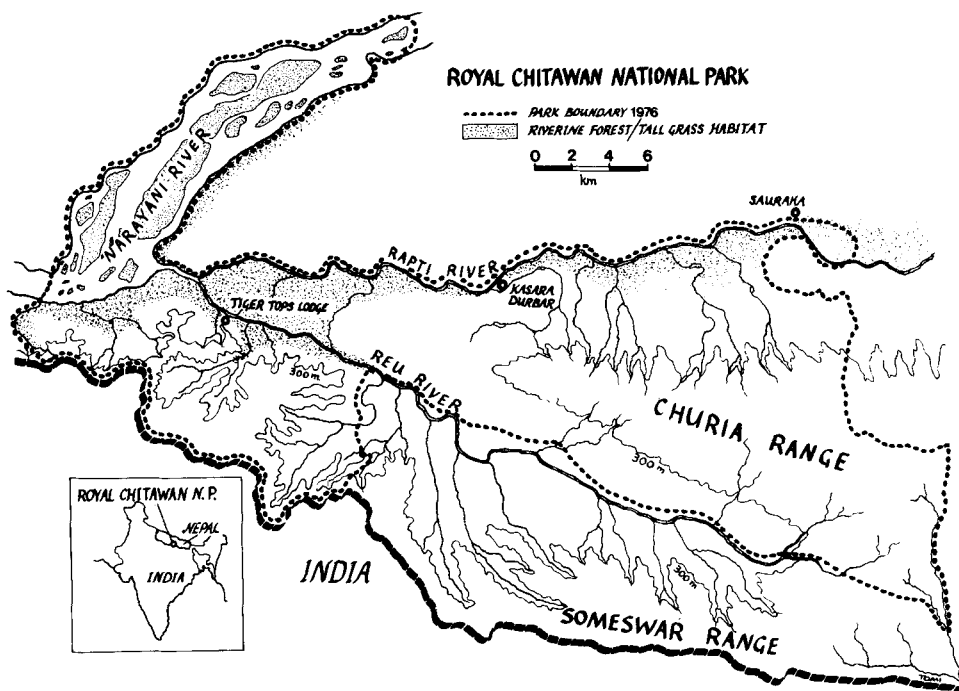


FIG. 2. Map of the Royal Chitawan National Park.

The altitude of the flood plain varies from 120 m to 200 m a.m.s.l. and the maximum height of the Churia Hills is 815 m. A resettlement and development programme in the 1950s destroyed large areas of forest and grassland in Chitawan, and most of the valley is now under cultivation. The hillsides are forested with deciduous or semideciduous trees, mainly sal (*Shorea robusta*), and the low lying areas along the rivers in the Park are a mosaic of riverine forest types and grasslands with grasses up to eight metres in height. Tree species

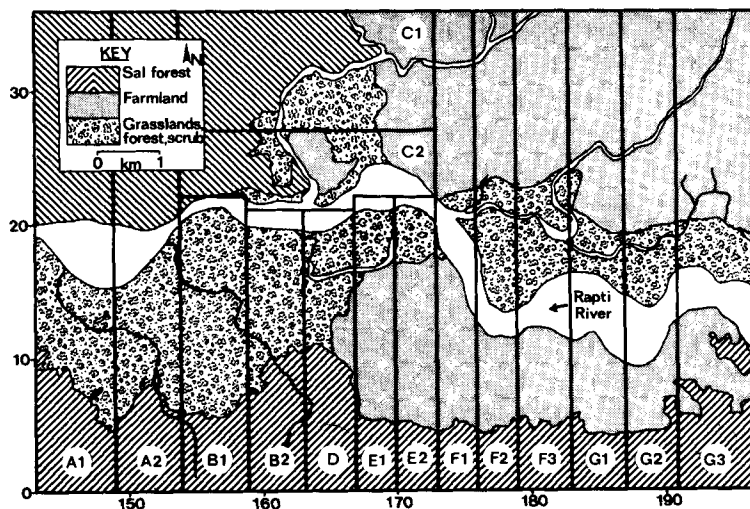


FIG. 3. A map of the Sauraha study area, showing the distribution of the major vegetation types and the arrangement of the seven blocks and 15 sub-blocks into which it was divided.

include *Bombax ceiba* and *Trewia nudiflora*, and the tall grass species include *Saccharum*, *Themeda* and *Narenga* species (see Plate I(a) & (b)).

The climate is monsoonal with a mean annual rainfall of 2400 mm, 90% of which falls between May and September. Temperatures reach a maximum of 38°C in May, becoming slightly lower, with a smaller daily range, during the monsoon and falling steadily until January when the minimum recorded was 6°C. Humidity is high all the year round; the relative humidity at dawn is frequently 100%, particularly during the monsoon and winter months.

There are rapid and very marked seasonal changes in weather and vegetation. Annual fires and floods and frequent changes in river courses combine to maintain a high diversity of early successional types of vegetation on the valley floor. The activities of man and his domestic stock increase the vegetational diversity at the Park boundaries.

In addition to the Indian rhinoceros the wild large mammal fauna of Chitawan includes Axis deer (*Axis axis*), Hog deer (*Axis porcinus*), Sambhar (*Cervus unicolor*), Muntjac (*Muntiacus muntjac*), Wild pig (*Sus scrofa*), Gaur (*Bos gaurus*), Tiger (*Panthera tigris*), Leopard (*Panthera pardus*), Sloth bear (*Melursus ursinus*) and Gangetic dolphin (*Platanista gangetica*).

For analysis of the data the year in Chitawan was divided into three seasons: monsoon (June–September), winter (October–January) and spring (February–May). The vegetation was classified into seven main types: sal forest, riverine forest, tall grassland, short grassland (including river banks), lakes, scrub and cultivated land.

## Methods

### General observation methods

The tall grasslands and dense woodlands of Chitawan made observations difficult, especially during the monsoon when much of the study area was flooded. Rhinoceroses were observed on foot, from

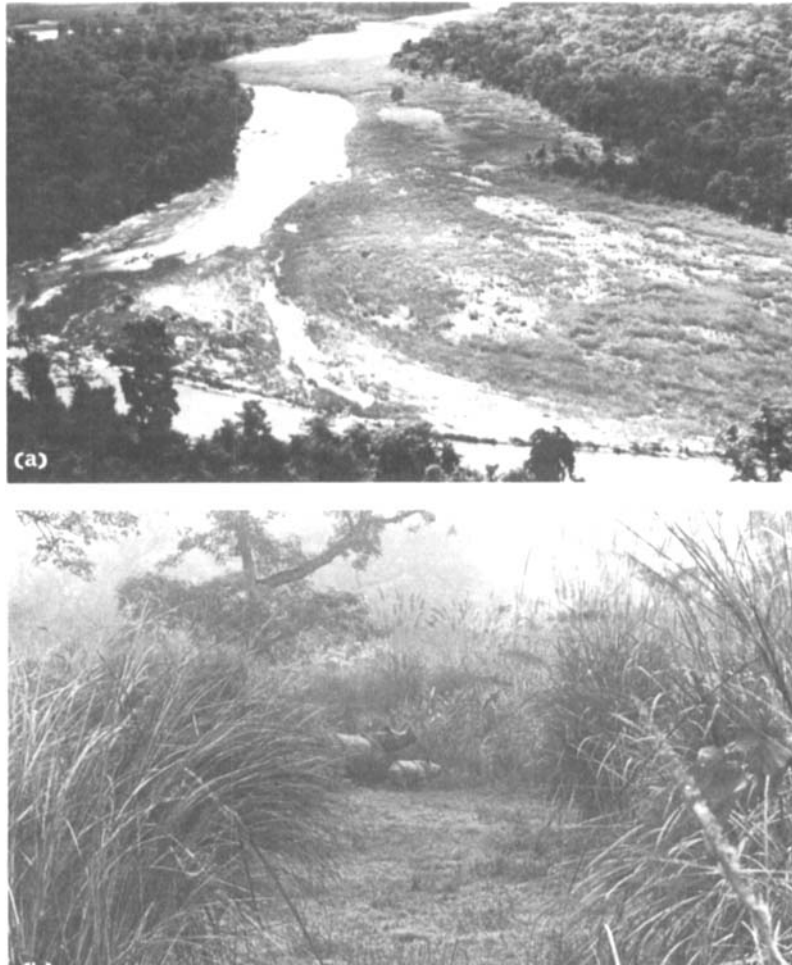


PLATE I. (a) An aerial view of a tributary of the Rapti at Sauraha. (b) A female Indian rhino with her calf in tall grassland, western Chitawan.

elephant back and from machans in trees or on the ground. The visibility of rhinos changed seasonally according to both the height of the grass and the frequency with which the rhinos wallowed in open water.

Observations were aided by  $9 \times 40$  binoculars and a  $22 \times 60$  telescope during the day and  $7 \times 50$  binoculars and a Rank SS20 image intensifier at night. Rhinos were seen on 6401 occasions and were watched for a total of 1182 h (3126 rhino h). They reacted to the presence of the observer on 38% of occasions, most frequently by running or walking away (80% of observations) but also by charging or advancing slowly towards the observer (10% of observations).

The duration of observations varied from brief glimpses of a few seconds to long periods of up to 33 h. Fifty-seven percent of observations were 10 min or shorter in duration because it was difficult to follow rhinos for long periods without being detected. Observations were of two general types: either a large area was covered and the numbers, locations, activities and identities of all rhinoceroses

encountered recorded; or selected individuals were followed for longer periods. Most adults and many immature animals could be distinguished individually using variations in horn sizes and shapes, skin folds and tubercles, scars, ear nicks and tail cuts. Sex determination was easy during long observations in the open but was often difficult during short observations in dense cover, especially with young animals. Rhinos were divided into seven age classes on the basis of their shoulder heights (estimated or photographically measured) and the development of their horns. Spatial locations were plotted on a 1 : 23,000 aerial photograph mosaic with accuracy usually within  $\pm 50$  m.

### *Study of food selection*

When it seemed likely that a feeding rhino could be kept under observation for 15 min or more, detailed records of the food available and the food eaten were kept by noting all plant types eaten during each minute and all plant types which had been within reach of the rhino during each minute.

Two indices, the utilization index ( $U$ ) and the preferability index ( $P$ ), were calculated as follows for each plant type:

$$U = (b/c) \times 100 \quad \text{and} \quad P = (b/a) \times 100$$

where,  $a$  is the number of minutes during which the plant type was available,  $b$  is the number of minutes during which it was eaten and,  $c$  is the total duration of the observation, in minutes.

## **Results**

### *Numbers, distribution and density*

The total rhinoceros population of the valley was estimated to be between 270 and 310 individuals. There were 226 individually identified rhinos within the study area in June 1975 and no individuals, apart from new born calves, were registered after that date. The rhinos' distribution coincides approximately with that of the grassland, riverine forest and scrub of the alluvial plains (Fig. 1). The sal forest supports a few animals in the vicinity of lakes and abandoned river beds.

Crude population densities varied from 0.38 to 1.79 rhinos/km<sup>2</sup>, and ecological densities (Eisenberg & Seidensticker, 1976) varied from 0.77 to 4.85 rhinos/km<sup>2</sup>. High population densities are associated with high diversity of vegetation types and ease of access to water and agricultural land.

### *Sex and age composition*

The overall composition of the registered population of 226 individuals was 73 (32.3%) adult females, 45 (19.9%) adult males, 48 (21.2%) sub-adults and 60 (26.6%) calves. The rates of sightings of rhinos of each sex and age class were approximately in the ratio of the proportions of each class in the registered population (Laurie, 1979). This indicates that there was no significant bias in frequency of sightings towards any particular sex or age class.

### *Births and mortality*

Births were recorded in each month of the year; there were slight but insignificant ( $\chi^2 = 6.67$ ,  $P > 0.05$ , d.f. = 5) peaks between November and February and in July and August. Females first gave birth aged between six and eight years, the average age being 7.1 years. The median of 50 inter-calving intervals was approximately 34 months and the

maximum was 50 months. Some adult cows were without calf during the whole study period: during the three years from December 1972 until November 1975, 42 cows produced 36 calves, two of which died shortly after birth. This is an overall birth rate of one calf per cow per 3.5 years or, adjusted for perinatal mortality, one calf per cow per 3.7 years.

Twenty-seven deaths were recorded during the study period; six of them due to poaching, which was confined almost entirely to the first year. Intraspecific fighting, particularly among males, accounted for six (almost 30%) of the deaths due to causes other than poaching. Three calves were recorded killed by tigers and other cases of tiger predation were suspected. Minimum annual mortality rates were estimated as 5.6% perinatal, 8.5% for calves, 1.2% for sub-adults and 3.4% for adults.

### *Feeding behaviour and ecology*

#### *Diet*

Parts of 183 species of plants from 57 botanical families were recorded eaten by rhinos. Tall grasses, mainly *Saccharum* species, were the most frequently recorded food type. Other food included short grasses, sedges, submerged and floating aquatic plants, herbs, creepers, ferns, shrubs and the leaves, twigs and fruits of trees and saplings. Quantitative conclusions about the composition of the rhinos' diet were complicated by the considerable seasonal and spatial differences in food availability and in visibility.

Vegetation transects repeated in each season in five vegetation types (Laurie, 1979) showed that the most marked seasonal changes were in the tall grassland where burning of the mature grasses in the spring was followed by the lush regrowth of young *Saccharum* and other tall grasses among the charred stems of grasses and shrubs. There was a marked increase in grass growth, mainly *Saccharum spontaneum* and *Cynodon dactylon*, in short grassland, river beds and scrub just before and during the early part of the monsoon, although these were often covered by flood water and silt later in the monsoon. Short grass, herbs, ferns, sedges and creepers increased in abundance in riverine forest during the monsoon, and the fallen fruits of *Trewia nudiflora* were abundant during June and July. In agricultural land maize plants were available from June to August, rice from August to December and wheat and mustard from December to March. Herbs and grasses flourished in the fields during the monsoon and rhinos often ate these to a greater extent than the planted crops. Aquatic plants were available year round but were often difficult for rhinos to reach during the monsoon.

Considering five vegetation types and four main categories of food, Table I shows the major components of the observed diet in each season for each vegetation type. There were significant differences in diet between all vegetation types and between all seasons within each vegetation type. There were also seasonal changes in diet within the food categories used in Table I; for instance, in the relative proportion of young to mature *Saccharum* grasses in the tall grassland.

The data on first feeding observations were weighted according to differences in the extent of each vegetation type and the mean rates of sightings of feeding rhinos in each vegetation type and season. Part of the considerable seasonal differences in the rates of sightings of feeding rhinos can be attributed to seasonal changes in visibility. In general, visibility of feeding rhinos was highest from January to May when the grass was burned, and was low from June to December as the vegetation grew up after the dry season. To correct for seasonal changes in visibility the mean rates of sightings of feeding rhinos in each season

TABLE I

*Seasonal differences in the distribution of first feeding observations\* in five vegetation types*

	Spring	Monsoon	Winter
Tall grassland <i>n</i> = 1329	Tall grass 96%	Tall grass 70%	Tall grass 65%
Short grassland <i>n</i> = 784	Short grass 57%	Short grass 70%	Short grass 60%
Permanent Lakes <i>n</i> = 321	Aquatic plants 67%	Aquatic plants 70%	Aquatic plants 84%
Riverine Forest <i>n</i> = 265	Tall grass 64%	Browse 49%	Browse 54%
Scrub <i>n</i> = 175	Browse 74%	Short grass 67%	Browse 47%

\*To avoid bias towards greater observed dietary diversity in seasons or vegetation types of better visibility, only the first food item to be eaten during each observation is included in this analysis. Only food types comprising more than 30% of the observations in any one season and vegetation type are shown in the table. Overall  $\chi^2 = 317.2$ ,  $P < 0.001$ .

were expressed as a percentage of the total of the rates in each vegetation type. Table II shows the calculated overall composition of the rhinos' diet in each season, considering six food types and disregarding sal forest and cultivated land, where there were too few observations.

More detailed analysis of the rhinos' diet and food preferences was attained by using data collected during close observation of food selection by the method described above. In general a wide variety of food types was eaten but the bulk of the diet consisted of relatively few types. Rhinos ate 83 (64.3%) of the available plant types, but only 24 types (18.6%) were eaten during 10% or more of the minutes of observation in any one vegetation type or season. Very few of the abundant plant species were completely avoided in all habitats and seasons (20 of the common sal forest species but only three: *Calotropis gigantea*, *Clerodendron viscosum* and the foliage of *Trewia nudiflora*, of the common species from other vegetation types).

TABLE II

*Estimated percentage composition of the rhinos' diet in each season*

	Spring	Monsoon	Winter
Grass			
Mature tall grass	14.5	29.4	35.3
Young tall grass	58.4	7.0	0
Short grass, herbs, sedges	13.5	52.3	35.1
Browse			
Leaves, shrubs, saplings	8.4	2.5	21.6
Fruits	0	3.1	0
Aquatic plants			
Floating and submerged	5.2	5.7	8.0



A rhino might be expected to feed best in an area where its most highly preferred food types are most abundant, i.e. where there is a high correlation between the utilization ( $U$ ) and preferability ( $P$ ) indices of the available food types. Table III shows rank correlation coefficients of these two indices for each vegetation type and season of all food types eaten during more than 2% of the minutes of observation. It shows that tall grassland is the most suitable type of feeding ground in the spring; short grassland during the monsoon; and scrub and short grassland during the winter. Young shoots of the tall grasses made up the bulk of the diet in tall grassland in spring and they were also the most preferred food items. During the monsoon, however, short grasses such as *Cynodon dactylon* and the tall grass *Saccharum spontaneum* were eaten most but the most highly preferred food types were the grass *Vetiveria zizanioides* and aquatic plants such as *Hydrilla verticillata* and *Ceratophyllum demersum*, which made up only a small proportion of the diet. For tall grassland there is a significant positive correlation between  $U$  and  $P$  in spring and a significant negative correlation in the monsoon.

TABLE III

*The relationship between the utilization and the preferability of food types according to habitat and season*

Season	Spring (FMAM)			Monsoon (JJAS)			Winter (ONDJ)		
	$r_s$	$n$	$P$	$r_s$	$n$	$P$	$r_s$	$n$	$P$
Habitat									
Tall grassland	+0.83	10	<0.01	-0.63	9	<0.05	+0.57	8	n.s.
Short grassland	-0.10	5	n.s.	+0.96	7	<0.01	+0.72	9	<0.05
Lakes	-0.54	6	n.s.	+0.13	7	n.s.	+0.80	4	n.s.
Riverine forest	+0.42	14	n.s.	+0.29	8	n.s.	+0.55	11	<0.05
Scrub	+0.83	6	<0.01	+0.44	13	n.s.	+0.82	7	<0.05

Spearman rank correlation coefficient,  $r_s$ .

The number of food types eaten during more than 2% of the minutes of time sampling observations,  $n$ .

Not significant at the 0.05 level, n.s.

### *Drinking and mineral licks*

Rhinos drank daily from streams, rivers, ox-bow lakes, small puddles and wallows, some of them heavily contaminated with urine. Four sites were found where rhinos and other ungulates regularly licked or ate soil or rock material. The one most frequently used by rhinos is a cliff of micaceous sandstone visited between November and May. Sodium, potassium, calcium and magnesium were present there in particularly high concentrations.

### *Wallowing*

Rhinos wallowed in ox-bow lakes, rivers and temporary pools, doing so most frequently between June and October (51% of all observations) and least frequently between December and March (4% of all observations). The frequency of wallowing was lower on cool, overcast days during the monsoon and immediately after a long period of rain but rain itself did not result in an immediate reduction in wallowing.

*Groupings*

Rhinos which moved together were considered members of a group. Cow-calf pairs were the commonest type of group, and there were only 946 (14.8%) sightings of rhinos in other types of group. Only seven groups consisted of more than three individuals. Figure 4 shows the types of associations formed, based on 293 observations of groups in which at least two members were classified, and considering cow-calf pairs as single units: 89.9% of the associations involved sub-adults; cow-calf pairs never formed groups with other cow-calf pairs, and single adults rarely associated with other adults of their own sex. Table IV gives the composition of the 174 groups in which all members were classified: 86 (49%) were of sub-adults only (15 of females only, 41 of males only and 30 of mixed sex), and 64 (37%) were of sub-adults and adults.

Temporary associations were formed at wallows and grazing grounds when animals rested or fed close to each other but moved independently. Sub-adults formed temporary associations significantly more frequently (35.5% of observations) than adults (20.6% of

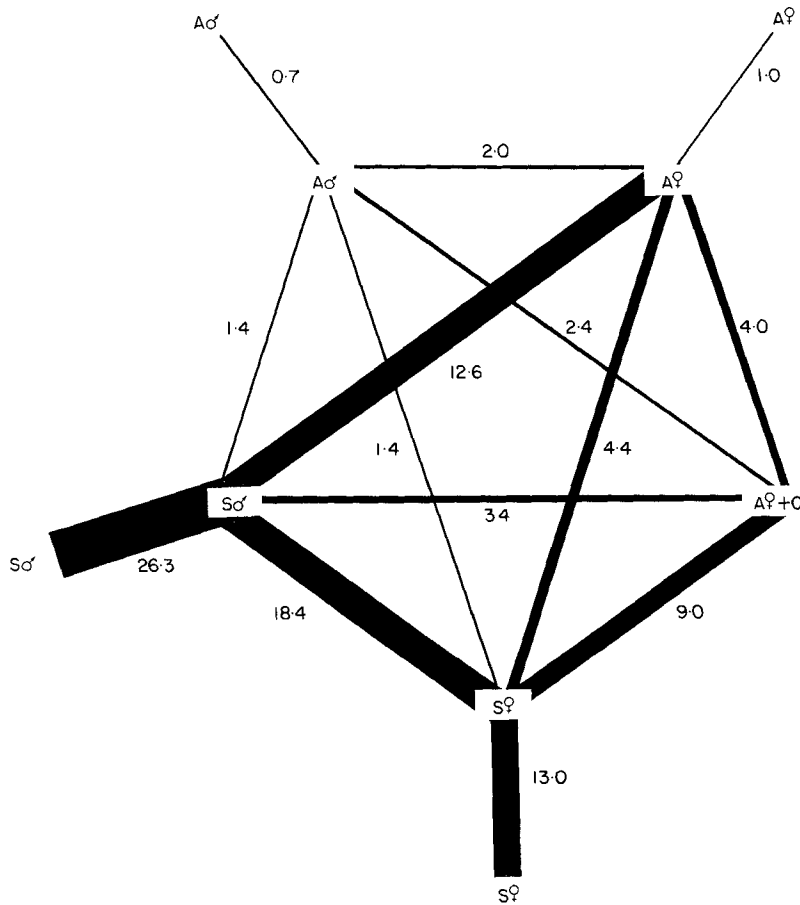


FIG. 4. Grouping tendencies for each sex and age class. The figures and the width of the lines joining each pair of classes indicate percentages of all associations in groups.

TABLE IV  
Composition of rhino groups

Companions	None	Number of observations		Cow-calf pair
		Adult male	Adult female	
Class or unit				
Adult male	(809)	2		
Adult female	(252)	6	3	
Cow-calf pair	(1507)	7	6	0
Sub-adult male	(320)	3	28	5
Sub-adult female	(321)	4	5	13
Sub-adult group	86	1	5	

observations) ( $\chi^2 = 62.6$ ,  $P < 0.001$ ). For analysis of social interactions the proportion of the total observation time for each sex and age class spent within 20 m of each other was calculated.

### Communication

#### Auditory signals

Ten types of sounds were distinguished. Table V summarizes the contexts in which nine vocalizations were heard. The tenth, the *humph*—a wheezing, thoracic-oral aspiratory sound uttered in time with the rhino's pace, was heard only from rhinos fleeing the observer.

TABLE V  
The contexts in which each of nine types of sounds were heard from undisturbed rhinos

Context	Number of series*												Total
	(i)	(ii)	(iii)	(iv)	(v)	(vi)	(vii)	(viii)	(ix)	(x)	(xi)	(xii)	
Type of sound:													
snort	273	58	73	55	6	18	—	—	—	13	35	57	588
honk	58	15	19	10	107	—	51	81	21	—	4	144	510
bleat	—	—	—	—	75	—	—	52	—	—	—	4	131
roar	—	—	—	—	47	—	—	34	—	—	—	20	101
squeak-pant	4	—	—	—	—	—	—	101	2	3	6	23	139
moo-grunt	—	—	18	—	2	—	—	1	5	173	13	—	212
shriek	—	—	—	—	1	—	—	4	—	—	—	7	12
groan	—	—	—	—	15	—	—	—	—	—	—	—	15
rumble	3	—	1	—	—	6	—	—	—	—	12	—	22

\*A series of sounds of the same type were treated as a single unit if they were separated by less than two minutes and directed at the same individual under the same circumstances.

Key to contexts: (i) on the approach of another rhino; (ii) on approaching another rhino; (iii) at another rhino which was nearby; (iv) in response to an initial honk or snort from another rhino in contexts (i) to (iii); (v) during face to face agonistic interactions, including courtship fights; (vi) just after a brief agonistic interaction; (vii) during flight from another rhino after a brief interaction; (viii) during prolonged chases (including courtship chases); (ix) during playful sparring; (x) as a contact call between cow and calf; (xi) while walking, grazing or wallowing, but not directed at a particular individual; (xii) unknown + others (often because insufficiently close observation).

TABLE VI  
*Actor recipient matrix for vocalizations*

	Snort	Honk	Bleat	Roar	Squeak-pant	Moo-grunt
Adult male						
Actor	44.2	39.5	10.5	5.8	50.0	0
Recipient	103.5	98.8	46.5	20.9	17.4	7.0
Adult female						
Actor	81.6	44.8	18.8	15.2	3.2	2.2
Recipient	76.2	36.1	11.6	9.4	7.6	60.6
Sub-adult						
Actor	35.3	32.5	4.7	2.8	0.9	6.6
Recipient	33.4	28.1	1.6	2.2	4.7	5.4
Calf						
Actor	34.5	12.3	1.3	0.5	0	76.8
Recipient	20.9	6.4	0.5	2.7	1.8	3.6

Figures are rates of vocalization per 100 h of observation of each sex and age class in association with other rhinos. Rates for adult females and calves refer to associations other than between mothers and their own calves.

Table VI gives the rates of vocalizations uttered and received per 100 h of observation for each sex and age class in association with each other.

*The snort* is produced by expulsion of air in a series of quick bursts through the lips and nostrils. It is used mainly as an initial contact call on meeting another rhino. Adult females snorted at the highest rate and all classes directed snorts most frequently at adult males.

*The honk* is a loud, low-pitched guttural vocalization of metallic, echoing nature emitted as a single burst or in a succession of short bursts. It was heard most frequently during prolonged agonistic interactions. Its distribution among sex and age classes was similar to that of the snort but, despite being one of the loudest vocalizations and audible from a great distance, the honk was heard less frequently.

*The bleat* is a loud, blaring single tone vocalization typically uttered with head held low, mouth open, tusks bared and ear pinnae held back. Bleating occurred during agonistic interactions and was normally associated with submission or flight during prolonged chases. It was used predominantly by adult females and sub-adults (mainly females) during interactions with adult males but also by adult females and adult males among themselves.

*The roar* was confined almost entirely to face to face agonistic interactions or prolonged chases and was directed predominantly by adult females at adult males and adult females.

*The squeak-pant* is a very variable sound, half aspiratory and half vocal which consists in its full form of a shrill squeak followed by a sharp exhalation of breath somewhere between a honk and a snort. It was heard most frequently from males during prolonged chases; usually from the pursuer only.

*The moo-grunt* or *gronk* is a short grunt made deep inside the throat with the mouth either open or shut. It has a curious ventriloquistic property to human ears and yet seemed to be used mainly by calves as a contact call with their mothers, often prior to suckling.

The almost self descriptive *shriek*, *groan* and *rumble* were recorded only rarely (Table V).

Rhinos showed interest in all rhino sounds, including tape recordings played back to them. Most reacted with brief glances in the direction of origin of the sounds or moved off quickly.

Some adult males, however, and occasionally sub-adult and adult females, showed particular interest in sounds of fighting and moved off in the direction of their origin.

### *Olfactory signals*

Rhinos often paused to sniff the ground and showed particular interest in the sites of urination and defecation of other rhinos. They followed each other by scent and it is likely that olfactory signals include odours left by the pedal scent glands, in addition to those of urine and dung. There are special actions associated with urination and defecation, particularly in adult males, apparently related to the leaving of persistent scent marks in the environment.

*Urination.* Rhinos urinated in two distinct ways: either in a continuous stream falling to the ground less than half a metre behind them or in a series of jets squirted up to three or four metres behind them. Females squirted their urine only during oestrus but some adult males always urinated in this way (Plate II(a)), spraying urine onto the surrounding vegetation and often dragging their hind toes in the earth and rubbing head and horn in low vegetation at the same time. Adult males performing this type of display left a trail of broken vegetation and furrows in the ground with urine covering the vegetation and upturned earth. Such displays were performed in response to the sight or scent of other rhinos on crossing a line feature or in response to disturbance by the observer.

*Defecation.* Rhinos tended to defecate near other rhino dung: only 13% of 1080 freshly deposited faeces were more than 10 m from visible dung, and during normal activities rhinos defecated on dung piles on 88% of occasions. Rhinos occasionally mouthed or ate dung ( $n = 6$ ), or scraped backwards with one or both hindfeet, spreading earth onto the freshly deposited dung ( $n = 14$ ). The proportion of defecations on dung piles was higher for adult males (21/27 or 78%) than for other social classes (59/97 or 61%) [ $\chi^2 = 14.9$ ,  $P < 0.01$ ]. Dung piles were often found at the borders of forest and grassland, on the banks of rivers or wallows and on paths or manmade roads and ditches. Dung piles were used by all social classes and frequency of use varied directly according to the number of rhinos using the area. Established dung piles were more likely to be added to than single defecations, and the latter only developed into piles if on a well frequented route.

*Reactions to scents.* Perfunctory sniffing of the air, ground or vegetation was so frequent that each occurrence was not recorded. Of 103 prolonged reactions to scents 20 were to rhino dung, 35 to rhino urine or tracks and eight to human scents. Adult males accounted for 34% of the 103 observations. On 62 (60%) of occasions a rhino sniffed intently, raised its nose, curled back its lips and held this posture for a few seconds (Plate II(b)). This action corresponds to the *flehmen* response described by Estes (1972) for a wide variety of mammals. Adult males (5.0 occurrences per 100 h of observation) and sub-adults (3.4/100 h) performed *flehmen* significantly more frequently than cows and calves (1.1/100 h), and adult males reacted predominantly to female tracks or urine, whereas other sex and age classes reacted most often to adult male tracks and urine.

### *Visual and tactile signals*

Although 20 types of movements or gestures which seemed of potential communicatory significance were distinguished, they are described below under *Interactions* because some are better considered as directly functional actions than as ritualized displays. They were

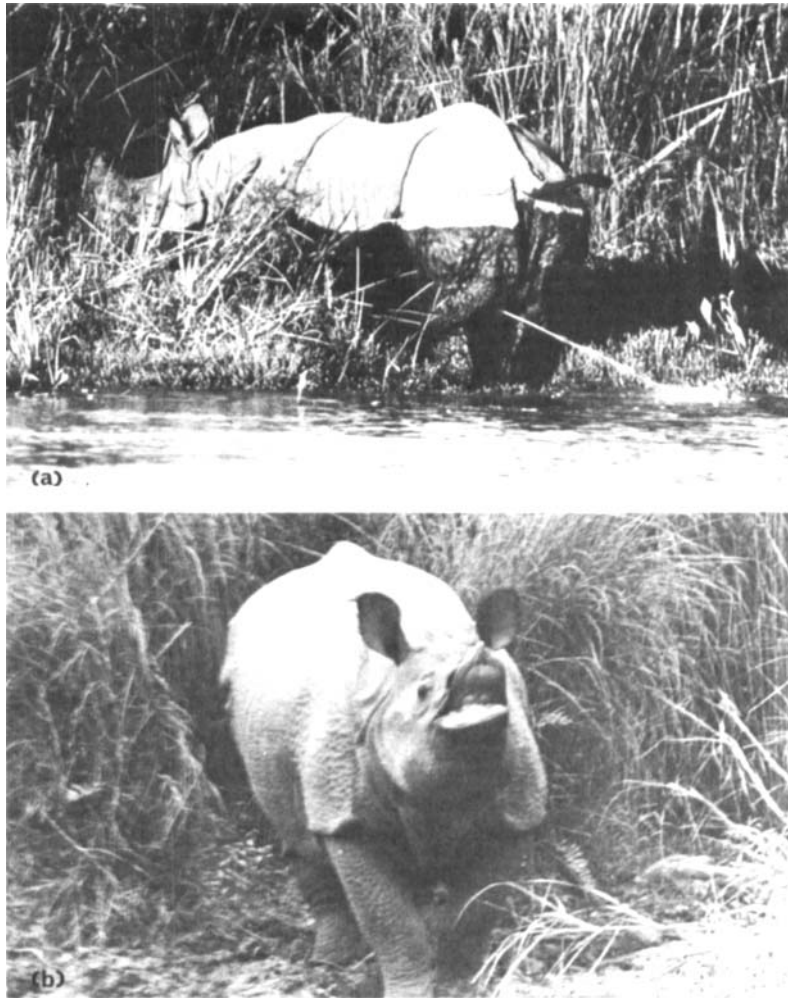


PLATE II. (a) An adult male squirt urinating. (b) A sub-adult female performing *flehmen*.

frequently accompanied by vocalizations. The main visual signals involved the posture of the head (whether it was held high or low and whether the animal faced another) and the display of the tusks in the lower jaw by curling back the lips.

#### *Ranging behaviour*

##### *Ranges*

Rhinos live in a long narrow strip of suitable habitat stretching east–west along the Rapti River. Sightings of individual rhinos were generally restricted to relatively small parts of the study area. Figures 5 and 6 compare the distributions of sightings on the E–W and N–S axes of the 37 most frequently seen individuals ( $n \geq 20$  sightings; maximum = 211) with the distributions of total or total regional sightings. Thirty-six individuals differed significantly

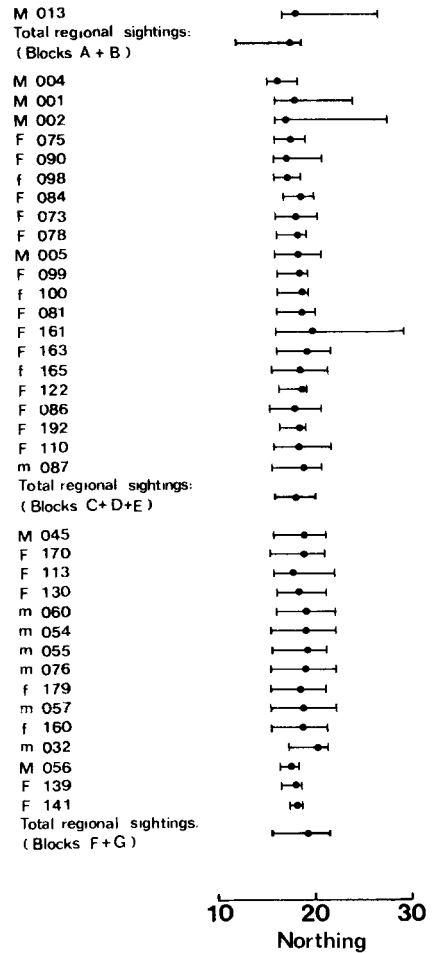
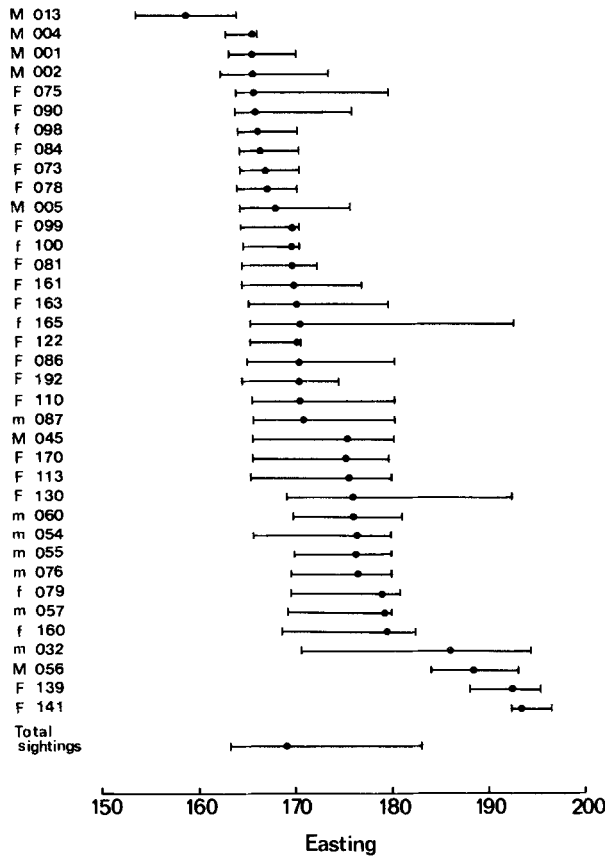


FIG. 5 (left). Medians and 90% ranges on the E-W axis. The 90% range includes 90% of all locations, with equal numbers on each side of the median location.

FIG. 6 (right). Medians and 90% ranges on the N-S axis.

in the distributions of sightings on the E-W axis but only nine differed significantly on the N-S axis (Kolmogorov-Smirnov one sample tests  $P < 0.01$ ). The study area can be considered as a series of overlapping ranges aligned east-west along the river with relatively few differences in north-south movement patterns.

Individual rhinos' ranges differed in size and location and were not exclusive. For comparison, the rectangles formed by the 90% ranges (Fig. 5) on each axis were called core ranges. These are smaller than the areas actually used by rhinos and they varied in size from 0.44 to 8.86 km<sup>2</sup>. Table VII shows that mean core range size increased, from block D to block F, with decreasing diversity of vegetation types.

Principal component analysis (Gower, 1966) was used to calculate a correlation matrix for the numbers of sightings of the 37 individuals distributed over the 15 sub-blocks of the study

TABLE VII  
Core range areas in relation to location

Block	Number of rhinos with median easting in the block	Mean core range area (km <sup>2</sup> )
D	9	2.15
E	12	3.51
F	11	4.26

Kruskal-Wallis one-way analysis of variance:  $P < 0.05$ ,  $F > D$ , Mann-Whitney  $U$  test:  $P < 0.01$ .

area. The first two principal components accounted for 64% of the variance, and the analysis indicated that the ranges of 57 of the 58 most frequently sighted individuals ( $n \geq 10$ ) could be divided into eight fairly discrete categories of size, location and pattern of use (Fig. 7).

### Seasonal movements

There were clear seasonal differences in the rates of sightings of rhinos in each block: during the spring the highest rates were in the tall grass of blocks D and E; during the monsoon and winter rates were highest in blocks F and G. However, seasonal changes in visibility affected the frequency of rhino sightings, so to avoid this bias seasonal differences in the rates of sightings of individuals in each block were considered. Figure 8 shows data for an adult female (F110) which was seen significantly less frequently than expected in the western blocks during the winter and more frequently than expected in the eastern blocks during the monsoon. Table VIII summarizes similar data for the 15 rhinos with sufficient sightings to test for significance in both the western and eastern parts of the study area. During the spring 14 rhinos (93%) were seen more frequently than expected in the west and 11 (73%) were seen

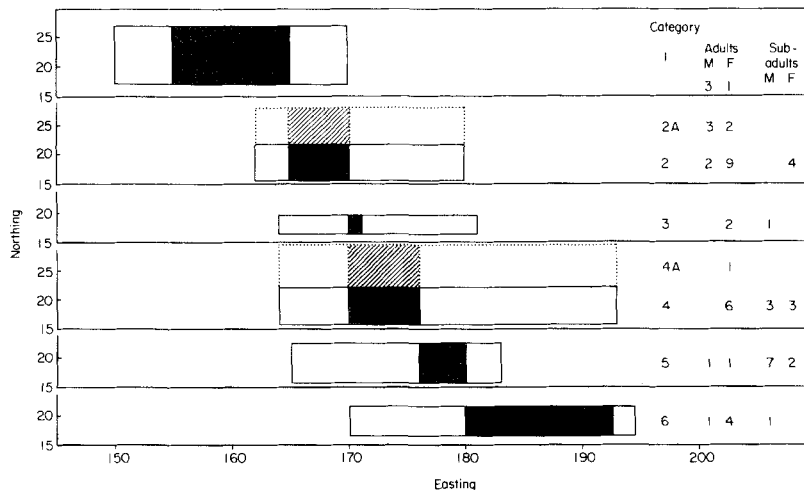


FIG. 7. Eight categories of rhino ranges: the rectangles enclose all the core ranges and the shaded portions all the median locations.



TABLE VIII

*The numbers of individuals seen significantly more and less frequently than expected from the number of visits in each season in the west and east of the study area*

Seasons	West Blocks A-E or A-D			East Blocks E-G or F-G		
	Spring	Monsoon	Winter	Spring	Monsoon	Winter
Frequency of sightings:						
> expected	14	0	0	0	12	1
no significant difference from expected	1	11	2	4	3	9
< expected	0	4	13	11	0	5

The study area was divided into two at the block boundary nearest to median location of the individual on the E-W axis: the D/E boundary for 10 rhinos and the E/F for five.

less frequently than expected in the east. There were similar but less marked differences in the other seasons which indicated a general trend for rhinos to move from blocks F and G into blocks D and E during the spring and out again to blocks F and G during the monsoon. The degree of movement varied between individuals, with some coming in from considerable distances and others staying in the central or outer blocks year round.

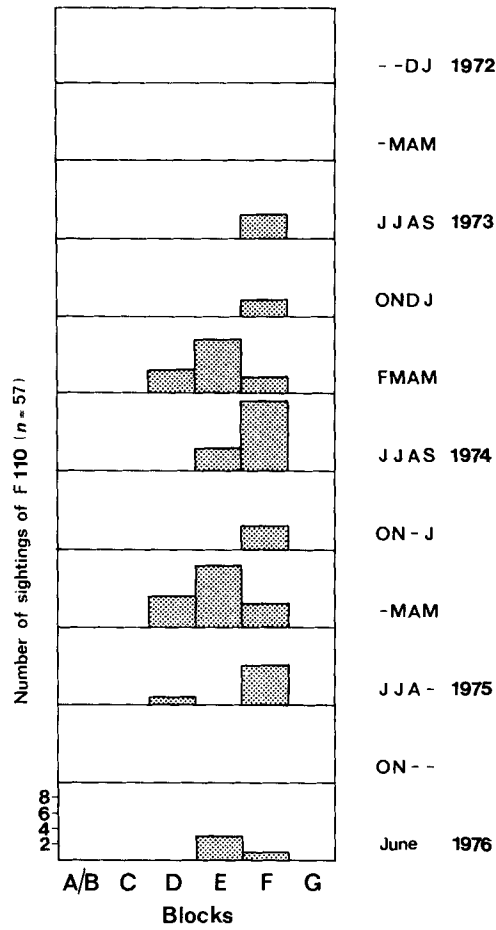
#### *Range changes*

Rank correlation coefficients were calculated for each pair of years of the study period, of the rates of sightings of each individual in each block of its range. For example, adult female F073 (Fig. 9) had  $r_s$  values of +0.918 (1973 with 1974), +0.783 (1973 with 1975) and +0.718 (1974 with 1975) and a relatively consistent pattern of range use from year to year. Table IX summarizes the data and divides the 37 most frequently sighted individuals, according to sex and age class, into those with consistent and inconsistent patterns of range use. Adult males were significantly more likely to change their ranges than adult females: 71% (five) of the seven males were in the inconsistent class as opposed to 28% (five) of the 18 females (Fisher exact probability test  $P = 0.007$ ).

#### *Interactions*

##### *Prolonged physical contact (n = 366)*

Two rhinos, normally members of the same group, often lay together with their flanks touching or rested their heads on each others flanks. Slight disturbance such as the approach of other rhinos caused calves to move into physical contact with their mothers ( $n = 20$ ). Prolonged licking of a companion's skin ( $n = 40$ ), mostly by sub-adults and calves but also by cows, typically occurred in wallows, with one rhino lying down and the other standing over it and licking for periods of up to 10 min at exactly the same spot on the skin. Other types of prolonged physical contact included mounting ( $n = 18$ ) and nose to nose nuzzling ( $n = 58$ ). Cows with calves spent 10.6% of their time in physical contact with their calves. The frequency of physical contact among other sex and age classes was highest in sub-adults (56.6 h or 8.4% of observation time) and lowest in adult males (5.3 h or 1.3%).



	Blocks A-E				Blocks F-G			
	Spring	Monsoon	Winter	Total	Spring	Monsoon	Winter	Total
Visits seen	22 (13.0)	7 (9.2)	0 (6.8)	29	5 (10.9)	18 (8.5)	5 (8.6)	28
Visits not seen	207	154	119	480	162	112	127	401
Total visits	229	161	119	509	167	130	132	429

$\chi^2 = 14.8, P < 0.001, \text{d.f.} = 2$

$\chi^2 = 16.39, P < 0.001, \text{d.f.} = 2$

The figures in brackets are the expected numbers of sightings on the null hypothesis that F110 did not show seasonal changes in range use.

FIG. 8. Seasonal variation in the locations of sightings of adult female F110.

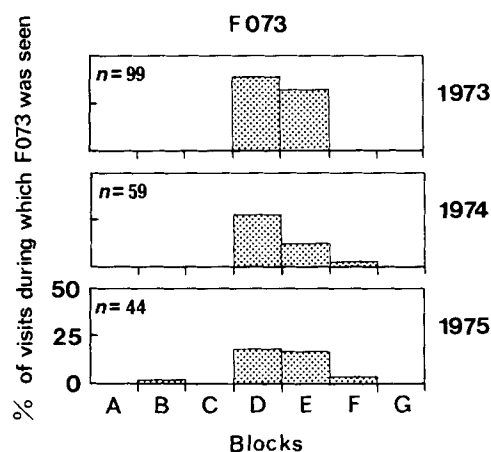


FIG. 9. The annual rates of sightings of adult female F073 in each block.

TABLE IX

*The consistency of range use classified according to the rhinos' sex and age classes*

	Adults		Sub-adults		Total
	Male	Female	Male	Female	
Consistent pattern of range use.					
All $r_s \geq +0.500$	1	3	11	2	17
Seen in two blocks or fewer	$\frac{1}{2}$	$\frac{2}{5}$	$\frac{2}{13}$	$\frac{1}{3}$	$\frac{6}{23}$
Inconsistent pattern of range use.					
All $r_s$ positive but one or more $r_s < +0.500$	1	0	1	0	2
One or more $r_s \leq 0.000$	$\frac{4}{5}$	$\frac{2}{2}$	$\frac{4}{5}$	$\frac{2}{2}$	$\frac{12}{14}$
Total	7	7	18	5	37

Spearman rank correlation coefficient ( $r_s$ ) for each pair of years of the study period, of the rates of sightings in each block.

#### *Peaceful interactions (n = 105)*

Play and peaceful behaviour between sub-adults and between cows and calves normally took place after the individuals had been wallowing together. Periods of nuzzling were frequently interspersed with spells of running and gambolling around a companion ( $n = 21$ ), and calves occasionally picked up sticks in their mouths and shook their heads like young puppies ( $n = 4$ ). Such behaviour between sub-adults and cows or sub-adults and calves normally followed immediately after meeting. A slow approach ( $n = 114$ ) was usual and one individual often bobbed its head or waved it rapidly from side to side ( $n = 23$ ) while walking or grazing towards the other rhino. The approached rhino usually stretched its nose forward and nuzzled the newcomer. Sub-adults and calves frequently extended the playful behaviour into sparring contests; facing each other with their horns touching and delivering mild blows

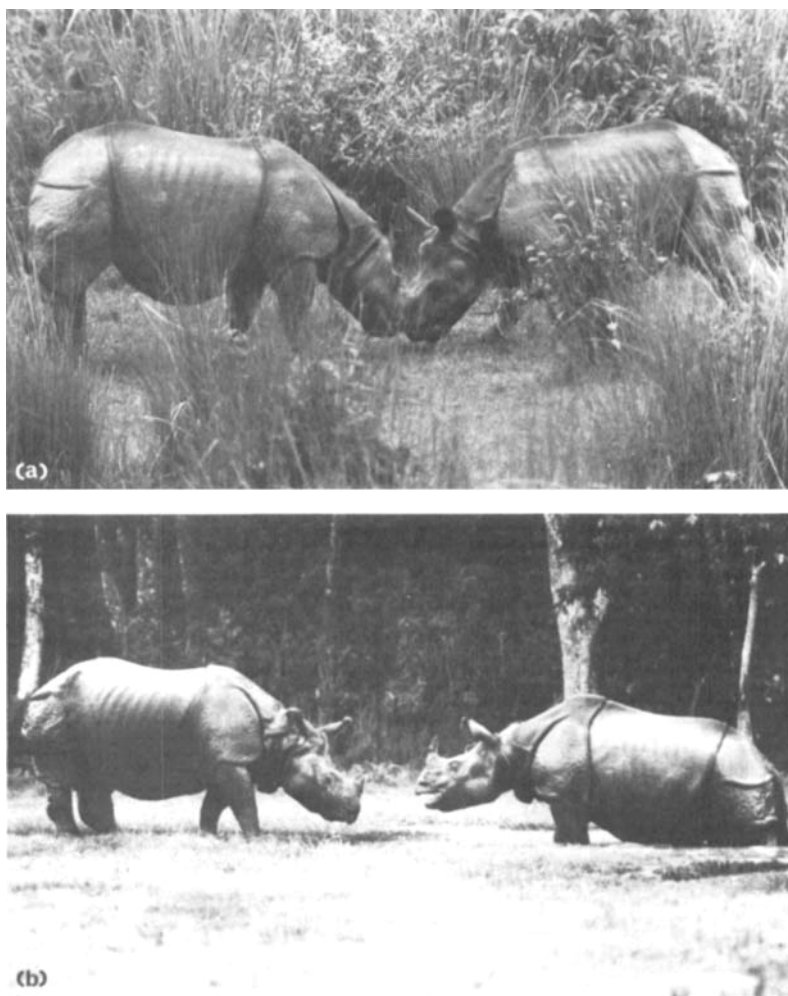


PLATE III. (a) Two sub-adult males sparring. (b) An agonistic interaction between two adult females at a wallow.

with the horn and side of the head to their opponent's head while parrying their opponent's blows (Plate III(a)). Of the 91 sparring contests observed, 79 involved sub-adults (Table X).

*Agonistic interactions (n = 417)*

When rhinos of different groups met there were frequently brief agonistic interactions. Eighty-five (22%) of 384 fully observed interactions ended in the immediate panicky flight of one or more of the rhinos. More frequently a rhino turned to face an intruder and stood still, watching its movements. One hundred and fifty-eight (41%) of the interactions ended after initial displays which included:

*Lip curl (n = 304)*: snorting or honking with head held high and lips curled back to show the lower tusks.

*Advancing steps* ( $n = 241$ ): walking forward quickly with head held low and accompanied by snorts or honks.

*Charge* ( $n = 92$ ): trotting silently forward with lowered head.

One hundred and forty-one (37%) of the interactions progressed to some kind of horn to horn confrontation such as:

*Horn to horn stare* ( $n = 141$ ): standing with horns touching at ground level.

*Tusk display* ( $n = 145$ ): honking and bleating with head lowered, mouth wide open and tusks bared (Plate III(b)).

*Horn clash and lunge* ( $n = 99$ ): delivering blows with the horn and tusks to the head and body of the opponent. Lunges, accompanied by short forward rushes and loud roars, were aimed mainly at the head region but, if the opponent turned, blows were delivered to the neck, flanks and rump and a prolonged chase sometimes developed ( $n = 31$ ) during which serious injuries were inflicted. These chases lasted up to several kilometres and were accompanied by loud squeak pants, honks and bleats.

The most prolonged interactions were between adult males and between adult males and adult females. Immediate flight was significantly more frequent among sub-adults and calves ( $n = 65$  or 25% of interactions) than among adults ( $n = 20$  or 4%) [ $\chi^2 = 76.3$ ,  $P < 0.001$ ]. Adult males chased more often than other classes: in 56 out of 70 chases observed the pursuer

TABLE X

*Numbers of observations of three different types of interactions between rhinos of each sex and age class*

	Prolonged physical contact	Peaceful interactions	Agonistic interactions
Adult male			
vs adult male	0	0	20
vs adult female	8	2	67
vs sub-adult	15	1	41
vs calf	4	1	12
Adult female			
vs adult female	1	0	97
vs sub-adult	7	2	88
vs calf	242	18	36
Sub-adult			
vs sub-adult	71	61	33
vs calf	15	15	15
Calf			
vs calf	3	3	8
Totals for:			
adult male ( $n = 191$ )	27 (14%)	4 (2%)	160 (84%)
adult female ( $n = 666$ )	259 (39%)	22 (3%)	385 (58%)
sub-adult ( $n = 529$ )	179 (34%)	140 (26%)	210 (40%)
calf ( $n = 386$ )	267 (69%)	40 (10%)	79 (21%)

TABLE XI

*Results of agonistic interactions between rhinos of different sex and age classes*

	Won	Lost	Neutral	Total
Adult male	66 (55%)	19 (16%)	35 (29%)	120
Adult female	100 (52%)	37 (20%)	54 (28%)	191
Sub-adult	7 (5%)	102 (71%)	34 (24%)	143
Calf	12 (19%)	27 (44%)	23 (37%)	62

Numbers of interactions refer to those with rhinos of other sex and age classes. The results of interactions were classified according to which, if any, individual fled or moved aside.

was an adult male. Tables X and XI show that adult males are the most aggressive class and also win most of their agonistic interactions.

### *Reproductive behaviour*

#### *Oestrus*

External signs of oestrus were difficult to see and could only be confirmed by observed copulation ( $n = 3$ ) or the female's acceptance of the male's advances ( $n = 10$ ). An actively maintained association between an adult male and a female was taken as an indication that the female was either entering, in, or leaving oestrus ( $n = 43$ ).

Oestrus recurred at intervals of between 27 and 42 days throughout the year, with a slightly higher, statistically insignificant, frequency between January and June. The earliest recorded post-partum oestrus was just over one month after the birth and almost immediate death of the calf. Otherwise no oestrus was recorded in females with calves less than ten months old and the median age of calves of oestrous females was 22 months ( $n = 19$ ).

#### *Courtship and mating*

Adult males often followed the tracks of a female, sniffing the ground intently from time to time and performing *flehmen*. Having located an oestrous female the male accompanied her intermittently for up to several days ( $n = 28$ ), occasionally making attempts to approach her more closely. The female usually repelled the male's advances by simply turning and snorting, but on some occasions the male continued to advance head down until the animals were facing each other horn against horn. Fights developed ( $n = 37$ ) with both rhinos trying to push each other back, the female in particular roaring and bleating loudly between lunges, horn clashes and tusk displays. Once a male turned a female over on her back and several times deep tusk wounds were inflicted.

If the female turned and ran the male chased her, sometimes over several kilometres. The male generally *squeak-panted* during such chases while the female *honked* or *bleated* very loudly. After such a chase the male usually caught up with the female again by following her scent. He attempted to approach her from behind and rest his chin on her rump while she walked. Both male and female squirt-urinated frequently and at this stage the female sometimes followed the male persistently and sniffed his penis.

Mounting was usually achieved only after several attempts and copulation lasted up to more than an hour ( $n = 3$ :  $> 30$ ,  $> 48$  and  $> 60$  min). The male appeared to ejaculate at

intervals of between 45 and 170 s ( $n = 57$ ;  $\bar{x} = 65$  s). Towards the end of copulation the female started to move more often and the male struggled increasingly to stay mounted, eventually sliding off on his belly. After two of the observed copulations the pair were seen together for the two following days. No further attempts at copulation were observed but it is possible that the male's presence prevents the female mating with another male.

### *Maternal care*

Females grew aggressive shortly before parturition and were less often found in the company of other rhinos. They usually chose secluded areas of thick vegetation in which to give birth and remained particularly wary and aggressive after the birth. Up to the age of six months calves were left alone for periods of up to 90 min ( $n = 10$ ) while their mothers fed up to 800 m away. Calves were suckled frequently up to the age of one year and started to feed on grass, herbs and creepers at the age of two to three months. Second year calves were suckled less frequently and only five calves were recorded being suckled over the age of 18 months.

Mothers were generally more aggressive than single adult females: they charged the observer on 13% of occasions ( $n = 58$ ) compared with 4% ( $n = 93$ ) for single cows ( $\chi^2 = 9.28$ ,  $P < 0.01$ ). Calves and sub-adults tended to approach and play with each other but cows drove off intruding rhinos. Despite repeated attacks, some sub-adults, mainly females, persisted in accompanying a cow-calf pair and the frequency of attacks by the cow eventually decreased.

Calves were separated from their mother at least a week before the birth of the mother's next calf, the process of separation being either sudden and final or gradual with periodic reunions over a period of four months or more. Cows drove away their calves violently only during the week before parturition: before that they simply snorted or threatened with a tusk display. Male calves left their mothers at a mean age of  $39.4 \pm 4.8$  months ( $n = 7$ ) compared with  $34.1 \pm 2.9$  months for female calves (Mann-Whitney  $U$  test two-tailed,  $P < 0.05$ ). Furthermore, one four-year-old male rejoined his mother after the death of his mother's new calf, and several other observations of single adult females with sub-adult males may have been cows with their four or five year old calves.

### *Individual differences in behaviour*

#### *Sub-adults*

Sub-adults were generally more timid than adults and some individuals became noticeably less timid and more curious as they grew older. Sub-adult males formed groups more frequently than sub-adult females (Fig. 10) and while in groups they were never attacked by adult males although lone sub-adult males were frequently attacked.

Two young males changed their ranges when they left their mothers and became independent, whereas three young females retained the ranging habits of their mothers. The higher numbers of sub-adult females in blocks D and E and of sub-adults in blocks F and G also suggest that there may have been pressures on sub-adult males to move out of the central, more highly populated areas.

#### *Adult females*

There were considerable differences between individuals in grouping behaviour and

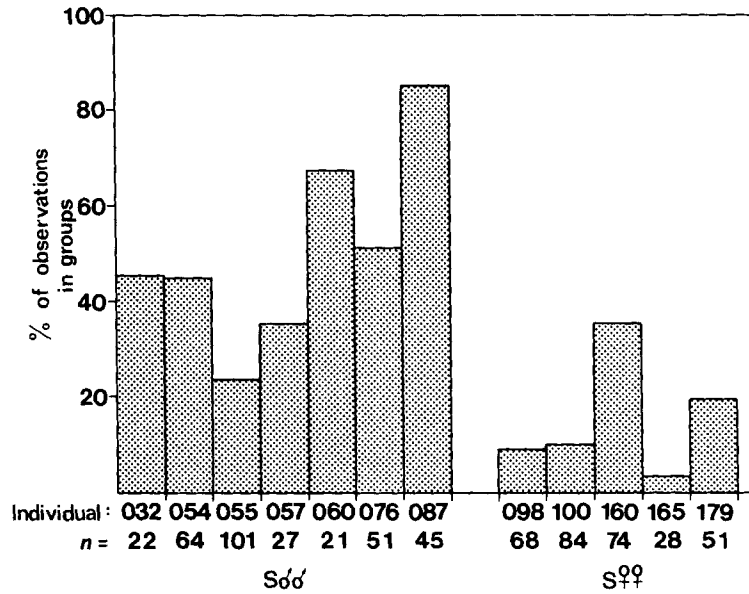


FIG. 10. The frequency of group formation by individual sub-adults.

frequency of agonistic interactions, particularly at wallows. There was evidence that cows living in the central blocks had to endure more attacks by other cows than those living in the outer blocks. No dominance hierarchy was indicated but the high rate of agonistic interactions between adult females at wallows may cause some individuals to avoid the most contested wallows.

#### *Adult males*

Adult males were divided into two classes, "strong" and "weak", on the basis of differences in social behaviour. Strong males associated more frequently with females, squirt-urinated and foot-dragged more frequently, and were the only males seen copulating. Although males were classified as "strong" or "weak" they lay on a continuum of "strength" and their positions on the continuum changed over the study period.

Adult males rarely associated with other adult males, and although there was a high rate of agonistic interactions between adult males when they were together, the number of such interactions was small. Only eight were observed involving the five adult males seen most frequently in the central blocks. During 1973, M001 chased M004 and M003 in block D, and M003 chased a strange adult male in block C. During 1974, M002 and M004 were both chasing F086 in block D, when M004 turned and chased off M002. Also during 1974, M005 was seen walking slowly across the Rapti from block F to block E with M045 following about 100 m behind. During 1975 M062, which had been seen only in block A up to that time, appeared in block D on two occasions. On the first occasion M062 chased M001, M004 and two adult females: a month later M062 was fatally wounded in a fight with M001 in block D and returned to block A where he died about 10 days later.

The wounds frequently acquired by adult males suggested that fights were common. However, some males lived in the same area together with very little mutual aggression, and



it appeared that most fights were between strange males and resident males. Weak males in particular, such as M002, were often seen in the vicinity of other adult males, and on one occasion three adult males wallowed 30 m apart in the same stream. However, such proximity can be misleading, as the vegetation is generally very thick and visibility poor. M001 and M003 were once wallowing 10 m apart but, when disturbed by the observer, M001 suddenly lunged at M003 and chased him off into the grass.

M004 was seen very infrequently during the second year of the study period, and it is likely that he moved either outside or to outlying regions of the study area during that year. M002 was also seen infrequently during the second year and died of old age during the third year. M045, M005 and M001 all showed clear evidence of changes in the use of their home ranges over the study period. Figure 11 shows that M045, although seen very rarely during the first year, accounted for nearly 90% of the sightings of the adult males in blocks F and G during the second and third years. M005 was seen in blocks B to G during the first year but reduced its range each year, moving out of block F in the second year as M045 moved into it. There was a corresponding change in block D with M005 moving in and M001 moving out to block C.

Thus, although adult males' ranges overlapped considerably, there was some degree of range exclusivity among strong males. Violent fights occurred, for example the one which ended in M062's death, but gradual changes in ranges with respect to known, neighbouring strong males seem to have resulted in considerable range overlap among the three strong males in the central blocks at Sauraha.

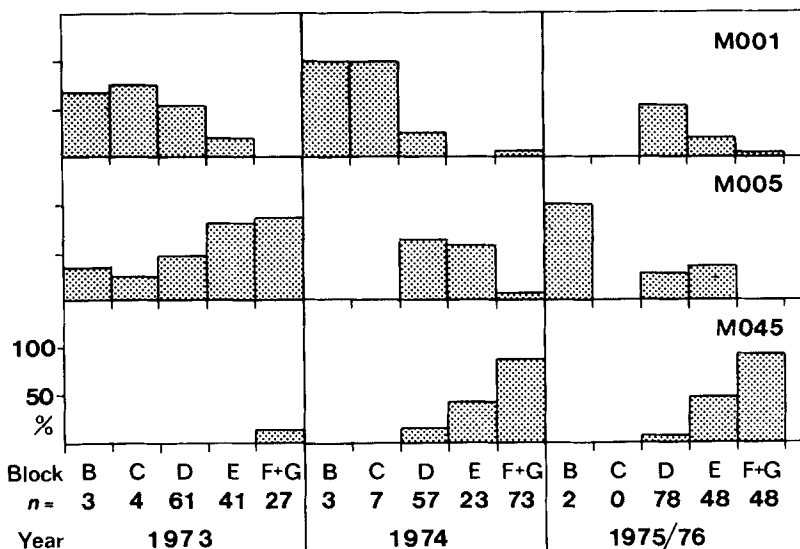


FIG. 11. Changes in the ranges of three adult males over the study period. Percentages are of all sightings (*n*) of the three adult males in each block in each time period.  $\chi^2$  test for differences between three years in the distributions of the sightings:

Blocks F + G M005 vs M045  $\chi^2 = 86.89$   $P < 0.001$  d.f. = 2  
 Block D M001 vs M005  $\chi^2 = 18.24$   $P < 0.001$  d.f. = 2

## Discussion

### *Relationships between rhino social organization and ecology*

The evolution of social organization in ungulates has been discussed by several authors, and all have emphasized the general correlation between various ecological factors and social organization (Eisenberg & Lockhart, 1972; Jarman, 1974; Geist, 1974; Estes, 1974; Owen-Smith, 1977). Interactions with the environment influence the communication mechanisms, grouping behaviour and movement patterns of individuals and hence the reproductive strategies employed by males, and the overall social organization of the species.

Table XII summarizes some physical, ecological and behavioural information on the five species of rhinoceros and is frequently referred to below. When considering the evolution of the social organization of the Indian rhinoceros the following ecological and morphological factors are of particular importance: (a) large body size, (b) marked seasonal and unpredictable variation in the distribution of resources in time and space, (c) habitats of generally poor visibility.

### *Grouping behaviour*

In Chitawan 0·2% of observations of Indian rhinos were of groups of more than three individuals and 5·2% were of more than two individuals. These figures compare with 1·7% and 10·6% for black rhinos and 3·4% and 17·2% for white rhinos (Owen-Smith, 1973). Javan and Sumatran rhinos form groups rarely (Borner, 1979; Hoogerwerf, 1970; Laurie, 1979) but may have been slightly more gregarious in the past when they were more numerous (Pollok & Thom, 1900; Wroughton & Davidson, 1918; Sody, 1959).

Large body size protects adult rhinos from predation but sub-adults in groups are further protected from predation and attacks by adult males. The relationships between group size and habitat in rhinos roughly parallel Jarman's (1974) correlations for African antelopes. The relatively gregarious white rhino is found in open habitats with a uniformly distributed abundant food supply whereas for the almost solitary rain-forest species (Table XII) visibility is poor and food is widely scattered and not quickly renewable. Indian rhinos form aggregations in open feeding grounds and at focal points such as wallows, but are generally less social than the two African species.

### *Sexual dimorphism and sex ratio*

All rhinos are sexually dimorphic in skull and horn size (Pocock, 1946; Groves, 1967, 1972, 1975) but only the White and Indian show marked sexual dimorphism in body size (Table XII). High ratios of adult females to adult males are generally reported for these two species, whereas the Black, Javan and Sumatran rhinos show more even adult sex ratios (Table XII). This conforms with Jarman's (1974) generalization for antelopes that small browsing species exhibit little sexual dimorphism and have even sex ratios, whereas large grazing species show considerable sexual dimorphism and a high ratio of adult females to males.

### *Maternal behaviour*

Leaving young calves unattended has not been previously recorded for Indian rhinos, but Joubert & Eloff (1971) had evidence that a Black rhino cow left her young calf alone while

she was feeding, and Bartlett (1873) concluded from observations in captivity that Sumatran rhinos did the same. Owen-Smith (1973) did not observe such behaviour in White rhinos. Indian rhinos and Black rhinos are large enough to protect their calves from predation, so the short hiding phase in these species may arise from the high energy requirement of the lactating cow and the calf's need for rest at an early age. The dense vegetation in these species' habitats may favour hiding (Lent, 1974). Walther (1964) suggested that, in "hiding" species, the following response of young animals is often imperfectly developed: this accords with observations that the calves of the Indian rhino, Black rhino and Sumatran rhino frequently run beside or in front of their mothers but White rhino calves normally follow at heel (Selous, 1881; Gee, 1953; Goddard, 1967; Coenraad-Uhlig, 1933; Owen-Smith, 1973).

### *Communication*

The Indian rhino has one of the largest and loudest repertoires of vocalizations, which is in accord with it being a relatively solitary animal which lives in habitats of poor visibility. The White rhino has more close range signals in its repertoire and possibly relies more on sight for long distances.

The eyesight of rhinos is widely held to be very poor but studies on the visual discriminatory ability of the Black rhino (Fasnacht, 1971) indicated that this was not so for that species. Indian rhinos rarely look up above eye-level but their detection of movement even against a dark background and at distances of up to 80 m is good (Laurie, 1979).

The main emphasis in visual signals of Indian rhinos is on direct actions and the display of the dangerous tusks in the lower jaw and the size of the head in front view. Unlike many other ungulates, there is no broadside display (Leuthold, 1977) in rhinos. This is consistent with the closed nature of the habitat. The postures associated with head to head confrontations, such as raised ears or pulled back ears, the lip curl which bares the tusks and the head-on view of the large bib and neck folds of the adult males are all visual signs effective at close quarters.

All the breeding males in Chitawan had very large head-on profiles and bibs but their horns varied from a 10 cm stump to 45 cm in length. The horn may not be as important in displays and dominance as the size of the animal. The long horns of the Black rhino and the White rhino contrast strikingly with the short horns of the Asian rhinos. Possibly they were developed as long distance visual signals suitable for open habitats but ineffective in forests and tall grasslands. The Woolly rhinoceros (*Ceolodonta antiquitata*) lived in the open tundra and had two long horns, whereas its close relative, the Sumatran rhino lives in forests and has very short horns.

Olfactory communication is particularly important in habitats of poor visibility and among animals such as the Indian rhino which have overlapping ranges but tend to move and forage alone. The main difference in olfactory communication between *Rhinoceros* and the other rhinos lies in the pedal glands which presumably leave scent marks on the furrows of earth turned up by foot-dragging, as well as during normal walking.

Foot-dragging occurs also in other rhino species (Table XII), but it appears to be best developed in the Indian rhino; possibly because of its visual significance in a wet environment. Borner (1979) noted that the Sumatran rhino twists saplings at points along the paths in such a way as to appear as visual signals to other rhinos (Table XII). On the other hand, the Indian rhino and the south-east Asian rhinos rarely scrape their hind-feet in their dung,

TABLE XII

*Some physical, ecological and behavioural comparisons of the five species of rhinoceros. (Numbers in italics refer to the literature listed at the end of the Table)*

	Sumatran rhinoceros ( <i>Dicerorhinus sumatrensis</i> )	Javan rhinoceros ( <i>Rhinoceros sondaicus</i> )	Indian rhinoceros ( <i>Rhinoceros unicornis</i> )	Black rhinoceros ( <i>Diceros bicornis</i> )	White rhinoceros ( <i>Ceratotherium simum</i> )
Adult female body weight (kg)	800-900 (1.8)	?1500 (10.11)	1600 (6.60)	720-1300 (4.7,9,13,45,72)	1600 (5)
Sexual dimorphism (A♂ body weight as % of A♀ body weight)	c. 100 (56,57,59)		129 (6)	c. 100 (4,7,9,13)	128-141 (5)
Adult shoulder height (cm)	121-138 (1.8,23.56,57,59)	140-170 (2.49)	159-186 (6.11,12,60)	165 (7)	171-186 (5)
Mean skull length (mm)	466 (Borneo)-528 (Malaya) (14)	506 (Vietnam)-529 (Sumatra) (14)	560-635 (11)	523 (Tana)-667 (Cape) (43)	664 (North)-693 (South) (48)
Dentition	Brachyodont, Protocone fold	Brachyodont	Hypsodont, Protocone fold	Brachyodont	Hypsodont
Hair	Long body hair (1.70)	Hair present only on ears and tail (21,70)	Hair present only on ears and tail (11,70)	Hairless, but hair follicles present (70)	Hairless, but hair follicles present (70)
Skin thickness (mm)	—	30 (neck shield) (35)	>25 (neck folds) (11)	—	45 (nuchal hump) 19 (belly) (71)
Gestation period (days)	c. 212-240 (36,42,44)	—	462-488 (mean = 478 ± 7, n = 27) (6,41,46,61,62)	419-476 (mean = 454 ± 15, n = 11) (40)	476-484 (n = 8) (5,38,39)
Habitat types	Rainforest (highland + low forest) (11,14,15,22,57,63)	Rainforest, but previously occurred in alluvial plain habitats (11,14,19,20,65)	Alluvial floodplains—grassland, swamps and riverine forest (11)	Wide range: from semi-desert to montane forest (24,26,27,28,34,66)	Short grass plains (5,37)
Feeding habits	Saplings, leaves, twigs, shrubs, fruits (15,56,57,63)	Saplings, shrubs, fruits, leaves, twigs, tall grass, herbs, palms (19,20,21,23)	Short + tall grass, shrubs, herbs, leaves, occasionally fruits, aquatic plants (11)	Leaves, twigs, shrubs, herbs (27,29,50,67)	Grass, herbs—very occasionally shrubs (5,37)
Population density (per km <sup>2</sup> )	0.02-0.04 (15,22)	0.15 (present) previously > 0.30 (16,19)	0.45-1.79 (11,51)	0.02-0.90 (17,18,24,25,50)	0.60-5.70 (5,37)
♀ Home range size (km <sup>2</sup> )	c. 30 (22)	'quite small' (23)	2-10 (11)	(Great variation according to habitat type) 2.6-90.0 (17,18,24,26,50) (as above)	4-15 (5)
Adult sex ratio (♂/♀ as % of total)			34-48 (Nepal) (11)	43.5-46.0 (27,28)	44.4 (overall) 38.7-53.0 (regionally) (5)

Grouping behaviour: % of observations of > two individuals	Very rare (15,32,33,52)	Rare but more common than in <i>D.s.</i> (11,20,21)	5-2 (11)	10-6 (26)	17-2 (3)
Visual displays	Tusks Tree twisting? Two short horns c. 250, 100 mm (max 380) Drag-marks rare (10,11,15)	Tusks Neck folds One short horn c. 150 mm in ♂ max (rarely in ♀) max 250 mm Drag-marks (10,11,20,21)	Tusks Very prominent neck folds and bib in A♂♂ One horn c. 400 mm max 600 mm Drag-marks (A♂♂) (11)	Two long slender horns (up to 1000 mm) Drag-marks (17,27)	Two long horns (up to 1000 mm) Drag-marks rare (3,5)
Olfactory displays	Squirt-urination Wallows + mud rubbing Dung-piles very rare (11,15,22,56,57)	Squirt-urination Wallows + mud rubbing Dung-piles rare Dung-scraping rare Pedal scent gland present (11,19,20,21,30) c. 9 distinct types, many similar to <i>R.u.</i> (11,21)	Squirt-urination Wallows + mud rubbing Dung-piles Dung-scraping rare Pedal scent gland present (11)	Squirt-urination Dung-piles Dung-scraping (17,20)	Squirt-urination Dung-piles Dung-scraping Preputial glands present (3,5,31)
Vocalizations	Wide variety, but descriptions confusing. Include loud and soft sounds (23,56,63,68,69) Fights occur (♂ vs ♀) but rather rare. Most courtship peaceful (15)	c. 9 distinct types, many similar to <i>R.u.</i> (11,21) Fights (♂ vs ♀) (20,21)	10 distinct types, mostly loud and controlling spacing between rhinos (11) Fierce fights + long chases (11,53,54)	Wide variety of sounds, ranging from loud roars to soft mewes (11,17,73) Fights between ♂ + ♀ and between rival males (27,34,55)	A very wide variety of sounds, particularly of close range signals (3,5) Peaceful containment of ♀ within a ♂'s territory, but fights also occur (3,37)
Courtship behaviour	—	—	Some range exclusivity but no true territoriality (11)	Territorial or nomadic/dominance—varies according to habitat type and availability of water (17,26,27)	Territorial: breeding males hold 1-2 km <sup>2</sup> Territories from which other breeding males are excluded (3)
Male mating systems	—	—	—	—	—

(1) Skaife (1961); (2) Medway (1969); (3) Owen-Smith (1975); (4) Hitchins (1968); (5) Owen-Smith (1973); (6) Lang (1961); (7) Meinertzhagen (1938); (8) Sonne-Hansen (1972); (9) Freeman & King (1969); (10) Lekagul & McNeely (1977); (11) Laurie (1979); (12) Maharajah of Cooh Behar (1908); (13) King (1969); (14) Groves (1967); (15) Borner (1979); (16) Schenkel & Schenkel-Hulliger (1977); (17) Goddard (1967); (18) Hitchins (1971); (19) Sody (1959); (20) Schenkel & Schenkel-Hulliger (1969b); (21) Hoogerwerf (1970); (22) R. Flynn (pers. comm., 1976); (23) Hazewinkel (1933); (24) Joubert & Eloff (1971); (25) Western & Simdiyo (1972); (26) Hitchins (1969); (27) Schenkel & Schenkel-Hulliger (1969a); (28) Roth & Child (1968); (29) Goddard (1970); (30) Cave (1962); (31) Cave (1966); (32) Wroughton & Davidson (1918); (33) Pollok & Thom (1900); (34) Guggisberg (1966); (35) Franck (1934); (36) Sanyal (1982); (37) Player & Feely (1960); (38) Schaurte (1969); (39) Pienaar (1970); (40) Jarvis (1969); (41) Tong (1960); (42) Bartlett (1873); (43) Groves (1972); (44) Anderson (1872); (45) Wilson & Edwards (1965); (46) Krishne Gowda (1969); (47) Morris & Jarvis (1959); (48) Groves (1975); (49) MacNaught (1932); (50) Mukinya (1973); (51) Lahan & Sonowal (1973); (52) Mjöberg (1930); (53) Gee (1953); (54) Berg (1933); (55) Goddard (1966); (56) Hubback (1939); (57) Strickland (1967); (58) Prater (1971); (59) Evans (1905); (60) Lang (1967); (61) Lang *et al.* (1975); (62) Buechner *et al.* (1974); (64) Shortridge (1915); (65) Peacock (1933); (66) Joubert (1971); (67) Goddard (1968); (68) Thom (1943); (69) Antonius (1937); (70) Cave (1969); (71) Cave & Allbrook (1959); (72) Denney (1969); (73) Frame & Goddard (1970).

as has frequently been reported for the African rhinos (Table XII). Goddard (1967) showed that rhinos could distinguish between the scent of different individuals' dung dragged in a bag behind a Landrover. The scent of dung on the feet quickly disappears in a wet environment so such a form of scent-marking would be ineffective in the Asian rhino habitats.

The Asian species of rhinos frequently wallow in small pools which smell strongly of urine. Hoogerwerf (1970) and Schenkel & Schenkel-Hulliger (1969*b*) concluded that regular impregnation of the skin with the smell of a wallow helps to mark the paths used by Javan rhinos, which pass through dense vegetation. In Chitawan the mud which was scraped off onto vegetation by Indian rhinos leaving similar wallows had a strong smell of urine and may have had olfactory significance for parts of the year.

### *Movements and ranges*

The patchy and variable distribution of food restricts the possible diet of Indian rhinos in any season and location. The distances Indian rhinos have to move between vegetation types to take advantage of the seasonal availability of resources such as food, wallows or mineral licks, determine the sizes of their ranges. Thus ranges, as would be expected, are larger in areas of lower vegetational diversity, and the lower limit of range size is *higher than in* species living in more uniform habitats.

Hitchins (1971) found home range sizes of 5.8–7.7 km<sup>2</sup> for three Black rhino cows in Hluhluwe. These are slightly smaller than the 5.3–9.6 km<sup>2</sup> home ranges of White rhino cows in Umfulozi (Owen-Smith, 1973), but there are considerable variations within species according to habitat type (Table XII). Sumatran and Javan rhinos feed largely on saplings and shrubs in rainforest. Such food is widely scattered and the home ranges of these species appear to be correspondingly large. Both species improve the food supply by bending saplings over until they break and feeding from the new shoots on subsequent visits (Hoogerwerf, 1970; Borner, 1979); such behaviour was also recorded in Indian rhinos in Chitawan (Laurie, 1979).

### *Mating systems*

Indian rhinos are large animals which possess directly functional, potentially dangerous weapons, and which do not form large groups and are relatively localized in their movements. These characteristics are typical of territorial ungulates (Owen-Smith, 1977) in that the costs associated with direct contests for mating or for the establishment of dominance hierarchies would be expected to be high. However, the Indian rhino's mating system appears to be a type of dominance hierarchy partially determined by location.

Breeding White rhino bulls hold territories of between 0.8 and 2.6 km<sup>2</sup> in which they maintain exclusive mating rights (Owen-Smith, 1975). Such a mating system would not be feasible in Chitawan since the great seasonal and unpredictable annual changes in the distribution of resources mean that male Indian rhinos cannot restrict their movements to such small areas as the White rhino males in South Africa, where there are smaller variations in forage productivity (Owen-Smith, 1975).

In the rapidly changing habitats of the Indian rhino, males have adopted wider ranging habits and thus increase their chances of finding both new, rich food sources and females already feeding on them. Poor visibility in the alluvial plain habitats also selects against territoriality. Although territories can be marked olfactorily (Owen-Smith, 1971) it is easier

for an Indian rhino male to intrude into another male's range, than it is for a White rhino in its open short grassland habitats. It is obviously to a male's advantage to progress into another male's territory: as long as he is undetected, he has a chance of mating.

The strongest Indian rhino males lived in the areas of highest adult female concentrations and moved around constantly over core ranges of up to 6 km<sup>2</sup>. The amount of overlap between their ranges varied but it was greatest in the areas of highest population density. Adult males probably benefit from occupying such areas because the chances of finding an oestrous female are higher and the food resources are better in those areas. Strong males were almost entirely solitary and were never seen together in groups. They distributed scent marks around their ranges but did not refrain from entering another strong male's range. Two neighbouring strong males rarely fought each other but strange strong males entering another's range were often attacked and sometimes killed. Weak or subordinate males are tolerated by strong males; presumably it is too costly in time and energy to exclude them and the chances of them mating are small. Furthermore, they may actually increase a strong male's chances of breeding by detecting an oestrous female and drawing the attention of the strong male by driving her.

The Black rhino's mating system appears to vary considerably according to habitat type, being similar to that of the White rhino in wet habitats but apparently not territorial in dry areas (Owen-Smith, 1973; Schenkel & Schenkel-Holliger, 1969a; Mukinya, 1973).

Little is known of the mating systems of the Sumatran and Javan rhinos. The wide ranging Sumatran rhinos would not be expected to hold exclusive mating territories in rainforest and competition between males would be expected in the vicinity of an oestrous female unless dominance relationships had already been determined. Hubback (1939) reported a fight between two males in the presence of a female and there are several reports of males accompanying females (Voltz, 1912; Shortridge, 1915; Peacock, 1933). However, there are many other reports which state that it is unusual to find pairs together (Hazewinkel, 1933; Hubback, 1939; Van Strien, 1974). Males probably accompany females for quite long periods before oestrus, and there may have been selection for females to delay oestrus thus increasing the chance of another male finding the pair and challenging her mate.

The Javan rhino appears to have been originally an animal of the lowland swamp forest and forest-edges whereas the Sumatran species was more typical of the high mountains (Peacock, 1933; Groves, 1967). I suggest that it was ecologically separated from *R. kendengicus* in Java (Hooijer, 1946) and *R. unicornis* in India by being unable to graze on short grasses but that it ate tall grasses and palms (Table XII). At present, apart from living at considerably lower population densities than formerly (Sody, 1959; Table XII), the Javan rhino is restricted to rainforest. It is very likely that individuals have larger ranges in rainforest than in lowland swampforest, and that originally the Javan rhino had a mating system similar to that of the Indian rhino.

### *Courtship and mating*

Indian rhino courtship chases and fights are extremely noisy and the loud vocalizations of the female advertise the courtship over a radius of at least one kilometre, with the result that strong males in the vicinity are attracted to the courting pair. Although courtship in ungulates often contains an element of aggressive behaviour, and the male commonly drives the female (Fraser, 1968; Leuthold, 1977), unmitigated aggression is unusual (Leuthold, 1977). Similar but less violent behaviour has been observed in Black rhinos (Guggisberg,

1966; Ritchie, 1963), Javan rhinos (Hoogerwerf, 1970) and Sumatran rhinos (Loch, 1937) but not in White rhinos (Owen-Smith, 1973).

Apart from directly testing the male's strength, one of the "functions" of the long, noisy chases and fights of the Indian rhino's courtship could be to ensure that the female is eventually mated by a strong male. The loud vocalizations used by female elephant seals when resisting copulation could serve a similar function (Cox & Le Boeuf, 1977), and the same could be true of Orang-utans (MacKinnon, 1974). The differences between the more peaceful courtship of the White rhino and that of the Indian rhino are probably related to differences in habitat structure and hence visibility. Briefly, in a habitat with low visibility in which males do not hold territories, an oestrous female may increase her chances of being mated by a stronger male if she resists copulation and advertises her readiness for copulation with loud vocalizations. Strong males, on the other hand, may obtain more matings by following the sounds of fighting between another male and female. It is also possible that adult females in oestrus may approach a consort pair, being attracted by both smell and vocalizations, as a male with a female is likely to be a strong male.

### *Conservation*

The massive reduction in the range of the Indian rhino has been caused primarily by the disappearance of most of the alluvial plain grasslands and woodlands, the rhino's preferred habitat, which is also the most suitable for wet rice cultivation. Now that almost all the surviving rhinos are confined to two National Parks containing a total of 500 km<sup>2</sup> of suitable habitat, any catastrophe such as an epidemic disease, severe flooding or a breakdown in protection measures could drastically deplete the total rhino population. Furthermore, in these small patches of alluvial plains there is a danger that changes in the courses of the rivers could result in vegetational succession proceeding to a climax condition unsuitable for early successional species such as the Indian rhino. As a result of increased deforestation in the Himalayas, the flood levels and extent of erosion in the plains increase every year. Small changes in the courses of these rivers could destroy the rhino's habitats, and the human population pressure on the surrounding land is such that alternative refuges are scarce.

In the small protected areas which remain, it will be difficult to ensure that the present diversity of suitable vegetation types is maintained. Enlargement of existing protected areas and the creation of buffer zones should be employed where possible, and it seems feasible that with careful planning rhinos could be taken from Kaziranga National Park to protected areas within the former range of the species, thus reducing overcrowding in Kaziranga, and spreading the risk of catastrophe.

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