5. SOCIAL BEHAVIOUR

Methods

5.1.1 Types of information recorded

General methods of observing rhinos and recording data are described in Section 2.3. The vast amount of information collected on social behaviour can be divided conveniently into three categories:- associations, communication and interactions.

(a) Associations (see Section 5.2).

I was interested in the frequency with which individuals of each sex and age class associated with other individuals. I distinguished two types of association because some were considerably more permanent than others. Thus I considered individuals which moved together or lay in physical contact with one another as members of a group (*e.g.* Plate 26), and individuals which were within 20 metres of each other at any one time though not necessarily moving together (*e.g.* Plate 27), as members of an aggregation.

As most observation periods were very short, some individuals remained within 20 metres of each other for the whole observation period and displayed no evidence one way or the other of independent orientation. In these cases previous knowledge of the individuals concerned was used to classify the association as a group or an aggregation. For instance, a cow-calf pair was always classified as a group.

I recorded, if possible, the age class, sex and identity of each individual, and indicated the types of associations between individuals at the start of each observation. Subsequent temporary associations were also described fully in the notes.

(b) Communication (see Section 5.3).

I noted all occurrences of auditory, visual and olfactory communication and any actions which I thought might be connected with such communication. I described and, when possible, tape-recorded all the types of sounds which I heard rhinos make and was able to refer to 10 distinct types and their variations when describing the contexts in which they were used. All obvious visual and olfactory displays and reactions to them were described in detail.

Particular attention was paid to occurrences of urination and defecation as it seemed likely that the scents of urine and dung played a part in olfactory communication.

(c) Interactions (see Section 5.4).

All interactions between rhinos were described in detail. Such descriptions were made easier by the classification of vocal, olfactory and visual displays into a number of discrete categories. I was also able to classify interactions as peaceful or playful, agonistic and those observed solely during courtship or mating.

5.1.2 Computer analysis

The use of the IBM 370 computer at Cambridge University is described in Section 4.1. It was impossible to code all the data recorded in the notebooks for inclusion on the computer cards because of the limitations of space on the punch cards, the complexity of many of the interactions observed and the variety of circumstances in which they occurred. However, in addition to using the computer in analysis of the data, I also used it as an easy reference file for finding data on certain types of behaviour,which I then analysed in more detail with further reference to my notebooks.

Listed below, with brief explanatory notes, are the variables used to summarize social behaviour. This brief summary of the coding system used for computer analysis is intended for quick reference only. Details of the types of behaviour listed are given in later sections.

(a) Associations

(i) Group size

(ii) Aggregation size

(iii) Age classes, sexes and identification numbers, if known, of all associated individuals.

(b) Communication

(i) Vocalizations

The occurrences of 10 types of vocalizations were listed. The context of each vocalization was not defined, but a distinction was made between vocalizations made in response to the observer or his elephant and those made in other circumstances - mostly elicited by other rhinos.

(ii) Defecation and urination

The numbers and types of defecations and urinations observed were coded. Two types of defecation - on and away from dung-piles - and two types of urination - normal and squirt urination - were distinguished. Associated behaviour such as foot-scraping, foot-dragging and tree-bashing was also coded.

(iii) Reactions to scents

The following reactions were coded:

1. Prolonged sniffing at the ground or vegetation
2. Following another rhino's tracks
3. Flehmen
4. Coprophagy
5. Licking urine.

(c) Interactions

(i) Peaceful interactions

The following types of peaceful interactions or passive physical contact between individuals were coded with details also of whether individuals were lying or standing and with which sex and age class of rhino the interaction took place.

1. Greeting with head waving or bobbing
2. Passive physical contact
3. Mounting flanks or rump
4. Rubbing flanks against flanks
5. Nuzzling the flanks or rump
6. Nuzzling the head region
7. Licking head or flanks
8. Suckling: duration and whether from behind or the side
9. Horn to horn sparring
10. Playfully running around
11. Playing with twigs in the mouth
12. Other peaceful interactions.

(ii) Agonistic interactions

I classified agonistic interactions according to which individual initiated the interaction and which individual was the apparent victor. All details of agonistic interactions were referred to, if needed, in the notebooks. Three types of results of interactions were coded:

1. Moved aside or ran away
2. Chased for more than 20 metres by the other individual
3. Neutral: no obvious victor.

Up to three agonistic interactions per observation could be coded, together with the sex and age classes of the opponents in each interaction. The numbers of additional agonistic interactions were also listed but without detail. However, there were rarely more than three agonistic interactions per observation of an individual, and details of any extra ones were available in the notebooks. Occasions when rhinos fled immediately at the sight or sound of other rhinos and in the absence of any agonistic interactions, were also coded.

5.1.3 Sound recording and experiments with played back sounds

I used a Sony 800 TC reel to reel tape-recorder to record nine types of sounds made by rhinos. I played back sounds of various types made by rhinos of different ages and sexes, and observed several individuals' reactions to them (Section 5.3.1.1).

5.1.4 Scent marking investigation

5.1.4.1 Dung piles

The tendency of rhinos to defecate on previously deposited dung is described in Section 5.3.2. In addition to the direct observations of defecation, a number of other methods were used to investigate the phenomenon of repeated defecation in the same place. For the first year of the study I kept a careful look out for all kinds of defecations and classed them as dung-piles or as single defecations. I defined dung-piles as groups of defecations none of which was more than 10 metres from another. In order to investigate the types of sites where dung-piles grew up, and the frequency with which dung-piles were used for defecation in comparison with other sites, I regularly recorded the number of dung-piles and the frequency of their use on set circuits within the study area. This was done at three stages during the project for periods of 10 to 29 days in December 1973, July 1974 and March 1975. A map was made of the chosen circuits and the sites of all dung-piles or single defecations were numbered and marked on the map. On subsequent daily visits,all new defecation sites within 10 metres of the circuit trail were assigned a number and marked on the map,and a record was kept of the location of all new defecations.

5.1.4.2 Dung and urine repositioning experiments

In addition to watching the reactions of rhinos to naturally deposited urine and dung, I collected samples of urine and dung,and placed them where I could watch rhinos' reactions to them. I collected dung from the Tiger Tops area and took it to the Sauraha area to investigate any possible reaction to dung from strange individuals. The results of these experiments are given in Section 5.3.2.

Results

5.2 Associations between rhinos

I distinguished (in Section 5.1.2) between temporary associations or aggregations of rhinos,and more permanent associations or groups. I consider here the frequencies of both types of associations between rhinos of different ages and sexes.

5.2.1 Group sizes and compositions

(a) Group size

Table 5.1 shows the frequencies of group sizes for 4,352 observations of rhino groups over the study period in both study areas. Obviously these observations of group sizes include many repeated observations of the same groups. However, it was shown in Section 3.6.4 that there were no significant differences between the sex and age classifications of registered individuals and of total sightings of rhinos. I concluded,in Section 3.9.2,that the frequencies of observations of group sizes and compositions can be considered as approximately equivalent to the actual frequencies of each type of group in the population.

Note that I have called solitary individuals groups of one, for easier

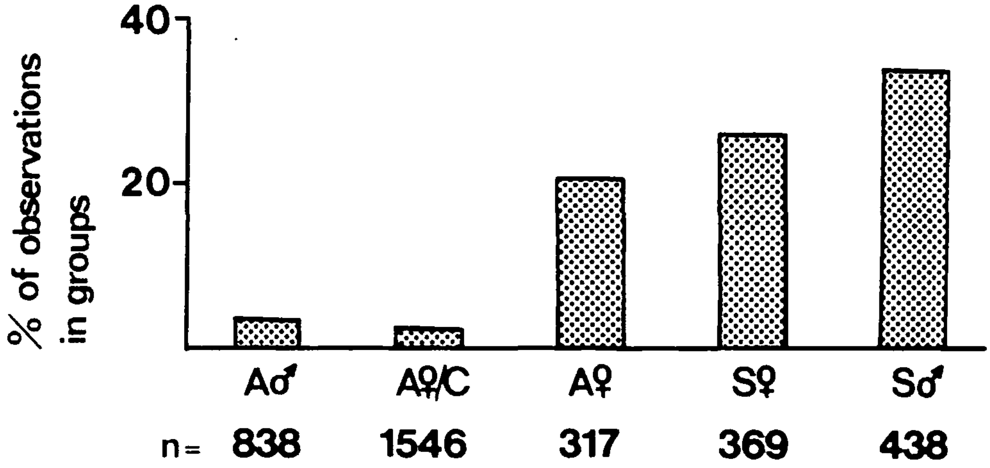
Table 5.1. The sizes of rhino groups.

No. of individuals in the group	No. of observations
1	2,426 (55.7%)
2	1,827 (42.0%)
3	92 (2.1%)
4	6 (0.1%)
5	0 (0.0%)
6	1 (0.1%)
Total	4,352

presentation of the data. It can be seen in Table 5.1 that 55.7% of the observations were of solitary individuals. Furthermore, 1,507 or 82.5% of the 1,827 groups of two rhinos consisted of cows with their calves. Thus, only 419 or 9.6% of observations were of groups other than solitary individuals or cow-calf pairs.

Fig. 5.1 shows the frequencies of group formation between individuals classified according to their sex and age classes. Adult females are subdivided into those with and without calves; cow-calf pairs are considered as single units because calves were rarely seen away from their mothers (see Section 5.5.4.2 for exceptions). It can be seen in Fig. 5.1 that there were considerable differences between the sex and age classes in the proportion of occasions that they were seen in groups with other individuals (significant differences are shown in Fig. 5.1). Adult males and cow-calf pairs associated least with others,and there was an increase in sociability in adult females, sub-adult females and sub-adult males, in that order.

The use of the χ^2 test on numbers of sightings of individuals is



χ^2 tests on differences between classes:- p values shown in matrix

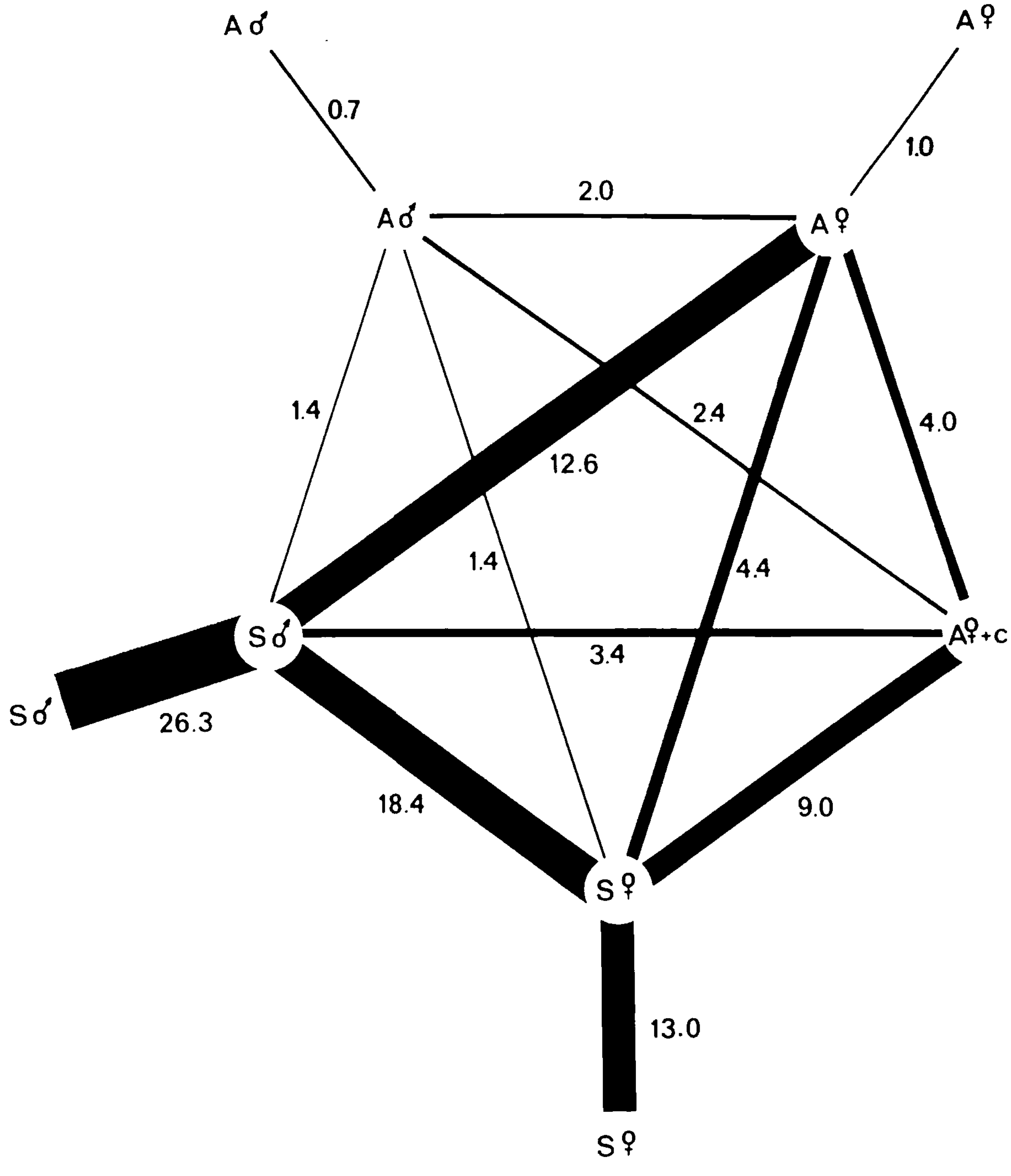
	Ao	A♀ + c	A♀	S♀
A♀ + c	>0.05			
A♀	<0.001	<0.001		
S♀	<0.001	<0.001	>0.05	
So	<0.001	<0.001	<0.001	<0.02

Fig. 5.1. A comparison of the grouping behaviour of rhinos of different sex and age classes.

difficult because it could be argued that repeated sightings of the same individuals inflate the N and so increase the likelihood of detecting a significant difference between two distributions. However, because they were separated by over 12 hours in most cases, I regarded successive sightings as independent. Furthermore, I showed evidence in Section 3.6.4 that the numbers of sightings of individuals of different sexes and ages closely reflected the numbers of individuals of those sex and age classes in the population.

(b) Group composition

Having demonstrated significant differences among the sex and age classes in the frequency of group formation, I now examine the types of groups which were observed. Fig. 5.2 shows, in schematic form, the likelihood of seeing rhinos of any two sex and age classes in the same group. The diagram is based on 293 observations of associations in groups between units of known sex and age classes. Cow-calf pairs were treated as single



The width of the lines joining each pair of classes indicates the number of associations between them in groups expressed as a proportion of all recorded associations in groups between rhinos of known sex and age class (n = 293). Lines pointing outwards from the polygon indicate associations between rhinos of the same class.

Fig. 5.2. Schematic representation of the likelihood of seeing rhinos of any two sex and age classes in the same group.

units for the reasons given above.

Fig. 5.2 shows that most (57.5%) of the observed associations were between sub-adults and in particular between sub-adult males. Also, 12.6% of the observed associations were between single adult females and sub-adult males. However, many of these observations were of a cow with her previous calf which had rejoined her after the death of her infant (discussed in Section 5.6.3). Cow-calf pairs never formed groups with other cow-calf pairs, and single adult females and adult males rarely associated with others of their own class.

For more detailed analysis of the types of groups formed, I have considered only those observations of rhino groups during which I determined the sex and age classes of all members of the group. There were 3,383 such observations and a summary of the sex and age compositions of the groups is shown in Table 5.2. Groups of two or more sub-adults are considered as single units in this table, and the compositions of these exclusively sub-adult groups are summarized in Table 5.3. When considering preferences of sex and age classes for grouping with any other sex and age class, it is necessary to take into account the numbers of each sex and age class in the population (shown in Table 3.10). As 98% of all observations of groups in Table 5.2 were made in the Sauraha study area, I considered the population composition in the Sauraha area only.

Adult males were seen on very few occasions with any other individuals, and they showed no significant preferences for any sex and age class (Kolmogorov-Smirnov one sample test $p > 0.20$). Looking at significant differences only, cow-calf pairs were seen significantly more frequently than expected in groups with sub-adult females and significantly less frequently than expected with other cow-calf pairs (Kolmogorov-Smirnov one sample test $p < 0.01$). On the other hand, single adult females were seen significantly more frequently than expected with sub-adult males and less frequently than expected with adult males and cow-calf pairs (Kolmogorov-Smirnov one sample test $p < 0.01$).

Table 5.2. The sex and age compositions of rhino groups.

Companions	Number of observations			
	None	A♂	A♀	A♀ + c
Class or unit				
A♂	809	2		
A♀	252	6	3	
A♀ + c	1507	7	6	0
S♂	320	3	28	5
S♀	321	4	5	13
Sub-adult group	86	1	5	

Based on 3,383 observations of rhino groups in which the ages and sexes of all members were determined.

Table 5.3. The sex compositions of sub-adult rhino groups.

Companions	Number of observations			
	1♀	2♀♀	1♂	2♂♂
1♀	15			
2♀♀	-	-		
1♂	20	2	33	
2♂♂	8	-	7	1

Based on 86 observations of sub-adult groups in which the sexes of all members were determined.

Sub-adult males formed sub-adult groups and associated with single adult females in groups more frequently than sub-adult females did (Tables 5.2 and 5.3). The latter formed groups less frequently overall but associated with cow-calf pairs to a greater extent than sub-adult males did. It was mentioned in Section 3.2.1 that it was easier to determine the sex of sub-adult males than of females. As this may have introduced a bias into the results for the frequency of sub-adults of both sexes seen in groups, I compared (in Table 5.4) the numbers of sightings and the numbers of registered individuals for sub-adults of both sexes. There is no significant difference between these two sex ratios (Table 5.4). However, there are clear significant differences between the sexes in the numbers of sightings of sub-adults in groups with adult females, with cow-calf pairs and other sub-adults (Table 5.4). Sub-adult males associated significantly more frequently with other sub-adult males and single adult females, whereas sub-adult females associated more frequently with cow-calf pairs. Furthermore, it can be seen from Table 5.3 that there was a higher tendency for sub-adult males to form all-sub-adult male groups than there was for sub-adult females to form all-sub-adult female groups ($\chi^2 = 8.31 \quad p < 0.01$).

5.2.2 Aggregations

Having considered the sizes and compositions of rhino groups, I now look at temporary associations between rhinos. One thousand and one (23.0%) of the 4,352 groups recorded were in aggregations with other groups of rhinos. They made up a total of 434 aggregations ranging in size from two to nine individuals as shown in Table 5.5. Looking first at the tendencies of social units to associate with others, I show in Table 5.6 the numbers of observations of each unit within 20 metres of another rhino or group of rhinos at the start of observation periods. Expressed as a percentage of the numbers of observations of each unit alone, these figures indicate tendencies to form aggregations. There were no significant differences between the sexes among adults or sub-adults in the proportions of occasions on which they were seen in aggregations. Solitary sub-adults, however, were significantly more likely to be associated with other

Table 5.4. A comparison of the frequency and types of groups formed by sub-adult males and females.

	Males	Females	Total	Significance of differences from the sex ratio of registered individuals (χ^2 one sample test)		
Numbers of registered sub-adults	21	17	38			
Total sightings of sub-adults	401	370	771	ns	$\chi^2 = 3.28$	$p > 0.05$
Sightings of sub-adults with cow-calf pairs	5	13	18	♀>♂	$\chi^2 = 5.63$	$p < 0.01$
Sightings of sub-adults with single adult females	28	5	33	♂>♀	$\chi^2 = 12.2$	$p < 0.001$
Sightings of sub-adults with other sub-adults	129	62	191	♂>♀	$\chi^2 = 11.60$	$p < 0.001$
Sightings of sub-adults with sub-adult females	38	30	68	ns	$\chi^2 = 0.10$	$p > 0.05$
Sightings of sub-adults with sub-adult males	91	32	123	♂>♀	$\chi^2 = 17.40$	$p < 0.001$

Table 5.5. The sizes of rhino aggregations.

Number of individuals in aggregation	Number of observations
2	119 (27.4%)
3	192 (44.2%)
4	70 (16.1%)
5	25 (5.8%)
6	14 (3.2%)
7	8 (1.8%)
8	4 (0.9%)
9	2 (0.5%)
Total	434

Table 5.6. The tendencies of different social units to form aggregations.

Unit type	Number of observations of the unit	Number of times another unit was within 20 metres
A♂	809	147 (18.2%)
A♀	252	56 (22.2%)
A♀+ c	1,507	325 (21.6%)
S♂	320	117 (36.6%)
S♀	321	110 (34.3%)
Sub-adult group	86	· 31 (36.0%)

individuals in aggregations than were solitary adults or cow-calf pairs (adults vs sub-adults $\chi^2 = 62.5$ $p < 0.001$).

Table 5.7 shows the types of aggregations formed, considering the 315 aggregations in which the sex and age classes of all rhinos were determined. Adult males associated mainly with adult females; cow-calf pairs also formed frequent aggregations with sub-adults (mainly females), and aggregations solely of sub-adults (mainly males) accounted for 14% of all the observations. Thus, the compositions of aggregations are similar to those of groups (described in Section 5.2.1).

5.2.3 Time in association with other rhinos

The analysis so far has been restricted to initial observations of rhinos in groups or aggregations. However, in order to look at the relative frequencies of various types of interactions between rhinos, I calculated the proportions of the total observation time for each sex and age class spent in aggregations with each other. The results (shown in Table 5.8) form the basis for the calculation of rates of vocalizations (Section 5.3.1) and interactions (Section 5.4).

Table 5.7. The sex and age compositions of rhino aggregations (n = 315 observations).

a) Aggregations of adults and of adults with sub-adults (n = 271).

Companions	Number of observations			
	A♂	A♀	A♀+c	2A♀♀+cc
Unit				
A♂	18			
A♀	16	1		
A♀+c	39	16	42	
2A♀♀+cc	1	5	6	1
S♂	9	1	20	2
S♀	9	2	51	4
Sub-adult group or groups	9	5	5	2

Also: one aggregation of three adult males and six mixed aggregations of between six and nine rhinos of all age and sex classes.

b) Aggregations solely of sub-adults (n = 44).

Companions	Number of observations		
	1♀	1♂	2♂♂
1♀	6		
1♂	6	14	
2♂♂	2	6	2
3♂♂	4	1	0
5♂♂	3	0	0

Table 5.8. The time spent by rhinos of each sex and age class in association with others.

Class or unit	Time (hours) spent in associations* (% of total observation time)	Time (rhino hours) spent in associations* with					
		A♂	A♀ + c	Single A♀	S♂	S♀	S?
A♂	86 (20.6%)	13	-	-	-	-	-
A♀ + c	220 (24.5%)	32	91	-	-	-	-
Single A♀	57 (36.8%)	26	64	-	-	-	-
C	900 (99.7%)	32	91	994	11	42	18
S♂	152 (64.1%)	18	11	27	192	-	-
S♀	93 (50.3%)	18	42	9	54	14	-
S?	72 (55.0%)	4	18	2	23	9	82

* Associations include groups and aggregations.

5.3 Communication

5.3.1 Auditory communication

5.3.1.1 Types of vocalization

Rhinos make a wide variety of sounds: I distinguished 10 different types which seemed to function in communication. None of these sounds were recorded on tape. There was considerable variation within each type, and some sounds were intermediate between two types. However, most sounds heard were clearly one of the following types.

(a) Snort

The snort is a non-vocal sound produced by the expulsion of air in a succession of quick bursts through the lips and nostrils. It varied in intensity and sounded almost explosive when the air was expelled at very high pressure. It also varied in length and in the number of bursts. The number of snorts per series varied from one to 20 (mean 2.0 ± 2.1) on 442 occasions, and was greater than 20 on 146 occasions.

(b) Honk

The honk is a loud low-pitched guttural vocalization of metallic echoing nature. It was emitted as a single burst or as a succession of short bursts and the mouth was normally held partly open. Alternate bursts were often of different tones.

(c) Humph

The humph is a mixture of thoracic-oral aspiratory sound and a wheezing type of vocalization. Reminiscent of the puffs of a steam engine, it is made by air expelled from the throat and was uttered in time with the pace of the rhino - usually when it was running.

(d) Bleat

The bleat is a loud blaring single tone vocalization similar to the prolonged lowing of domestic cattle. It was made with head low, mouth open, tusks bared and ear pinnae held back.

(e) Roar

The roar is similar to the bleat but louder and more forcible, made with the head raised and mouth open. It varied more in intensity and volume than the bleat did: similar to the bellowing of cattle.

(f) Shriek

The shriek is a very loud and high pitched vocalization variable in tone and reminiscent of the trumpeting of elephants or the squealing of a pained dog.

(g) Squeak-pant

The squeak-pant is a very variable sound, half aspiratory and half vocal in nature. It consists in its full form of a sharp squeaking noise similar to a squeaking wheel or machinery, followed by a panting noise which is a sharp exhalation of breath somewhere between a honk and a snort. The lips are sometimes vibrated during the pant. The intensity of the squeak-pant varied considerably. Sometimes the squeak was the only audible component: the lip vibration showed that the pant component was not omitted but became too faint to be heard.

(h) Moo-grunt

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 which makes its origin difficult to locate. Moo-grunts varied from short gruff grunts to long drawn out squeaky grunts which sounded like a rusty hinge opening. Although there were occasions when only one or two moo-grunts were recorded, moo-grunts were normally repeated regularly at rates of five to 40 per minute for 30 minutes or more.

(i) Groan

The groan, although similar to the moo-grunt, is a louder and longer grating vocalization usually made with the mouth open. It was not common.

(j) Rumble

The rumble is an outflow of breath which vibrates the throat in a way reminiscent of the rumbling of a horse's lips.

(k) Other sounds

Various other sounds were emitted by rhinos but seemed to have no function as signals, being merely the consequence of abdominal air pressure. Loud burping and farting noises were very common and occurred most frequently when the rhinos were rolling in wallows or lying and shifting position on the ground. A long loud exhalation almost invariably followed when a rhino lay down either in a wallow or on dry land. One particular sub-adult female wheezed and rattled noisily on many occasions and sounded like an asthmatic. These respiratory noises were emphasized when she ran or was alert or suspicious.

Although not an oral sound, a peculiar slapping sound caused by kicking the belly sharply with the hind feet may also have had some signal function.

5.3.1.2 Contexts of auditory displays

Reactions to the observer

Table 5.9 shows that there was a significant difference in the frequencies of the different types of rhino sounds heard (a) during reactions to the observer (Section 2.3.2) and (b) in other contexts ($\chi^2 = 37.2 \quad p < 0.001$). The snort and the humph were heard significantly more frequently in reaction to the observer than in other contexts, and the snort, honk and humph together accounted for 94.5% of all sounds heard during reactions to the observer.

Table 5.9 also shows the frequencies of sounds made by rhinos during each of the eight types of reaction to the observer (Section 2.3.2). The snort was used frequently in all reaction types as an initial warning or keep away signal. The honk was a more aggressive signal, often heard during charges, but also when a rhino was fleeing; the humph was almost entirely restricted to flight from the observer.

TYPE OF SOUND:	Number of series*											
	Snort	Honk	Humph	Bleat	Roar	Shriek	Squeak-pant	Moo-grunt	Groan	Rumble	Others	Total
(a) In reaction to the observer												
TYPE OF REACTION:												
Silent alert	14	0	0	0	0	0	0	0	0	0	0	
Turn in alarm	10	2	0	0	0	0	0	0	0	0	1	
Sudden flight	108	108	70	0	0	0	1	2	0	1	11	
Charge	21	26	7	0	2	0	3	0	0	0	0	
Curious advance	20	15	8	0	0	0	0	0	0	0	0	
Run and look back	62	25	18	0	0	0	1	3	0	0	3	
Walk away	57	2	1	0	0	0	0	0	0	5	0	
TOTAL (in reaction to the observer)	292 (48.1%)	178 (29.3%)	104 (17.1%)	0 -	2 (0.3%)	0 -	5 (0.8%)	5 (0.8%)	0 -	6 (1.0%)	15 (2.5%)	607
(b) From undisturbed rhinos	588 (33.2%)	510 (28.8%)	17 (1.0%)	131 (7.4%)	101 (5.7%)	12 (0.7%)	139 (7.8%)	212 (12.0%)	15 (0.9%)	22 (1.2%)	25 (1.4%)	1773
TOTAL (all sounds)	880	688	121	131	103	12	144	217	15	28	40	2380

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

Table 5.9. The frequencies of different types of rhino sounds heard (a) in reaction to the observer and (b) from undisturbed rhinos.

Other contexts

Table 5.10 summarizes the contexts in which each of the main types of sounds were heard among rhinos not disturbed by the observer. Here, considering each of the main types of sound in turn, I describe contexts, responses and distributions among the sex and age classes. Individuals which uttered sounds are called 'actors', and individuals at which sounds were directed are called 'recipients'.

(a) Snort (n = 588)

(i) Contexts (see Table 5.10).

The approach of another rhino to a grazing or wallowing individual commonly elicited a single or double snort, and wallowing individuals often stood up just before or after they snorted. Although I recorded fewer snorts from rhinos approaching other rhinos - 58 as against 273 - it was more common,especially at wallows, for one or two individuals to approach a larger aggregation of rhinos than vice-versa. Snorts were directed at rhinos which were grazing or lying nearby on 73 occasions. The distances between the rhinos was mostly less than 20 metres, but on one occasion a male rhino snorted as another male came into view 200 metres away.

The snort was used as a contact call between cow and calf, nine times by the cow initially and three times by the calf initially, although there were sometimes lengthy exchanges of snorts. In response to snorts made in contexts of initial proximity, the recipient snorted back on 55 of the 404 occasions. After agonistic interactions which ended with one rhino running away, the vanquished individual often turned to look back at its opponent and snorted. The rhino then turned to flee again or retraced its steps back towards its opponent.

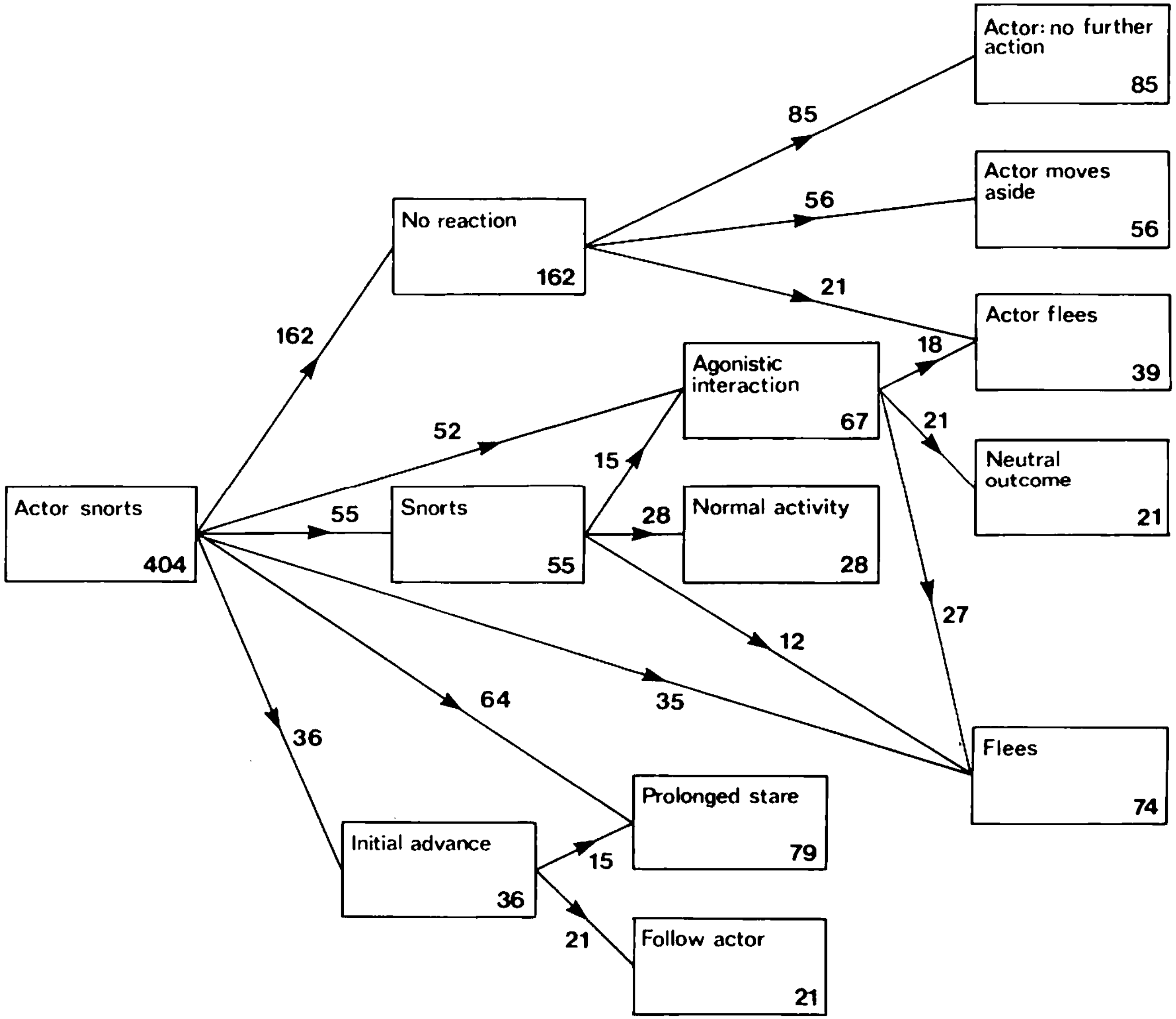


Fig. 5.3. The frequency of various types of responses to snorts made in contexts of initial proximity (n = 404).

the encounter was neutral. Thus the outcomes of encounters which started with a snort were not related to which individual snorted first (Wins: actor vs recipient $\chi^2 = 2.14$ $p > 0.10$); the snort therefore seems to be a sound directed at nearby rhinos as a contact or warning signal informing them of the actor's presence.

(iii) Distribution among the sex and age classes (see Table 5.11).

The matrix in Table 5.11 shows the frequency with which snorts were directed by each of four sex and age classes at each other for the 452 occasions when the classes of both actor and recipient were known. Rates of snorting are expressed as the numbers of snorts per 100 hours of observation of each pair of sex and age classes in associations together (Table 5.8). Although snorts were often directed at rhinos not in the same group or aggregation, the numbers of hours in associations together are the best measure I have of the possibility of interactions between rhinos of two classes.

Adult females snorted at the highest rate; followed by adult males and sub-adults. All classes snorted most frequently at adult males and, in order of decreasing frequency, at adult females, sub-adults and calves. Calves often snorted at the same individual as their mothers did (n = 20) but also snorted independently - often during curious approaches to other rhinos while their mothers grazed.

(b) Honk (n = 510)

(i) Contexts (see Table 5.10).

There was considerable variation in the lengths of bouts of honking. Single honks were sometimes employed in a manner similar to snorts, as a keep away signal, but were usually preceded by one or more snorts. On the approach of another rhino, a single honk was heard on only 16 occasions

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

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.

† A series is defined in Table 5.9.

Table 5.10. The contexts in which each of nine types of sounds were heard from undisturbed rhinos.

Rhinos snorted apparently at no other particular individual on 35 occasions. On 10 of these occasions they responded to the noises made by other rhinos fighting; generally honks, bleats or squeak-pants which were sometimes heard and responded to from a distance of up to two kms. Rhinos snorted on three occasions after intensely sniffing the ground or the water in a wallow and on two of these occasions they also performed 'flehmen' (Section 5.3.2.3). On six occasions rhinos snorted on walking across a path, ditch, river or forest boundary, and one snort immediately followed the noisy fall of fruit from a nearby tree.

(ii) Responses (see Fig. 5.3).

Snorts were often the starts of encounters between rhinos (Section 5.4) and are therefore analysed in detail. Fig. 5.3 shows the frequency of various types of responses to snorts made in contexts of initial proximity (i to iii in Table 5.10). It can be seen that on 162 occasions (40.1%), the recipient rhino made no response (other than pricking its ears and quickly glancing in the direction of the snorts). On these occasions the actor either continued its normal activities (n = 85), fled at speed (n = 21) or, if in a wallow or a restricted place, moved aside to make room for the other rhino (n = 56). On 35 occasions (8.7%) the recipient fled almost immediately. On 55 occasions (13.6%), the recipient rhino responded with a snort. More complicated agonistic interactions developed on 67 occasions (16.6%). Other reactions to snorts included prolonged staring (n = 79), sometimes preceded by an inquisitive advance towards the actor (n = 15). On a further 21 occasions a tentative advance resulted in the rhino following the actor - sometimes over long distances.

Overall, the actor fled or moved aside on 95 occasions and the recipient on 74 occasions, and there were 235 occasions when the result of

Table 5.11. The actor-recipient matrix for snorts.

		RECIPIENT				Total
		A♂	A♀	S	C	
ACTOR	A♂	8 61.5	21 36.2	7 17.5	2 6.3	38 44.2
	A♀	43 74.1	111 71.6	43 39.4	29 18.7	226 81.6
	S	25 62.5	40 36.7	45 12.0	2 2.8	110 34.7
	C	13 40.6	39 25.2	11 15.5	13 14.3	76 34.5
	Total	89 103.5	211 76.2	106 33.4	46 20.9	452

The upper figure in each cell is the number of occasions the vocalization was recorded. The lower figure is the rate of vocalization per 100 hours that the two age and sex classes were observed in associations together, or, in the margins, the rate of vocalization per 100 hours of observation of each age and sex class in associations with other rhinos.

Rates for adult females and calves refer to associations other than between mothers and their own calves.

without a preliminary snort. Honks directed at other rhinos nearby usually followed some kind of disturbance which alarmed the rhino. For example, a sleeping rhino, on being suddenly woken, honked and lunged with its horn or tusks at a nearby rhino. Cows even attacked their own calves in this way (n = 2). On one occasion an exchange of honks took place between two sub-adults grazing 40 metres apart but, in general, rhinos rarely responded with a honk to an initial snort or honk from another individual.

Honks were heard most frequently during prolonged agonistic interactions - either face to face or during flight and prolonged chases (Section 5.4.2). During such interactions several honks were uttered in quick succession, and during chases they were usually in groups of three, each group separated by a few seconds. Although it was sometimes difficult to be certain which individuals were honking during prolonged interactions and chases, there was a positive correlation between honking and flight. After a brief encounter (context vii) it was always the fleeing rhino which honked (n = 51). In 39 of 47 closely observed chases, only the fleeing individual honked, and in eight cases both individuals honked. There was no correlation between honking and flight during face to face agonistic interactions. During playful sparring between two individuals, if one rhino honked the other normally responded with a honk. Lone individuals honked rarely: when they did, it was in response to the sounds of distant fighting (n = 2), or for no apparent reason.

(ii) Distribution among the sex and age classes (see Table 5.12).

The distribution of honks among the sex and age classes is very similar to the distribution of snorts (see Table 5.12). The rate of honking per 100 hours in aggregation was highest in adult females, followed by adult males, sub-adults and calves in that order (Table 5.12).

Table 5.12. The actor-recipient matrix for honks.

		RECIPIENT				Total
		A♂	A♀	S	C	
ACTOR	A♂	17 130.8	8 13.8	8 20.0	1 3.1	34 39.5
	A♀	36 62.0	50 32.3	31 28.4	7 4.5	124 44.8
	S	23 57.5	29 26.6	47 12.6	4 5.6	103 32.5
	C	9 28.1	13 8.4	3 4.2	2 2.2	27 12.3
	Total	85 98.8	100 36.1	89 28.1	14 6.4	288

The matrix is explained in Table 5.11.

Rhinos of all sex and age classes honked most frequently at adult males when they were with them, and least frequently at calves. Despite being one of the loudest vocalizations and audible from a great distance, the honk was heard less frequently than the snort.

(c) Bleat (n = 131) (see Tables 5.10 and 5.13)

Seventy-five (57.3%) of the bouts of bleating heard were during face to face agonistic interactions. Bleating was linked with submission; both contestants were heard bleating on only four occasions out of 71. The submissive individual typically backed away, bleating, with the head held low down near the ground (Section 5.4.2). Bleats were also heard during prolonged chases (n = 52 or 39.7%): they were normally associated with honks, and on 21 out of 22 clearly observed chases, only the fleeing individual bleated.

The bleat 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 (Table 5.13). Only weak adult males (Section 5.6.4.2) were recorded bleating.

Table 5.13. The actor-recipient matrix for bleats.

		RECIPIENT				Total
		A♂	A♀	S	C	
ACTOR	A♂	9 69.2	0 0.0	0 0.0	0 0.0	9 10.5
	A♀	21 36.2	27 17.4	3 2.8	1 0.5	52 18.8
	S	9 22.5	4 3.7	2 0.5	0 0.0	15 4.7
	C	1 3.1	1 0.5	0 0.0	0 0.0	2 1.3
	Total	40 46.5	32 11.6	5 1.6	1 0.5	78

The matrix is explained in Table 5.11.

(d) Roar (n = 101) (see Tables 5.10 and 5.14)

Roars were confined almost entirely to face to face agonistic interactions (n = 47) or prolonged chases (n = 34). The pursued individual was roaring during eight of 11 chases which I observed closely, and the pursuer roared on only two occasions. It was more difficult to be sure which individual was roaring during face to face agonistic interactions, but, among adult females, it appeared to be used more often by those which later 'won' the contest.

Table 5.14 shows a similar distribution of roars among the sex and age classes as shown for bleats in Table 5.13. The roar was used predominantly by adult females against adult males and other adult females, and by sub-adults against adult males.

Table 5.14. The actor-recipient matrix for roars.

	RECIPIENT				Total
	A♂	A♀	S	C	
ACTOR A♂	2 15.4	2 3.4	0 0.0	1 3.1	5 5.8
A♀	10 17.2	23 14.8	5 4.6	4 2.6	42 15.2
S	6 15.0	1 0.9	2 0.5	0 0.0	9 2.8
C	0 0.0	0 0.0	0 0.0	1 1.0	1 0.5
Total	18 20.9	26 9.4	7 2.2	6 2.7	57

The matrix is explained in Table 5.11.

(e) Squeak-Pant (n = 139) (see Tables 5.10 and 5.15)

Squeak-pants were heard most frequently from males during prolonged chases. They were associated with honks and bleats in 83 of the 100 prolonged chases which were seen or heard. In 30 of the 35 chases which were seen clearly, only the pursuer was squeak-panting. Adult males chased adult females or other adult males over long distances, and squeak-panted regularly throughout. Squeak-panting after a five or 10 minute chase often continued for up to another 10 minutes as the rhino wandered back along the path of the chase sniffing the ground. On two occasions adult males followed a female's tracks, squeak-panting as they went.

There were three cases of adult females using the squeak-pant as a contact call while searching for their calves. Adult and sub-adult females squeak-panted during oestrus when following an adult male (Section 5.5.2) and in response to scents on the ground. Sub-adults squeak-panted occasionally while sparring, and a sub-adult female once fled, startled by a sambhar's alarm call, and squeak-panted from 50 metres away for about 10 minutes.

Table 5.15. The actor-recipient matrix for squeak-pants.

		RECIPIENT				Total
		A♂	A♀	S	C	
ACTOR	A♂	10 76.9	21 36.2	11 27.5	1 3.1	43 50.0
	A♀	4 11.1	0 0.0	2 1.8	3 1.9	9 3.2
	S	1 2.5	0 0.0	2 0.5	0 0.0	3 0.9
	C	0 0.0	0 0.0	0 0.0	0 0.0	0 0.0
	Total	15 17.4	21 7.6	15 4.7	4 1.8	55

The matrix is explained in Table 5.11.

(f) Moo-grunt (n = 212) (see Tables 5.10 and 5.16)

The moo-grunt, although recorded less frequently than snorts or honks, is probably one of the most frequent vocalizations as it is of low intensity and does not carry over long distances. It was directed predominantly (78%) by calves at their mothers as a contact call.

A calf moo-grunted while grazing or walking near its mother (n = 101), at the approach of another individual (n = 28) and while lying or wallowing near or in physical contact with its mother (n = 24). A calf stopped moo-grunting when it returned close to its mother after wandering away (n = 23) and, after lying silently beside its mother, started moo-grunting on walking away from her (n = 17). A calf's rate of moo-grunting decreased after returning to its mother from a distance (n = 7). A mother rarely moo-grunted in reply to its calf (n = 8): and when she did so it was normally desultorily. On two occasions, a mother moo-grunted once in response to a long series of moo-grunts from its separated calf. On another occasion, however, it was the mother which moo-grunted frequently and the calf which remained silent, lying in physical contact with an adult male (Section 5.6.1). Calves moo-grunted frequently during play and before suckling (Section 5.6.1). One calf moo-grunted while being attacked by an adult male, and two others moo-grunted while following sub-adults. A lost 11 month old calf moo-grunted frequently during the two days that it was separated from its mother.

Sub-adults moo-grunted while grazing or walking together (n = 10), although answering moo-grunts were rare (n = 2). Sub-adults also moo-grunted while sparring with each other (n = 5) and one did so during an agonistic interaction with an adult male. On two occasions a sub-adult followed an adult male moo-grunting regularly on his trail, and on three occasions a sub-adult moo-grunted while following a cow-calf pair. An adult female once moo-grunted on being chased by an adult male and an adult male once moo-grunted while walking alone.

Table 5.16. The actor-recipient matrix for moo-grunts.

		RECIPIENT				Total
		A♂	A♀	S	C	
ACTOR	A♂	0 0.0	0 0.0	0 0.0	0 0.0	0 0.0
	A♀	1 1.7	0 0.0	0 0.0	8 0.8	9 3.2
	S	3 7.5	3 2.8	15 4.0	0 0.0	21 6.6
	C	2 6.3	165 16.6	2 0.4	0 0.0	169 18.8
	Total	6 7.0	168 60.6	17 5.4	8 0.9	199

The matrix is explained in Table 5.11, but note that associations between mothers and their own calves were included when calculating rates of moo-grunting.

(g) Shriek (n = 12) (see Table 5.10)

The shriek was heard only during intense agonistic interactions between rhinos (Table 5.10), but the rhinos were seen on only three occasions. Two of these three occasions were during mating or courtship chases when the adult female shrieked as she turned to face and fight the pursuing male (Section 5.5.2). On the third occasion the shriek was used by one of two adult males fighting each other in thick vegetation.

(h) Groan (n = 15) (see Table 5.10)

The groan was typically heard during a lull in face to face agonistic interactions when both participants stood facing each other, heads held rather low and mouths open preliminary to joining in combat again (Section 5.3.3). There was no correlation between the eventual winner of such an interaction and whether that individual groaned or not. The groan seemed to be a warning signal rather than a submissive signal, and was used while advancing slowly as well as while stationary. It was only once heard by both participants during the same interaction. On most occasions it was an adult female (n = 10) or sub-adult female (n = 4) which was groaning, and in most cases the groans were directed at adult females (n = 12).

(i) Rumble (n = 22) (see Table 5.10)

As in reactions to human disturbance (Table 5.9), the rumble was used most frequently by adult males (n = 15). They rumbled while walking or grazing alone (n = 3), on crossing the border of two vegetation types or a river bank (n = 2), while walking off, squirt-urinating, after smelling the ground intently (n = 4), in response to the approach of sub-adult males (n = 4) or after a brief interaction with another rhino (n = 2). Adult females and sub-adults rumbled after brief interactions with other rhinos (n = 5) or while grazing near other rhinos (n = 2).

(j) Humph (n = 17)

The humph was only used by rhinos fleeing after brief encounters with other rhinos; it was sometimes preceded by exchanges of snorts and honks. It had little social significance beyond being a signal that the individual was fleeing.

5.3.1.3 Reactions to sounds played back on a tape-recorder

Rhinos showed interest in all rhino sounds played back near them. Most individuals' reactions were either to glance briefly in the direction of origin of the sounds or else to move off quickly. However, some adult males showed particular interest in sounds of fighting such as honks, squeak-pants, bleats and roars, and approached the tape-recorder, often squirt-urinating and dragging their feet (Sections 5.7 and 6.2.2.2). Some adult males moved off in the direction of real sounds of fighting, and sub-adult and adult females also showed interest in such sounds on a few occasions, particularly during oestrus (Section 5.5.2).

5.3.2 Olfactory communication

Rhinos often paused, while walking, to sniff the ground, and showed particular interest in the sites of urination and defecation of other rhinos. They followed each other by scent: on several occasions I watched one of a temporarily separated pair of rhinos rejoin its companion by sniffing along its tracks. Pedal scent glands occur in *Rhinoceros* (Cave, 1962), and it is likely that olfactory signals include odours left on the trail from these glands, in addition to those of the urine and dung. There are some special actions associated with urination and defecation, particularly in adult bulls, apparently related to the leaving of persistent scent-marks in the environment. Urination, defecation and other associated actions of relevance to scent marking are described below.

5.3.2.1 Urination

I describe here two methods of urination used by rhinos, the contexts in which they were used and the frequencies with which each sex and age class urinated. I saw rhinos urinating during 390 of my encounters with them and I counted 622 occurrences of urination. I later divided these occurrences into 433 series of from one to over 20 urinations that were of the same type (see below) and appeared to be triggered by the same stimuli. Most of these series lasted only a few minutes, but some lasted much longer. For example, if a rhino was grazing steadily and urinating once every few minutes over a period of an hour or more, all the urinations were counted as a single series.

(a) Methods of urination

(i) Normal urination.

The normal method of urination was in a regular continuous stream which fell to the ground less than half a metre behind the rhino. Both males and females invariably lifted their tails and curled them over their backs or held them straight out behind them, during urination. Rhinos stopped all activity while urinating normally: this is in marked contrast to squirt-urination (see below).

(ii) Squirt-urination.

Both males and females are capable of squiring their urine behind them in one or more jets. Males can urinate with the greatest force, squirting jets of urine up to three or four metres backwards (see Plate 28). The number of squirts per urination in males varied from one to 17 with a mean of 2.7 (n = 143). The urine was often sprayed onto vegetation behind the rhino up to a height of more than a metre. Although females can squirt their urine up to about 1.5 metres behind them, they normally did so only during oestrus (Sections 5.5.1 and 5.5.2). Both sexes squirt-urinated while stationary, walking or running.

(b) Contexts and frequency of urination by rhinos of different sex and age classes

Fig. 5.4 shows the contexts in which 433 series of urinations were recorded. Urination was particularly frequent in certain contexts: for example, 120 (27.7%) of the series of urinations occurred during reactions to the observer, and 113 (26.1%) appeared to be in response to other rhinos or to scents on the ground. In Table 5.17 the contexts of urination are shown for each sex and age class of rhinos. Adult males were seen urinating more frequently than any other sex and age class (see below) and a higher proportion of their urinations were in response to the observer, to the sight or scent of other rhinos, or on crossing a line feature.

Table 5.18 shows that adult males urinated four times more frequently

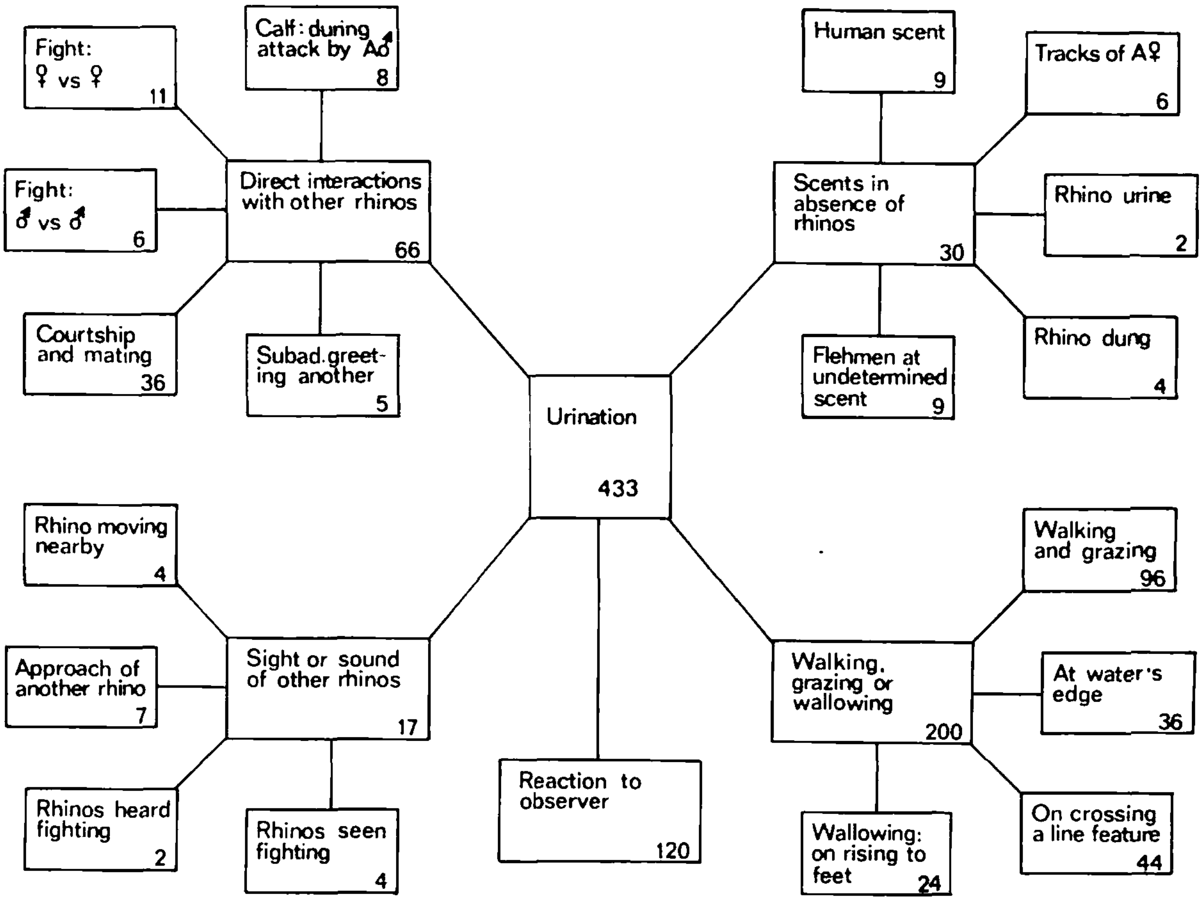


Fig. 5.4. The contexts in which rhinos were observed urinating (n = 433).

Table 5.17. The contexts of urination by rhinos of each sex and age class.

Class	Number of observations				Total
	A♂	A♀	S	C	
Context					
(i) Disturbed by observer	75 (34.7%)	27 (22.7%)	16 (24.2%)	2 (6.5%)	120 (27.7%)
(ii) As a reaction to other rhinos	41 (19.0%)	21 (17.6%)	13 (19.7%)	8 (25.8%)	83 (19.2%)
(iii) As a reaction to scent	17 (7.0%)	4 (3.4%)	4 (6.1%)	5 (16.1%)	30 (6.9%)
(iv) While walking or grazing	32 (14.8%)	32 (26.9%)	24 (36.4%)	8 (25.8%)	96 (22.2%)
(v) While wallowing	4 (1.9%)	14 (11.8%)	4 (6.0%)	2 (6.5%)	24 (5.5%)
(vi) On entering water	12 (5.6%)	16 (13.5%)	2 (3.0%)	6 (19.3%)	36 (8.3%)
(vii) On crossing a line feature	36 (16.1%)	5 (4.1%)	3 (4.5%)	0 (0.0%)	44 (10.2%)
Total	217	119	66	31	433

Table 5.18. The relative frequencies of normal and squirt-urination by rhinos of each sex and age class.

	Number of series of urination seen			Rate (number of series per 100 hours of observation)
	Squirt type	Normal type	Total	
Class				
A♂	206	11	217	52.0
A♀	7	112	119	11.3
S	15	51	66	11.9
C	3	28	31	3.4
Total	231	202	433	

Total rates of urination:-

A♂ > A♀ ≈ S > C $p < 0.001$

Overall $\chi^2 = 489.0$ $p < 0.001$

Other p values:-

	A♂	A♀	S
A♀	<0.001		
S	<0.001	>0.05	
C	<0.001	<0.001	<0.001

Squirt urination vs Normal:-

Squirt urination > Normal : A♂ $\chi^2 = 300.1$ $p < 0.001$

Normal urination > Squirt : A♀ $\chi^2 = 145.9$ $p < 0.001$

S $\chi^2 = 28.7$ $p < 0.001$

C $\chi^2 = 27.5$ $p < 0.001$

during observation periods than adult females or sub-adults did. Furthermore, 48% of adult males' series of urinations were of more than a single urination, compared with only 12% of adult females', 10% of sub-adults' and 6% of calves'. Table 5.18 also shows that adult males not only urinated more frequently but were the only class to squirt-urinate significantly more frequently than they urinated normally.

The higher rate of urination by adult males was not a result of a greater number of reactions to the observer or longer spent with other rhinos. Table 5.19 shows the numbers of occasions on which each sex and age class urinated during reactions to the observer compared with their

Table 5.19. The frequency of urination by rhinos of each sex and age class in reaction to the observer.

Class	Number of occasions disturbed by observer	Number of occasions when rhinos urinated
A♂	323	75 (23.2%)
A♀	705	27 (3.8%)
S	403	16 (4.0%)
C	601	2 (0.3%)

Overall $\chi^2 = 186.7$ $p < 0.001$

total number of reactions to the observer. Adult males urinated on 23% of 323 occasions whereas the other sex and age classes urinated on only 3% of 1,431 occasions (Table 5.19). Similarly, adult males were less frequently near other rhinos (Section 5.2, Table 5.8) yet urinated more frequently in reaction to them ($\chi^2 = 153.1$ $p < 0.001$ on rates of urination per hour in aggregations). One of the most marked differences between adult males and other classes was the frequency of urination in crossing line features such as the boundary of two vegetation types (see Table 5.17). This is discussed below in Sections 5.6.4.2 and 5.7.

(c) Behaviour associated with squirt-urination

Squirt-urination in adult males was often accompanied by other behaviour patterns peculiar to adult males. These included vigorously rubbing the head and horn in low vegetation, and walking stiff-legged, dragging the hind toes in the earth, thus creating a pair of parallel furrows in the ground.

A rhino performing this type of display often wandered on and off any paths, breaking down vegetation on either side in a wide trail which crossed and recrossed the main path. The result was a trail of broken vegetation with furrows in the ground, and urine covering the vegetation and upturned earth. Drag-marks were often more than 100 metres long, and one extended for 600 metres. They were associated with dung-piles on eight occasions, either starting at them or passing through them (*e.g.* Plate 29).

Both foot-dragging and head-rubbing were strongly associated with squirt-urination: I saw foot-dragging on 38 occasions, on 37 of which it was accompanied by squirt urination and on six by head and horn-rubbing. Table 5.20 shows the contexts in which foot-dragging occurred: they are similar to those in which squirt-urination was observed by adult males (Tables 5.17 and 5.18). On six occasions foot-dragging accompanied urination after a male had chased a female. The male pushed down trees with his horn on two such occasions, and once he charged a small tree at high speed and hit it with his horn. On 12 occasions there was no immediately preceding interaction with another rhino. Five of these observations were at the border of grassland and riverine forest as the rhino entered the forest.

Table 5.20. The contexts of foot-dragging by adult males.

(i)	Disturbance by observer	11
(ii)	Reaction to other rhinos	10
(iii)	Reaction to scent on the ground	5
(iv)	While walking/grazing	7
(v)	While crossing boundaries of vegetation types	5
	Total	38

Apart from direct observations of foot-dragging, I also found 59 places where there were signs of foot-dragging. The numbers of drag marks found in each calendar month over the study period are shown in

Table 5.21, together with the rates of finding drag marks per 100 hours in the field. the differences are not significant, although the rates are highest between April and July. Foot-dragging is discussed in Sections 5.6.4.2 and 5.7.

Table 5.21. The frequency of observations of drag-marks in each calendar month.

	Number of drag marks	Number of drag marks per 100 hours in the field
January	7	1.1
February	4	1.3
March	9	1.1
April	20	2.4
May	14	1.6
June	8	1.3
July	17	2.5
August	4	1.1
September	3	0.6
October	3	0.6
November	5	0.9
December	3	0.9
Total	97	1.4

Overall χ^2 on pairs of months: $\chi^2 = 9.42$ $p > 0.05$

5.3.2.2 Defecation

(a) Contexts

I observed defecation 124 times and also collected data on the accumulation of dung-piles. Only 13% of 1,080 freshly deposited faeces examined were more than 10 metres from other visible dung. This indicates that rhinos are stimulated to defecate when they encounter rhino dung. I confirmed this by direct observations, although there was a complication in that rhinos often defecated in reaction to disturbance by the observer. Table 5.22 shows the numbers of defecations observed during normal activities and after disturbance, on and away from dung-piles. During normal activities rhinos defecated on dung-piles on 88% of occasions (n = 94).

The members of cow-calf pairs and sub-adult groups often defecated within a few minutes of each other even if they were not at a dung-pile. Rhinos tended to choose particular spots to defecate even in the absence of a dung-pile. Bushes, the bases of trees and clumps of grass were favoured, and there was a very strong attraction to any kind of hollow in the ground. Dung-piles normally grew up as a result of other rhinos reacting both to the smell of the dung and to its position. This was particularly noticeable when men had been digging ditches around their fields or around the park boundary. Rhinos defecated when they crossed the ditches, but a sizeable dung-pile accumulated only when the rhinos were confined by fences or deeper ditches to a single crossing place. The sunken stone markers for the airstrip in the park were continually being used as defecation sites.

Table 5.22. The frequencies of defecation by rhinos of each sex and age class on and away from dung-piles and its relation to disturbance by the observer.

	Number of observations					Rate of defecation per 100 hours of observation
	During normal activities		In reaction to observer		Total	
	On dung-pile	Away from dung-pile	On dung-pile	Away from dung-pile		
Class						
A♂	16	4	5	2	27	6.5
A♀	24	11	1	12	48	4.5
S	16	1	1	6	24	4.3
C	12	5	0	2	19	2.1
?	5	0	0	1	6	
Total	73	21	7	23	124	

Rates of defecation:-

Overall: $\chi^2 = 14.9$ $p < 0.01$ df = 3

A♂ > A♀ = S > C $p < 0.02$

On dung-pile vs away from dung-pile:-

Overall: $\chi^2 = 6.53$ $p < 0.05$

(b) Frequency of defecation in each sex and age class

Table 5.22 shows the numbers of defecations per 100 hours of observation for each sex and age of rhinos. It can be seen that adult males defecated significantly more frequently than the other sex and age classes. Furthermore, the proportion of defecations on dung-piles was highest for adult males. There are smaller differences between the sex and age classes if defecations in response to disturbance by the observer are excluded from the comparison.

(c) Behaviour associated with defecation

Rhinos normally walked straight up to a dung-pile or defecation site and evacuated their bowels either over it or beside it. On several occasions a rhino swivelled its hindquarters round to bring them over the dung-pile, but a rhino stepped backwards onto a dung-pile on only three occasions.

I saw undisturbed rhinos sniffing the defecation site before defecation on 17 (18.1%) of observations, and 15 of these sites were dung-piles. A rhino mouthed previously deposited dung before defecating on four occasions, and ate its own dung immediately after defecation on two occasions. Mouthing of dung and coprophagy were recorded for calves and sub-adults only.

Rhinos normally walked off immediately after defecation, but on seven occasions I saw a rhino scrape backwards with one or both hindfeet, thus spreading earth over the freshly deposited dung. I saw signs of dung-scraping on seven other occasions, and tracks indicated that the rhino had backed up to defecate on two of these occasions. Ten of the 14 scrapes observed were on dung-piles, and in one case no fresh dung had been added to the pile. Three observations were made of rhinos walking up to a dung-pile and lifting their tails in readiness to defecate, then lowering them again and walking away without defecating. All sex and age classes were implicated in scraping; some from direct observation and some from evidence of tracks. Dung-scraping is compared in Sections 5.7 and 6.3 with similar behaviour in other species of rhinos.

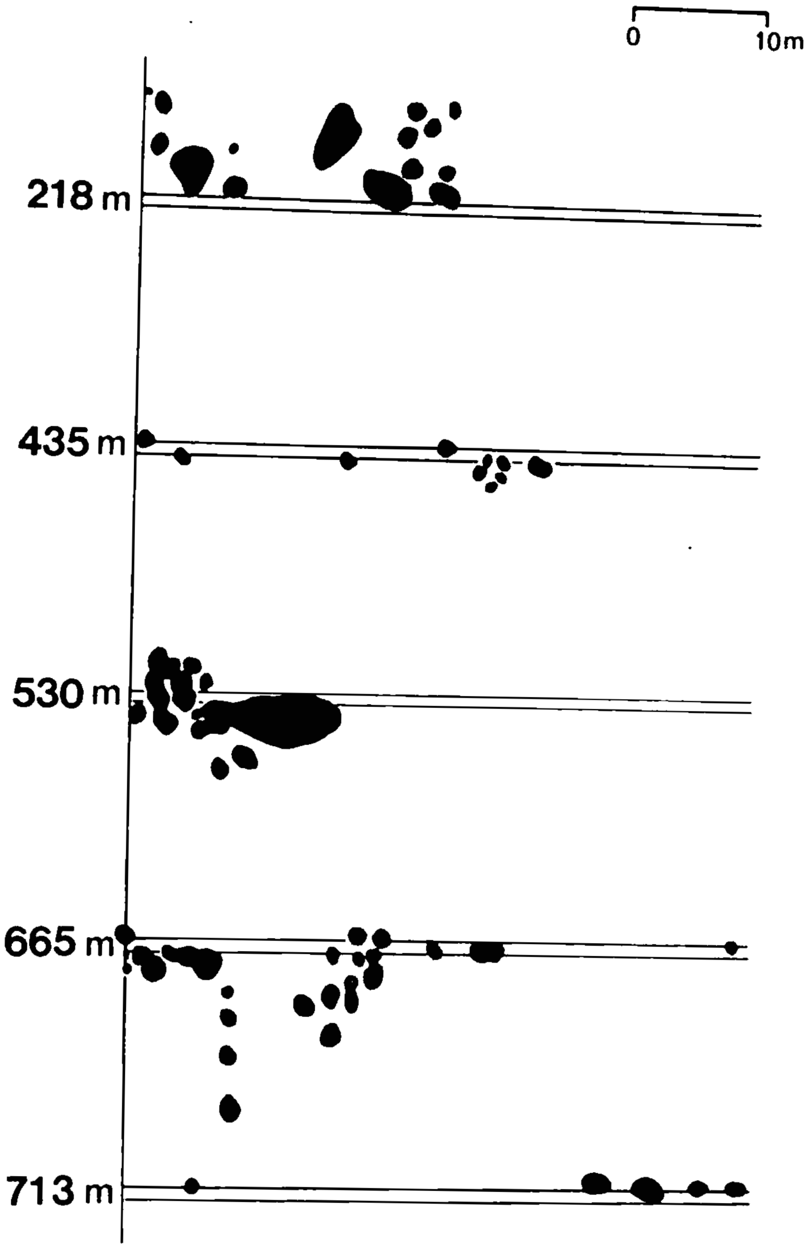
(d) The origins and frequency of use of dung-piles

Table 5.23 shows the types of locations of 180 dung-piles on straight-line transects in the Sauraha study area. Dung-piles were often found at the borders of riverine forest and grassland or on the banks of rivers and wallows, and also occurred on paths, especially at path junctions and beside man-made roads and ditches. Such locations are similar to those where adult males tended to urinate (Section 5.3.2.1).

Table 5.23. The types of locations of 180 dung-piles on straight-line transects at Sauraha.

Type of location	Number of dung-piles
1. On rhino paths:	
(a) Near a wallow	26
(b) Near a boundary between vegetation types or on a road	23
(c) Other locations	79
	128
2. Away from rhino paths:	
(a) In burnt grassland	48
(b) In woodland	4
	52

Fig. 5.5 shows plans of dung-piles along a path in open grassland. Dung-piles varied in the degree of piling up, and some were scattered over a wide area. (I defined dung-piles (Section 5.1.4) as including all defecations within 10 metres from any other.) The maximum height of



Measurements to the left refer to the distance from the origin: no dung was recorded on the intervening sections of the path.

Fig. 5.5. A plan showing the distribution of rhino dung along a path in tall grassland.

piles recorded was 80 cms, but most piles were only about 20-30 cms at their highest points.

The frequency of use of dung-piles varied directly according to the number of rhinos using the area. Piles which had been disused for many weeks were suddenly re-used by several rhinos in succession when rhinos moved into an area which provided a temporary food supply. Twenty-five dung-piles were checked in block F on 10 consecutive days in December 1973 and July 1974. In December 14 dung-piles were used a total of 36 times and in July 24 dung-piles were used a total of 123 times. The dung-piles at the base of a cliff where rhinos come to a mineral lick during the winter months (Section 4.3.9), were used frequently during the winter but hardly ever during the monsoon. The dung-piles in unburnt areas of grassland very rarely had fresh dung on them in December and January, but after burning, and during the period of grass regrowth, most of the old dung-piles were used again and some new ones were created.

I recorded all dung and defecations on set circuits in the Sauraha study area (described in Section 5.1.4). On a six kilometres circuit in the Sauraha study area, there were 25 defecation sites on 19 March 1975 and 54 on 24 May 1975. Between these dates, my brother and I walked the circuit on 38 days. During these days rhinos defecated on the original 25 sites 237 times; on the other hand, the 29 additional sites were used only 38 times, only four of them being used more than once.

Thus, established piles are more likely to be added to than single defecations. Sites of single defecations are only likely to develop into dung-piles if on a well frequented rhino route. As rhinos tend to defecate when they find some dung, those rhinos on well-frequented routes are far more likely to defecate on piles than away from piles simply because of the numbers of rhinos which have preceded them and defecated on the route.

5.3.2.3 Reactions to scents

Perfunctory sniffing of the air, ground or vegetation was so frequent that I did not record each occurrence. However, I did record the details of 103 prolonged reactions by rhinos to scents on the ground or the vegetation. During long observation periods from machans, I was able to watch the reactions of rhinos to the tracks or urine of rhinos which I had seen earlier. There were 20 reactions to rhino dung, 35 to rhino urine or tracks and eight to human urine or tracks. On 40 occasions I could not determine what the rhinos were sniffing. Adult males accounted for 35 of the 103 observations.

On 62 (60.7%) of the occasions, a rhino sniffed intently with its nose close to the ground and then either raised its nose with the head held low, or raised its whole head high in the air, curling back the lips and holding the position for a few seconds (Plate 30). This action has been described as the *flehmen* response in a wide variety of mammals (Estes, 1972). On 26 occasions the rhino repeatedly sniffed the ground and performed *flehmen* - sometimes up to eight times within a few minutes.

Table 5.24 shows the frequency of *flehmen* by rhinos of different sex and age classes, and the scents to which they reacted. It can be seen that adult males and sub-adults performed *flehmen* significantly more frequently than adult females and calves. There was also a significant difference between the adult males and the other sex and age classes in the relative numbers of male and female rhinos' tracks or urine to which they responded (Fisher exact probability test $p < 0.002$). Adult males reacted predominantly to female tracks or urine; on five occasions after or during courtship or mating, and on four occasions on finding and sometimes following a female's scent trail. Other sex and age classes reacted more often to adult male tracks or urine, normally not after direct interactions of any kind.

Urination took place on 11 occasions within a few minutes of *flehmen*. Snorts ($n = 3$) and moo-grunts ($n = 2$) also accompanied *flehmen*, although there were no other rhinos nearby. Licking urine from vegetation ($n = 4$) and eating the vegetation ($n = 4$) preceded or followed *flehmen* on several

Table 5.24. The frequency of flehmen *as a reaction to various scents by rhinos of each sex and age class.*

	Number of observations of flehmen in response to:				Total	Rate (number per 100 hours of observation)
	Tracks or urine of					
Class	Male rhino	Female rhino	Human	Unknown scent		
A♂	2	9	1	9	21	5.0
A♀	3	1	2	6	12	1.1
S	9	2	1	7	19	3.4
C	2	1	1	6	10	1.1
Total	16	13	5	28	62	

Differences in rates of flehmen:-

Overall $\chi^2 = 38.2$ $p < 0.001$

χ^2 between each pair of age and sex classes:-

	p values		
	A♂	A♀	S
A♀	<0.001		
S	>0.05	<0.01	
C	<0.001	>0.05	<0.01

A♂, S > A♀, C $p < 0.01$

occasions. *Flehmen* was accompanied on two of these occasions by defecation and urination.

For 28 of the observations of *flehmen*, the scent to which the rhinos reacted was not known. Two adult males performed *flehmen* on entering the same wallow within an hour of each other, and an adult female and her calf did so within a few minutes of each other at the same place on a river bank. Eight of these 28 occurrences of *flehmen* were at small stagnant wallows or pools just after a rhino had entered and either drunk a little water or sniffed the surface. Another eight occurrences directly followed interactions with other rhinos and were probably in response to the scent of those rhinos. One sub-adult male was chased off by an adult female; he returned 15 minutes later and performed *flehmen* where she had urinated.

Male rhino urine and tiger urine placed at two points on a river crossing point received varying attention from rhinos. No rhinos performed *flehmen* at the tiger urine but two females performed *flehmen* at the rhino urine having deviated from their path to reach it. Dung placed at various points along rhino paths was defecated on, but there was no difference between the rhinos' reactions to local dung and to dung brought from Tiger Tops to Sauraha.

5.3.3 Visual and tactile communication

Rhinos used visual and tactile signals less strikingly than they used sounds. I distinguished 20 types of movements or gestures which seemed of potential communicatory significance, although some are better interpreted as directly functional actions rather than as ritualized displays. I have divided them into three main groups according to the contexts in which they occurred:-

(a) prolonged (more than two minutes) physical contact between individuals
(b) peaceful interactions and play behaviour
(c) agonistic interactions.

Vocalizations were frequently associated with the special action patterns described below.

(a) Physical contact

Rhinos often maintained physical contact with each other for long periods, normally while resting either in wallows or on dry land. The individuals involved normally knew each other well. Five types of physical contact were distinguished.

(i) Flanks touching flanks (n = 698).

Rhinos stood or, more normally, lay together with their flanks touching (*e.g.* Plate 25). Sometimes one or both individuals rubbed its flank against its companion.

(ii) Head on flank or head (n = 219).

One rhino put its head up on its companion's flank, rump or head, and either kept it there motionless or rubbed or nuzzled its companion (*e.g.* Plate 31). This occurred most frequently while resting in physical contact, but also during other activities. One individual was normally the more active in any pair, in keeping its head in contact with its companion, but on some occasions the behaviour was reciprocated and both individuals lay with heads resting on each other, or engaged in mutual nuzzling and rubbing. The head region attracted most attention during nuzzling, especially the horn and immediately behind the horn. The ears, the chin and the folds of the skin around the neck were also frequently nuzzled, particularly by calves.

(iii) Licking (n = 40).

Prolonged licking of a companion's skin was seen on 40 occasions. Typically one individual was lying down and its companion stood over it and licked for periods of up to 10 minutes at exactly the same point on the skin (*e.g.* Plate 32). A fold of skin was often the site chosen for licking. Normally the lower lip only, but sometimes both lips, were rested on the skin, and the tongue was moved rapidly in and out about 100 times per minute. Licking was sometimes accompanied by chewing motions which were continued after leaving the companion.

(iv) Mounting (n = 18).

Mounting consisted of raising the forelegs onto a companion's head, flank or rump while it was either lying or standing. A calf sometimes climbed right up onto its mother's back while she was wallowing (*e.g.* Plate 33). Most observations were of mounting the flanks near the head and the head itself.

(v) Nose to nose nuzzling (n = 58).

Both rhinos of a pair stood facing each other and touched noses. They sometimes opened their mouths and lightly mouthed each other's horns.

(b) Play and peaceful interactions

The five types of behaviour described under prolonged physical contact also occurred in shortened forms during play and peaceful interactions. Rubbing, nuzzling and mounting were all combined in playful interactions between two companions. Nuzzling developed into open-mouthed caressing of the horn and biting of the ears and was frequently mutual. Apart from these more active forms of physical contact, five other components of play and peaceful interactions were distinguished.

(i) Slow approach (n = 114).

The rhino advanced slowly towards another, often pausing with head stretched forward, low, near the ground. The slow relaxed movements were in contrast to the direct approach described below under agonistic interactions, and almost always preceded peaceful interactions.

(ii) Head bobbing (n = 23).

The rhino bobbed its head rapidly up and down from the ground to above shoulder level. There was sometimes a circular or waving component to the movement. This action was performed either while approaching or standing near another rhino.

(iii) Sparring (n = 182).

Sparring developed from nose to nose nuzzling and was a form of playful fighting. Individuals faced each other with their horns touching and delivered mild blows with the horn and side of the head to their opponent's head while parrying their opponent's blows (*e.g.* Plate 34).

Circular and bobbing movements of the head frequently developed as each rhino tried to get beyond the other's guard. Horns clashed audibly and, during nuzzling, the mouth was often open and attempts at biting occurred.

(iv) Running around (n = 17).

Rhinos frequently interspersed periods of active nuzzling, caressing and sparring with spells of running and gambolling around their companions. The two companions normally stayed within a few metres of each other but some individuals (mainly calves) ran over 100 mètres from their companion and back again.

(v) Playing with sticks (n = 6).

Calves picked up sticks in their mouths on four occasions and played with them by running around their mothers, shaking and flinging their heads like young puppies. The sticks were small in diameter and less than 1½ metres in length. On two occasions adults also played with branches and sticks, pushing and pulling them while lying in wallows.

(c) Agonistic interactions

Encounters between rhinos varied greatly in duration and in the extent of interaction between individuals. Some rhinos fled immediately on the approach of another individual,even in the absence of any threatening gestures from the latter. Some rhinos took to immediate and panicky flight on hearing noises which could have been made by approaching rhinos. However, prolonged and complicated sequences of agonistic behaviour took place on many occasions and sometimes resulted in injuries. The more complicated sequences of behaviour observed are described in Section 5.4.2. Ten simple components of agonistic behaviour are described here. The 'n's refer to numbers of observations during 384 fully observed interactions between individuals of known sex and age class (see Section 5.4.2).

(i) Sudden turn (n = 62).

On detecting the presence of another individual, the rhino turned suddenly to face the other. I distinguished between sudden panicky turns and the more normal slow and unhurried turns.

(ii) Prolonged stare (n = 359).

Having turned to face an intruder, the rhino stood still,watching its movements. The head was held either low down near the ground or high up with ears erect and facing forwards.

(iii) Lip curl (n = 304).

While facing another individual with head held high, the rhino snorted or honked as described in Section 5.3.1.2; during the vocalization the lips were curled back and the mouth opened slightly, displaying the lower tusks. The head was stretched forwards high up level with the spine, and the lips curled up and forwards so that the prehensile tip of the upper lip projected towards the opponent and vibrated with the snort. The ears were held erect and directed forwards. This display also occurred without the accompanying snorts.

(iv) Advancing steps (n = 241).

The rhinos took several steps in the direction of its antagonist. The head was normally lowered,and honks and snorts often accompanied the approach, which was normally quick and led right up to the antagonist.

(v) Charge (n = 92).

The charge differed from advancing steps in that the rhino trotted forward silently and lowered its head as it approached the other rhino (as in Plate 9).

(vi) Horn to horn stare (n = 141).

The rhino stood with its head low down near the ground and its horn pressed up near to or against the other's horn. The posture was held for short periods before and during more serious attacks as the two animals tried to push each other backwards.

(vii) Tusk display (n = 145).

The mouth was opened wide and the tusks bared (Plate 35). This display was accompanied by honks and bleats and was performed either with the head held high, or, more commonly, with the head held low down near the ground. It was often coupled with bleating and slow backing away from an approaching rhino. The ears were often held back during this display.

(viii) Horn clash and lunge (n = 99).

Blows were delivered with the horn and the tusks to the head of the antagonist. Horns sometimes clashed but more often no contact was made, and the lunges, which were accompanied by short rushes forward and loud roars, generally stopped short of their target. Lunges were often made from side to side as well as forwards and the head was always held low down. Lunges were mainly aimed at the head region but, if the opponent tried to turn round, blows were delivered to the neck, flanks and rump and a chase sometimes developed during which serious injuries were inflicted (*e.g.* Plates 36 and 37). Prolonged chases took place over several kilometres with accompanying loud vocalizations.

(ix) Submissive lying (n = 8).

On a few occasions a rhino reacted to the approach of another by lying down and making no effort to defend itself. When wallowing, individuals submerged their bodies so that only their horns, eyes and ears were above water. They either faced the approaching rhino or, in the case of some calves, turned their backs and hid their faces in the bushes at the side of the wallow.

(x) Tail curling.

Although this behaviour almost certainly has no signal value it did seem to be an indicator of tension in rhinos. The tail was curled up in a spiral on the back or held straight out behind. The tail was always curled during defecation and urination but also frequently during chases and face to face agonistic encounters.

5.4 Interactions between individuals

Peaceful and agonistic interactions between rhinos were observed most frequently in or near wallows and on open grazing areas. Fig. 5.6 shows the locations of all observations during which such interactions occurred. More than 60% of the interactions took place at wallows, where I knew by experience that the rhinos congregated, and where I spent most time watching. Although peaceful interactions frequently occurred away from wallows, agonistic interactions probably took place predominantly at the places where I watched. Many of the interactions were accompanied by loud vocalizations, and such sounds were frequently heard coming from the directions of the wallows.

5.4.1 Peaceful interactions

5.4.1.1 Physical contact

(a) Contexts

More than half of the observations of prolonged physical contact between rhinos (n = 366) were made while rhinos were wallowing together and touching flanks. The remaining observations were made either while rhinos were resting together on dry land or during feeding periods.

On 20 occasions, slight disturbances such as my approach or the approach of other rhinos caused calves to move into contact with their

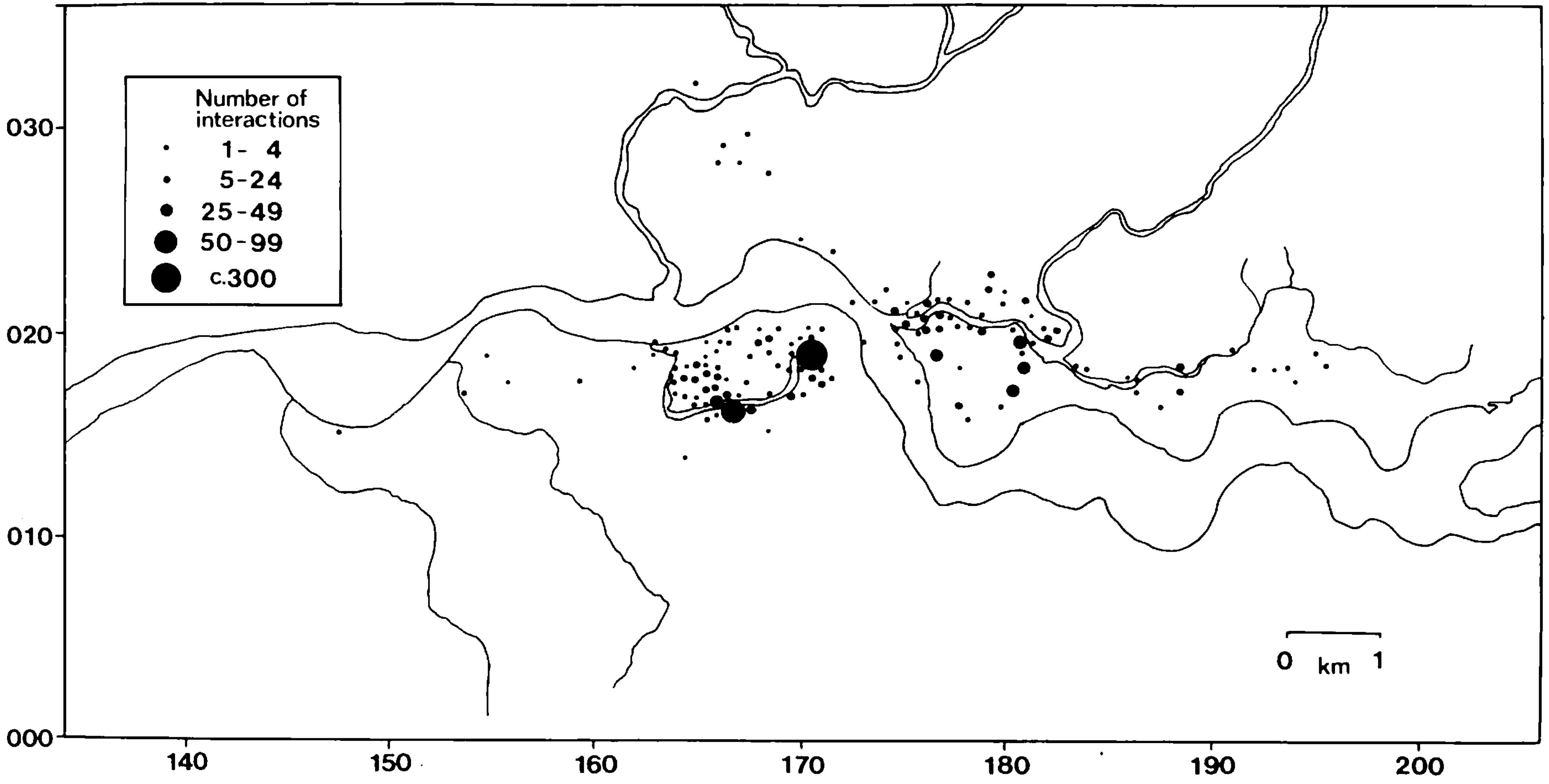


Fig. 5.6. A map of the Sauraha study area showing the locations of all observations during which peaceful or agonistic interactions took place (n = 1,185).

mothers and remain in contact for some time afterwards (*e.g.* Plate 38). This behaviour was seen in young and old calves alike and was also observed while cows and calves were grazing together. In the latter cases the calf sometimes ran over 20 metres to its mother - on one occasion over 100 metres - and stood with its head up on her flank or neck. The mother sometimes reciprocated the gesture by putting her head on the calf's back. When wallowing, a calf sometimes lifted its head onto its mother's back without shifting position and let it slide off again shortly after the potential danger was past. No such reassurance contact was observed between sub-adults or other sex and age classes.

On the rare occasions when calves or sub-adults were in physical contact with adult males, they were wallowing, and the calf or sub-adult put its head up on the flank or rump of the adult male. Adult males often attacked sub-adults that made such approaches, and only certain well known individuals were allowed to remain in physical contact for long periods (see Sections 5.6.3, 5.6.4.2 and 6.2.2.2). Sub-adults on two occasions approached adult males which were wallowing, and licked their flanks. Apart from one case of a sub-adult licking an adult female, all other observations of licking were between sub-adults or between cows and calves, although not necessarily their own calf. In all these cases the animal being licked rolled over in a relaxed way as if inviting its companion to lick other parts of its body.

(b) Frequency and social distribution

Prolonged periods of physical contact between rhinos were observed on 366 occasions. Simple flank to flank contact was maintained for some time on almost all these occasions. Resting of the head on a companion's flanks or head, mounting, licking and nose to nose nuzzling were more rarely observed, and there were differences between the sex and age classes in the frequency with which they displayed these behaviour patterns. Table

5.25 shows the total numbers of observations of physical contact with other rhinos for various sex and age classes and the percentage of these totals during which the five forms of physical contact were seen. During normal flank to flank contact the individual which initiated contact was normally the calf in cow-calf pairs and the sub-adult in all combinations which included sub-adults. Calves and sub-adults also displayed the rarer forms of physical contact to a greater extent than adults (Table 5.25).

Table 5.25. The frequencies for each sex and age class of various forms of prolonged physical contact between rhinos.

	Total number of observations of prolonged physical contact	Number of observations and percentages of the total for the five forms of physical contact:				
		Flanks on flanks	Head on head or flanks	Mounting	Licking	Nose to nose
Class						
A♂	27	23 (85%)	6 (22%)	-	-	1 (4%)
A♀	259	249 (96%)	20 (8%)	-	6 (2%)	5 (2%)
S	179	165 (92%)	47 (26%)	-	18 (10%)	38 (21%)
C	265	260 (98%)	146 (55%)	18 (7%)	16 (6%)	14 (5%)

The total lengths of time spent by each sex and age class of rhinos in physical contact with others is shown in Table 5.26, expressed both in hours and as a percentage of the time spent by those sex and age classes in associations together (see Table 5.8). I watched rhinos for long periods while they were wallowing, and as they were more likely to be in physical contact while wallowing than during other activities, the proportions of time spent in physical contact should be regarded only as comparisons between different sex and age classes and not as indicators of the overall proportion of time spent in physical contact.

Cows with calves spent 10.6% of their time in physical contact with their calves. They occasionally lay in physical contact with other rhinos, but only for 1.7% of the time that they were in associations. Calves were

Table 5.26. The time spent in physical contact by rhinos from each pair of sex and age classes.

	Hours in physical contact				
	A♂	A♀ with C	Single A♀	S	C
A♂	0	-	-	-	-
A♀ with C	0	0	-	-	-
Single A♀	1.3 (n = 8) (5.0%)	0.6 (n = 1) (0.9%)	0	-	-
S	3.3 (n = 15) (8.3%)	1.9 (n = 3) (0.9%)	2.1 (n = 4) (5.5%)	17.5 (n = 71) (9.4%)	-
C	0.7 (n = 4) (2.2%)	95.5 (n = 240) (10.6%)	0.5 (n = 2) (0.8%)	4.3 (n = 15) (6.0%)	0.1 (n = 2) (0.1%)
Total for each sex and age class	5.3 (6.2%)	99.3 (11.1%) (1.7% if time in association with own calf is excluded)	4.5 (7.9%)	46.6 (12.5%)	101.2 (11.2%) (2.5% if time in association with mother is excluded)

The upper figure in each cell is the number of hours spent in physical contact.

The lower figure in each cell is the number of hours in physical contact expressed as a percentage of the time spent by those sex and age classes in associations with each other.

'n's are the numbers of observations of prolonged physical contact.

in physical contact with others on a few more occasions, mostly with accompanying sub-adult females. The frequency of physical contact among other sex and age classes was highest in sub-adults and lowest in adult males; this parallels the time spent in associations by these classes (shown in Table 5.8). The proportion of time spent by calves in physical contact with their mothers decreased slightly with age (see Section 5.6.2).

5.4.1.2 Play and peaceful behaviour

(a) Contexts

Play and peaceful behaviour between sub-adults and between cows and calves normally took place after the individuals had been resting together for some time at a wallow. Such behaviour between sub-adults and cows or sub-adults and calves normally followed immediately after meeting. A slow approach was usual and one individual often bobbed its head or waved it rapidly from side to side while walking or grazing towards the other rhino. Head bobbing seemed to act as a gesture of peaceful intentions: it was also seen occasionally in agonistic interactions as an appeasement gesture. The approached rhino rarely displayed the same behaviour pattern but usually stretched its nose forward and nuzzled the newcomer. Cows and sub-adults normally grazed peacefully beside each other after such a greeting, while calves and sub-adults normally extended the playful behaviour into sparring contests.

(b) Frequency and social distribution

Play and peaceful behaviour was observed on 105 occasions. Sparring (n = 91) was the most commonly observed form of such behaviour and it was normally preceded by a slow approach and nuzzling, with occasional head bobbing. Table 5.27 shows the numbers of observations of sparring and associated behaviour patterns between different sex and age classes and the corresponding frequencies per 100 hours of association. It can be seen that sparring took place predominantly among sub-adults and between sub-adults and calves. Although there were 31 sparring contests between two sub-adult males and only four between two sub-adult females, there was no significant difference between the sexes in the numbers of sparring contests per 100 hours of observation together, because sub-adult male associations were so much more common (Section 5.2).

The remaining observations of play and peaceful behaviour involved mainly cows and calves. Prolonged periods of physical contact often developed into play as the calf ran around the mother and played with sticks. Such behaviour was more common in the younger calves (Section 5.6.2).

Table 5.27. The frequency of sparring between rhinos of each sex and age class.

	A♂	A♀	S	C
A♂	0	-	-	-
A♀	2 3.4	0	-	-
S	1 2.5	2 1.8	61 32.6	-
C	1 2.5	6 0.6	15 21.1	3 6.6
Total for each sex and age class	4 4.7	10 3.6	140 44.2	28 12.7

The upper figure in each cell is the number of observations of sparring, and the lower figure is the rate of sparring expressed as the number of observations per 100 hours of association. Rates for adult females and calves refer to associations other than between mothers and their own calves.

5.4.2 Agonistic interactions

(a) Contexts

Whenever two or more rhinos approached each other, either at wallows or on grazing grounds, there was usually a reaction by at least one of them. Most interactions were short, and one individual normally fled or moved aside. The most prolonged interactions were between adult males and between adult males and adult females. These often developed into chases over long distances. The variations in the types and outcomes of interactions between different sex and age classes are described below.

(b) Frequency and social distribution

I watched the full sequence of agonistic behaviour following an encounter between two or more rhinos of known sex and age class on 384 occasions; parts of such sequences were seen or heard on more than 100 further occasions, on many of which I could not determine the classes of the individuals involved. The frequencies of the major components of agonistic behaviour described in Section 5.3.3, and the sequences in which they occurred, are shown in Fig. 5.7 for the 384 fully observed interactions. It can be seen that 64.5% of the interactions were short, and lunges and severe attacks took place only rarely.

The frequencies with which each component of agonistic behaviour was displayed by different sex and age classes are shown in Table 5.28. It can be seen that young animals (sub-adults and calves) fled at once more often than adults ($\chi^2 = 76.33 \quad p < 0.001$). Adult males chased more often than others did. I often saw only the later stages of the prolonged chases, and these observations are not included in Table 5.28. I could see clearly both the fleeing and pursuing rhinos on 70 occasions, and on 56 of these occasions the pursuing individual was an adult male. Adult females performed more of most agonistic displays than other sex and age classes did: their interactions frequently continued for some time as horn to horn confrontations, whereas those involving adult males and younger animals came to quicker conclusions when one of the individuals fled or moved aside.

The frequencies with which agonistic interactions were observed between rhinos of each sex and age class are shown in Table 5.29. There are striking differences between the distributions of agonistic and peaceful interactions (see Table 5.27). The high rate of agonistic behaviour among adult males corresponds to their solitary habit (Section 5.2) and the absence of mutual peaceful interactions (Table 5.27). Only among sub-adults was the frequency of peaceful interactions higher than that of agonistic interactions. Calves and sub-adults were not aggressive among themselves, but sub-adults were involved in agonistic interactions with adults of both sexes. Adult females showed a high rate of agonistic interactions among themselves and with adult males: many of the latter took

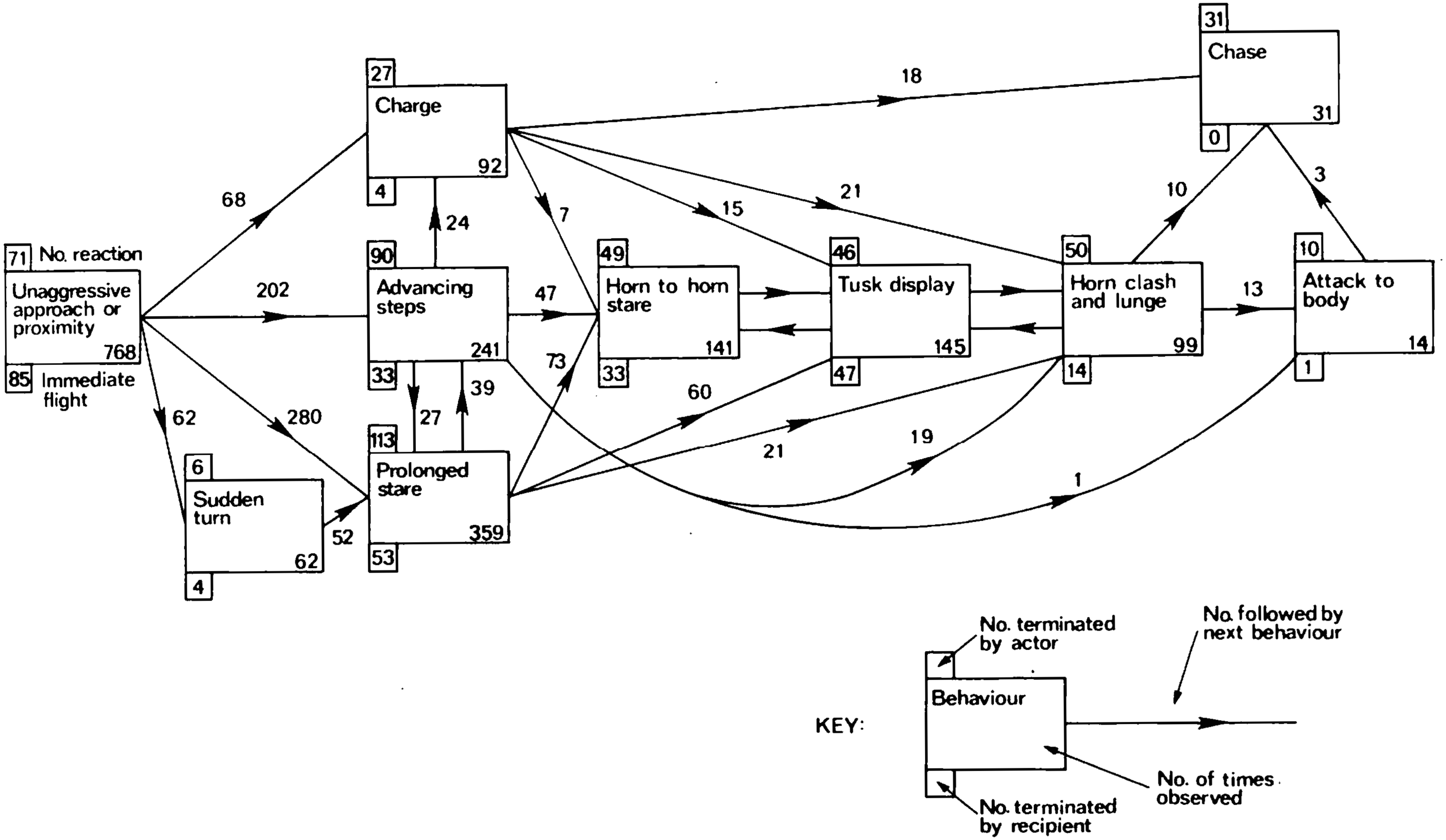


Fig. 5.7. The frequencies and sequences of the major components of agonistic behaviour in 384 fully observed interactions between rhinos.

Table 5.28. The frequencies of agonistic behaviour components displayed by rhinos of each sex and age class.

	A♂ (n=151)	A♀ (n=358)	S (n=185)	C (n=74)	Total (n=768)
Component					
(i) Sudden turn	7 (4.6%)	43 (12.0%)	9 (4.9%)	3 (4.1%)	62 (8.1%)
(ii) Prolonged stare	24 (15.9%)	236 (65.9%)	67 (36.2%)	32 (43.2%)	359 (46.7%)
(iii) Lip curl	15 (9.9%)	212 (59.2%)	56 (30.3%)	21 (28.4%)	304 (39.6%)
(iv) Advancing steps	61 (40.4%)	112 (31.3%)	49 (26.5%)	19 (25.7%)	241 (31.4%)
(v) Charge	11 (7.3%)	71 (19.8%)	2 (1.1%)	8 (10.8%)	92 (12.0%)
(vi) Horn to horn stare	26 (17.2%)	66 (18.4%)	44 (23.8%)	5 (6.8%)	141 (18.4%)
(vii) Tusk display	9 (6.0%)	114 (31.8%)	21 (11.4%)	1 (1.4%)	145 (18.9%)
(viii) Horn clash + lunge	17 (11.3%)	77 (21.5%)	5 (2.7%)	0	99 (12.9%)
(ix) Submissive lying	0	2 (0.6%)	3 (1.6%)	3 (4.1%)	8 (1.0%)
(x) Tail curling	Not recorded accurately				
(xi) Immediate flight	7 (4.6%)	13 (3.6%)	44 (23.8%)	21 (28.4%)	85 (11.1%)
(xii) Prolonged chase	19 (12.6%)	8 (2.2%)	2 (1.1%)	2 (2.7%)	31 (4.0%)

The upper figure in each cell is the number of observations.

The lower figure is the frequency of each component expressed as a percentage of the total number of interactions recorded for that class.

place during courtship (Section 5.5.2).

(c) Responses to agonistic behaviour

The sequences of agonistic behaviour shown in Fig. 5.7 give some idea of the responses during interactions. Either one individual fled immediately on the approach of another, or there was some type of horn to horn confrontation which varied in intensity but sometimes led to both individuals lunging at each other with tusks and horns, and occasionally

Table 5.29. The frequency of agonistic interactions between rhinos of each sex and age class.

	A♂	A♀	S	C
A♂	20 307.7	-	-	-
A♀	67 115.5	97 125.2	-	-
S	41 102.5	88 80.7	33 17.6	-
C	12 37.5	36 23.2	15 21.1	8 8.8
Total for each sex and age class	160 186.0	385 139.0	210 66.2	79 35.9

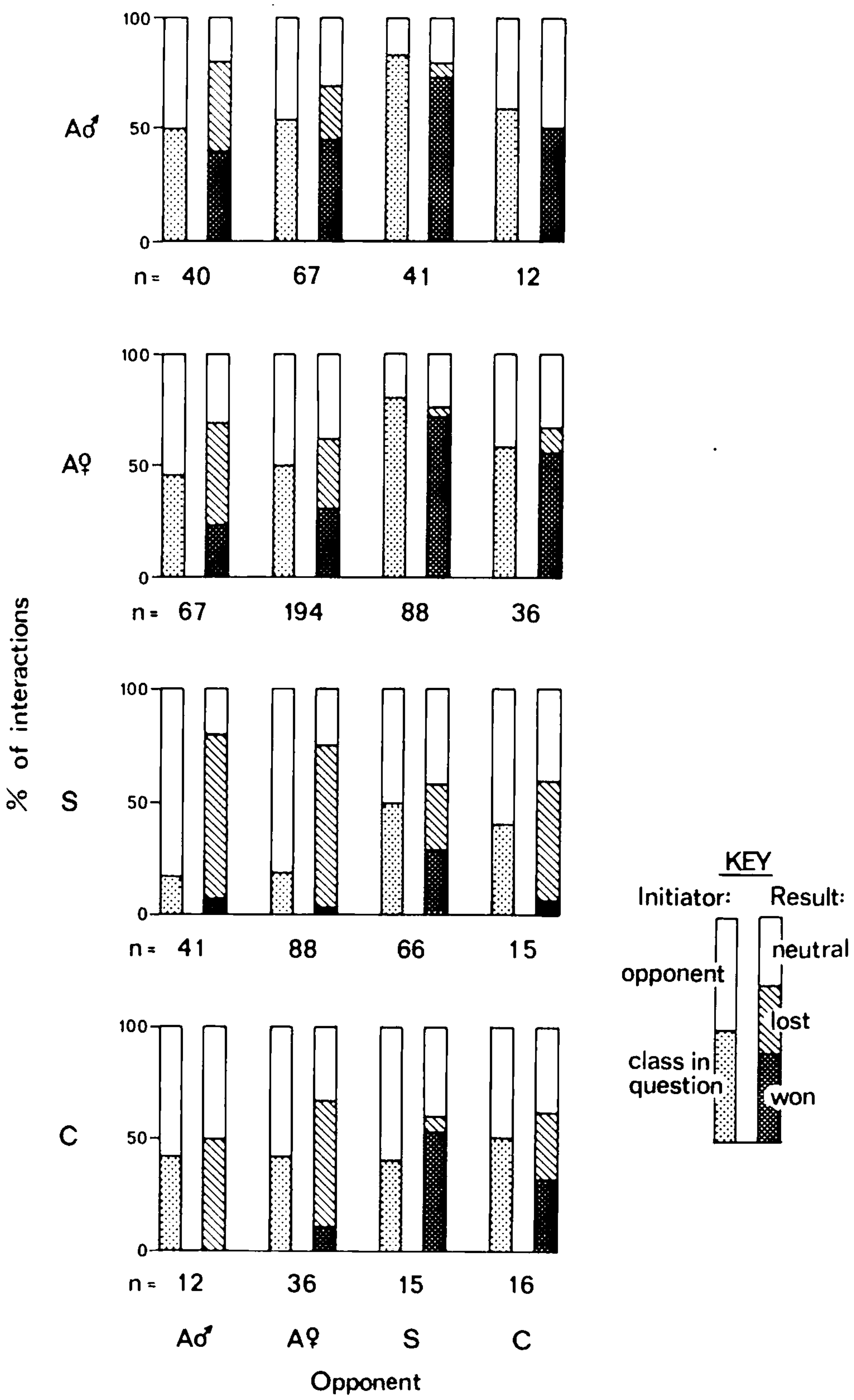
The upper figure in each cell is the number of agonistic interactions observed, and the lower figure is the rate of agonistic interactions expressed as the number of observations per 100 hours of association. Rates for adult females and calves refer to associations other than between mothers and their own calves.

to severe injuries. Fig. 5.8 summarizes the results of interactions between rhinos of each sex and age class in a simplified manner as

(i) neutral
(ii) fled or moved aside (lost)
(iii) opponent fled or moved aside (won).

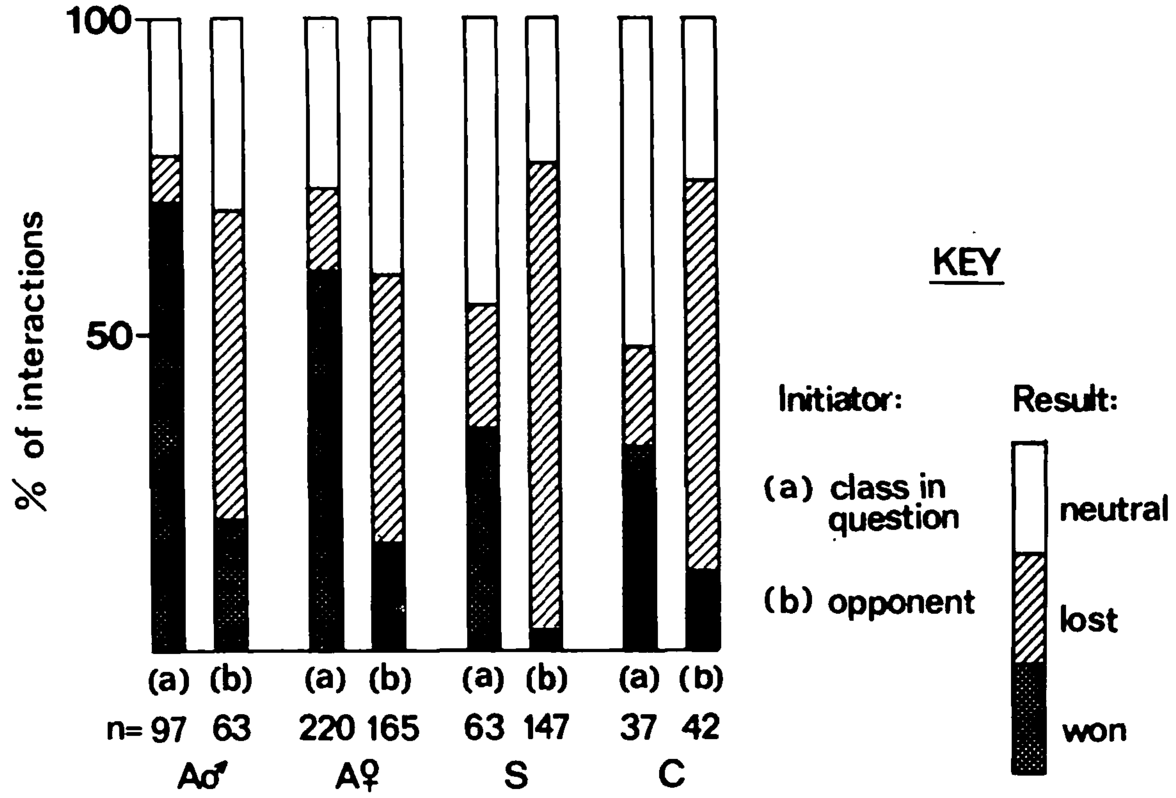
The proportions of interactions initiated by rhinos of each class are also shown.

Fig. 5.8 shows that adult males won the highest proportion of their interactions, followed by adult females, calves and sub-adults in that order. Every class won interactions with sub-adults more than with any other class. Fig. 5.9 shows the results of interactions for rhinos of each class, according to whether they initiated the interactions. The initiator won on significantly more occasions than the opponent did. Sub-adults initiated significantly fewer interactions than adults or calves



Wins: Losses + Neutral   Overall $\chi^2 = 80.03$ $p < 0.001$
Percentage of wins highest in Ao > A♀ > C ≈ S $p < 0.05$

Fig. 5.8. A summary of the results and initiators of agonistic interactions between rhinos of each sex and age class.



Proportions of interactions initiated: Overall $\chi^2 = 50.00$ $p < 0.001$
Percentage of interactions initiated by Ao ≈ A♀ ≈ C > S $p < 0.001$

Initiator won on 56.4% of occasions)
Opponent won on 13.6% of occasions) $\chi^2 = 182.4$ $p < 0.001$.

Fig. 5.9. The relationships between initiation and the results of agonistic interactions involving each sex and age class.

did (Fig. 5.9), but even sub-adults won 19% of the interactions which they initiated. On the other hand, sub-adults won only 3% of 147 interactions which their opponents initiated whereas adult males won 21% of the 63 interactions which their opponents initiated and almost all the interactions which they initiated themselves. These results are discussed in Section 5.6.

5.5 Reproductive behaviour

5.5.1 Oestrus

External signs of oestrus were difficult to see, so information on reproduction is limited to that obtained from recording births (Section 3.7) and from behavioural observations. It was shown in Section 5.2.1 that adult males were usually solitary and, when found in aggregations, were most frequently with adult females. Most of these aggregations and most of the brief agonistic interactions observed (described in Section 5.4.2) were the result of rhinos converging independently on wallows and favoured grazing grounds. During short observations it was difficult to determine whether associations between adult males and females were being actively maintained or not. However, a series of short observations of the same pair of rhinos in different places on a single day indicated that the rhinos were moving around together. During longer observations it was often clear that one individual was following another.

Oestrus was confirmed by observed copulation or the female's acceptance of the male's advances (Section 5.5.2.1) on only six occasions; all during actively maintained associations between adult males and females, which were known to have lasted intermittently for three days or more. The behaviour patterns observed before copulation (Section 5.5.2.2) were also seen on other occasions; all during actively maintained associations. Therefore, 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.

I had difficulty in determining the duration of oestrous periods and the frequency with which they occurred. There were considerable problems (described in Section 2.3) in locating individual rhinos at will, or in following them for long periods. Thus, on most occasions when I saw a pair of rhinos actively associating on a certain day, neither of them were located on the following day, so I did not know whether they were still together or not. Furthermore, even if I relocated one or both of a pair of rhinos, I could not be sure that their association had terminated. It was quite possible for two individuals to be separated temporarily and for one to rejoin the other very quickly by following its tracks (as described in Section 5.3.2).

The intervals between successive sightings of individual females in actively maintained associations with adult males are plotted in Fig. 5.10. The intervals show a bimodal distribution with peaks at 1-2 days and 28-32 days. This is not caused by an uneven distribution of sightings, as all nine females which contributed to the data were seen frequently during the intervals between their associations with adult males. The mid-point between the two peaks in Fig. 5.10 is at 15-16 days; therefore, for the purposes of this analysis, if the interval between two observations of a female in actively maintained association with an adult male was less than 15 days, both observations were regarded as within the same oestrous period. If the interval was 15 days or more, I regarded the two observations as in different oestrous periods.

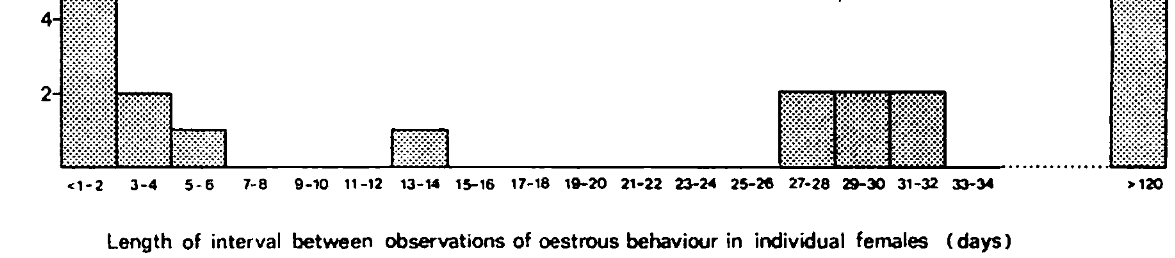


Fig. 5.10. The lengths of intervals between successive observations of oestrus in individual females.

(a) Lengths of oestrous periods

I was not able to follow individuals for long periods or to find them at will, so I was unable to determine the lengths of oestrous periods. Fig. 5.11 shows the spans of my observations of known females actively associating with males within one oestrous period. Twenty of the 29 occurrences of oestrus were observed on only one day, and on some occasions the females were seen away from males on the next day. However, other females were later seen with males again, and during the longer spans the females were seen away from adult males on almost as many occasions as they were seen with them. For instance, during one 10 day period I saw a certain adult male and female together on four days and apart on three days, and on the remaining three days I saw neither of them. Thus, although most of the occurrences of oestrus which I observed were not shown to last more than one day, I suspect that there were more intermittent associations with adult males which spanned two days or more.

(b) Frequency of oestrus

Most associations between adult males and females and hence most oestrous periods were probably not detected, because of the difficulties of locating and following individuals. Only 43 occurrences of oestrus were recorded during the study period.

Recurrences of oestrus were most frequently at intervals of 27-32 days (Fig. 5.10). These are the intervals between the beginnings or first detections of actively maintained associations. Further evidence on the frequency of oestrus comes from one female which was seen copulating and then, 42 days later, was seen accepting a male's advances, and seemed about to copulate again.

Fig. 5.12 shows the frequencies of oestrus observed in each month of the study period. Fig. 5.13 compensates for differences in searching

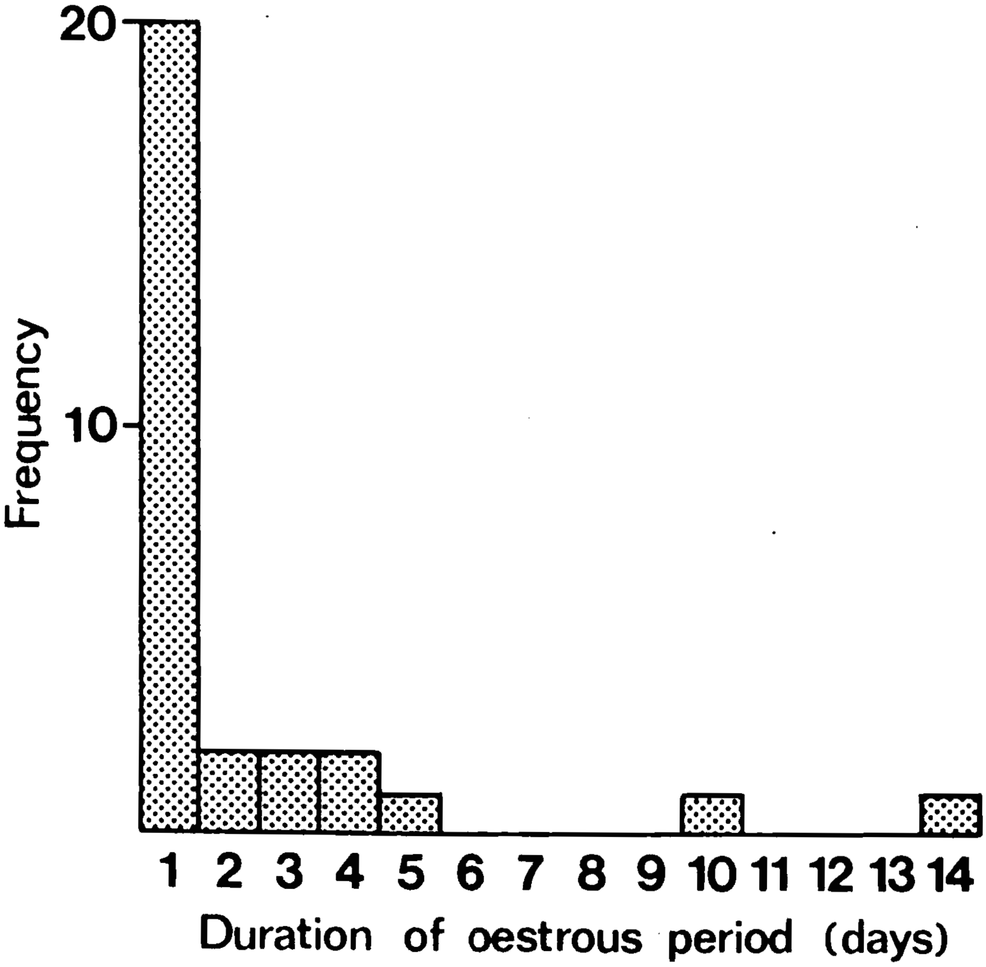
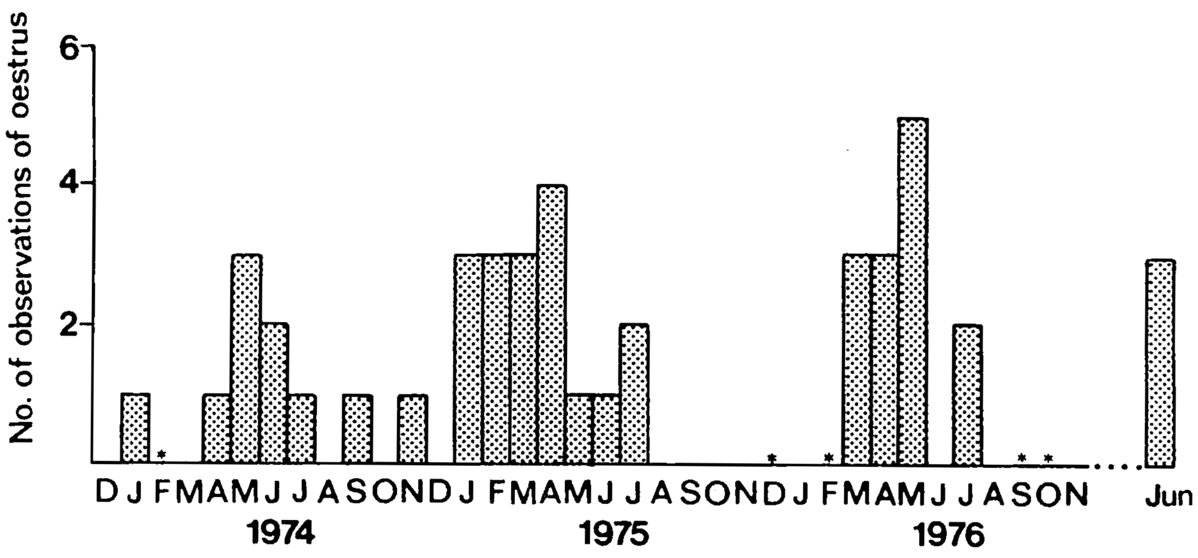


Fig. 5.11. Frequency distribution of the duration of oestrous periods.



* denotes less than 3 days spent in the field.

Fig. 5.12. The numbers of observations of oestrus in each month.

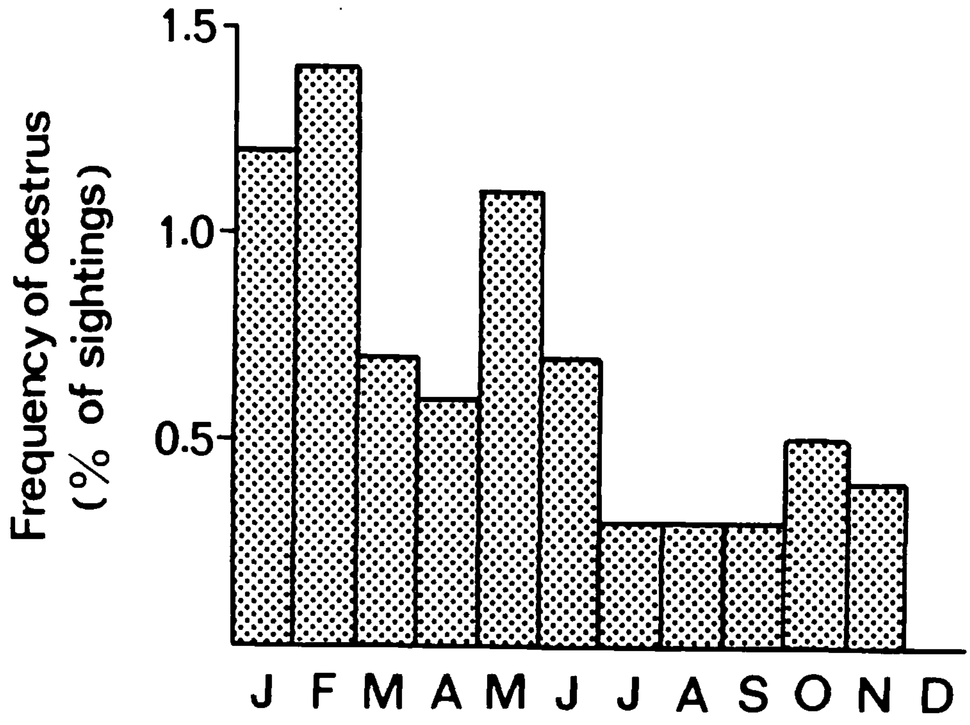


Fig. 5.13. Seasonality of oestrus.

effort by expressing the frequencies of oestrus as a percentage of the numbers of sightings of rhinos in each calendar month. The distribution of recorded oestrus is not significantly different from the distribution of all sightings of rhinos over the 12 months (Kolmogorov-Smirnov test $p > 0.20$). No significant peaks in birth rate were found either (Section 3.7.2). Oestrus was slightly more frequent between January and June than between July and December, and births (Section 3.7.2) were slightly more frequent in July and August and between November and February. The gestation period of the Indian rhino is about 16 months (Lang *et al.*, 1977; see Table 6.1). Thus there is no convincing correlation between the slight seasonal peaks in oestrus and births, although the monsoon peak in births corresponds to the spring peak in oestrus. However, this is not surprising as (a) a high proportion of observed oestrous periods did not result in conception (see below) and (b) we are looking at a set of oestrus records and a set of birth records that are a year out of step.

In conclusion, the evidence suggests that oestrus recurs at intervals of 27-42 days throughout the year but with a slightly higher frequency between January and June.

(c) Timing of oestrus in relation to the age of the accompanying calf

The earliest recorded post-partum oestrus was deduced from a subsequent birth to have been just over one month after the birth and almost immediate death of the previous calf (Section 3.7.1). Apart from that case, no oestrus was recorded in females with calves of less than 10 months old. Fig. 5.14 shows the frequency of recorded oestrus in females, according to the ages of their calves. It can be seen that the median age of the calves of oestrous females was 22 months.

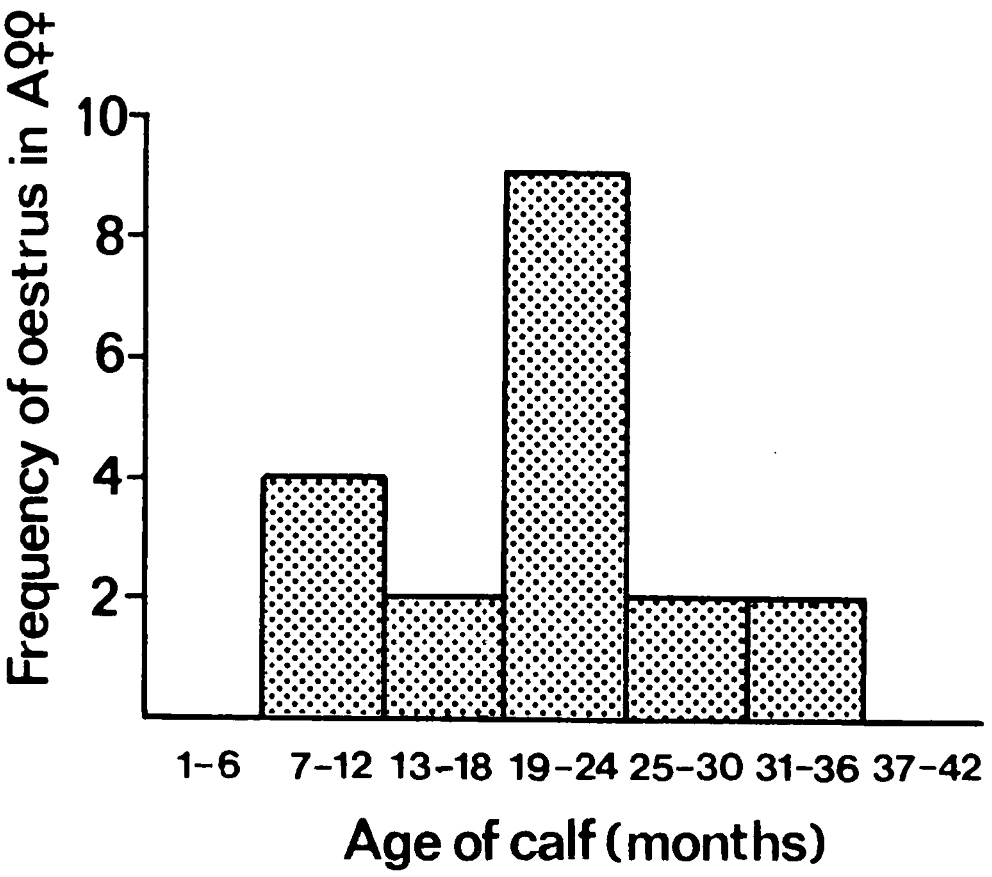


Fig. 5.14. The frequency of oestrus in females, according to the ages of their calves.

5.5.2 Behaviour of adult males and females during oestrus

5.5.2.1 Pre-mating behaviour

On the three occasions that mating was observed it was preceded by several distinct behaviour patterns. Four main types were distinguished:-

(a) Accompanying
(b) Fights and chases
(c) Peaceful approaches and physical contact
(d) Mounting

These components of behaviour, also observed on other occasions, are described below.

(a) Accompanying (n = 28)

One animal, normally the male, persistently accompanied an animal of the opposite sex. Adult males often followed the tracks of adult females, sniffing the ground intently from time to time and performing *flehmen* (Section 5.3.2.3). Having located a female, the male accompanied her intermittently for periods of up to several days, occasionally making attempts to approach her more closely. The female often repelled advances of males by simply turning and snorting (see Section 5.3.1) although more serious fights sometimes developed (see below).

On most occasions the female was accompanied by a calf, and all three individuals grazed, rested and wallowed near each other. If they became separated, the male relocated the female by following her tracks. On a few occasions an adult female was seen persistently following an adult male, and on these occasions the male showed little interest in the female.

(b) Fights and chases (n = 37)

I distinguished between brief agonistic encounters and prolonged fights and chases in Section 5.4.2. Most of adult males' approaches to females were repelled by the females simply turning and snorting. However, on some occasions the male continued to advance head down until the male and female were facing each other horn against horn. Both rhinos tried to push each other back, often roaring loudly between lunges, horn-clashes and tusk-displays. During lulls in such fights, both rhinos sometimes backed away and the male often *flehmened* after smelling the ground nearby. The male normally restarted the fight by charging at the female's head or neck. The female lay down submissively on some occasions and then the male made no attack but either stood over her or lay down nearby, sometimes opening and shutting his mouth as if biting the air. An adult male put his head under an adult female's neck on one occasion, and then lifted her front legs off the ground and turned her right over on her back: she lay apparently winded for about a minute while the male stood over her and then walked away.

On such occasions the male attacked the female only if she moved again. If the female ran, the male chased her; sometimes over several kilometres. Both sexes squeak-panted but the male did so more frequently, while the female either honked or bleated (see Section 5.3.1.2). The tails of both male and female were usually held curled up or horizontally extended behind. Both sexes urinated frequently during chases and fights, and the smell of urine was very strong nearby. Severe wounds were often inflicted, especially if the female turned to run from a horn to horn position and received blows from the male on her flanks and rump.

A calf accompanying the female was normally left behind during prolonged chases, and sometimes was not reunited with its mother for up to two days (see Section 5.6.2). The male usually gave up chasing eventually, and either followed the female by scent or wandered off in another direction. In either case the male normally continued to squeak-pant for several minutes after the chase and, on one occasion, a male put his head down, charged and hit a small tree with his horn.

(c) Peaceful approaches and physical contact (n = 10)

If a male and female were still together after a chase, the male often approached the female from behind and put his head up on her rump. The male continued to try to keep his chin resting on the female's rump, whether she stood still or walked. The male often squirted urine as he walked, and his penis was often partly enlarged, with the red glans showing. The penis also became enlarged sometimes when males were grazing alone or near a female (see Section 6.3.5). Placing of the chin on the rump of the female was a preliminary to mounting,but the posture was often held for periods of several minutes with no attempt made at mounting.

The female also squirted urine in little jets and on some occasions advanced on the male, squeak-panting softly and urinating more frequently than him. She sometimes followed the male persistently even if he trotted away, and on two occasions I saw a female put her head between the male's hind-legs and sniff at his penis.

(d) Mounting (n = 5)

Males' attempts at mounting females were very clumsy, and successful mounting took a long time. After prolonged periods of following a female and resting his chin on her rump, a male made intention movements with his forefeet as if to lift them up onto her back. Launching himself forward with his hind-legs he often managed to raise himself so that his neck rested on the female's rump, only to slide off again. I made only one observation of the whole sequence of a successful mounting; it proceeded in stages with the male working his way forward with his forefeet resting on the female's back until they were in front of her front cross folds and his chin was above her neck fold. In this case no intromission took place and the male slid off again as the female walked forward. This was the main cause of failure in most attempts at mounting, as it is very difficult for the male to raise himself forward on the female's back and intromit, at the same time as keeping step with the female by moving the hind-legs.

5.5.2.2 Mating behaviour (n = 3)

Copulating pairs of rhinos were seen on three occasions, on all of which the male had already mounted and intromitted (Plate 39). The male's forefeet occasionally slipped down the female's flanks, but each time he replaced them on her back. The female mainly stood still, looking around and moving her feet occasionally. Whenever she walked forward the male had to suffle along making small quick steps with the hind-legs. At regular intervals the male jerked his hind-quarters, wagged his tail once, then lifted his tail to a horizontal position where it quivered for a moment erect and taut with the whole hind-quarters also shivering momentarily. His head rose at this point and he struggled to thrust his hind-quarters and keep his feet up on the female's back.

Between these spasms there was no action on the part of the male apart from occasional shuffling, grunting and flapping of the ears. The interval between the spasms varied from 45 seconds to two minutes 50 seconds (n = 57) with a mean of 65 seconds. Towards the end of the copulation, the female's movements increased in frequency and she often opened and shut her mouth, gasping like a fish, before moving forward. The male struggled increasingly to stay mounted and he eventually slid off on his belly. I watched copulations for 30, 48 and 60 minutes but never saw the start; so they lasted longer than this.

5.3.2.3 Post-mating behaviour (n = 3)

After the male had dismounted, the female either walked away fast and disappeared from view, or grazed about 40-50 metres away. On two occasions the male stood still, grazed for a few minutes and then lay down. On one occasion he performed *flehmen* and retraced his and the female's tracks, bobbing his head up and down as he went. Although the pair always separated immediately after copulation they were seen together again within two days after two of the observed copulations. No further copulations or attempts at mounting were observed during these periods. It is possible that this behaviour is adaptive as it ensures that no other male mates with the female.

5.5.3 Oestrous behaviour in pregnant females

Three females which displayed oestrous behaviour were known from subsequent parturitions to have been pregnant at the time of their associations with an adult male. One 12 months pregnant female was accompanied also by her three year old female calf, and it is possible that the male was attracted by the calf's oestrus. He accompanied the pair for three hours, grazing near them and on one occasion having a horn to horn encounter with the female while the calf stood behind her mother.

On two other occasions the females were without calves and they were *c.*12 and *c.*15 months pregnant. No aggressive interactions took place between the males and females during the observations which lasted eight hours and two and a half hours respectively. The two pairs moved together, grazed and lay down together and in both cases the female put her head on the male's flank, in one case licking it for over 10 minutes (discussed in Section 6.3.5).

5.5.4 Maternal behaviour

5.5.4.1 Parturition

The behaviour of females changed considerably shortly before parturition: they become more aggressive in encounters with man or other rhinos, and were found less often in the company of other rhinos.

I saw pregnant females with very swollen udders on several occasions, but there was always an interval of several days, during which I did not see them, before they reappeared with their new-born calves. Although I did not observe any births, I saw four calves which were between two and seven days old. In all cases, the new-born calves were near thick grassland or forest, and I suspect that females tended to choose areas of thick vegetation in which to give birth. However, females around the edge of the park must have given birth in the open or under sparse cover,in places considerably disturbed by villagers and domestic stock. Two villagers told me that they had watched births during the afternoon at the edge of open stock-grazing areas outside the park.

5.5.4.2 The behaviour of females with young calves

Females with new-born calves very rarely formed aggregations with other rhinos: they were particularly wary and attacked other rhinos if they were approached. However, this behaviour did not persist for long: there were no significant overall differences between females with calves of different year classes in the tendencies to form aggregations or to attack other rhinos. There was a difference, however, in their behaviour towards the observer.

Fig. 5.15 shows the frequency with which mothers with calves of different ages (a) detected the observer, and (b) charged the observer after detecting him. Mothers with first year calves were more likely to detect the observer ($\chi^2 = 8.41 \quad p < 0.01$) and to charge towards him ($\chi^2 = 5.74 \quad p < 0.02$). However, the higher rate of detection of the observer by mothers with first year calves is partly due to the calves being more curious and inquisitive at an early age (Section 5.6.1) and thus often being aware of the danger before their mothers were. If a

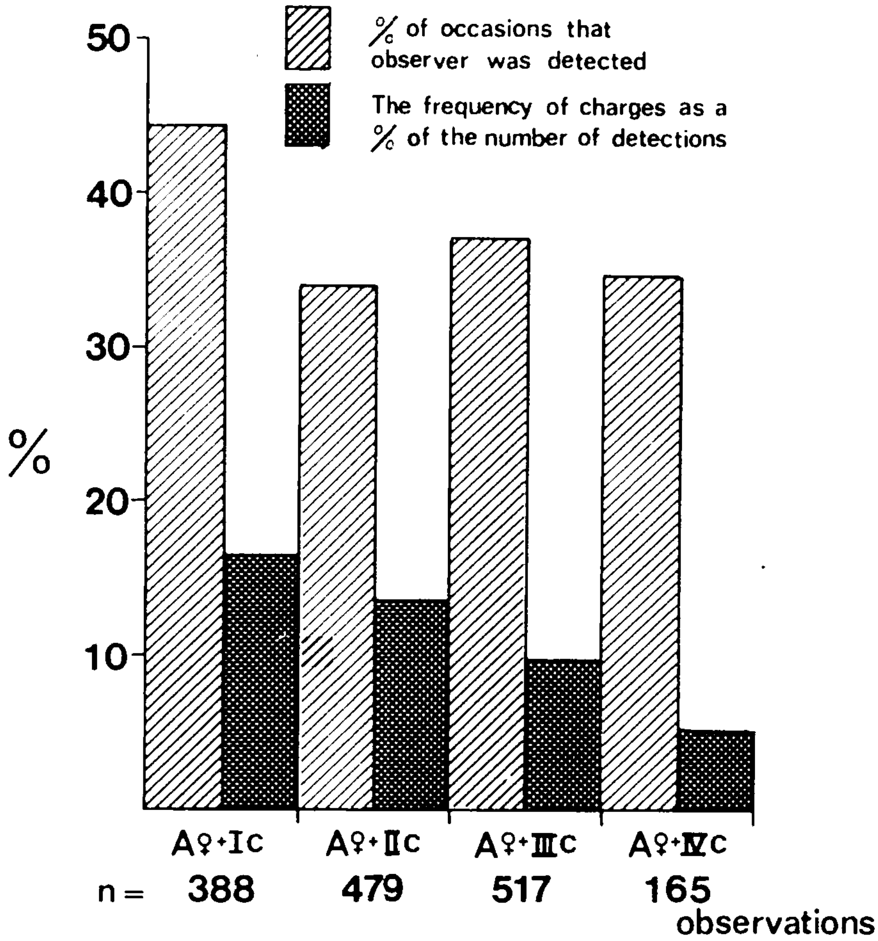


Fig. 5.15. The relative frequencies with which females with calves of different ages detected and charged the observer.

young calf became scared, it turned and ran back to its mother who either turned to face the potential danger or ran off behind her calf. Only rarely did a female lead the retreat. This behaviour is discussed in Section 6.3.3 with reference to the other species of rhinoceros. The reactions of mothers of first year calves towards the observer probably reflects the higher risk of predation on first year calves.

Up to the age of six months, calves were left alone by their mothers for periods of up to 90 minutes and possibly for longer. On a total of 10 occasions, I saw five females with calves aged six, four, four, three and two months respectively, feeding alone up to 800 metres from their calves. Older calves were often separated from their mothers during chases by adult males but were never left intentionally by their mothers.

Intentional leaving of calves was restricted to females with calves aged less than six months: one female which left her calf at least five times before it was three months old was never seen away from her calf when it was older than three months. 'Hiding' of the calf is discussed in relation to other ungulates and to the risk of predation in Section 6.3.3.

5.5.4.3 Suckling

Suckling was observed on 56 occasions. Thirty-eight observations were of first year calves, 17 of second year calves and one of a third year calf. These correspond to rates of suckling of once every 5.5 hours for first year calves and once every 13.4 hours for second year calves. However, during a single observation period of three and a half hours an 11 month old calf was suckled four times for a total of 11 minutes. The overall observed rates of suckling are probably lower than the actual rates, because a high number of observations are included during which the rhinos were disturbed and remained wary of the observer. However, they do show that second year calves are suckled about one third as frequently as first year calves. Five different calves were suckled over the age of 18 months; one up to 26 months.

The method of suckling varied: the calf was either suckled standing to one side of the female and facing her rear at an angle of 45° to the line of her body (n = 39), or from the rear with its head between the female's hind-legs (n = 17). There was strong individual preference for one or other of these two methods. Of the two cow-calf pairs seen suckling on more than nine occasions, one suckled exclusively from the rear (n = 9) and the other exclusively from either side equally (n = 10). Both sets of observations spanned more than one year. Only two out of eight cow-calf pairs seen suckling more than once displayed both methods.

Females always stood while suckling except that once a female lay on her side and her calf stood beside her.

Before suckling, calves often nuzzled the female (n = 15), mounted her flanks (n = 5), ran around her in play (n = 4), butted her teats (n = 2), or licked her flanks (n = 2). Females only nuzzled calves on two occasions before suckling. Play and physical contact maintained by the calf were strongly associated with subsequent suckling (see Table 5.30). Sixteen observations of suckling directly followed disturbance by either humans (n = 7) or other animals or rhinos (n = 9). Whether the rhinos were wallowing or grazing before the disturbance, the calf seemed to take advantage of the mother's change in activity, and started to feed while she stood looking in the direction of potential danger. On only three of these occasions was the calf seen in physical contact with the mother or playing around her before the disturbance. On a further nine occasions, the calf approached the female, moo-grunting, and started to feed immediately.

Table 5.30. The relationship between play and subsequent suckling during observations of first and second year calves.

	Suckling	No suckling	Total
Play	21	37	58
No play	29	1,382	1,411
Total	50	1,419	1,469

Fisher exact probability test $p < 0.001$

The duration of suckling bouts varied from 10 seconds to nine minutes with a mean of 3.3 ± 1.5 minutes. On six occasions there was a break in suckling while the calf either butted the teats or, on one occasion, changed teats. It was always the calf which terminated a bout of suckling. The cow invariably stood still and stopped eating, until the calf had stopped suckling: only then did she resume feeding or walk off (discussed in Section 6.2.2.1).

Suckling took place at all times of day, and during either feeding or resting periods. There was no significant association with any other activity ($\chi^2 = 3.64 \quad p > 0.05$) or with any particular four hour period ($\chi^2 = 3.86 \quad p > 0.05$).

5.5.4.4 The behaviour of mothers towards other rhinos and man

There were differences in behaviour between single adult females and adult females with calves, which appeared to be related to calf protection. In particular, mothers were generally more aggressive than single adult females. For example, single adult females fled on 56% of occasions and charged on 4% of occasions when they detected the observer (n = 93). Mothers, on the other hand, fled on 41% and charged on 13% of occasions (n = 58) ($\chi^2 = 9.28 \quad p < 0.01$). Similarly, although the sample size was small, single adult females rarely initiated attacks on other rhinos except during the advanced stages of pregnancy (Section 5.5.4.1).

Calves had a strong tendency to approach other rhinos and to play with other calves and sub-adults (Sections 5.4.1 and 5.6.2). Sub-adults similarly approached calves and tried to initiate peaceful interactions (Sections 5.4.1 and 5.6.3). Almost all of the agonistic interactions between adult females and sub-adults and between adult females and calves followed such approaches. On four occasions a mother attacked an adult male after her young calf had approached it and lain down in physical contact with it.

Despite repeated attacks by adult females, some sub-adults persisted in accompanying a cow-calf pair (see Section 5.6.2), and the number of attacks by the female eventually decreased. Peaceful associations between cow-calf pairs and sub-adult females are described in Section 5.2. Single adult females associated more frequently with sub-adult males (Section 5.2), but in at least one case the sub-adult male was the female's previous calf, and the same may have been true in other cases (Section 5.6.2). These observations are discussed in Section 6.2.2.

5.6 Changes in behaviour with age, and individual differences in behaviour

In this section the behavioural changes associated with increasing age are described. Since the span of the study was short in relation to the rhinos' potential life span (Section 3.8), the behavioural changes described are all short term changes in particular individuals or differences between age classes, which are pieced together to give an idea of the changes occurring in individuals throughout their lives. I also investigate individual differences in behaviour among rhinos of each sex and age class, with particular attention to adult males. I distinguished five stages of the life cycle:-

(a) Infancy (0-1 year): the period of dependence on the mother for nourishment and protection from predators (Class 1).

(b) Juvenilehood (1-3 or 4 years): the period after weaning during which the individual remains with the mother (Classes 2 and 3).

(c) Adolescence: the period of independence from the mother prior to the attainment of social maturity (Classes 5 and 6).

(d) Adulthood: the period of social maturity (Class 7).

(e) Senescence: the terminal stage during which the animal no longer plays an integrated role in the reproductive population (Class 7).

5.6.1 Infancy

The skin of the four calves seen within one week after birth was a pinkish colour and remained so for about 15 days. Each calf was initially a little unsteady on its feet and walked around its mother, rubbing against her flanks, or lay down beside her. It solicited suckling by butting the teats and rubbings its mother's head and flanks (Section 5.5.4.3).

During most of the day an infant lay beside its mother who grazed or rested nearby. Sometimes the mother left her young calf and moved away to feed or drink (Section 5.5.4.2). On these occasions, the calf did not move from the spot where it had been left. In the presence of the mother, the infant was very active and ran around and back and forth from the mother, rubbing its flanks and head on her flanks and head, and occasionally picking up sticks in its mouth (Section 5.4.1.2). Infant rhinos showed considerable interest in their surroundings, and frequently sniffed at vegetation, logs and pools of water, and rubbed their heads and flanks on trees. They approached other rhinos (*e.g.* Plate 40), but interactions with other rhinos were usually disrupted by the infants' mothers (Section 5.5.4.4).

5.6.2 Juvenilehood

Calves remained with their mothers for three to four years (Section 3.7), during which time their behaviour became less curious and playful, and increasingly timid. Table 5.31 shows the frequencies of physical contact and play behaviour with the mother for the three age classes of calves. Older calves more frequently rushed back to the mother for reassuring physical contact than their infants did. They also initiated fewer peaceful interactions with other rhinos and attacked intruding rhinos more frequently than infants did.

Table 5.31. Changes with age in the amount of physical contact and play observed in rhino calves.

(a) Rates of physical contact and play compared for different age classes.

Class	Rates (number of observations per 100 hours) of Physical contact with mother	Play with mother	Play with other rhinos
I (0-1 year)	23.0	4.8	1.4
II (1-2 years)	20.6	0.9	2.6
III-IV (>2 years)	17.6	0.6	1.9

(b) Numbers of observations of play with the mother and with other rhinos.

	Number of observations		Total
	Play with mother	Play with other rhinos	
Class I	10	3	13
Classes II-IV	5	15	20
Total	15	18	33

$\chi^2 = 8.18$ $p < 0.01$

During short separations from its mother, a juvenile often searched for her, moo-grunting frequently, and sniffing the ground carefully. The mother's reaction varied: on two occasions I saw a cow lie silently in a river while her calf searched for her on dry land. On one of these occasions the calf repeatedly walked up to a nearby sub-adult female and nuzzled her: on the other occasion, the calf followed an adult male half way across the river and then turned back when it heard its mother snorting. A juvenile was often separated from its mother during courtship and mating, and on these occasions both the mother and the juvenile searched for each other. The juvenile often approached other rhinos and followed them for short distances: one juvenile male approached an adult male who eventually killed it after attacking it repeatedly over several days (see Plate 37). Another juvenile wandered for three days before its mother found it, but another remained hidden and quiet like an infant despite the fact that its mother passed by its hiding place several times, squeak-panting loudly.

Juveniles were attacked more frequently by adult males than infants were, and although the sample size is not great enough to be conclusive, it appeared that attacks were directed more at juvenile males than at juvenile females. This may explain the tendency, demonstrated in Table 5.32, for males to remain longer with their mothers than females. The estimated ages at which males left their mothers were significantly higher than the ages at which females left, but this difference could have been caused by underestimation of the difference in growth rates of male and female calves. However, the calves whose ages were most accurately known confirm the trend demonstrated by the other calves (Table 5.32). Furthermore, one male (m087) rejoined his mother after the death of the mother's new calf, and several other observations of single adult females with sub-adult males may have been cows with four year old calves.

Suckling was terminated during the juvenile period but I never saw cows force their calves to stop suckling (Section 5.5.4.3). Juveniles were separated from their mothers at least a week before the birth of the mother's next calf but the process of separation was either sudden and final, or there were periodic reunions and separations over a period of four months or more. Male's separations, in accordance with the data in Table 5.32, were more often of the latter type and females' of the former type. I only saw an adult female drive away its calf violently during the week before parturition. Before that, a cow simply snorted when the juvenile approached, and sometimes threatened it with the tusk-display (Section 5.4.2).

Table 5.32. Differences between the sexes in the ages at which calves left their mothers.

Male calves		Female calves	
Individual	Age (months) at leaving mother	Individual	Age (months) at leaving mother
*074	39	079	34
076	36	082	36
087	38 (55)	085	36
091	50	100	31
094	42	114	40
146	36	*131	32
*193	35	136	30
		165	35
		*162	33
Mean ± SD	39.4 ± 4.8		34.1 ± 2.9

Mann-Whitney U test, $p < 0.05$ (two tailed test)

* denotes calves born after January 1972, whose ages were therefore known more accurately than calves born earlier.

The figure in brackets is explained in the text.

5.6.3 Adolescence

Sub-adult is the term used for adolescent rhinos (Section 3.2.2). Sub-adults were generally more timid than adults (Section 5.4.2). The typical reaction to my presence of one sub-adult male (m055) changed during the study period from immediate rapid flight to a curious approach. The same individual was seen in a group on 29% of occasions (n = 63) during the year after its first sighting and on 16% of occasions (n = 38) during the next year ($\chi^2 = 2.10$ $p > 0.05$). Although this result is not significant, it indicates a possible trend towards less timid and more solitary behaviour.

(a) Grouping behaviour

The tendency of sub-adults to form groups is described in Section 5.2.1. These groups were variable in composition, frequently splitting and amalgamating with other groups. Sub-adults in groups were never attacked by adult males although lone sub-adult males were frequently attacked (Section 5.4.2). The possible protective advantage of groups is discussed in Section 6.3.2.

Fig. 5.16 shows the proportions of occasions on which each of the most frequently sighted sub-adults were seen in groups. It confirms that sub-adult males generally formed groups more frequently than sub-adult females (see Section 5.2), but it also shows that there were considerable variations within the sexes.

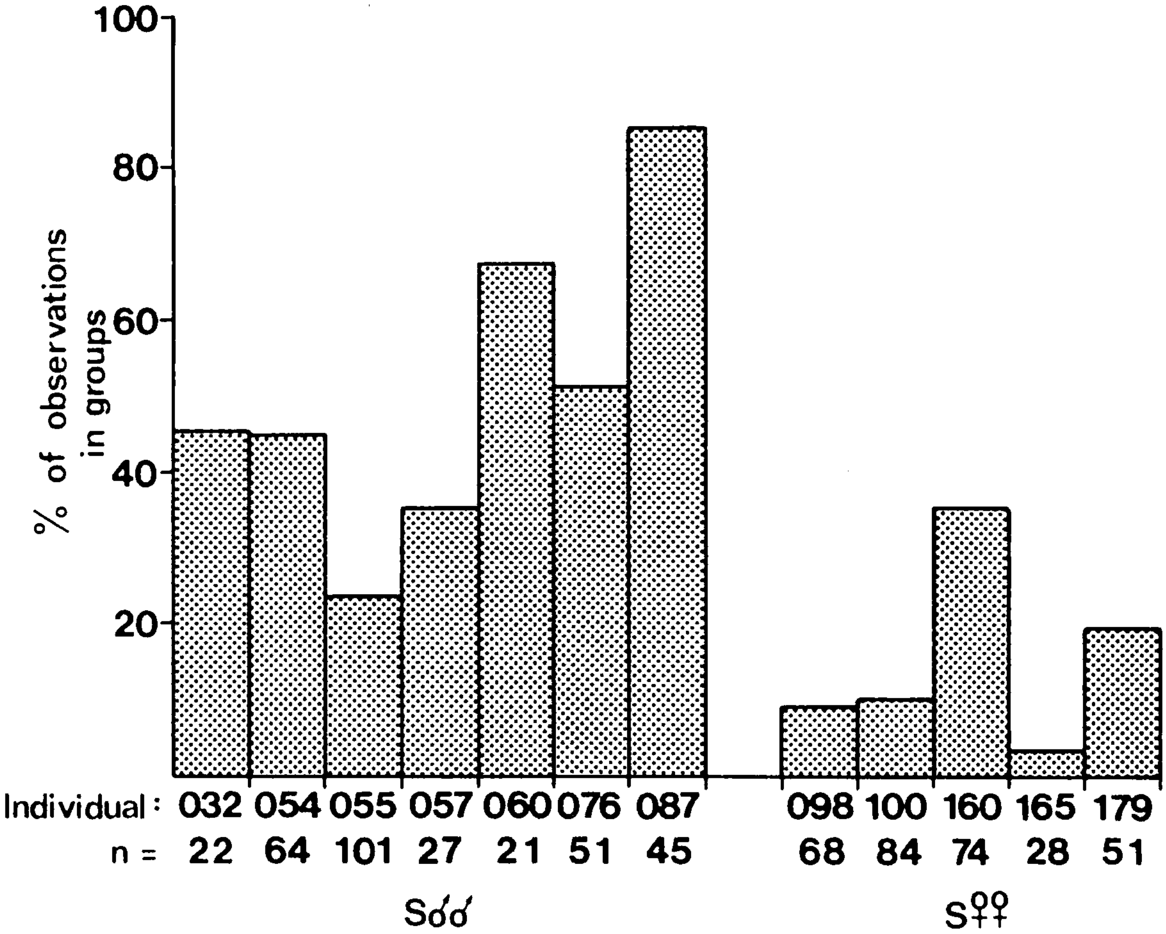


Fig. 5.16. The frequency of group formation by individual sub-adults.

The individual composition of sub-adult groups also varied greatly. The seven most frequently sighted males formed groups with between three and 11 other sub-adults. However, certain individuals were seen together more frequently than would be expected by chance: m076 was with m054 on seven occasions and with m055 on six of the 25 occasions it was seen in a group. The sub-adult m087 was almost always with its mother (F086) after she had lost her calf (088) to a tiger. Among the most frequently sighted sub-adult males, m055 was the only one seen in groups with adult males: it was twice seen lying in physical contact with M045 (see Plate 41), although on other occasions it was chased off by the same adult male (discussed in Section 6.2.2.3). Among the most frequently sighted sub-adult females, f160 was with F086 and m087 on 12 of the 26 occasions it was seen in a group (discussed in Section 6.2.2.3).

(b) Range changes after leaving the mother

Three individuals, m076, m087 and f100 were each seen more than 20 times as calves and more than 20 times as sub-adults. Both the sub-adult males showed changes in range use after leaving their mothers, but the sub-adult female did not (Section 4.6.3.5). The ranges of the sub-adult males shifted eastwards from blocks D and E to block F and the range of f100 remained in blocks D and E. Furthermore, two very distinctively marked sub-adult females, f165 and f160 were thought by the Itami guards to have been born and reared mainly in block G. However, these sub-adult females were subsequently seen in blocks D and E. Although this data is obviously inconclusive, the higher numbers of sub-adult females in blocks D and E and of sub-adult males in blocks F and G (Sections 3.5 and 4.6.3.3) suggest that there may have been pressures on sub-adult males to move out of the central highly populated areas (discussed in Sections 6.2.2.3 and 6.2.1).

5.6.4 Adulthood

5.6.4.1 Adult females

Some differences in behaviour between single adult females and mothers are described in Sections 5.2.1 and 5.5.4.4. Apart from these differences, there was considerable variation in behaviour between individuals. Fig. 5.17 shows the proportions of occasions on which each of the most frequently sighted adult females was seen in a group with sub-adults.

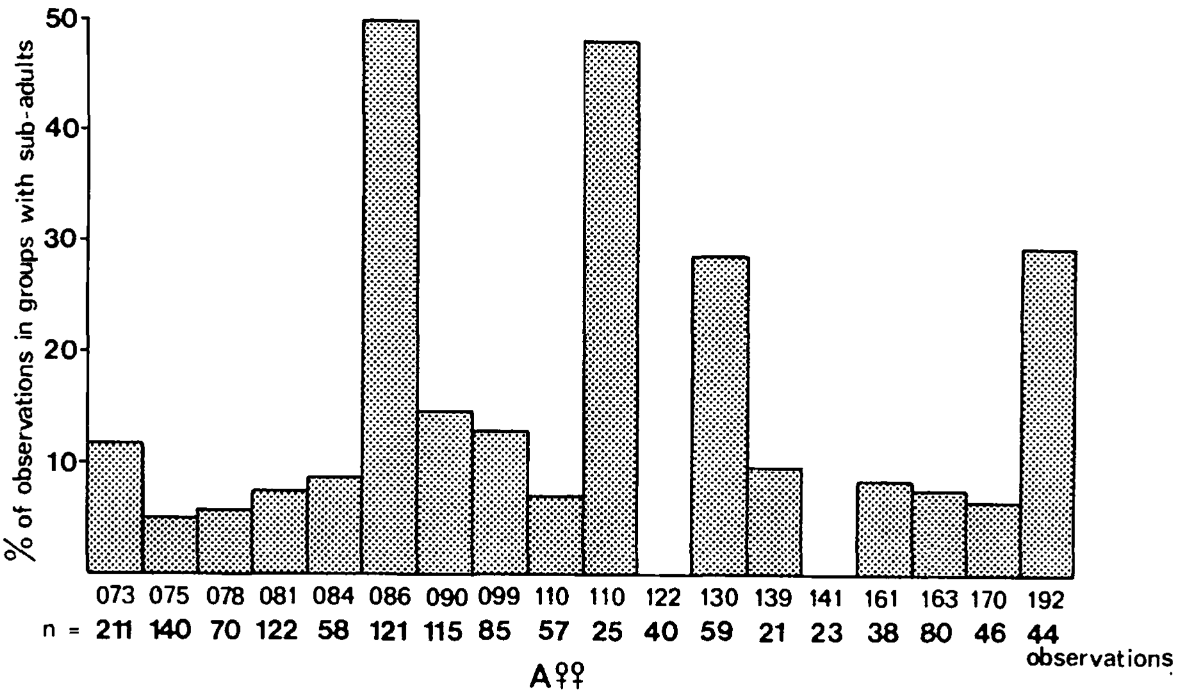


Fig. 5.17. The frequency of group formation with sub-adults by individual adult females.

Table 5.33 shows the numbers and the results of agonistic encounters involving these individuals. There was a significantly higher rate of agonistic interactions between adult females of range category 2 (Section 4.6.3.3) than between other females. This result might be interpreted as increased competition among adult females in the more densely populated regions. However, there are alternative explanations. Firstly, most of the interactions took place at wallows, and I spent longer observing

Table 5.33. The numbers and results of agonistic interactions involving the most frequently sighted adult females.

Individual	Number of agonistic interactions observed	% of occasions that opponent fled	The rate of agonistic interactions with adult females (The number per 100 hours of observation)
Adult females of range categories 1 to 3			
F073	42	42.9	17.0
F075	28	35.7	14.2
F078	18	38.9	33.3
F081	31	35.5	24.7
F084	17	41.2	27.5
F090	16	31.3	8.8
F099	33	33.3	40.4
F122	15	20.0	24.0
F192	17	52.9	40.9
			Mean = 25.6 ± 10.6
Adult females of range categories 4 to 6			
F086	45	48.9	17.9
F110	14	22.0	28.6
F113	3	33.3	15.0
F130	15	80.0	6.7
F139	3	66.7	0.0
F141	1	0.0	0.0
F161	7	85.7	0.0
F163	8	25.0	4.7
F170	5	80.0	16.7
			Mean = 10.0 ± 9.5

Mann Whitney U test on the difference between the groups in rate of agonistic interactions with adult females: $U = 13$, $p < 0.01$.

rhinos at wallows in blocks E and F than in other blocks. Secondly, the rates of agonistic interactions have been calculated per hour of observation, and do not take into account the times spent in association with other individuals. Thirdly, no account is taken of changes in behaviour or range use over the study period.

Therefore, I carried out a detailed analysis of the interactions between adult females at particular temporary wallows during single monsoons. For example, Fig. 5.18 shows the times spent away from other adult females by different individual females in one particular wallow, about 20 metres by 10 metres, in block E during the monsoon of 1973.

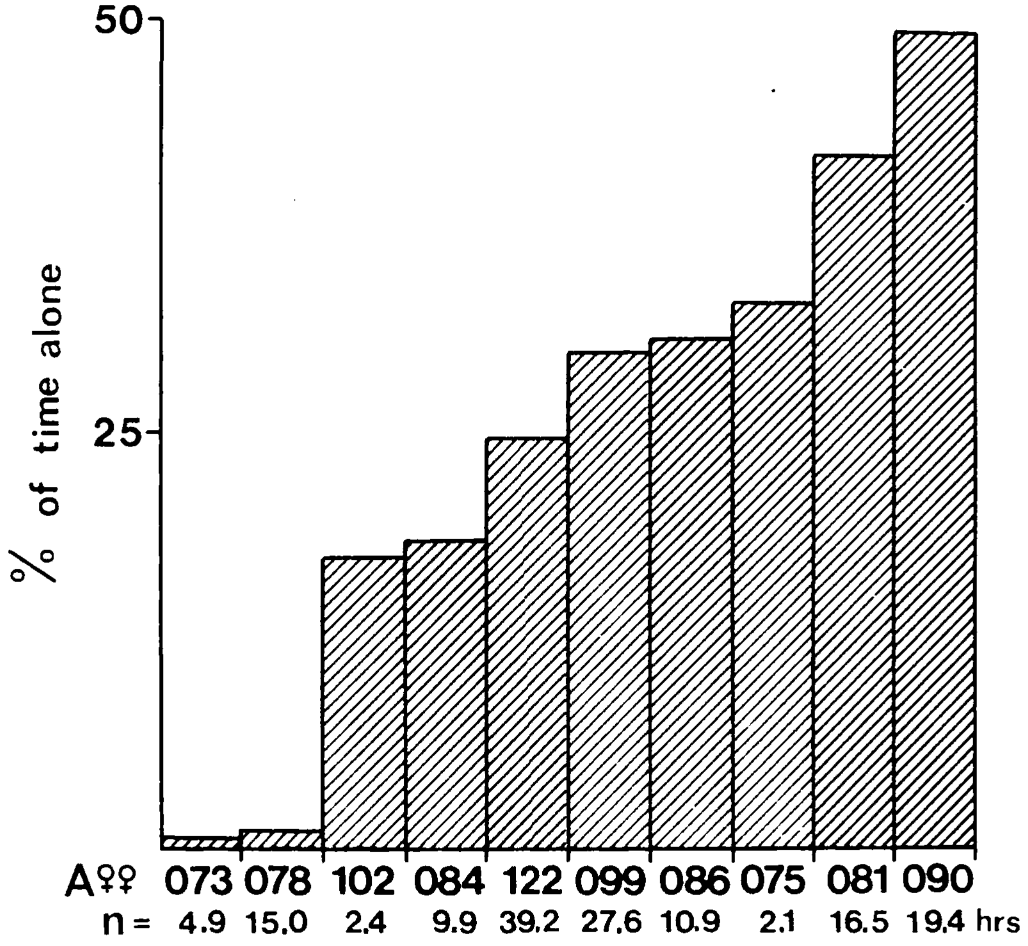


Fig. 5.18. The degree of association by individual adult females with other adult females in a certain wallow during the 1973 monsoon.

Table 5.34 shows the rates of agonistic interactions between each individual per hour that they were together in the wallow, and the identity of the individual in each pair which won most interactions. Such analysis on this and other wallows cannot be presented in full in this report, but it did not indicate a dominance hierarchy among the adult females. There

Table 5.34. Rates and results of agonistic interactions between individual adult females in one wallow during the 1973 monsoon.

	A 073	B 075	C 078	D 081	E 084	F 086	G 090	L 099	M 103	Y 122
B 075	X									
C 078	10.0 A	7.5 B								
D 081	7.5 D	1.1 D	0.0 -							
E 084	30.0 A	1.1 B	15.0 C	1.2 D/E						
F 086	0.0 -	X	0.0 -	0.2 F	8.6 F					
G 090	1.2 G	0.0 -	0.0 -	0.3 G	0.0 -	0.4 F				
L 099	0.0 -	0.0 -	0.6 L	0.5 L	0.2 L	0.7 L	0.6 G			
M 103	14.1 A	X	X	X	X	X	1.2 M	3.4 L		
Y 122	0.4 A	X	0.4 C	0.0 -	0.5 E	0.0 -	0.0 -	0.2 L	0.8 Y	
Total interactions per hour with others	2.05	2.17	0.52	0.94	1.24	0.80	0.51	0.73	4.10	0.35
Total wins minus losses	+6	+1	+1	-3	-2	+2	+1	+10	-6	-10

Identifying letters and numbers are used for each individual.

The individuals in the body of the table won more interactions than their opponents.

The figures in the body of the table are rates of agonistic interactions per hour that each pair of rhinos were together.

X denotes not seen together.

D/E denotes equal numbers of interactions won by each animal.

was also no relationship between the frequency of observed agonistic interactions and the time spent in the wallow with other rhinos. However, the high rate of agonistic interactions between adult females may cause some individuals to avoid the most contested wallows (discussed in Section

6.2.2.1). Note that F122, the only single adult female, at that time, among the 10 individuals, had the lowest success rate in interactions with the other cows.

5.6.4.2 Adult males

Adult males are treated in more detail here than other sex and age classes because I was most interested in the ways in which individual differences in their behaviour affected their breeding success. I show here that only certain adult males regularly courted and mated with females. For convenience, I have divided adult males into two social classes on the basis of differences in social behaviour. I describe social interactions between adult males and changes in their use of their ranges over the study period.

(a) Associations with other rhinos

Adult males were usually solitary (Section 5.2). There were, however, variations among the adult males in the extent to which they associated with other rhinos, and in the sex and age classes with which they tended to associate. I show in Table 5.35 the numbers of occasions on which each of 13 adult males were seen in associations with other rhinos classified according to their age and sex.

The numbers of sightings varied considerably between individuals. No statistical significance can be placed on the differences between the proportions of sightings in associations, for individuals seen on only a few occasions. However, for the five individuals seen on over 30 occasions I show (in Table 5.35) the results of chi-squared tests between each pair of individuals on the proportions of sightings in which they were in associations. The table and the matrix show that M005 and M045 were seen significantly more frequently in groups or

Table 5.35. The frequencies with which individual adult males associated with rhinos of each sex and age class.

Individual	Number of sightings in associations	Number of associations with A♂	A♀	S♀	S♂	Total number of sightings
M001	25 (19.0%)	11	14	4	3	131
M002	4 (10.5%)	4	1	2	1	38
M003	4 (28.6%)	1	2	0	0	14
M004	7 (11.9%)	6	2	2	1	59
M005	45 (24.2%)	4	42	9	2	186
M013	4 (18.2%)	0	2	1	1	22
M034	1 (7.1%)	1	0	0	0	14
M045	47 (29.2%)	0	32	12	25	161
M052	0 -	0	0	0	0	4
M053	3 (30.0%)	1	2	0	0	10
M056	6 (30.0%)	0	6	1	0	20
M062	5 (29.4%)	3	1	0	0	17
M070	0 -	0	0	0	0	7

Results of χ^2 test on differences between individuals in the proportion of sightings in associations:

p values

	M001	M002	M004	M005
M002	>0.05			
M004	>0.05	>0.05		
M005	>0.05	<0.05	<0.05	
M045	>0.05	<0.02	<0.01	>0.05

aggregations than M002 and M004. Furthermore, M005 and M045 were seen more frequently with adult and sub-adult females than with adult males, whereas the opposite was true for M002 and M004 (Fisher exact probability test $p < 0.001$). M001 seems to be intermediate between these two pairs of individuals, being not significantly different from either of them in its proportion of sightings in aggregations. It was seen more often with adult females than with adult males, but relatively more frequently with the latter than were M005 and M045.

The associations between adult males and females considered above include chance aggregations and actively maintained associations, as defined in Section 5.4.1. I now consider the numbers of actively maintained associations with females recorded for each individual adult male. The difficulties in determining whether an association was or was not actively maintained are discussed in Section 5.5.1. It was clear that longer observation periods made it easier to detect actively maintained associations. There was considerable variation in the mean observation duration for each of the 13 adult males: in general, as for all observations of rhinos, durations of observations were longer in the central blocks of the study area. Table 5.36 shows the total observation times, numbers of sightings and mean durations of observations for the 13 adult males classified according to the blocks in which they were seen most frequently. The five individuals seen most frequently in the central blocks had significantly longer mean durations of observations than individuals in the outlying blocks (Mann Whitney U test $p < 0.001$).

In Table 5.37 I have compared the frequencies with which individual adult males were seen in actively maintained associations with females. As longer observation periods increased the chance of detecting actively maintained associations, individuals seen most frequently in the outlying blocks are considered separately from those in the central blocks. It can be seen that all males in the latter group actively associated with females at some time during the study. The rates of associations per 100 hours of observation are not significantly different between individuals ($\chi^2 = 5.07$ $p > 0.05$), but it is clear that M005 and M045 associated the most frequently with females in the central blocks, and M005 also associated with females in blocks B and G.

There were differences between individual adult males in the frequency of squirt-urination and foot-dragging displays. The frequencies of these displays by the five adult males considered above are shown in

Table 5.36. The numbers of sightings and the durations of observations of individual adult males classified according to where they were seen most frequently.

Individual	Total observation time (hours)	Numbers of sightings	Mean observation duration (minutes)	Block in which most frequently seen
(1) Individuals seen most frequently in the central blocks (D,E,F)				
M001	60.6	131	28.0	D
M002	17.9	38	28.0	D
M004	26.4	59	27.0	D
M005	126.9	186	41.0	D
M045	85.7	161	32.0	F
(2) Individuals seen most frequently in the outlying blocks (A,B,C,G)				
M062	5.3	17	18.5	A
M003	1.8	14	7.0	B
M013	3.1	22	9.0	B
M034	1.2	14	5.0	B
M052	0.6	4	9.0	B
M070	1.6	7	14.0	B
M053	3.2	10	19.2	C
M056	4.4	20	13.2	G

Mean observation durations:- Central blocks 31.2 ± 5.2
Outlying blocks 11.9 ± 4.9

Central blocks > Outlying blocks Mann Whitney U test $p < 0.001$

Table 5.38. It can be seen that there were significant differences between individuals in the frequencies of both displays. I observed M045, M005 and M001 mating in the central blocks during the study period, and these three individuals were different from the other two in several behavioural characteristics. They all squirt-urinated more frequently than M004 and M002, although M001 did so slightly less frequently than M005 and M045. The latter two males also dragged their feet significantly more frequently than the other three. I showed above that M005 and M045

Table 5.37. The numbers of actively maintained associations between individual adult males and females, arranged according to the blocks in which they were observed.

BLOCK	Number of associations observed						
	A+B	C	D	E	F	G	Total
Individual No.							
(1) Individuals seen most frequently in the central blocks D,E,F.							
M001	0 (5)	1 (10)	4 (95)	0 (18)	0 (3)	0 (0)	5 (131)
M002	0 (4)	0 (3)	4 (27)	0 (1)	0 (3)	0 (0)	4 (38)
M004	0 (2)	0 (0)	1 (56)	0 (1)	0 (0)	0 (0)	1 (59)
M005	1 (3)	0 (1)	5 (87)	3 (62)	3 (32)	1 (1)	13 (186)
M045	0 (0)	0 (0)	1 (14)	3 (32)	13(112)	0 (3)	17 (161)
(2) Individuals seen most frequently in the outlying blocks							
M062	0 (10)	0 (0)	0 (7)	0 (0)	0 (0)	0 (0)	0 (17)
M003	0 (5)	0 (3)	0 (5)	0 (0)	0 (1)	0 (0)	0 (14)
M013	1 (14)	0 (4)	0 (4)	0 (0)	0 (0)	0 (0)	1 (22)
M034	0 (12)	0 (0)	0 (2)	0 (0)	0 (0)	0 (0)	0 (14)
M052	0 (3)	0 (0)	0 (1)	0 (0)	0 (0)	0 (0)	0 (4)
M070	0 (4)	0 (0)	0 (2)	0 (1)	0 (0)	0 (0)	0 (7)
M053	0 (0)	1 (10)	0 (0)	0 (0)	0 (0)	0 (0)	1 (10)
M056	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (20)	1 (20)

Figures in brackets refer to the total number of sightings of each individual in a particular block.

differed from the others in the degree of associations with other rhinos and in particular with females. Although the rates of actively maintained associations with adult females were not significantly different among the five individuals, M045, M005 and M001 had the highest absolute frequencies of such associations, and these individuals were also seen most frequently throughout the study period. I regarded them as the 'strong' males of the central blocks.

There were also differences in rates of squirt-urination and foot-dragging among the less frequently observed adult males (Table 5.38).

Table 5.38. A comparison of the frequencies of squirt-urination and foot-dragging displays performed by individual adult males.

Individual No.	Squirt-urination		Foot-dragging	
	Number	Rate (No/10 hrs)	Number	Rate (No/10 hrs)
(1) <u>Central blocks</u>				
M001	29	4.8	3	0.5
M002	0	0.0	1	0.6
M004	2	0.8	0	0.0
M005	99	7.8	13	1.0
M045	69	8.1	18	2.1
χ^2 = 34.8		$p < 0.001$	χ^2 = 14.4	$p < 0.01$
M045, M005 > M001 > M002, M004			M045 > M005 > M001, M002, M004	
(2) <u>Outlying blocks</u>				
M003	3	17.0	0	0.0
M013	4	12.8	1	3.2
M034	0	0.0	0	0.0
M052	1	16.2	0	0.0
M053	2	6.3	0	0.0
M056	6	13.7	1	2.3
M062	4	7.6	0	0.0
M070	3	18.0	1	6.3

These differences are not significant, and the higher rates of urination were caused partly by a high frequency of disturbance by the observer (see mean observation durations, Table 5.36). However, it is worth pointing out that M034, the only male seen neither to squirt-urinate nor foot-drag, was a very timid individual, similar in behaviour to M002. Furthermore, of the three males seen in actively maintained associations with females (Table 5.37), two (M056 and M013) were seen both squirt-urinating and foot-dragging. It appeared that these displays were the mark of breeding males but, due to the small numbers of observations of many individuals, it was necessary to use other clues such as the degree of timidity to decide whether a certain individual was likely to be breeding in a particular area. I classified males roughly into 'strong' males and 'weak' males, but they lay on a continuum of 'strength', and their positions on the continuum changed over the period of the study.

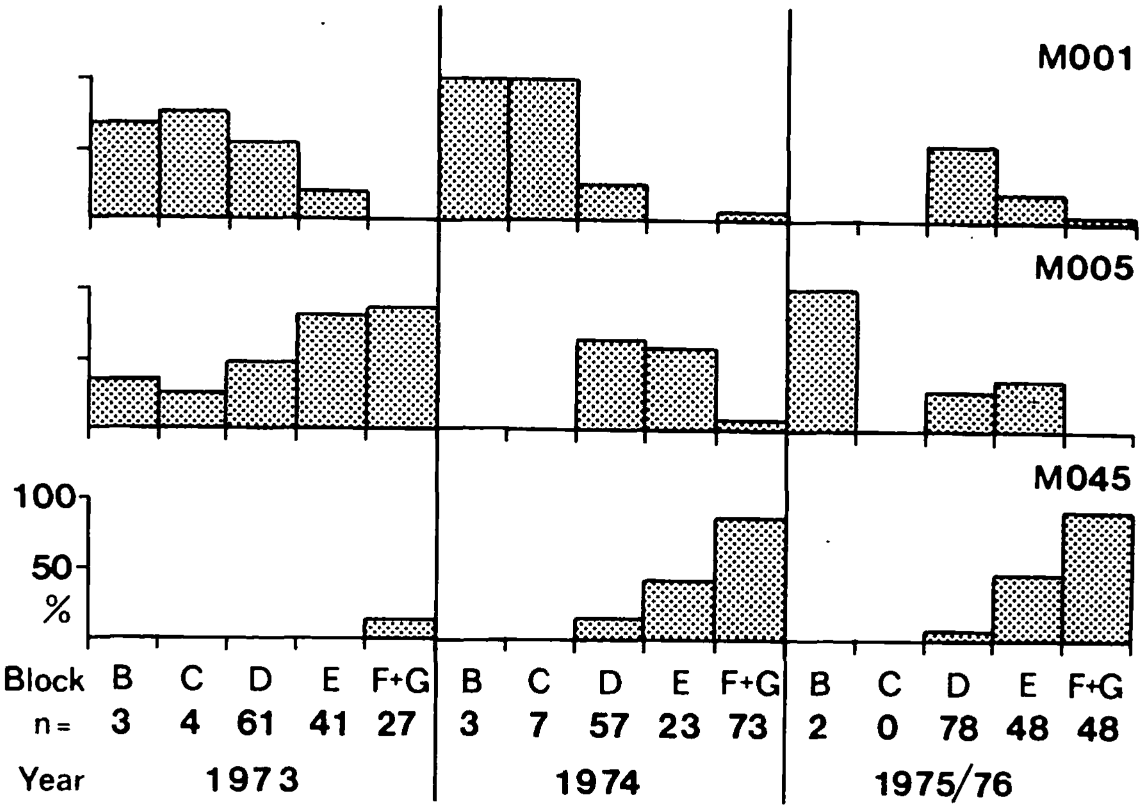
(b) Interactions between adult males

Adult males rarely associated with other adult males (Section 5.2), and although there was a high rate of agonistic interactions between adult males when they were together (Section 5.4.2), the number of such interactions was small. I observed only eight 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 metres 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 (see Plate 36) 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. The deaths caused by fighting were listed in Table 3.15. 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 metres apart in the same stream. However, such proximity can be misleading, as the vegetation is generally very thick, and visibility poor (discussed in Section 6.3.2). M001 and M003 were once wallowing 10 metres apart but, when disturbed by the observer, M001 suddenly lunged at M003 and chased it off into the grass. The interactions between adult males are discussed in Section 6.2.2.2 in relation to their ranges (see below).

Table 4.9 showed the distribution of sightings of all individuals over the whole study period. It can be seen that M004 was seen very infrequently during the second year of the study period, and it is likely that it 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 evidence of changes in the use of their home ranges over the study period (Section 4.6.3.5, Table 4.16). Fig. 5.19 shows these changes more clearly, by considering only sightings of these three adult males, and plotting the numbers of sightings of each individual in each block and year as a proportion of the number of sightings of all three individuals in that block and year. It can be seen 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 (see Section 6.2.2.2 for discussion of these results).

In conclusion, it appears that, 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 seems to have resulted in considerable range overlap among the three strong males in the central blocks of the Sauraha study area.



Percentages are of all sightings (n) of the three adult males in each block in each time period.

χ^2 test for differences between three years in the distributions of the sightings

Blocks F + G	M005 vs M045	$\chi^2 = 86.89$	$p < 0.001$	df = 2
Block D	M001 vs M005	$\chi^2 = 18.24$	$p < 0.001$	df = 2

Fig. 5.19. Changes in the ranges of three adult males over the study period.

5.7 Discussion on communication

I discuss here the types of signals used by rhinos for communication, considering various aspects of structure and function and the relationships between the environment and the types of signals used. This is preliminary to a detailed discussion in Section 6 about the relationships between ecology and social organisation and the consequences of interactions between rhinos.

The extent to which ungulates communicate with each other, and the types of signals used depend largely on the spatial distribution of the individuals (see Section 6.3.1) and the nature of the environment. The habitat type, the distance over which the signals are transmitted and whether they are transmitted by day or by night all appear to influence the nature of the signals used (see Marler (1967) for a discussion of the relationship between the structure and function of communicatory signals).

The signals used by animals to exchange information about their motivational states and their intentions are difficult to classify either descriptively or functionally. Differences between the sensory abilities of observers and animals can cause observers to perceive a very different set of signals from that which the animal under study perceives. There are also difficulties in distinguishing discrete signals in what often appear to be continua of expression in several sensory modalities (Marler, 1967). Ungulate signals have been classified functionally into four broad categories:- attraction (*e.g.* courting and calling the young), repulsion (*e.g.* threat), submission, and alarm (Leuthold, 1977). However, many signals as perceived by human observers occur in widely different contexts, and Kiley (1972) concluded from work on domestic ungulates that most auditory signals, or vocalizations, merely signal the state of excitement of the animal and have to be interpreted in the context of other behaviour such as visual displays and direct actions. The latter hypothesis accords with observations of vocalizations such as the squeak-pant occurring in different circumstances (Section 5.3.1), but it is possible (a) that the rhinos can distinguish differences between the sounds uttered in each context or between sounds uttered by males and females and (b) that sounds may perform more than one communicatory function without ambiguity.

Most communication appeared to be concerned with the control of spacing between individuals (Section 5.3). The large number of signals associated with the defence of "personal space" (Hediger, 1950; Marler and Hamilton, 1966), *i.e.* increasing or maintaining distance between individuals, is unusual among ungulates: an equivalent emphasis has been found only in other rhino species, in particular the white rhino (Owen-Smith, 1973; see Section 6.3). I now consider auditory, olfactory and visual signals in turn.

(a) Auditory signals

Vocalizations were the most frequently recorded type of signal (Section 5.3). This is in accord with the rhino being an animal which forms groups rarely (Section 5.2) and lives in habitats where the visibility is poor (Section 2.1.5).

The great volume of the sounds such as the squeak-pant, bleat, roar and honk suggest that they may function in long distance communication, although they were recorded mainly during face to face agonistic interactions and chases. Apart from their direct functions as a display of strength or submission, these loud vocalizations may indeed serve as long distance signals to other rhinos. Adult males in particular moved off in the direction of such sounds, which were sometimes recordings played back on a tape-recorder (Section 5.3.1.3). Adult and sub-adult females also moved towards the sounds of fighting, and one adult female followed a consort pair for almost one hour using a combination of olfactory and auditory clues.

In the context of courtship behaviour (Section 5.5.2), females may increase their chances of being mated by a stronger male if they resist copulation and advertise their 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 a female. It is also possible that adult females in oestrus may approach a consort pair, being attracted by both smell and vocalizations: a male with a female is likely to be a strong male and hence worth mating with. These functional hypotheses are discussed further in Section 6.2.

Marler (1955) concluded that to be easily locatable, calls should be low frequency, regularly repeated grunts. However, long range calls, especially in thick vegetation, should be of high frequency in order to carry the distance. The squeak-pant, honk and bleat are obviously well adapted for long distance advertisement; they could also function as indicators of strength at close quarters, but the rarity with which adult males use vocalizations in face to face interactions does not support this hypothesis (see Section 6.2). The moo-grunt, on the other hand, is a low frequency, regularly repeated short range contact call, but I found it to have a ventriloquistic property - perhaps merely because the mouth was rarely opened, and a moo-grunting rhino could even continue feeding (Section 5.3.1).

Unlike the auditory repertoire of most ungulates, that of the rhino appears to contain no specific alarm call, although the snort and subsequent humphs on fleeing do serve to alert other rhinos to a disturbance. However, although sub-adults are very jumpy and run at the slightest disturbance, most adult rhinos are unconcerned about disturbances and have developed no responses to the alarm calls of chital, sambhars, wild pigs, langurs, macaques and birds. This is probably a result of their large body size which renders them invulnerable to the attacks of predators.

(b) Visual signals

The eyesight of rhinos is widely held to be very poor, but recent studies on the visual discriminatory ability of the black rhino by Fasnacht (1971) indicated that this is not so of the black rhino. I came to the conclusion that, although Indian rhinos rarely look up above eye-level, their detection of movement even against a dark background and at distances of up to 80 metres was good (Section 2.3.2).

The main emphasis in visual signals of 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 signals.

All the breeding males (Section 5.5.4.2) had very large head-on profiles but their horns varied from a 10 cm stump to 45 cms in length (Plates 13, 41). The horn may not be as important in displays and dominance as the size of the animal. As horns are lost quite frequently during fights and even by charging at trees in redirected aggression, it could be adaptive for individual males to be ranked on actual size and strength rather than the size of a temporary attachment such as a horn. Visual signals are combined with auditory signals in all but adult males. The latter seem to rely on their large size and intimidatory slow, confident approach, together with accompanying body scents to threaten antagonists. Owen-Smith (1973) noted similar behaviour in white rhino males. The long horns of the black rhino and the white rhino contrast strikingly with the short horns of the Asian rhinos. They probably developed as long distance visual signals suitable for open habitats but ineffective in forests and tall grasslands. The woolly rhinoceros (Appendix B) 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 (discussed in Section 6.3).

Apart from direct visual signals there are also possible visual components in the long dragmarks made by the hind feet (Section 5.3.2). Borner (1977) 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 6.1; discussed in Section 6.3).

(c) Tactile

Tactile contact such as rubbing and licking flanks and heads was recorded most frequently between cows and calves and between sub-adults (Section 5.4.1). All such behaviour is bond-reinforcing: it occurs also during courtship and is frequently accompanied by moo-grunts (Section 5.4.1).

(d) Olfactory

The release and deposition of scent permits exchange of information among animals and is particularly adaptive in closed habitats and among animals such as the Indian rhino, which have overlapping ranges but tend to move and forage alone. The wet nature of the Indian rhinos' habitat decreases the effectiveness of olfactory communication but,judging from the reactions of rhinos to scent marks (Section 5.3.2), there is no doubt of its importance.

The foot-dragging display has already been mentioned above with reference to the visual component of the drag-mark signal. As it is usually accompanied by squirt-urination, it is also of obvious olfactory significance. Furthermore, the pedal scent gland (Cave, 1962) is probably associated with the display and leaves a scent mark on the up-turned earth and disturbed vegetation. It is also possible that the smell of freshly up-turned earth and the sap of broken branches and barked trees draws attention to such marks (Eisenberg and Kleiman, 1972).

Foot-dragging occurs also in other rhino species (see Table 6.1), but it appears to be best developed in the Indian rhino; possibly because of its visual significance in a wet environment. I saw a short stretch of drag marks made by a Sumatran rhino in Endau Rompin, Malaysia, but such behaviour is not widely reported for the south-east Asian rhino species; perhaps not surprisingly, since the rhinos are rarely observed and drag marks do not persist for long periods. On the other hand, the Indian rhino and the south-east Asian rhinos rarely scrape their hind-feet in their dung, as has frequently been reported for the African rhinos (Table 6.1). Goddard (1967b) showed that rhinos could distinguish between the scent of different individuals' dung dragged in a bag behind a Landrover. The pedal scent gland of *Rhinoceros* may have evolved because the scent of dung on the feet quickly disappears in a wet environment, and there was selection pressure for an alternative form of scent-marking to the impregnation of the feet with the scent of dung.

Indian rhinos of all sex and age classes performed *flehmen*, and it appeared to be connected with olfactory communication via the urine (Section 5.3.1.3). Although all urine could contain some chemical signals, the distinctive squirt-urination display which sprays the urine onto surrounding vegetation and over a wide area was most often performed by 'strong' breeding males which are individuals of high social status (*c.f.* Ralls, 1974).

Squirt-urination was performed frequently during encounters between individuals and in reaction to the scent of other individuals, their dung or their urine. In the latter cases, it may be viewed as the result of an indirect encounter with another individual as suggested by Schenkel and Schenkel-Hulliger (1969a) for the black rhino. Squirt-urination has been reported for all species of rhinoceros (Hubback, 1939;

Goddard, 1966; Schenkel and Schenkel-Hulliger, 1969a, 1969b; Owen-Smith, 1975; see Table 6.1).

The Asian species of rhinos frequently wallow in small pools which smell strongly of urine. Hoogerwerf (1970) and Schenkel and Schenkel-Hulliger (1969b) 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 part of the year. Weir (1969) reported that certain clays effectively bind scent: thus urination in wallows and rubbing of mud from wallows onto trees may function in communication between individuals (discussed in Section 6.3).

Dung-piles were used by Indian rhinos of all sex and age classes in Chitawan (Section 5.3.2.2), and similar findings have been reported for other species of rhinos (Owen-Smith, 1973). For the white rhino, dung-piles appear to have a territorial marking function (Owen-Smith, 1973). However, there was no evidence in Chitawan that dung-piles were territorial markers, although they probably do indicate the range of some individual rhinos. The effects of seasonality and fast changes in the vegetation on the movements of rhinos are discussed in relation to territoriality in Sections 6.1 and 6.3.

Scent-marks such as dung-piles can be regarded as bulletin-boards which aid in individual spacing and convey information on the reproductive state of individuals. There was evidence that the urine of both oestrous female Indian rhinos and breeding males was of more interest to males and females respectively, than the urine of non-oestrous females or non-breeding males (Section 5.3.2.3).

Dung-piles and sites of squirt-urination were concentrated at wallows, the junctions of paths and at borders between habitat types - particularly at borders between forest and grassland. Similar observations have been reported by Peter Jarman (pers. comm., 1978) for various species of macropods, and Buechner *et al.* (1975) reported that a captive male *R. unicornis* commonly squirt-urinated on crossing the threshold between his shed and his outer enclosure. Focal points in the environment and their importance for social communication are discussed in Section 6.3.

Displays and interactions between rhinos are discussed in more detail in Sections 6.2 and 6.3 with reference to the other rhino species and their evolution.

5.8 Summary

1. Rhinos are[3] predominantly solitary: only 9.6% of observations were of groups other than single individuals or cow-calf pairs.

2. The most frequent types of group consisted of two or more sub-adults - most frequently sub-adult males. Adult males very rarely associated with other rhinos, and adult females only did so with sub-adults.

3. Ten different vocalizations were identified. Many are of high intensity and used to maintain spacing between individuals, and possibly to advertise the location of fights. There is no specific alarm call.

4. Olfactory communication is important to rhinos. Scents are carried in the urine, the dung and the pedal scent-glands. Adult males squirt

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[3] The use of the present tense is for convenience in summarizing the main findings: it should not be regarded as signifying general conclusions applicable outside the area or period of the study.

their urine and drag their feet in a display not performed by the females or the sub-adults.

5. The emphasis in visual displays is on the head-on view of the neck folds and bib and the large tusks in the lower jaw. There is no lateral or broadside display.

6. Tactile communication involves rubbing and licking, and is most frequent in play and peaceful interactions between cows and calves, sub-adults and courting pairs. It is often accompanied by low intensity vocalizations.

7. Agonistic interactions are most frequent between adult males and between cows with calves. Attacks on sub-adult males by adult males are also frequent. Fights between males often end in death to one of the combatants. Agonistic behaviour also plays a large part in courtship.

8. The initial stages of courtship are particularly aggressive: the male chases the female over long distances and they join in face to face combat. Loud vocalizations are used throughout, especially by the female. Later stages of courtship are peaceful, and copulation lasts over an hour. After copulation the male stays with the female for one or two days but does not copulate again.

9. Pregnant females become particularly aggressive shortly before and for the first year after the birth of a calf. Cows often leave very young calves while they feed some distance away.

10. Calves are inquisitive and spend long periods playing with objects in their environment and approaching other rhinos. Mothers discourage such contact by attacking the other rhinos.

11. Female calves leave the mother earlier than male calves. The latter are often attacked by adult males, and sometimes killed. Male calves, on finally leaving the mother, are more likely to associate with other young males than are female calves. They are less likely to be attacked by adult males when in a group than when alone.

12. The most aggressive adult females live in the best parts of the study area, *i.e.* in the parts with the greatest habitat diversity where there is also the highest population density of rhinos.

13. Adult males can be divided into two types. Weak males do not display, rarely initiate agonistic interactions with other males, and rarely court females. Strong males, on the other hand, display regularly, attack other males - especially strange strong males - and court and mate with females.

6. DISCUSSION ON ECOLOGY AND BEHAVIOUR

The following discussion is in three main parts. I consider first, temporal and spatial variations in resource availability and how these affect the ranging behaviour of rhinos. I then discuss individual differences in behaviour and consider how these differences affect individual and inclusive fitness. Thirdly, I discuss the evolution of the observed patterns of behaviour, considering the relationships between social organisation and ecology among ungulates generally and among rhinos in particular.

6.1 Variations in the distribution of resources and their effects on the distribution of rhinos

6.1.1 Temporal and spatial variations in food availability and diet

The diversity of vegetation types within small areas is characteristically high in alluvial plain environments; and the effects of man and his domestic stock further increase the diversity (Wharton, 1968; Eisenberg and Lockhart, 1972). The interspersion of different vegetation types in Chitawan results in a very uneven distribution of rhino food, and the availability of food is also affected greatly by seasonal variations in the weather, and by floods, fires and the activities of other animals, including man (Section 2.1).

The patchy and variable distribution of food restricts the possible diet of rhinos in any season and location (Fig. 4.3). The rhinos' diet changed seasonally, and movements between habitat types resulted in a more varied diet (Section 4.3.4). Seasonal changes in the use of ranges were related to the distribution and seasonal availability of different food types in the study area (Section 4.3.4). The immediate influx of rhinos to tall grass areas after fires, and the movements of rhinos to the scrubby areas along the river-beds and the cultivated land, during the monsoon, are examples of such seasonal changes. Grass fires occurred seasonally in the tall grassland, but the distribution of burns was patchy and differed from year to year. Rhinos quickly found newly burned patches and immediately ate the charred grass stalks and licked the ash from the stalks (Section 4.3.4). Some shrubs such as *Colebrookia oppositifolia* were eaten only when charred: similar observations were reported by Goddard (1968) for the black rhino.

Apart from the seasonal changes in distribution of food, there were more permanent changes resulting from erosion during the monsoon floods (Section 2.1.4).[4] Large areas of riverine forest or grassland were rapidly transformed into bare sandbanks which were later recolonized by grasses, herbs, shrubs and, eventually, trees (Section 2.1.5).

The spatial variations in soil types (Section 2.1.2), the monsoonal climate and the action of fires and floods combine to make the distribution of food rather unpredictable. The same is true to a lesser extent of the distribution of wallows and mineral licks.

6.1.2 Movements and ranges

Dietary diversity was maintained throughout the year (Section 4.3): rhinos adopted temporary daily movement patterns, visiting different food sources, but they appeared to discover new sources of food very quickly, presumably by moving regularly around their ranges (Sections 4.6 and 4.7.2). The availability of wallows also influenced movement patterns: after one wallow was washed away by floods, rhinos in the Sauraha study

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[4] At the height of the floods the Rapti was carrying approximately 1,500 large trees per day past Saurah (57% *Trewia nudiflora* and 25% *Bombax ceiba*).

area used previously unvisited wallows more than half a kilometre distant.

The greatest concentrations of rhinos were in the border areas of the park where there was maximum diversity and interspersion of habitat types (Sections 2.1.5 and 3.5). There also appeared to be a correlation (inverse) between habitat diversity and range sizes. Habitat diversity is greatest in the central blocks of the Sauraha study area where cultivated land, scrub, riverine forest, sal forest, tall and short grassland and river-beds all intermingle (Sections 2.1.5 and 4.6.1). In Section 4.6.3.2 I showed that rhinos whose ranges were centred in these blocks had smaller ranges, on average, than rhinos whose ranges were centred in outlying blocks with a lower diversity of habitat types. Possibly the distances which rhinos have to move between habitat types to take advantage of the seasonal availability of resources such as food, wallows or mineral licks, determine the sizes of their ranges.

In areas where the degree of interspersion of habitat types is high, it is to be expected that rhinos can satisfy their requirements for food, water, minerals and wallows within a smaller range than in areas of more uniform habitat type. Thus, although the scrub and river-bed habitats in the east of the Sauraha study area are very productive of food at certain times of year, the variety of habitat types is not as great as in the central blocks, and rhinos are forced to move further (especially during the spring) in order to satisfy their resource requirements, and their ranges are larger.

Although an animal might be able to satisfy its requirements for food, water, minerals and wallowing by continual wandering over new ground, it is probably an advantage to be familiar with one area and the distribution of resources within that area. Such familiarity can be expected to result in more efficient exploitation of the resources and more successful escapes from predators (Leuthold, 1977). In the case of the Indian rhino, with a rather unpredictable environment, some degree of wandering is expected to be selected for, although I found that most rhinos did stick to particular ranges over the study period.

6.1.2.1 Comparisons of ranging behaviour with other species

The sizes and locations of ranges quoted for different studies of animals are often difficult to compare with each other because of differences in the methods of determination of ranges and the time span over which they were determined. Jewell (1966) defined the *home range* of an animal as the area over which it normally travels in pursuit of its routine activities. Geist (1971) considered that migrating species had several seasonal home ranges with fixed routes of travel connecting them. Jewell (1966) considered the sum of all these ranges including the routes as the 'life-time range' and Jay (1965) termed it the 'annual range'. When determining the ranges of individual rhinos, I took into account all locations during the study period. For almost all animals the annual range was the same as the study period (3½ years) range (Section 4.6.3.5). However, the ranges of rhinos as defined in this report (Section 4.6.3.1) are smaller than annual ranges determined by including all locations of particular individuals (*e.g.* Goddard, 1967b; Owen-Smith, 1973).

Jarman (1974) showed that the movement patterns of antelopes are affected by the degree of dispersion of food items and seasonal variations in food availability and distribution. In general there are fewer fluctuations in the food supply in forests than in grasslands. Thus small forest-dwelling browsers which have a sparsely scattered but relatively constant food supply are commonly sedentary; whereas the large grazers with a seasonally fluctuating food supply are more mobile, and often exhibit seasonal migrations (Jarman, 1974).

Hitchins (1971) found home range sizes of 5.8 - 7.7 km^2 for three black rhino cows in Hluhluwe. These are slightly smaller than the 5.3 - 9.6 km^2 home ranges of white rhino cows in Umfolozi (Owen-Smith, 1973). However, there are considerable variations within species according to habitat type (see Table 6.1). For instance, Goddard (1967b) showed that black rhinos around Ngorongoro had home ranges of 2.5 km^2 in the Lerai forest, 15 km^2 in the surrounding grassland and up to 88 km^2 at Olduvai in dry thorn-scrub. Hitchins (1969) found a home range size of only 3 km^2 for a black rhino cow inhabiting mainly thicket, compared with 5 km^2 for a cow in nearby savanna, and Owen-Smith (1973) showed that white rhino cows fed over a wider area during the dry season than the wet season-up to more than 20 km^2.

Owen-Smith (1973) concluded that white rhino female home ranges in favourable habitat tended to be larger than those of black rhinos under similar conditions, and he postulated that the difference could be related to the white rhino's larger body size and the advantages to a grazer of being opportunistic in its movement patterns and thus discovering the unpredictable variations in food supply typical of grasslands.

Sumatran and Javan rhinos feed largely on saplings and shrubs in rainforest (Table 6.1). Such food is widely scattered, and the home ranges of these species appear to be correspondingly large (Table 6.1). However, the feeding behaviour of the south-east Asian rhinos is adapted to improve the food supply. Both species commonly feed by bending saplings over until they break: on subsequent visits to the site, the rhinos feed from the shoots growing from the bent over saplings (Hoogerwerf, 1970; Borner, 1977; Laurie, unpubl. data). Similar behaviour was observed in Chitawan in Indian rhinos, although it probably did not increase the food supply significantly (Section 4.3.6).

It appears that rainforest rhinos have large home ranges that include various good feeding areas which are revisited at intervals of several weeks. Hoogerwerf (1970) reported that Javan rhinos often walked seven to eight kilometres in one night and probably up to 20 kms in a single day, but they also stayed up to several days within a half km^2 if there was a particularly rich food source. Occasional landslips cause gaps in the canopy, and result in profuse growth of secondary vegetation on which Javan rhinos feed (Schenkel and Schenkel-Hulliger, 1969b; Hoogerwerf, 1970; Laurie, unpubl. data). Borner (1977) reported that Sumatran rhinos walked up to seven kms per day and he suspected that their home ranges were in excess of 20 km^2.

The south-east Asian species of rhino, particularly the Sumatran species, are smaller than the African and Indian species (Table 6.1). This conforms with Jarman's (1974) generalization for African antelopes that browsers are smaller than grazers. However, Jarman (1974) also found that grazers generally have larger ranges than browsers: this does not hold for the rainforest rhinos, presumably because food is particularly sparse near the ground in rainforest (Whitmore, 1975) and a large range is therefore essential. Although both the Javan and Sumatran rhinos inhabit rainforest today, there is evidence for previous ecological separation, which is discussed in Section 6.3.

Indian rhinos are mixed grazers and browsers and thus, by seasonal changes in diet and habitat use, live in ranges, the sizes of which are influenced largely by habitat diversity. The sizes of ranges given in Section 4.6.3.1 are smaller than the total ranges quoted for other rhino species, as a result of the method of calculation (Section 4.6.3). Allowing for this, the ranges of adult female Indian rhinos are about the same size or slightly larger (up to 21.3 km^2) than those of white rhino females (Owen-Smith, 1973), but adult male Indian rhinos have considerably larger ranges than white rhino males. Breeding white rhino bulls hold territories of between 0.8 and 2.6 km^2 in which they maintain exclusive mating rights (Owen-Smith, 1975). In Chitawan, however, such small territories could not include all the habitat types required by a rhino throughout the year. Furthermore, annual floods in Chitawan change the habitat distribution so much that permanent male territories such as the white rhino's are not possible for the Indian rhino (further discussed in Section 6.3.3).

6.2 The selective consequences of individual differences in behaviour patterns

Darwin (1859) held that both behaviour and morphology were subject to natural selection acting on individual differences in reproductive success. Wynne-Edwards (1962) suggested that differences in social behaviour evolved in order to control population size within the limit set by the food supply, and that this was possible through interdemic or 'group' selection for altruist genes. He implied that some individuals would act to their own detriment but to the benefit of the species or the population. It has since been demonstrated that although interdemic selection can take place, the necessary conditions, namely small groups with low migration rates, occur only rarely (Wilson, 1974; Maynard-Smith, 1976). However, it is possible that individuals would be selected to behave in such a way that they decreased their individual fitness but increased their inclusive fitness (Hamilton, 1964) by acting altruistically towards close relatives (Hamilton, 1963; Williams, 1966). Since individuals share a large proportion of their genes with close relatives, they can ensure the replication of some of their own genes by assisting close relatives to reproduce.

Individual fitness is influenced by differences in survival, reproductive output, progeny viability and progeny quality at maturity

(Hamilton, 1963; Crook, 1972). However, behaviour that maximizes fitness can be expected to vary markedly between the sexes and between different age classes (Trivers, 1972). Females, unlike males, cannot have offspring by successive matings, and errors in mate selection are therefore more serious for females than for males. It is expected, therefore, that females will exhibit greater selectivity in mating and will prefer males likely to contribute genes that will increase their offspring's viability and quality at maturity (Fisher, 1958; Maynard-Smith, 1958).

Mate selection by the females can also be influenced by the more immediate role of the male in increasing the offspring's chances of survival by providing food, defending a territory or protecting both the female and the offspring from predation (Orians, 1969). It follows that a male on a superior-quality habitat will attract more and more females until the increased number of females in the area decreases the attractiveness of the male and the area, and makes advantageous a monogamous mating with a male on poorer habitat (Verner and Willson, 1966). In most mammals, the male plays a very minor role in the care of the offspring and, as expected from the arguments above, monogamy is relatively rare (Eisenberg, 1966).

I examine below differences in ranging behaviour and patterns of interactions between and within each sex and age class of rhinos. After considering differences in ranging behaviour, I consider the interactions of adult females first, because it is their distribution and movements which largely influence the reproductive strategies adopted by males (Jarman, 1974).

6.2.1 Differences in ranging behaviour

Not all differences in ranging behaviour can be explained by the distribution of resources in different areas (Section 6.1). There were some differences which appeared to be socially induced. For example, sub-adult males were restricted to scrubby areas away from the central blocks of the Sauraha study area; and both breeding and sub-adult females were more common in the central blocks where the diversity of habitat types was greatest (Sections 3.5 and 4.6.3.3).

Adult males were more widely distributed than sub-adult males but they were relatively scarcer in the areas of highest adult female density. The adult sex ratio in the Tiger Tops study area was one to one but at Sauraha, where the population density was 75% higher than that at Tiger Tops, the adult sex ratio was almost two females to one male (Section 3.6.3). The males living in the best areas for resources appeared to be the strongest ones (Section 5.6.4.2).

Crook (1970) and Eisenberg and Lockhart (1972) suggested that it is adaptive for male animals to reduce the competition for forage between other individuals and the females which will bear their offspring. It could also be adaptive for males to reduce competition by assuming different food habits from the females (Geist, 1974). Gaardarsson and Moss (1970) found that during the breeding season, Icelandic ptarmigan (*Lagopus mutus*) had different food habits according to sex, and that both sexes occupied the same habitat types.

However, by excluding other males, a breeding male not only reduces feeding competition, but also competition for mating with females. Competition between males for females appears to be the most likely explanation of the higher number of females in many species. Walther (1964) described differences in the spatial distribution of male and female Thomson's gazelles: territorial males staked out large territories in the home ranges of females, and relegated bachelor herds to less good habitats. Division of habitat utilization between males and females has also been noted for buffalo in Sri Lanka (Eisenberg and

Lockhart, 1972), for the mountain goats and mountain sheep of North America (Geist, 1971), and for the Asian elephant (Olivier, 1978).

Owen-Smith (1975) reported that territorial white rhino males reduced competition for mating by maintaining dominance over other males within their territories (see Section 6.3.5), but there was no exclusion of subordinate males from territories, and hence no reduction of feeding competition. As female white rhinos are not restricted to a male's territory, there is little advantage to a territorial male in reducing the number of subordinate males feeding in his territory.

In Chitawan, it is possible that relegation of sub-adult male rhinos to areas of inferior habitat reduces competition for forage in the areas of best habitat. However, it seems more likely that differences in ranging behaviour are more closely related to mating opportunities (discussed in Section 6.2.2).

Competition between adult females (Section 5.6.4.1) could be the cause of differences in their ranges. Although food is abundant in Chitawan, its patchy and variable distribution means that competition could occur at small temporary food sources. However, there was no evidence of such competition except at focal points of the environment such as wallows. The advantages to a female of living in the areas of most varied and high quality habitats fall into two main classes. Firstly, cows are likely to increase their chances of rearing a calf because both cow and calf can feed themselves better than in poorer quality habitats. Secondly, the strongest adult males live in the best areas, and calves sired by them are likely to inherit qualities which improve their chances of reproduction (Section 6.2.2.1).

6.2.2 Differences in patterns of interactions

6.2.2.1 Adult females

A female rhino gives birth only once every three or four years and may produce a maximum of perhaps nine offspring in her lifetime (Section 3.7). As explained above, females are expected to select their mate more carefully than males, and to invest considerable energy in the care and rearing of each calf.

(a) Mate selection

A notable feature of courtship in Indian rhinos is that it is extremely aggressive, the male often chasing and fighting with the female repeatedly before mating occurs. 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 behaviour has been observed in the black rhino (Guggisberg, 1966), but is considerably rarer in both the African rhinos (Owen-Smith, 1973) (further discussed in Section 6.3.5).

In the Indian rhino, the chases and fights were noisy, and the loud vocalizations of the female advertised the courtship over a radius of at least one kilometre, with the result that strong males in the vicinity were attracted to the courting pair (Section 5.7). Thus, apart from directly testing the male's strength, one of the functions of the long, noisy chases and fights could be to ensure that the female is eventually mated by a strong male.

It is reasonable to assume that the characteristics associated with being a strong male are genetic, and also that these characters lead to greater reproductive success (Section 5.6.4.2). Thus a female's male offspring are likely to inseminate more females if she mates with a strong male: *i.e.* a female increases her inclusive fitness by mating with a strong male.

The long mating chases could therefore be adaptive to the female, although they are of negative or zero adaptive value to the chasing male (see Section 6.2.2.2). The loud vocalizations used by female elephant seals when resisting copulation could serve a similar function (Cox and Le Boeuf, 1977), and the same could be true of orang-utans (MacKinnon, 1974).

Although Guggisberg (1966) and Ritchie (1963) reported severe fights between male and female black rhinos during courtship, Goddard (1966) did not observe such behaviour, and it appears that the black rhino cows play a more passive role in courtship than Indian rhino cows. In the white rhino, the driving phase is very different to that of the Indian rhino's courtship: the bull white rhino quietly but firmly attempts to keep an oestrous female within his small territory.

The female white rhino thus tests the male on his persistence and his show of strength, and his success in maintaining his dominance within a territory. The differences between the more peaceful courtship of the white rhino and that of the Indian rhino probably evolved as a result of differences in habitat structure and hence visibility (discussed in Sections 6.2.2.2 and 6.3.5). Briefly, in a habitat with low visibility in which males do not hold territories, a female could be mated by any male if she remained quiet, but can attract other (stronger) males by means of loud vocalizations.

Little is known about the courtship of the Javan and Sumatran rhinos (see Table 6.1). Fights between male and female were reported to occur during the courtship of Javan rhinos (Hoogerwerf, 1970). Borner (1977) concluded from tracks and signs that only peaceful interactions took place during the courtship and mating of Sumatran rhinos, but Hubback (1939) found indications of two male Sumatran rhinos fighting over a female (see Section 6.3.5 for further discussion).

(b) Maternal behaviour

Indian rhino cows were particularly aggressive towards other rhinos and man shortly before giving birth and for a year or more afterwards (Section 5.5.4). Such behaviour could be simply competition for food or for space in a wallow (Sections 4.3 and 4.4), or, alternatively, an effort to drive out the opponent permanently, and thus improve the quality of the area for rearing calves. However, as food for rhinos is locally abundant, it is more adaptive to concentrate on feeding rather than attacking a feeding neighbour (see also Kruuk, 1972) and this is what was normally observed (Section 5.2). Jarman and Jarman (1973) concluded that adult male impalas could only expect to increase the food available to their mates and offspring by 3-5% by driving out subordinate males.

A third possibility is that the agonistic behaviour of adult females is primarily an adaptation to protect their own calves and to prevent misdirection of the cow-calf bond. The formation of a bond between mother and young is very important for the survival of the calf, and the period of seclusion around parturition is generally held to be an adaptation to facilitate imprinting of the calf on the mother and vice-versa (Tschanz, 1962; Lent, 1964). In closed habitats such as those of Chitawan the chances of a calf getting lost or attaching itself to another individual are relatively high, and lost calves were seen on several occasions (Section 5.6.2). When a calf is young it may be important for the female to stay apart from other individuals so that her calf knows who to follow: predation and attacks by adult males and other adult females could select for this behaviour.

Cows with calves were involved in agonistic interactions most frequently with other cows with calves (Section 5.4.2). However, adult females did accept the company of sub-adults, some of which were previous calves (Section 5.2). An accompanying sub-adult possibly reduces the risk of predation on the calf and, because she accompanies the cow and calf for long periods and becomes attached to the pair, the danger of the calf getting lost by following her is not so great as with another adult.

Calves normally left their mothers shortly before the birth of a sibling. Several factors may favour a female driving off her young before the birth of her next calf. First, though perhaps unlikely, there is the possibility that the new calf may become attached to her previous calf, and follow it instead of her. Secondly, the older calf might compete for the milk supply, and could do this even before the birth of the new calf. The calf is separated from its mother usually several days to weeks before the birth of a new calf (Section 5.6.1). Separation often occurs gradually, with the calf spending increasingly long periods away from its mother prior to leaving her finally. Male calves tended to stay longer with their mothers than female calves, possibly because they were attacked more often by adult males when away from their mothers (Section 6.2.2.3). Predation and attack by adult males may have played a large part in selection for long periods of maternal care in rhinos. The ratio of intercalving interval to gestation period is 2.5 : 1 in Indian rhinos compared with 2 : 1 in most antelopes, cervids and caprids. This difference possibly relates to the fact that the young ungulates which live in female-young herds, are less subject to predation and attacks by adult males.

6.2.2.2 Adult males

In common with most ungulates, adult male rhinos do not exhibit any direct parental care. The main process by which an adult male can increase his individual fitness is by increasing his reproductive output, and individual males differed greatly in their breeding success (Section 5.6.4.2). The behaviour of adult males towards each other and towards females, led me to divide them into two categories: strong and weak males. Although weak males were probably capable of breeding, and occasionally associated with oestrous females, strong males probably performed almost all matings (Section 5.6.4.2). Note that there is a continuum from weak to strong males: the dichotomy is for clarity and is not a mirror of reality.

(a) Strong males

The strongest males lived in the areas of highest adult female concentrations and moved around constantly over ranges (90% ranges: see Section 4.6.3) of up to six km^2. The amount of overlap between their ranges varied, but it was greatest in the areas of highest population density (Section 5.6.4.2). Adult males probably benefit from occupying such areas because the chances of finding an oestrous female are higher. Secondly, the food resources are better in those areas, and this affects both their own condition and possibly the survival of their offspring, provided that females remain in the area of mating to rear their young (see below).

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 home range were often attacked and sometimes killed (Section 5.6.4.2). There are different levels of the same course of action among strong males, distinguished by the area over which the male wanders and fights other males.

(i) Some strong males maintain their dominance and mating rights year round in areas of low population density, which are good feeding grounds only seasonally. They have to survive on poorer food at some times of the year, but their larger body size means that they are adapted to a poorer diet than cows and calves (Section 4.7). M056 and M053 are examples of such males (Section 5.6.4.2).

(ii) Other strong males maintain their dominance in areas of varied habitat types where there are large resident populations of females, and which other females visit seasonally. There is of course more competition for females in these areas, and only the strongest males can breed. However, strong males known to each other rarely fight over females (Section 5.6.4.2), presumably because it is more advantageous to the challenger to spend time and energy looking for another female than fighting for one which he might not get anyway (see Kummer *et al.*, 1978). M001, M005 and M045 showed this level of strong male behaviour (Section 5.6.4.2).

(iii) The third level of strong male tactics is shown by those individuals which frequently wandered over large areas of both high and low habitat diversity, and attempted to enforce their dominance over resident strong males. Although some matings were undoubtedly obtained by such males, intrusion of this sort often led to fierce fights (Section 5.6.4.2). Only the very strongest males can succeed in obtaining matings over a wide area: the risks of injury and death may be too high for most individuals. M005 ranged over a wide area in the first year of the study period but reduced his range thereafter. M062, however, was not so successful: he was killed by one of the strong males in the central blocks (Section 5.6.4.2).

It is noted in Section 6.2.2.1 that the long mating chases are of zero or negative adaptive value to adult males. However, if males cannot obtain matings without chasing females, and chases are adaptive for females (Section 6.2.2.1), chases will be selected for. In a habitat with poor visibility it is obviously adaptive for a male to follow a female and try to mate with her even if it means entering another strong male's range.

However, if the hypothesis that chases are of adaptive value only to females is to be supported, the loud squeak-pant vocalizations of the adult males (Section 5.3.1) have to be explained. It appears maladaptive for a male to advertise the presence of an oestrous female to other males. There are several possible explanations but the most likely one is that males only squeak-pant while chasing a female if they are dominant over other males in the area. This is supported by the observation (Section 5.3) that even when two males are chasing each other, it is the pursuing one which squeak-pants. The high frequency squeak-pant may also be more difficult to locate than the honks and bleats of the females (Marler, 1967), and if the female is making enough noise for other males to locate her, there is not going to be selection against vocalizations by pursuing males.

Most interactions between strong males and adult females were either courtship interactions, in which cases the male normally initiated them, or attacks by adult females in protection of their calves (Section 5.4.2). Strong males rarely attacked anoestrous females: it is in their interests to encourage females to stay within their home ranges, thus increasing the chances of later finding an oestrous female. Occasional unprovoked attacks perhaps indicate to the females how strong they are. Owen-Smith (1973) noted similar attacks by white rhino males.

Peaceful interactions between strong males and adult females with calves were all confined to courtship: at other times, cows with calves never allowed adult males to approach closely (Section 5.5.4). However, single adult females, sub-adults of both sexes and, occasionally, calves approached an adult male and lay in physical contact with him (Section 5.6). Such associations with females (adults and sub-adults) may have been part of courtship. In the case of sub-adult males, it is in the interests of a sub-adult male to remain in the high quality home ranges and perhaps eventually to take over the mating rights from the strong male (Section 6.2.2.3). A strong male only allowed particular sub-adult males to lie in physical contact with him, and demonstrated his dominance by occasionally jumping up and chasing off the sub-adult (Section 5.6.3).

Aggression directed at sub-adults and calves by a strong male, and occasional deaths resulting from it, might reduce the adult male's inclusive fitness if the sub-adults or calves were related to him. However, the indications were that males remained dominant in a particular area for only two to three years at a stretch (Section 5.6.4.2). As the time from conception to independence is of the order of five years (Section 5.6.2), it is unlikely that sub-adults or calves just about to leave their mothers are related to the resident strong male.

Strong males sometimes attacked calves during courtship and drove them away from the female, perhaps thereby reducing the female's maternal defence reactions and making it easier to subdue her (Section 5.5.2). In such cases the male could be attacking one of his own progeny since it would be normally only 2½-3½ years since the calf was conceived, but the movements of females in and out of a strong male's range (particularly during the spring: Section 4.6.2) make it unlikely that all the calves born or reared in his range were sired by himself. In two cases of a calf of known parenthood being separated during courtship, the courting male was not the father of the calf, and the female was about two and a half kms distant from the site of her previous conception and in a different strong male's range.

Weak males (see below) occasionally associated with strong males but they were sometimes attacked and chased over long distances by the latter. However, weak males were not excluded from the ranges of strong males. Possible reasons why strong males should tolerate the presence of subordinates fall into two categories: (a) it is too costly to exclude them and (b) it is not expensive to keep them. In more detail:

(i) the costs in time and energy of excluding them are too high,

(ii) their effects on the viability of the strong male's progeny by the depletion of food reserves are negligible,

(iii) the chances of them mating are small (Section 5.6.4.2)

and (iv) they may actually increase the strong male's chances of breeding, by detecting an oestrous female and drawing the attention of the strong male by driving her (Section 6.2.2.1).

(b) Weak males

Weak males are often young animals but include some old individuals which have been strong males in the past but are too old to maintain their dominance over others. It is possible that some males may spend two or more periods as strong males separated by periods as weak males, following severe injuries from which they require time to recuperate, unharrassed by other rhinos.

Weak males, unlike sub-adult males, were frequently found in the best areas of habitat. They probably benefit not only from the better resources, but also from occasional matings. However, if challenged by a strong male, they relinquish oestrous females, and do not risk injury or death. Being long-lived animals, they are likely to benefit from waiting until they are strong enough to have a good chance of victory in a fight and be able to dominate other individuals. Furthermore, by remaining within the areas of highest population density, the weak males may learn about the distribution of resources and females, become familiar with the resident strong males and improve their chances of becoming strong males themselves.

6.2.2.3 Sub-adults and calves

(a) Dispersal of sub-adults

Geist (1974) developed a theory that the young of animals living in stable, self-regenerating climax habitats are expected to remain in their home area after leaving their mothers. On the other hand, the young of species from unstable early seral habitats are expected to disperse because there is no advantage in acquiring traditional knowledge of food sources from their parents or from their herds, and there is a good chance that they will discover new unoccupied habitats.

The riverine grassland and forest habitats of Chitawan are all early seral stages, but they are maintained as an edaphic climax by the combined effects of fire, flooding and river erosion. Thus all suitable habitat is expected to be occupied by rhinos, although unusual changes in river courses and burning regimes may create good feeding areas away from concentrations of rhinos.

Adult rhinos display quite detailed knowledge of the distribution of food, wallows and mineral licks at different times of the year, and their experience may be of benefit to sub-adults in exploiting their environment. There is no need for sub-adults to accompany the adults: they merely have to follow the adults by scent, and to use the communal paths which are well marked by dung-piles.

Sub-adult rhinos have probably more to gain by remaining near the area of birth than by dispersing widely. This is certainly true of present day rhino areas: in the past the relative advantages and disadvantages may not have been so clear cut. However, of the six calves in Chitawan which were recognized individually before they left their mother, four were later recognized in roughly the same home ranges as their mothers, although sub-adult males were restricted to the poorer quality regions as described below (Section 5.6.3).

(b) Behaviour of sub-adult males

Selection pressures acting on the behaviour of calves and sub-adults would be expected to act towards improving the chances of (a) immediate survival and (b) reproductive success later in life.

As strong adult males often attack sub-adult males (the risk of injuries to the adult is slight), the latter adopt the strategies of moving out of the areas of highest concentration of strong males, fleeing immediately when approached by other rhinos, and forming groups as a further defence against their attacks (Section 5.6.3). Sub-adult males are very similar in appearance to young adult females and there may have been selection for this resemblance. The long bib and the convoluted neck folds develop during adulthood. Resemblances between young males and adult females have been noted by Geist (1971) to reduce the number of attacks by adult male mountain sheep on young males. Furthermore, as strong adult males never form groups, the sight of several sub-adult males in a group may not trigger the aggressive reaction in the adult which the sight of a single sub-adult sometimes does (Section 6.3.2.1). Sub-adult male groups are known from several species, *e.g.* waterbuck (Spinage, 1969), plains zebra (Klingel, 1969) and warthog (Cumming, 1975), but mixed sex sub-adult groups appear to be unusual (Owen-Smith, 1973), although they occur in both the white rhino and the Indian rhino (Owen-Smith, 1973: Section 5.2.1).

A sub-adult male often attempted to approach and lie down in physical contact with a known strong male in a wallow. Although the strong male often chases him off, such behaviour may eventually benefit the sub-adult: by becoming familiar with a strong male, a sub-adult may increase his chances of later becoming dominant in the area. Perhaps also the stimulus of repeated attacks by adult males 'tells' the sub-adult that he is in a good area for obtaining matings later.

The costs of attacks have to be weighed against the benefits of later reproductive success. Two alternative strategies of taking over a group of females - direct fighting and gradually increasing familiarity - have been described in gelada baboons (Dunbar and Dunbar, 1975). Strong males may attack known sub-adult males less frequently than strange ones, although I have no conclusive data to show this. If so, sub-adult males may benefit from living in the poorer quality areas where only one strong male is likely to encounter them (Section 5.6.4.2), but on the edge of high quality areas where most matings are performed.

(c) Behaviour of sub-adult females

Females leave their mothers at the age of about 3-3½ years and are mated about 2-2½ years later. Their behaviour is similar in many ways to that of single adult females, although they are more timid and flee more readily from any disturbance.

It is in the interests of a sub-adult female to live in the best areas for calf rearing and to become familiar with the structure of a range suitable for breeding: she can do so by attaching herself to a cow-calf pair - sometimes her own mother and full or half-sibling. In the latter case there are mutual advantages to both the sub-adult and her mother. The mother improves her inclusive fitness by protecting her previous calf and gaining help in protection of her younger calf. The sub-adult gains traditional knowledge of the area and protection from predators and the advances of adult males, and also improves her inclusive fitness by protecting her young sibling.

If a sub-adult female is not accepted by a cow, she can follow the movements of the majority of cows and calves by using their paths. Sub-adult females are less frequently attacked by adult males than are sub-adult males, and can therefore occupy the best areas of habitat with impunity until they first come into oestrus.

(d) Behaviour of calves

Some common behaviour patterns of calves appear to involve risks to immediate survival, but might be important in improving the chances of successful integration into the community. For example, calves are very inquisitive and often wander away from their mothers to investigate objects and other rhinos (Sections 5.6.1 and 5.6.2).

Inquisitive behaviour risks injury or death by predation, attacks from other rhinos or starvation as a result of becoming separated from the mother. Calves make contact with other members of the population despite their mothers being strongly protective (Section 5.6). The inquisitive, exploratory behaviour of the calf may be adaptive in that it familiarizes the calf with its physical and social environment and hence may improve the calf's chances of survival and reproduction after leaving its mother. There could be therefore a conflict of selection pressures acting on both the calf and its mother: remaining close to the mother improves a calf's chances of immediate survival, and wandering away from the mother risks immediate survival but may improve subsequent chances of survival and reproduction.

Calves were often attacked by cows with calves, and occasionally by adult males (Section 5.4.2). Young calves in particular showed great interest in adult males who tolerated their approaches and even drove off the calves' mothers if the latter attempted to rejoin their calves (Section 5.6.1). Young hippopotamus calves showed similar interest in adult males, especially when they were defecating or urinating (Olivier and Laurie, 1974). In both species it appears that the calf tries to familiarize itself with members of its community, at the risk of being attacked and possibly killed. There are records of hippo males killing calves (Verheyen, 1954), and one third year male Indian rhino calf was killed in Chitawan by an adult male (Section 5.6.2).

It appeared that young males were attacked more frequently by adult males than young females were (Section 5.4.2). There was also evidence that male calves stayed with their mothers for longer than female calves (Section 5.6.2): perhaps there is selection for a longer rearing period for male calves.

I could not establish whether the rearing period only or whether the intercalving interval was also longer for the mothers of male calves. However, it is possible that the greater readiness of the female calf to leave the mother could decrease the mothers defensive actions and therefore allow the approach of an adult male at an earlier oestrus than if she had a male calf. The latter could stick so close to his mother and elicit her maternal defence so effectively that he stopped her mating again. It may be in his interests to do so, as the new calf will be only a quarter or half related to him, depending on whether it is a full or a half-sibling. Interestingly, male calves, having been driven off by their mothers before the birth of a new calf, sometimes rejoined their mothers in the event of the early death of their sibling.

6.3 Evolution of rhino behaviour patterns and social organisation

6.3.1 Relationships between social organisation and ecology among rhinos

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

In Section 6.2 I discuss the selective consequences of the patterns of relationships between individual rhinos, and point out how these relationships determine the type of society in the Indian rhino. Now I consider the evolution of the observed social organisation, comparing the different species of rhinos with respect to various aspects of their ecology and social organisation.

Table 6.1 summarizes the main facts in the literature about the five species of rhinos. I refer to this table throughout the following discussion instead of repeating the numerous references to the literature.

6.3.2 Grouping behaviour

6.3.2.1 Factors affecting grouping behaviour

Unlike many other ungulates, rhinos are essentially solitary: more than 90% of observations in Chitawan were of solitary individuals or cow-calf pairs (Section 5.2.1). Apart from cow-calf pairs, the only lasting rhino groups consisted of either two or more sub-adults - mostly sub-adult males - or of a sub-adult female with a cow-calf pair (Section 5.2.1). I consider here the likely selective pressures for solitariness, and discuss them with reference to other ungulates.

(a) Vegetation structure

Eisenberg and Lockhart (1972) suggested that the tendency of forest ungulates to be solitary could be partially explained by the poor visibility which makes co-ordination of cohesive groupings difficult. On this hypothesis, the rhinos which live in tall grasslands where the visibility is poor would not be expected to form herds. However, this hypothesis presumably applies to any forest animal, not just ungulates; yet large groupings of forest primates occur, suggesting that it might not be a very important factor. Furthermore, the bearded pig and the

Table 6.1. Some physical, ecological and behavioural comparisons of the five species of rhinoceros.

	Sumatran rhinoceros *Dicerorhinus sumatrensis*	Javan rhinoceros *Rhinoceros sondaicus*	Indian rhinoceros *Rhinoceros unicornis*	Black rhinoceros *Diceros bicornis*	White rhinoceros *Ceratotherium simum*
Adult female body weight (kgs)	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)	c100 *56,57,59*		129 *6*	c100 *4,7,9,13*	128-141 *5*
Adult shoulder height (cms)	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 (cms)	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)	c212-240 *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+ lowland), secondary 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*

* Numbers in italics refer to the literature listed at the end of the Table.

Continued/.....

Table 6.1 *(continued)*

	Sumatran rhinoceros *Dicerorhinus sumatrensis*	Javan rhinoceros *Rhinoceros sondaicus*	Indian rhinoceros *Rhinoceros unicornis*	Black rhinoceros *Diceros bicornis*	White rhinoceros *Ceratotherium simum*
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 (No./km^2)	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* (Great variation according to habitat type)	0.60-5.70 *5,37*
♀ Home range size (km^2)	*c*30 *22* 10 *57*	"quite small" *23*	2-10 *11*	2.6-90.0 *17,18,24,26,50* (as above)	4-15 *5*
Adult sex ratio (♂♂ as % of total)			34-48 (Nepal) *11* *c*50 (Kaziranga) *11,51*	43.5-46.0 *27,28* 53.7-56.1 *17,25,29,50*	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 *D.s.* *11,20,21*	5.2 *11*	10.6 5	17.2 *3*
Visual displays	Tusks Tree twisting? Two short horns *c*250,100mms (max 380) Drag-marks rare *10,11,15*	Tusks Neck folds One short horn *c*150 mms in ♂♂ (rarely in ♀♀) max 250mms Drag-marks *10,11,20,21*	Tusks Very prominent neck folds and bib in A♂♂ One horn *c*400mms max 600 mms Drag-marks (Aoo) *11*	Two long slender horns (up to 1,000mms) Drag-marks *17,27*	Two long horns (up to 1,000mms) Drag-marks rare *3,5*

Continued/.....

Table 6.1 (continued)

	Sumatran rhinoceros *Dicerorhinus sumatrensis*	Javan rhinoceros *Rhinoceros sondaicus*	Indian rhinoceros *Rhinoceros unicornis*	Black rhinoceros *Diceros bicornis*	White rhinoceros *Ceratotherium simum*
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*	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*	*c*9 distinct types, many similar to *R.u.* *11,21*	10 distinct types, mostly loud and controlling spacing between rhinos *11*	Wide variety of sounds, ranging from loud roars to soft mews *11,17,73*	A very wide variety of sounds, particularly of close range signals *3,5*
Courtship behaviour	Fights occur (♂vs ♀) but rather rare. Most courtship peaceful *15*	Fights (♂vs ♀) *20,21*	Fierce fights + long chases *11,53,54*	Fights between ♂+ ♀ and between rival males *27,34,55*	Peaceful containment of ♀ within a ♂'s territory, but fights also occur *3,37*
Male mating systems	-	-	Breeding males territorial but with considerable overlaps: 'territories' >3-4km^2 *11*	Territorial or nomadic/dominance - varies according to habitat type and availability of water *17,26,27*	Territorial: breeding males hold 1-2km^2 territories from which other breeding males are excluded *3*

Continued/.....

Table 6.1 (continued: the literature)

1. SKAFTE (1961)
2. MEDWAY (1969)
3. OWEN-SMITH (1975)
4. HITCHINS (1968b)
5. OWEN-SMITH (1973)
6. LANG (1961)
7. MEINERTZHAGEN (1938)
8. SONNE-HANSEN (1972)
9. FREEMAN and KING (1969)
10. LEKAGUL and McNEELY (1977)
11. LAURIE (This report and unpublished data)
12. MAHARAJAH OF COOCH BEHAR (1908)
13. KING (1969)
14. GROVES (1967a)
15. BORNER (1977)
16. SCHENKEL and SCHENKEL-HULLIGER (1977)
17. GODDARD (1967b)
18. HITCHINS (1971)
19. SODY (1959)
20. SCHENKEL and SCHENKEL-HULLIGER (1969b)
21. HOOGERWERF (1970)
22. FLYNN (pers. comm. 1976)
23. HAZEWINKEL (1933)
24. JOUBERT and ELOFF (1971)
25. WESTERN and SINDIYO (1972)
26. HITCHINS (1969)
27. SCHENKEL and SCHENKEL-HULLIGER (1969a)
28. ROTH and CHILD (1968)
29. GODDARD (1970a)
30. CAVE (1962)
31. CAVE (1966)
32. WROUGHTON and DAVIDSON (1918)
33. POLLOK and THOM (1900)
34. GUGGISBERG (1966)
35. FRANCK (1934)
36. SANYAL (1892)
37. PLAYER and FEELY (1960)
38. SCHAURTE (1969)
39. PIENAAR (1970)
40. JARVIS (1967)
41. TONG (1960)
42. BARTLETT (1873)
43. GROVES (1972)
44. ANDERSON (1872)
45. WILSON and EDWARDS (1965)
46. KRISHNE GOWDA (1969)
47. MORRIS and JARVIS (1959)
48. GROVES (1975)
49. MacNAUGHT (1932)
50. MUKINYA (1973)
51. LAHAN and SONOWAL (1973)
52. MJÖBERG (1930)
53. GEE (1953a)
54. BERG (1933)
55. GODDARD (1966)
56. HUBBACK (1939)
57. STRICKLAND (1967)
58. PRATER (1971)
59. EVANS (1904)
60. LANG (1967
61. LANG *et al.* (1977)
62. BUECHNER *et al.* (1975)
63. VAN STRIEN (1974)
64. SHORTRIDGE (1915)
65. PEACOCK (1933)
66. JOUBERT (1971)
67. GODDARD (1968)
68. THOM (1943)
69. ANTONIUS (1937)
70. CAVE (1969)
71. CAVE and ALLBROOK (1959)
72. DENNEY (1969)
73. FRAME and GODDARD (1970)

peccaries form large herds in forests (Medway, 1972; Sowls, 1974) maintaining cohesion by frequent vocalizations; and the swamp deer and water buffalo live in herds in the tall grasslands of northern India and Nepal (Gee, 1964).

(b) Food dispersion and abundance

Among African bovids, Jarman (1974) noted that those species which feed selectively on small unevenly distributed food items generally do not form large groups, whereas those species which feed relatively unselectively on abundant, continuously dispersed food, aggregate in large herds. In Chitawan, food for rhinos is locally abundant although it is patchily distributed in time and space (Section 4.3.3). Thus at most food sources there appears to be little competition for food between rhinos, and several individuals may congregate at the same food source (Section 5.2.2).

(c) Predation

For many species, predation has been invoked as a major selective pressure favouring aggregations of animals rather than solitary existence. Jarman (1974) considered that predation may set the lower limit on group size in ungulates because of the advantages conferred on animals in open habitats by aggregating. However, because of their size, adult rhinos are rarely preyed upon (Section 3.8.1), and there is no consequent selection for aggregations.

Sub-adults, on the other hand, may be attacked by tigers (R.N. Sonowal, pers. comm., 1976), which may explain partly their tendency to form groups among themselves and with cow-calf pairs (Section 5.2). There may also be a mutual advantage to cows with calves in having an accompanying sub-adult as an extra guard against predation of her calf (Sections 5.6.4.1 and 6.2.2.1).

(d) The passing on of traditional knowledge

In long-lived animals such as rhinos and elephants, the accumulation of traditional knowledge of food sources, mineral licks and wallows may be advantageous for survival in seasons which differ from normal. Elephants have no need to aggregate in herds for predator defence, yet they form large herds whose benefit to individual members may be the accumulation and utilization of traditional knowledge (Laws, 1969).

Rhinos, on the other hand, do not form large groups, although the long period spent with the mother, and the associations between adult females and sub-adults may be important in this context. However, rhinos are more sedentary than elephants, and there may be less traditional knowledge to be passed on.

(e) Attacks by conspecifics

Single sub-adult male rhinos were often attacked by adult males but groups of sub-adults were never attacked (Section 5.6.3). Attacks by adult males could be a selective pressure on sub-adults to form groups with each other or with cow-calf pairs (Section 6.2.2.3). Robertson *et al.* (1976) reported that parrot fishes (*Scarus croicensis*) reduced attacks by territorial males by schooling, although in that case it appeared that individuals were reducing the chances of attacks to themselves rather than inhibiting attacks by adult males on individuals in the school.

There are problems in deciding which of the above selective pressures are important in determining grouping behaviour. As Sinclair (1977) has pointed out, there is a danger of circularity in arguing for any one selective pressure, because all the factors are inter-related. Body size and feeding style are closely linked (Section 4.7.1) and both these influence habitat choice and anti-predator behaviour. Small-bodied species typically feed selectively on highly digestible and nutritious forage which is sparse and scattered, and available in the most constant supply in forested habitats. Large-bodied species, on the other hand, are adapted to feed relatively unselectively on forage of low energy content such as grass which is most abundant in open habitats. Small-bodied selective feeders which live in closed habitats can hide from predators and do so more efficiently when alone or in small groups. On the other hand, large unselective feeders which feed in the open have to either flee from or attack predators, and may gain an advantage by associating in groups (Eisenberg and Lockhart, 1972; Jarman, 1974).

These inter-relationships make it very difficult to distinguish between the hypotheses listed above. Among sub-adults, both predation and attacks by adult males select for aggregations. However, among adults there appear to be few selective pressures for aggregations, although occasional aggregations at abundant food sources are presumably not selected against because time spent competing with others is better spent feeding. A further selective pressure for adult males to be solitary is the resulting reduction in the probability of proximity of competitors during mating (discussed in Section 6.2.2).

The mother-calf bond is obviously very important in a slow maturing species such as the rhino, and mothers of young calves seem to be particularly aggressive towards other rhinos, tending to associate with others less than single females or the mothers of older calves. Thus, there may be selection acting on mothers to remain solitary: possibly the selective pressure is attacks by other rhinos on the calf, or the possibility of misdirection of the cow-calf bond (discussed in Section 6.2.2.1).

6.3.2.2 Comparisons of grouping behaviour with other species

Rhinos differ from most of the larger ungulates in being mainly 'solitary'. Other 'solitary' species include some suids (Frädrich, 1974), moose (Houston, 1974), sambar (Schaller, 1967; Laurie, unpubl. data) and tapirs (Medway, 1969). African antelopes, equids, elephants and hippos generally associate in large groups (Klingel, 1969; Douglas-Hamilton, 1972; Jarman, 1974; Olivier, 1978) although hippos forage on their own at night (Olivier and Laurie, 1974).

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 (Section 5.2.1; Table 6.1). These figures compare with 1.7% and 10.6% for black rhinos (Hitchins in Owen-Smith, 1973), and 3.4% and 17.2% for white rhinos (Owen-Smith, 1973). Borner (1977) found evidence of Sumatran rhinos associating in pairs only twice - the several hundred other tracks which he followed were of single individuals. When they were more numerous, Sumatran rhinos may have been slightly more gregarious than the recent evidence suggests: Pollok and Thom (1900) reported that although mainly solitary, three or four were sometimes found within one and a half kilometres of each other, and they once saw two females in one wallow. Wroughton and Davidson (1918) reported two groups of four and six individuals.

The evidence is similar for the Javan rhino: three individuals was the largest number tracked together by Hoogerwerf (1970) during many years in Ujung Kulon, and he only rarely found groups of two individuals, other than cow-calf pairs. Schenkel and Schenkel-Hulliger (1969b) found two to four individuals near each other on several occasions although not actually moving together. During my own brief visit to Ujung Kulon in 1975, I saw one pair of sub-adults moving together (Laurie, unpubl. data).

The relationships between group size and habitat in rhinos parallel some of Jarman's (1974) correlations among African antelopes. White rhinos live in open habitats with a uniformly distributed abundant food supply, and, although not found in herds, they form large groups more frequently than the other species. The black rhinos have more dispersed food sources but still form large groups more frequently than the Asian species - possibly because of their generally more open habitat types. Indian rhinos form aggregations in open feeding grounds and at focal points such as wallows, but are generally less social than the African species. Javan and Sumatran rhinos appear to form groups less frequently than the Indian rhino, although there is evidence that the Javan rhino may have been found in larger groups in the past (Sody, 1959). This is in accord with Jarman's (1974) correlation, since the south-east Asian species inhabit dense forest where visibility is poor, and their food items are widely scattered and not quickly renewable.

Correlations of this kind, including other factors such as body size and social organisation, are discussed further below. It should be pointed out, however, that loose correlations of this sort are rather crude when compared with similar ecological behavioural correlations for primates (*e.g.* Clutton-Brock and Harvey, 1977).

6.3.3 Maternal behaviour

Indian rhino cows charged intimidatorily at other rhinos and at human intruders, especially just before giving birth and during the first year of the calf's life. Owen-Smith (1973) stated that white rhino cows did not charge in defence of the calf; they differ in this respect from black rhinos (Schenkel and Schenkel-Hulliger, 1969a). Another difference between the species widely commented upon in the literature is that white rhino calves always flee behind their mothers while black rhino and Indian rhino calves always flee ahead of their mothers (Selous, 1881; Gee, 1951). In Chitawan, calves often led the retreat but they were influenced by the direction in which the mother started to run, and usually ended up behind her. The absence of an intimidatory charge in the white rhino is puzzling: perhaps it is a result of having evolved with a different set of predators (Owen-Smith, 1973).

Cow rhinos in Chitawan normally stayed close to their calves, but for the first three months they often left their young calves unattended and grazed up to 800 metres away for periods of one to two hours (Section 5.5.4). Such behaviour has not been recorded before in Indian rhinos but Joubert and Eloff (1971) had evidence that a very young black rhino calf was left similarly unattended, 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; it is probably not adaptive in species which inhabit open country where hiding places are scarce.

Walther in Lent (1974) first classified ungulate young into 'hiders' and 'followers', and Lent (1974) summarized some of the general differences in ecology and behaviour between the two types. Hiding of young has developed as an anti-predation device in those species living in closed habitats, or in small species able to hide in low cover in open habitats: followers are generally larger species typical of open habitats and are often characterised by great seasonal mobility. 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 a hiding strategy. Walther (1968) suggested that, in 'hiding' species, the following response of young animals is often imperfectly developed: this accords with the 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, 1953a; Goddard, 1967b; Coenraad-Uhlig, 1933; Owen-Smith, 1973).

The prolonged periods of physical contact of a cow with her calf, and the toleration of sometimes quite violent play behaviour without any overt signs of aggression (Section 5.4.2), are plainly adaptive to the adult female in maintaining the bond with her calf. I never saw a cow terminate a suckling period: it was always the calf who terminated suckling, and the cow readily responded to signals from the calf indicating the desire to nurse (Section 5.5.4.3). In many other ungulate species, the mother becomes more aggressive during suckling as her offspring grows older (Leuthold, 1977). However, African buffalo calves, which also have a long period of dependence on the mother, suckle for long periods and continue to nurse after their mothers have stopped lactating (Sinclair, 1977). This may be an adaptation to maintain family bonds in both buffaloes and rhinos. Owen-Smith (1973) also reported no aggression during suckling,between cow and calf white rhinos. Weaning conflict is generally expected to occur because the mother and her young have to act differently to maximize their inclusive fitness (Trivers, 1974). However, with a long inter-calving interval and weaning generally complete before the calf's independence, weaning conflict has not developed in rhinos.

6.3.4 Sexual dimorphism and sex ratio

Verner and Willson (1966) suggested that sexual dimorphism, selection for aggressive males extending body growth into adulthood, and polygamy were characteristic of birds living in fluctuating habitats with a large productivity gradient, such as marshes. Jarman (1974) noted a relationship between sexual dimorphism and the feeding styles or social classes of antelopes: small browsing species generally exhibit little sexual dimorphism and maintain pair territories, whereas grazing species which move more, and live in habitats of greater productivity gradient, exhibit considerable sexual dimorphism, and there are more adult females than males in the population.

Indian rhino adult males are about 129% of the adult female weight and are known to extend growth considerably into adulthood (Lang, 1967). The evidence for the white rhino is similar (Table 6.1). However, the black rhino and the Sumatran rhino show almost no sexual dimorphism in body size and, for Javan rhinos, the evidence is equivocal; Hoogerwerf (1970) maintained that females are heavier than males, but Schenkel and Schenkel-Hulliger (1969b) deduced from track measurements that females are smaller than males.

Although the black and Sumatran rhinos do not show any sexual dimorphism in body size, both these species, in common with the other rhino species, are sexually dimorphic in skull size, in particular nasal breadth, and horn size (Pocock, 1946; Groves, 1967a, 1972, 1975; see also Appendix M). Males generally have wider skulls and broader horns than females.

Adult sex ratio is difficult to measure, and the result depends upon the area considered. In Chitawan there are more adult females than males but in the best quality areas the sex ratio is particularly disparate (Section 3.6.3). More females than males are generally reported for the white and Indian rhinos, but four out of six reports for black rhinos indicate more males than females (Table 6.1), and the evidence for the southeast Asian species is inconclusive. Skafte (1961) caught only one male among eight Sumatran rhinos in a trapping operation in Riau, Sumatra, and Hoogerwerf (1970) concluded that there were more male than female Javan rhinos in Ujung Kulon. However, Schenkel and Schenkel-Hulliger (1969b) and Borner (1977) thought that the sex ratios were nearer unity in these two species.

The Sumatran and the black rhino, the only two species which are definitely not sexually dimorphic in body size, are also the smallest species, feed almost entirely on browse and live at the lowest population densities (Table 6.1). Thus, the rhinos appear to conform to Verner and

Willson's (1969) suggestion and Jarman's (1974) generalization. The two polygynous grazing species have developed considerable sexual dimorphism, with more emphasis on the horn size in the white rhino which lives in open habitats and on the neck folds and bib in the Indian rhino which lives in closed habitats (see Section 6.3.5). However, the black rhino is not monogamous (Goddard, 1966), and Borner (1977) was of the opinion that the Sumatran rhino is not monogamous either. Perhaps, therefore, the lack of sexual dimorphism in body size is simply a result of the limitations of a diet of browse (Bell, 1971; discussed in Section 4.7.1).

6.3.5 Mating systems

6.3.5.1 Competition between males

Competition between male animals for mating opportunities has generally been regulated socially. Overt fighters with dangerous weapons have generally been selected against, and displays and non-damaging fights selected for (Geist, 1974). Ungulates have reduced serious fights by ritualizing agonistic interactions (Geist, 1966; Maynard-Smith and Price, 1973), although fatal combat between males occurs in several species, particularly those which are not faced with high predation pressures, such as moose (Geist, 1971), bison (McHugh, 1958), hippos (Attwell, 1963; Olivier and Laurie, 1974) and rhinos (Table 6.1).

The ways in which male animals regulate competition for mating with females have been classified into two main groups: territorial systems and dominance systems. Territoriality is essentially a form of spatially localized dominance (Owen-Smith, 1971), which has been favoured evolutionarily under ecological, sociological and morphological conditions where the costs associated with alternative mating strategies are likely to be higher than those associated with holding a territory (Owen-Smith, 1977).

I discuss here the mating system of the Indian rhino in Chitawan, with reference to the mating systems of other rhino species, and possible evolutionary reasons for the observed differences between the systems.

Indian rhinos are large animals with directly functional, potentially dangerous weapons, which do not form large groups (Section 5.2) and are relatively localized in their movements (Section 4.6). 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, various morphological and ecological conditions of the Indian rhino in Chitawan have, I suggest, resulted in a mating system which is a type of dominance hierarchy partially determined by location.

Firstly, as mentioned above, the lack of predation pressure on adults reduces selection against intraspecific fighting, although, in their evolutionary past, rhinos were subject to predation by larger predators (Section 2.2). Other evolutionary reasons why the Indian rhino's mating system (see Section 6.2.2.2) differs from true territoriality fall into two main groups:

(a) those associated with the uneven distribution of resources over time and space (Section 6.1.1)

(b) those associated with the poor visibility in the closed habitats of the Indian flood plains (Section 5.7).

It is useful to compare here the white rhino with the Indian rhino. Territorial male white rhinos hold small (1 - 2 km^2) mutually exclusive territories in which they maintain mating rights to all females, but tolerate subordinate males so long as they do not display or engage in courtship (Owen-Smith, 1971). Females roam freely over many male territories, and, when in oestrus, are confined to one male's territory by the male's gentle blocking manoeuvres at the territorial boundaries (see below).

A mating system such as the white rhino's could not be favoured evolutionarily in Chitawan, since the great seasonal and unpredictable annual changes in the distribution of resources (mainly food, but also wallows) mean that male Indian rhinos cannot restrict their movements to such small areas as the white rhino males in South Africa, where there are relatively small variations (in time and space) in forage productivity (Owen-Smith, 1975).

Indeed, it may be adaptive for Indian rhino males (and females) to roam over wider areas than necessary for survival, because of the rapid changes in the distribution of habitat types. By adopting a wide ranging habit, males could increase their chances of finding (a) new, rich food sources and (b) aggregations of females already feeding on such food sources. I suggest that male Indian rhinos do not have a defendable resource (Brown, 1969), and would not therefore be expected to be strictly territorial. The area over which it is adaptive for males to move in search of food and females, is too large to defend against other males.

Secondly, in support of the above hypothesis, I suggest that the poor visibility in the alluvial plain habitats further 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 male 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 (Section 6.2.2.2). The difference in visibility between the African and Asian habitats is discussed in Section 5.7. Geist (1966) noted a negative correlation between the sizes of horns (for display) and tusks (for damaging attacks) in rhinocerotids and cervids. The African rhinos have lost their tusks, but their horns are considerably larger than those of the Asian species: presumably, in open habitats, horns (and possibly the nuchal hump and extended penis of the white rhino) can be used as distance displays, whereas in the closed habitats of Asia the emphasis in displays is on the neck folds, bib and tusks (Section 5.7).

In areas of high population density where several strong males' ranges overlap and where the males have become accustomed to each other over several years (Section 5.6.4.2), it would probably be adaptive for those males not to fight each other if evenly matched, especially as there is a good chance that the mating will not end in conception (Section 5.5.1). Hippo males also fight to decide dominance but rarely challenge a male in possession of an oestrous female (Verheyen, 1954; Olivier and Laurie, 1974). It should also be adaptive for weaker males to avoid fights, and for strong males to discourage weaker males from mating. The fact that fights between rhino males are frequently fatal, indicates that the advantages to be gained from winning fights must be great. However, a much longer term study is necessary to find out the magnitude of the enhancement of breeding success in strong males.

The expression of social behaviour in terms of population organisation is very sensitive to ecological influences (Crook, 1970): territoriality may be present in one population of a species and absent, or present in a different form, in another population, *e.g.* impala (Jarman and Jarman, 1974). Black rhinos appear to show similar variability. In wet habitats they exhibit a similar mating system to that of the white rhino (Hitchins in Owen-Smith, 1973), but they range more widely and at lower densities in dry areas (Schenkel and Schenkel-Hulliger, 1969a). The sparse distribution of food and water may make it not adaptive for males to establish territories in dry areas. The mating system of the Indian rhino could be subject to similar variability in different areas. However, in Kaziranga, rhinos appeared to have a similar social organisation to that in Chitawan (Laurie, unpubl. data), and their seasonal changes in ranges as a result of flooding were much greater.

The marked seasonality of forage production in the Indian rhinos' habitats may be another factor which has selected for a greater degree of direct competition between males than in the white rhino. For the Indian rhino there may well be an energy surplus during the spring and the monsoon (Sections 4.3 and 4.5), which can be expended on fights between males and on long courtship chases. In comparison, energy surpluses are probably small for the white rhino which lives in habitats where seasonal fluctuations in forage production are relatively small in relation to population levels. This may partly explain the absence of extended fights and chases both between males and between males and females.

Little is known of the mating systems of the south-east Asian rhinos, and, because they now live at much lower densities than previously (particularly the Javan rhino: see Appendix A and Table 6.1), recent studies may indicate different mating systems from those which operated in the past. Damaging fights have been recorded between males when population levels were higher (Table 6.1), but not recently. Borner (1977) suggested that male Sumatran rhinos maintain mating rights at focal points in the environment, such as mineral licks, visited by many females. However, it is not clear what the relative advantages would be to a male of (a) staying at one place and waiting for females or (b) moving around, perhaps feeding better, and finding females away from mineral licks.

Food is relatively predictable (in time and space) in the rainforest, and the Sumatran rhinos' method of feeding produces new growth of food for subsequent visits to the same area (Section 6.1.2.1). Therefore, a rhino's best feeding strategy is to roam widely but to return to familiar areas. Regular movements also increase the chances of finding new sources of food such as the rich growth of saplings and shrubs which grow at the sites of land-slips or tree-falls. Thus, a male Sumatran rhino's best strategy would appear to be to roam widely over a large home range, following rhino paths and visiting focal points where scent-marks might indicate the passage of an oestrous female.

Competition between males would then 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). I suspect that males accompany females for quite long periods before oestrus, and that there has been selection for females to delay oestrus for as long as possible to increase the chances of another male finding the pair and challenging her mate (see Section 6.3.5.2). The absence of sexual dimorphism in body size is discussed in Section 6.3.4, but Sumatran rhino males have larger horns and tusks than the females (Groves, 1967a), which indicates some degree of direct competition between males.

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, 1967a). I suggest that it was ecologically separated from *R. kendengicus* in Java (Section 1.3.1) and *R. unicornis* in India (Appendix B) by being unable to graze on short grasses, but that it ate tall grasses and palms (Table 6.1). At present, apart from living at considerably lower population densities than formerly (Sody, 1959; Table 6.1), the Javan rhino is restricted to rainforest. This should be remembered when making conclusions about the ecology and behaviour of the Javan rhino. For instance, it is very likely that individuals have larger ranges in rainforest than in lowland swamp-forest.

Little is known at present about the Javan rhinos' mating system, but

Hartmann Amman (pers. comm., 1978) is at present studying the species in Ujung Kulon. I suggest that originally the Javan rhino had a similar mating system to that of the Indian rhino. The conditions of unpredictable food supplies and poor visibility apply to both species, although the Javan rhino's food supply was probably more predictable in time and space than that of the sympatric *R. kendengicus*. Reports of fights between males and females and long noisy chases (Hoogerwerf, 1970) indicate similar courtship behaviour to that of the Indian rhino (see Section 6.3.5.2).

Horsfield (1824, in Sody, 1959) reported that Javan rhinos 'lived gregarious' in many parts of Java in the early nineteenth century, and Sody (1959) quoted many more,similar reports. Living at high densities (Table 6.1), competition between males would be expected to be regulated partially by a system of spatially localized dominance, as in the Indian rhino. Now, in Ujung Kulon, where Javan rhinos have to roam more widely at lower densities, such a system is unlikely to be operating. It is more likely that males are adopting the same mating strategy as the Sumatran rhino, which is primarily adapted for life in the rainforest (see above).

6.3.5.2 Courtship and mating

The aggressive courtship behaviour of Indian rhinos is unusual among ungulates, although similar behaviour has been recorded in black rhinos (Guggisberg, 1966), Javan rhinos (Hoogerwerf, 1970), Sumatran rhinos (Lock, 1937) and hippos (Attwell, 1963). Long noisy chases, however, appear to be restricted mainly to the Indian rhino although they also occur in the Javan rhino (Table 6.1; Hoogerwerf, 1970). I suggest in Section 6.2.2.1 that the noisy mating chases and fights of the Indian rhino are adaptive to the females in attracting stronger males (this is despite the fact that females are sometimes killed; Section 3.8.1; R.N. Sonowal, pers. comm., 1976). A seasonal energy surplus, lacking in the other (tropical) species, may have allowed this system to evolve.

Secondly, poor visibility is a selection pressure for such chases (Section 6.2.2.1). From this premise one might expect chases in the Sumatran rhino, but lower population densities and an emphasis on indirect visual and olfactory marks in the environment (Borner, 1977) combine to make long chases non-adaptive.

On the other hand, the good visibility in the white rhino's habitat has led to the female simply testing the male on his ability to defend a territory and to keep her within it. His silhouette in side view may be important in this context; perhaps also the nuchal hump and the extended penis (Owen-Smith, 1973). With reference to the penis, the white rhino is the only species shown to possess preputial scent glands (Cave, 1966). Perhaps the combination of visual and olfactory signals function in restricting oestrous females to single territories.

A characteristic of the mating of rhinos is the prolonged copulation - between 30 minutes and 75 minutes in black, white and Indian rhinos (Goddard, 1966; Owen-Smith, 1973; Gee, 1951; this report, Section 5.5.3). There is also evidence of repeated ejaculation during this period (Owen-Smith, 1973; this report, Section 5.5.3). The advantages to a large-bodied species of a long copulation and repeated ejaculation is that it could save effort in mounting. It is odd in this context why elephants, although larger still, copulate for only a few seconds (Eisenberg *et al.*, 1971). Alternatively, copulation may cause the release of ova. Rhinos rarely re-mount a female after copulation (Goddard, 1966; Owen-Smith, 1973; Section 5.5.2) although Indian rhino males remained with females for one or two days afterwards - perhaps thereby ensuring that no other male copulated with her. The associations observed between pregnant females and strong males (Section 5.5.3) are puzzling. Perhaps there are advantages to the females in attracting the attentions of males at a certain stage of pregnancy, but it is unclear what they are.

6.3.6 Conclusions

The social organisation of the Indian rhino, discussed above, has probably been favoured evolutionarily by the following conditions:

(a) large body size, leading to a low predation risk for adults, and the animals being dispersed singly or in small groups (cow-calf pairs or sub-adult groups).

(b) seasonal and unpredictable variations in the distribution of resources in time and space, leading to animals moving regularly around ranges, the sizes of which vary according to habitat diversity and productivity.

(c) generally poor visibility, combined with (b) (above), leading to (i) males being unable to defend territories and (ii) advantages to females in resisting and vocally advertising attempts at copulation.

(d) seasonality possibly leading to an energy surplus which can be expended in fights between males and in mating chases.

The Indian rhino has survived since the Pleistocene, whereas numerous other large ungulates, including several species of rhinoceros, elephants and hippopotamus have become extinct (Colbert, 1935). The Indian rhino's unselective feeding habits, its adaptibility to a wide variety of habitats and food types and its affinity for water have probably been important factors in its survival. In this context, it is interesting to compare the hippopotamus, which died out in India, with the Indian rhino.

I examine briefly here a possible example of convergent social organisation in the hippo and the Indian rhino, resulting from similar ecological conditions. Both species are large grazers associated with alluvial plain environments and affected by unpredictable variations in the distribution of resources. The nature of the essential resources and the extent of their unpredictability varies between the species. Changes in the distribution of vegetation types, and seasonal changes, are greater in India and Nepal and have a greater influence on the rhino. The hippo, with a form of fore-stomach fermentation may not require the same diversity of food as the rhino (Section 4.7), although changes in river courses will obviously affect food availability. However, the hippo's main limitation is its physiological requirement to remain in water for long periods of the day. Unpredictable variations in the water-level, particularly in rivers, cause hippos to aggregate in large herds when wallowing places are scarce and to split up into smaller groups when water-levels rise (Olivier and Laurie, 1974).

Thus, in both species, unpredictable variations in the distribution of resources affect the movements and distribution of adult females and hence the optimum mating strategies of the males. Such conditions favour a male mating system based on dominance rather than territoriality (Section 6.3.5). For the rhino, poor visibility is another factor which selects against territoriality. Visibility is better in the habitats of the hippo but, as the animals are confined to the water during the day, defence of a territory on land is impossible, and there is no advantage to be gained from holding a territory in the water, because of the unpredictable movements of the females.

There are several similarities in behaviour between the Indian rhino and the hippo; notably the frequent escalation of fights (sometimes involving long chases), the actual fighting technique using the lower tusks, displays which show off the lower tusks, attacks by adult males on young males, approaches by calves to adult males, and the fact that 'strong' males with oestrous females are rarely challenged by other males (Verheyen, 1954; Attwell, 1963; Olivier and Laurie, 1974).

Such close correspondence in social organisation is interesting in view of the similarities in the ecology of the two species. The fact that the Indian rhino survived in India and the hippo died out, may be explained by the greater variations in resource distribution (resulting from the high latitude and the monsoon) favouring the rhino which feeds, unlike the hippo, on browse and aquatic plants. If we take this speculation a step further, the hippo in Africa may occupy the equivalent niche of the Indian rhino, and this may explain why the African rhinos are not aquatic: the white rhino can swim only with difficulty, and its distribution is limited by rivers (Owen-Smith, 1973).

Further studies on the social organisation and ecology of hippos and rhinos should provide data to test some of the suggestions and hypotheses I have put forward (see also Laurie and Olivier, 1977). H. Klingel (pers. comm., 1977) is at present studying hippos in Uganda, and (as mentioned above) H. Amman (pers. comm., 1978) is studying Javan rhinos in Ujung Kulon. A continuation of my study, making use of the histories of known individuals, is also being considered.

7. CONSERVATION

Rhinoceros unicornis is an endangered species (IUCN[5], 1978), of which fewer than 1,200 individuals remain in the wild (Laurie and Olivier, 1977). It is desirable for many reasons to conserve the diversity of flora and fauna characteristic of natural ecosystems, and the conservation of a single species has to be considered as part of the conservation and management of whole ecosystems. Conservation should not be regarded as an unproductive form of land use; rather it can have important economic, social and educational values, and should be regarded as the management of natural resources for man's benefit now and in the future so as to achieve the highest sustainable quality of human life (McNeely, 1975).

In this section, I consider some of the implications of the results of this study for the conservation of the Indian rhino and its natural habitats. There is not space in this dissertation for a full discussion of the results with respect to conservation: this will be published in a separate report. I discuss here the threats to the rhino's continued survival in the wild and then suggest how its chances of survival might be increased in ways compatible with the other aims of conservation and other forms of land use.

7.1 Threats to survival

The massive reduction in the range of the Indian rhino (Section 1.3) was caused primarily by the disappearance of most of the alluvial plain grasslands of northern India. Many of the patches of such habitat which remained were too small to protect rhinos from the depredations of hunters, poachers and farmers (Section 1.3.2). The conflict between man and rhinos was heightened by the fact that the preferred habitat of the rhinos was also the most suitable for the cultivation of wet rice (Section 1.3.2). By

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[5] International Union for the Conservation of Nature and Natural Resources.

the middle of this century, rhinos were largely restricted to reserves, and their survival depended on the protection given to them by man (Section 1.4). The history of Chitawan illustrates the potentially disastrous effects on the rhino population, of a breakdown in law and order (Section 1.4).

The survival of the Indian rhino is still threatened by poaching (Section 3.8.1; Appendix C) and by human encroachment on the habitat (Section 2.1.7). However, there are now additional threats which stem from the concentration of the few remaining rhinos into a small number of tiny reserves. Nine hundred of the c1,100 surviving rhinos live in two National Parks containing a total of 500 km^2 of rhino habitat (Section 1.3.2). Any catastrophe in Chitawan or Kaziranga such as an epidemic disease, severe flooding or a breakdown in law and order 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 rhino (Section 2.1.5).

7.1.1 Poaching

As both males and females bear horns, rhinos of both sexes are killed by poachers. This fact, combined with the low reproductive rate (Section 3.7.1) makes extensive poaching likely to deplete rhino populations very quickly. However, the Indian rhino is fully protected in Nepal, India and Bhutan, and as long as the present high standard of protection is enforced, the dangers of severe losses from poaching are slight. Previous heavy poaching may have resulted in a low ratio of young to old animals in the population today.

In Nepal there have been no cases of poaching discovered since July 1975 (Section 3.8.1). Poaching was dramatically reduced in 1973 with the gazetting of the Royal Chitawan National Park (Section 1.4), and the reorganisation of the guard force. The Royal Nepalese Army took over the protection of the park in 1976 and, despite some antagonism of the local villagers and an initial unfamiliarity with life in the jungle, the soldiers have successfully controlled poaching (Section 2.1.7).

There is still a low rate of poaching in India, even in Kaziranga National Park (Appendix C): control of poaching is made more difficult than in Nepal by the fact that people are allowed to enter and even live inside most of the Indian reserves (Appendix C; Section 7.1.2). Thus poachers can pose as buffalo graziers or collectors of forest produce who have a legal right to be within the protected areas.

7.1.2 Encroachment and disturbance by man and his domestic stock

Cultivation and the grazing of domestic stock are prohibited within the Royal Chitawan National Park, and the collection of forest produce is strictly controlled. Thatch-grass cutting is restricted to certain areas and allowed during only one month per year. The rhinos suffer considerable disturbance during the grass-cutting season and are in increased danger from poachers posing as grass-cutters.

In most of the Indian reserves, including the Kaziranga National Park, buffalo graziers are allowed to live and graze their stock in return for fees paid to the Forest Department. Villagers are allowed to live in the Laokhawa Reserve if they work for the Forest Department for a few days each year. Fishermen and collectors of forest produce are also allowed to visit the smaller reserves on payment of fees.

Although the effects of stock-grazing and grass-cutting can sometimes be beneficial to wild animals by creating new habitat types, the rhinos require a diversity of habitat types which such practices threaten to destroy (Section 7.2).

Problems of encroachment and disturbance cannot be considered in isolation from the intrusions of rhinos into agricultural land. It is very difficult for villagers living on the edge of rhino reserves and national parks to understand why such a dangerous and troublesome beast as the rhino should be protected. Villagers are often killed by rhinos: five were killed in Chitawan during the three years I was there - four of them outside the National Park. Rhinos damage up to 20% of the rice crop on land within 800 metres of the park boundary (Section 4.3.7.1), and losses of maize and wheat are also high. Although at present crop-raiding and deaths are philosophically accepted as inevitable, the conflict between man and wildlife along the park boundary is likely to increase as both rhino and human populations increase.

7.1.3 Flooding and erosion

As a result of increased deforestation in the hills of Nepal and northern India, the flood levels and extent of erosion in the plains increase every year. Almost all the surviving rhinos are restricted to small areas of riverine forest and grassland in the flood plains of large rivers, namely the Rapti, the Teesta, the Manas and the Brahmaputra. Small changes in the courses of these rivers could destroy the rhinos' habitats; and the human population pressure on the land in surrounding areas is such that alternative refuges are very scarce. The Kaziranga National Park has decreased from 430 to 390 km^2 in area since 1966 due to erosion by the Brahmaputra. Similar changes are taking place in Chitawan (Section 2.4) and it is conceivable that heavy flooding in a single season or within a short span of years (Wadia, 1966; Eckholm, 1975) could change the entire flood plain area within the National Park to open bank vegetation. On the other hand, if the Rapti cut further north again into the middle of the valley, the absence of regular flooding and changes in river courses would lead to gradual deforestation and the loss of the grassland habitat

(Seidensticker, 1976).

A further problem in Chitawan is that the legal boundary of the park is the bed of the Rapti river, and the general trend of the river-bed is to move southwards, thus decreasing the area of flood-plain legally within the park.

7.1.4 Exotic plants

Habitat modification by the proliferation of exotic plants which have no specific local parasites or predators has been a serious problem in many areas of the world. A creeper, *Mikania scandens* and the water hyacinth, *Eichhornia crassipes* are causing problems for rhino conservation in north-eastern India.

(a) *Mikania scandens*

Mikania scandens was introduced from the southern United States to north-east India during the second world war, and there are strong reasons to believe that it has formed a hybrid with the Asian *M. cordata* (Choudhury, 1972). *M. scandens* or the hybrid has proliferated and spread over wide areas of west Bengal and Assam, and threatens to destroy large tracts of riverine forest and grasslands.

The climber forms a thick mat wherever sunlight is available, and grows very fast (about 8 cms per 24 hours) over trees and grasses alike until large areas of typical rhino habitat are transformed into a carpet of *Mikania* and *Mikania*-festooned tree trunks. Rhinos and other ungulates eat only the young shoots, so the loss of food resources and the change in habitat structure is very detrimental to the wildlife.

(b) *Eichhornia crassipes*

The water hyacinth (*Eichhornia crassipes*), a native of North America, was introduced to Assam during the last century. Apart from clogging up waterways all over south-east Asia, the water hyacinth causes special problems in the Kaziranga National Park.

It sinks with flood waters onto the open areas around the lakes or *bheels* after the monsoon, and prevents the regrowth of the short grasses which are an important food supply for the rhinos and the other ungulates. Although water hyacinth is eaten by rhinos and other ungulates when it is free floating, it is not eaten after being stranded on dry land, as it soon dies.

7.1.5 Overcrowding

At present there are over 600 rhinos in the 375 km^2 of Kaziranga National Park. As the populations both at Kaziranga and Chitawan are increasing and there are no alternative refuges for the rhinos, there are dangers in the future of facilitated disease outbreak and increased intraspecific fighting. Fifteen rhinos died of haemorrhagic septicaemia in Kaziranga in 1974, and the number of deaths from intraspecific fighting has been increasing (R.N. Sonowal, pers. comm., 1975).

7.2 Management

Rhino conservation and management have to be considered in relation to the conservation of the habitat and of other species, and to the productive utilisation of the protected areas. It is not for scientists to decide the management procedures which should be employed in protected areas. Rather it is for scientists to provide information which will enable predictions to be made on the results of a number of possible management procedures. Firstly, the aims of the protected areas must be defined. Before one can decide how best to manage a park, one must decide what the purpose of the park is supposed to be, and how one will reconcile its existence with the encroaching pressures of the environs (Myers, 1972; Laurie, 1974).

As the Indian rhino is an endangered species, its conservation has high priority within the national parks and reserves in which it occurs. However, the conservation of sympatric endangered species such as the tiger and the gharial have also to be considered (Bolton, 1975) and the suitability of the parks and reserves for game-viewing by tourists has to be taken into account (Laurie, 1973). In this report, I limit my discussion to the conservation of the rhino itself.

Management may involve either active manipulation of the plant and animal communities or protection from modification or external influences. As most biotic communities are in a constant state of change due to processes of ecological succession, it is often necessary to manipulate the habitat to maintain or attain a desired stage of succession. The alluvial plain habitats of Chitawan and Kaziranga are maintained by the flooding and changing of channels by the rivers during the monsoon. Fire also plays a part in maintaining the diversity of habitat types in various stages of succession.

In the small protected areas which remain, it will be difficult to ensure that the present diversity of suitable habitat types is maintained. I examine below several possible courses of action which could aid in the conservation of the rhino. Firstly, I consider possible forms of habitat management within the existing protected areas. Secondly, I discuss the possibilities of enlarging the present protected areas, and the creation of buffer zones. Thirdly, I consider the possibility of reintroducing rhinos to other protected areas within the former range of the species, thus spreading out the population and reducing the dangers to the whole population of a catastrophe in any one locality.

7.2.1 Management within existing protected areas

7.2.1.1 Nepal

The Royal Chitawan National Park is too small to guarantee the essential diversity of early successional vegetation types in the future (Section 7.1.3), and too small to include the total annual ranges of many of the rhinos. The high population density of rhinos at the boundaries of the park results from the high diversity of vegetation types. The scrubby woodland which occurs where domestic stock have been grazing, is attractive to rhinos during the monsoon because the grass is short and lush (Section 4.3.2).

Fencing, although useful to demarcate the boundary and to discourage cattle graziers, has not been effective in excluding rhinos from agricultural land (Laurie, 1973). During the monsoon, fences and ditches are rendered useless by the rapid changes in courses of even minor streams, and the rhinos quickly learn to cross a fence at weak points or at streams or rivers. Other ways to combat the problem of crop-raiding include the formation of buffer zones (Section 7.2.2) or changing the culturally inherited movement patterns of rhinos. The latter could be attempted by intensive scaring of particularly the younger animals in the fields, or discouraging animals from using the scrubby woodland areas outside the park as daytime refuges from nocturnal crop-raids. However, such operations are difficult, because crops are very attractive to rhinos, and may result in them having to feed for a shorter time than they would have to on other food. The edge of the park was certainly more attractive to rhinos partly because of the proximity of the agricultural land.

The main agents of habitat change within the park are flooding and erosion. These are difficult to employ as tools of management. However, the increased flooding during recent years is probably caused by deforestation in the hills of Nepal which increases the run-off and raises the level of the river beds. Afforestation in the hills could directly benefit the park by slowing down the gradual southward movement of both the Rapti and the Naryani Rivers.

Fire also helps to maintain the edaphic climax of the tall riverine grasslands in Chitawan. So far its effects have been left largely to chance. It was demonstrated that the new regrowth of grass after burning attracts rhinos from a wide area during the spring months (Section 4.6). Thus, potentially, fire is a promising tool of management. It could perhaps be used to draw rhinos away from the border areas where they come into conflict with the local people. However, the border areas are also visited by tourists who want to see rhinos: thus,protecting these areas from fire would hinder the game-viewing of the tourists.

The long term effects of burning annually and of not burning at all have been insufficiently investigated. Experiments are needed to decide the best management procedures, but the immediate policy should be to burn extensively, particularly in the central areas of the park, in the hope that rhinos will be attracted from the perimeter. Experimental quadrats should be set up with firebreaks and fences to investigate the effects of burning on the grass and on the subsequent utilisation of the grass by rhinos and other ungulates.

The guard force in the park are doing an excellent job: the changes in the grass cover in areas previously heavily grazed by domestic stock are evidence of this. Poaching has been virtually eliminated in Chitawan, and the only people allowed in the park are those passing through on the three rights of way and grasscutters during the month that cutting is permitted. The cutting of grass for thatch is essential for the people of Chitawan Valley, but every effort should be made to find alternative sites or alternative thatching material. A proportion of the revenue from tourism should be given to the local governments as compensation for putting up with the rhinos.

In Section 7.2.2 I suggest that "buffer zones" could be set up in which stock grazing was prohibited but thatch grass cutting was allowed. As long as cutting is permitted within the National Park, great emphasis should be put on its control and, as for fire, experiments should be set up to investigate the effects of annual cutting. It is possible that cutting of *Imperata cylindrica*, which is unpalatable to rhinos except in the very young stages, is a way of perpetuating the species. In areas where *I. cylindrica* has been burned, *Saccharum* spp. are becoming more common, especially in the wetter areas. However, more research is needed on the effects of both cutting and burning.

7.2.1.2 India

(a) Human disturbance

Although the idea of multiple land use is admirable, the juxtaposition and intermingling of wildlife reserves and cultivation is particularly problematical. In the 70 km^2 Laokhawa Reserve there are 2,000 people who cultivate rice and maize and graze 6,000 head of stock. Within such a small area there is bound to be conflict between man and wildlife and indeed the worst series of poaching incidents in recent years was in Loakhawa where 22 rhinos were killed in 1974.

The conflict between graziers and wildlife is not so severe, but when the numbers of domestic stock permitted is so high that large areas of the reserve are overgrazed, the wildlife is certain to suffer. This is the case at Orang Reserve in Assam and at some of the other small reserves (Laurie, 1975). In large reserves buffalo and cattle grazing could actually be increasing the carrying capacity of the reserve for wildlife by creating new habitat types (Section 4.3.2). Despite the possible advantages of limited stock grazing, there are dangers of transmission of disease from the stock to the wild populations of ungulates and there are dangers that the graziers could shelter poachers. The possibilities of multiple land use and the creation of buffer zones are discussed in Section 7.2.2.

(b) Fire

Fire is used effectively in Kaziranga to maintain its high population of rhinos. In other reserves which are also forest plantations, such as Orang, there have been no fires for six or seven years. The effects on the ungulate populations are noticeable, but in reserves which have more than a conservation aim, the rhinos have to take a lower priority than the trees. The aim of each reserve should be re-examined, and if it is decided to manage such reserves as Orang for conservation, burning should be implemented as a management procedure to increase the carrying capacity of the area for rhinos.

(c) Exotic plants

Jaldapara and Manas Reserves are particularly badly affected with the creeper, *Mikania scandens* (Section 7.1.4). In Jaldapara, the Forest Department of West Bengal have experimented by ploughing up small plots of *Mikania* covered grassland, and planting rice, millet, wheat, maize and Napier grass (*Pennisetum pedicillatum*) in an attempt to combat the spread of *Mikania* and to provide food for the rhinos and other ungulates. This solution is unsatisfactory as it destroys the natural habitat and, although it provides food for the rhinos as a temporary measure, it cannot be used on a large scale.

Foresters and tea-planters have investigated both chemical and biological methods for the control of *Mikania*. Spraying with 2,4-D is effective but has to be repeated three times per year and is quite expensive. Furthermore, it damages other plants: *Mikania* has to be removed from the tea bushes before being sprayed (Choudhury, 1972; M. Borah, pers. comm., 1976).

Biological control of *Mikania* using the parasitic dodder (*Cuscuta reflexa*) has been partially effective, but the parasite is not sufficiently host-specific, and has spread onto tea garden shade trees like *Acacia* spp. and *Cassia* spp. and also to some forest trees such as *Bauhinia* spp. and *Indigofera* spp. (Choudhury, 1972). It clearly is difficult to use dodder as a method of biological control of *Mikania* in natural ecosystems, and research into other parasites such as rusts and fungi is urgently needed if Jaldapara Reserve is to be saved.

The second problem connected with exotic plants is that of the stranding of water hyacinth on the grazing grounds of rhinos in Kaziranga (Section 7.1.4). Investigations are needed into solutions to this problem. One possible solution lies in regulating the speed of withdrawal of the flood waters at the end of the monsoon by the use of flood gates. Settling is worse in years when the floods recede slowly. Another possibility, probably the simplest, would be to clear the affected areas after the monsoon by mechanical means. Biological or chemical control is undesirable, as water hyacinth is a useful food source for buffaloes, swamp deer and rhinos during the monsoon and at other times of the year on standing water.

7.2.2 Extensions to existing protected areas

7.2.2.1 Nepal

The Royal Chitawan National Park was extended from 546 km^2 to 907 km^2 in 1977 (Section 2.1.7). Most of the extensions both to the east and the west were of sal and hill forest. Some rhinos live in these areas but most live in the lower riverine habitats. At present the range of the rhino in Nepal is considerably larger than the area of flood plain within the National

Park. Rhinos inhabiting sub-optimum habitats outside the park feed by crop-raiding through much of the year. Cultivated land and protected forest areas are interspersed, particularly to the east of the park, so that conflict between man and wildlife is great.

A basic principle in land use planning is that different land areas have different optimal uses which, when fitted together in an overall plan, will assure the optimal future productivity of the land. Bad planning can cause considerable difficulties: in particular when cultivation and settlement adjoin national park boundaries. The creation of 'buffer zones' around national parks has proved effective in reducing such problems. Limited collection of forest produce, stock grazing and hunting have been permitted in such buffer zones in Africa without serious detriment to the totally protected areas (Myers, 1972).

However, if the principle of buffer zones is applied to the problem of rhino conservation, there are some obvious difficulties. Firstly, limited stock-grazing and tree-felling enhance the environment for rhinos (Section 2.1.5.6) and attract rhinos even closer to the boundary of cultivation. The rhinos living permanently outside the park in depleted forest areas are evidence of this (Section 3.5). The protected forest areas outside the park are the equivalent to 'buffer zones' but such zones often aggravate the conflict between man and wildlife. In Chitawan the best approach to land use is to reduce the degree of interspersion of cultivated and protected land, and to reduce the availability of depleted forest areas adjacent to cultivation. Fortunately, the rivers of Chitawan provide useful natural boundaries that should be employed to full effect.

If the park was extended by a further 73 km^2 to include the area south of the Rapti River, between Jaimangala and Amritia, the rhinos at present living north of the Rapti in Janakpur and Katar forests would be able to move south into excellent habitat south of the river, and the areas north of the river could be brought under productive agriculture or allowed to grow thatch grass or to be grazed by domestic stock. Similarly, the narrow depleted forest strip along the northern bank of the Naryani in Nawalpur should not be allowed to serve as a daytime refuge for the rhinos which feed in the fields there. Guards could be retained to prevent poaching of rhinos which cross the Naryani, but the aim should be to limit rhinos to areas south of the Naryani and Rapti Rivers.

The movement and resettlement of the 4,200 villagers from the Padampur pachayat (HMG, 1974) cannot be undertaken lightly. The people are of a variety of castes including Tharus, Gurungs, Danuwars and Botés. There is a need for detailed sociological research before the area at present under cultivation could be included within the park.

7.2.3 Reintroductions

For the reasons given in Section 7.1, it is obviously wise to spread out the rhino population as much as possible. As well as insuring against a catastrophe in one reserve, removal of animals from the most densely populated areas would help to prevent overcrowding. In addition, some of the smaller isolated reserves in West Bengal and Assam would probably benefit from the introduction of new genes into their rhino populations.

There are several protected areas within the former range of the Indian rhino which might be suitable for reintroduction. Lal Suhandra N.P. in Pakistan, Corbett N.P. and Dudhwa N.P. in Uttar Pradesh and the Champaran Forest Reserve in Bihar are all possibilities. Krishne Gowda (1974) has also proposed the reintroduction of rhinos into South India. Within Nepal, the Karnali Wildlife Reserve and the Sukla Phanta Wildlife Reserve are both possible sites for reintroduction of rhinos (see Fig. 7.1).

Careful consideration should be given to the needs of the rhinos: the initial stage of a reintroduction scheme would involve a detailed study of

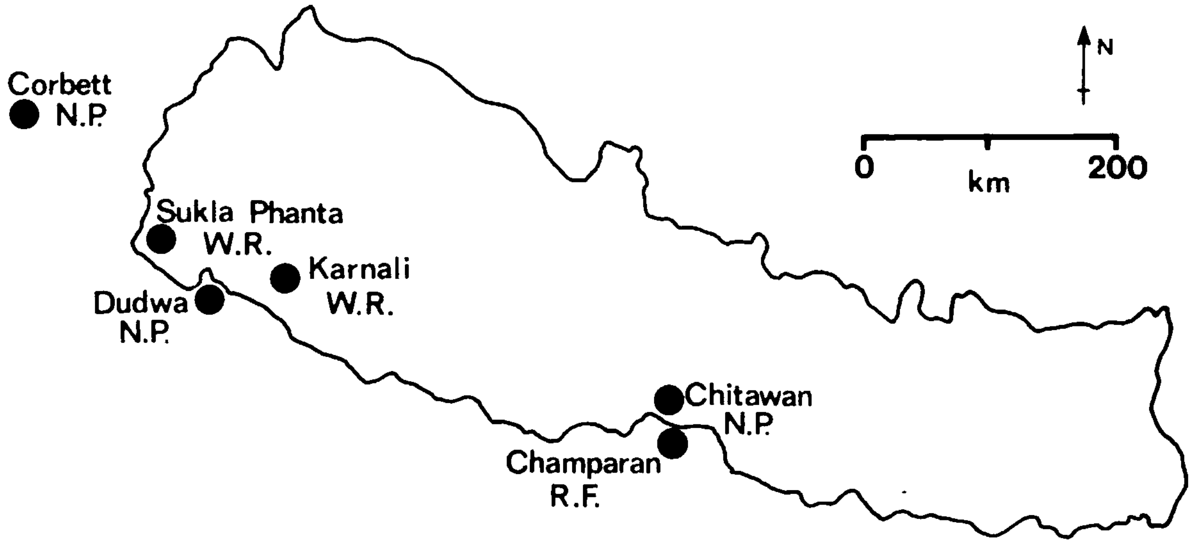

Fig. 7.1. Possible sites for reintroduction of rhinos.

the proposed sites for reintroduction in order to decide whether they were suitable. There should be adequate separation between farmland and rhino habitat to prevent excessive crop raiding. Dudhwa N.P. in India and Karnali Wildlife Reserve in Nepal would be particularly suitable, as they are largely separated from cultivation by rivers. It is also possible that newly introduced rhinos would be timid and reluctant to enter farmland.

If reintroductions to other reserves go ahead, the rhinos should be caught in overcrowded reserves or in areas outside protected areas which are destined to be turned over to agriculture (Section 7.2.2). Tranquilization using M.99 would be the most suitable method of capture. This drug has been used successfully in zoos and in the wild in Nepal. When the Nepalese east-west Highway is completed the trip from Chitawan to Karnali would be a matter of only a few hours.

Transfer within Nepal poses few problems but there are political complications for transfer between states in India. In particular, the Assamese State Government is concerned that their monopoly on the rhinos as a tourist attraction would disappear. However, such problems can be overcome, and it is essential for the future of the Indian rhino that every effort should be made to reintroduce it into suitable reserves.

APPENDIX A

A brief description of the five living species of rhinoceros with a summary of their past and present distributions

(a) *Dicerorhinus sumatrensis* G. Fischer, 1814; the Sumatran or Asiatic two horned rhinoceros.

D. sumatrensis is a relatively small rhino: both males and females stand only 1.2 - 1.4 metres at the shoulder and weigh 800 - 900 kgs (see Table 6.1). Three distinct subspecies are recognised; from Sumatra and Malaya, Borneo and mainland south-east Asia respectively (Groves, 1967a; Groves and Kurt, 1972). There are two distinctive skin folds; one encircling the trunk just behind the forelegs and another just anterior to the hind legs which does not go over the back. The skin is smooth but often very hairy. There are two horns in tandem (larger in males), the front one, on the tip of the muzzle, being considerably larger than the rear one (Groves, 1971). There is one pair of incisors in each jaw, the lower pair are modified as large sharp forward pointing tusks and the upper pair have large flattened crowns (Pocock, 1945). The pre-molars and molars are very similar to each other and relatively low crowned with transverse ridges of enamel (Walker, 1964) indicating a non-specialized browsing habit (Osborn, 1898).

Van Strien (1974) summarized the historical distribution of the Sumatran rhino. Until early in this century it was still widely distributed in hilly rainforest areas from Assam to Vietnam and on the islands of Borneo and Sumatra. Borner (1977), after three years of survey work, concluded that there were 56-84 Sumatran rhinos in five areas in Sumatra. R. Flynn (pers. comm., 1976) concluded that there were less than 30 in

West Malaysia, mainly concentrated in the Endau-Rompin region of the State of Johore. In Thailand the Sumatran rhino is reported from five areas, but populations are very small (McNeely and Laurie, 1977). There are several other small populations in Borneo and Burma (Borner, 1977) but the numbers are not known. The world population is probably less than 300 individuals and there are none in captivity. Strickland (1967) studied the feeding habits of a few individuals in Malaya, and Borner (1977) and R. Flynn (in prep.) have made recent studies of the ecology and behaviour of the species, mainly by following tracks.

(b) *Diceros bicornis* Linnaeus, 1758: the Black or Prehensile-lipped rhinoceros.

D. bicornis stands about 1.65 metres at the shoulder and weighs between 720 and 1,300 kgs (see Table 6.1). The skin is smooth, almost hairless, and is not folded to the extent of that of the Asian species of rhinoceros. The upper lip is triangular in shape, prehensile and very mobile. There are two horns in tandem which are very variable in proportions and shape, and measure up to 135 cms (Ward, 1935). *D. bicornis* has short-crowned molars and premolars - a brachyodont dentition - and there are no incisors or canines. The black rhino, in common with other rhinos, has a very high number of chromosomes ($2n = 84$; Hungerford *et al.*, 1967). The white rhino's diploid number is 82 (Heinichen, 1969); that of the Indian rhino is also 82 (Wurster and Benirschke, 1968).

The historical range of the black rhino extended through Africa from the south-western Cape northwards to Sudan and Nigeria, although it never occurred in rainforest regions. Today the black rhino still occurs in dry bush country and particularly in thorn scrub over much of this range but its numbers are being very rapidly reduced (E.M. Monks, pers. comm., 1977). Hitchins (1968a, 1969, 1970, 1971), Goddard (1966, 1967a, 1967b, 1968, 1969, 1970a, 1970b, 1970c), Schenkel and Schenkel-Hulliger (1969a), Joubert and Eloff (1971) and Mukinya (1973, 1976, 1977) have made recent ecological and behavioural studies of the species in the wild.

(c) *Ceratotherium simum* Burchell, 1817: the White or Square-lipped rhinoceros.

C. simum is the largest of all species of rhinoceros, with a shoulder height of 1.7 - 1.8 metres and a body weight of up to 2,300 kgs (Owen-Smith, 1975; Table 6.1). There are two subspecies of white rhinoceros: *C.s. cottoni* which was historically restricted to the west bank of the upper Nile (Heller, 1913), and *C.s. simum* which occurred over much of southern Africa from the Orange and Vaal Rivers in the south to the Zambezi river in the north (Player and Feely, 1960).

C. simum is distinguished from the sympatric *D. bicornis* by its larger size, its nuchal hump, its straighter back and its larger head with broad square lips. The lower lip bears a hardened pad (Van den Bergh, 1955). Skin-folds are little developed but Alexander and Player (1965) recorded considerable short body hair in the southern subspecies. There are two horns in tandem, the anterior one usually considerably larger than the other. The cheek-teeth are hypsodont, or high-crowned, and cement-covered and there are no incisors or canines in either jaw (Groves, 1972).

Owen-Smith (1973) summarized the past and present distributions of the white rhino and described the massive decline in numbers during the nineteenth century as a result of hunting pressure. Now the southern race is recovering in numbers, and populations have been re-established by translocation in several parts of its former range. However, there are probably not more than 4,000 individuals of the southern race and not more than 1,000 individuals of the northern race. Both races live in generally dry open mixed woodland and grassland habitats. Backhaus (1964) studied the northern race briefly but, apart from that study, the only long term scientific study of the species was by Owen-Smith (1971, 1972, 1973, 1975) on the southern race.

(d) *Rhinoceros sondaicus* Desmarest, 1822: the Javan or Lesser one-horned rhinoceros.

R. sondaicus has thick generally hairless skin with three folds across the back and others around the neck and legs. It stands 1.4 - 1.7 metres at the shoulder, and weights have been reported of between 1,500 and 2,300 kgs (Hoogerwerf, 1970; Lekagul and McNeely, 1977). There is a single rather short nasal horn, larger in males. Incisor tusks are present in both sexes in the lower jaw, and the molars and premolars are short-crowned or brachyodont. The upper lip is pointed and prehensile, and hangs over the lower lip when at rest.

The Javan rhino was found formerly in Java, Sumatra, West Malaysia, Thailand, Indochina, south-western China and parts of the Brahmaputra Valley and the Sunderbans (Pollok and Thom, 1900; Imbert, 1921; Bishop, 1933; Sowerby, 1936; Shebbeare, 1953; Sody, 1959; Groves, 1967a; Hoogerwerf, 1970). Today the only known population is in the rainforested Ujung Kulon Reserve of western Java where there were 45-55 individuals in August 1975 (Schenkel and Schenkel-Hulliger, 1977). It is possible that a few individuals survive in the Bolovens Plateau region of Laos (Neese, 1975), the Cardamom Mountains of Kampuchea (McNeely and Laurie, 1977) and the Tennasserim Range on the Burma-Thailand border (McNeely and Cronin, 1975).

Schenkel and Schenkel-Hulliger (1969b) studied the ecology and behaviour of *R. sondaicus*, and Hoogerwerf (1970) published a comprehensive account of many years of observations in Ujung Kulon. Hartmann Amman (pers. comm., 1978) started a study of feeding and ranging behaviour in Ujung Kulon in 1978.

(e) *Rhinoceros unicornis* Linnaeus, 1758: the Indian or Greater one-horned rhinoceros.

R. unicornis is a much more massive animal than *R. sondaicus*, higher at the shoulder (Table 6.1), with a larger head, and with more developed skin folds around the neck. Only two skin folds encircle the trunk, in contrast with three in *R. sondaicus*. Adults in captivity have weighed between 1,600 and 2,070 kgs with males being generally heavier (Lang, 1961, 1967). Both sexes have a single well developed nasal horn which reaches a maximum length of about 60 cms (Ward, 1935; Wazim Khan, pers. comm., 1975). Incisor tusks are also present, and the molars and premolars are hypsodont or high-crowned, with a complex enamel pattern.

Once distributed from Pakistan to Northern Burma along the River valleys Indus, Ganges and Brahmaputra (Section 1.3), there are now *c.* 1,100 greater one-horned rhinos restricted to seven small reserves in Assam and West Bengal and their environs and the Royal Chitawan National Park, Nepal.

APPENDIX B

The evolutionary origins of the living species of rhinoceros

The first known rhinoceroses are found in sediments of Eocene age: they probably arose from the hyrachyids, a group of primitive tapirs (Colbert, 1935). The true rhinoceroses or Rhinocerotidae were one of three families of rhinoceroses in the Eocene. The Hyracondontidae or running rhinoceroses and the Amynodontidae or aquatic rhinoceroses dominated the upland and lowland habitats respectively, but were largely replaced by the Rhinocerotidae in the Oligocene. The Rhinocerotidae remained a dominant family of mammals during the Oligocene and Miocene epochs with at least eight evolutionary lines occupying a wide range of grazing niches throughout Eurasia, Africa and North America (Thenius and Hofer, 1960). Evolutionary trends exhibited by these lineages included (i) an increase in general body size, (ii) the development of broad three-toed feet, (iii) molarization of the premolars, (iv) a lengthening of the crowns of the cheek teeth and (v) the development, on the skull,of horns which were unique in lacking a bony core (Colbert, 1935).

Among the many forms of rhinoceros was the giant hornless *Baluchitherium grangeri* from the Miocene of Mongolia, the largest land mammal known, with a shoulder height of nearly six metres and a total length of almost nine metres (Osborn, 1923). The primitive hornless or small horned Aceratheres and Diceratheres with two horns side by side were widespread in Europe and North America until the end of the Miocene. The Miocene and Pliocene Teleocerines are typified by *Teleoceras*, a squat heavy bodied North American form which resembled a hippopotamus with a single small horn at the end of the nose. The Teleocerines were aquatic in habit and lived in large herds (Osborn, 1923). During the Pliocene many rhinoceros species became extinct and only a very few lines continued into the Pleistocene when they had to contend with the selective pressures of a severe climate, hunting by early man and widespread habitat changes (Martin and Wright, 1967).

Among those forms which survived into the Pleistocene were the huge Elasmotheres with a single large horn on the frontal region and high crowned molars with a complex laminated enamel pattern (Osborn, 1923), evidently an adaptation for grazing the hard Eurasian steppe grasses. Apart from the Teleocerines which died out in the early Pleistocene, the other three forms of rhinoceros which survived into the Pleistocene are still represented among the five extant species of today, which may be grouped within three distinct sub-families: The Dicerorhinae, the Dicerinae and the Rhinocerotinae (Thenius and Hofer, 1960; Thenius, 1969).

The Dicerorhinae can be traced back 40 million years to the tapir sized *Dicerorhinus tagicus* of the Oligocene of Europe where the group evolved. The Dicerorhinae are characterized by two horns in tandem and a tendency towards ossification of the nasal septum. Zeuner (1934) concluded that there were three main lines of the Dicerorhinae; the first, distinct in the Pliocene, ended in the woolly rhinoceros, *Coelodonta antiquitatis*, which inhabited Europe during the later Ice Ages. In *Coelodonta*, incisors and canines were completely reduced, molars were hypsodont or high crowned and the skull was greatly lengthened; all adaptations to a graminivorous diet. The second line also developed in grass steppe and is represented by *D. hemitoechus* and Merck's rhinoceros, *D. kirchbergensis*, while the third line, one of the most primitive, adapted to the tropical rainforest and is now represented by *D. sumatrensis*. The earliest representative of the group in southern Asia is the flat nosed

Coelodonta ~~*Rhinoceros*~~ *platyrhynus* of the Indian Pliocene and Pleistocene. This species and *C. etruscus* from the Pliocene were forest dwelling browsing species which once lived in the broad forest belt which then extended from eastern England to northern India (Osborn, 1923).

The Dicerinae resemble the Dicerorhinae in having two horns in tandem, but the nasal septum is not ossified and there are no incisors or canines. At one time they were thought to have arisen from the incisor-less *Coelodonta* (Osborn, 1923) but this is unlikely, and their early phylogeny is still obscure. The aberrant *Paradiceros mukirii* of the late Miocene of Kenya indicates that the group had an independent African origin (Hooijer, 1966; Hooijer and Patterson, 1972). The late Pliocene *Cerathotherium praecox* of Kenya shows resemblances to both the modern species, *Diceros bicornis* and *C. simum*, and indicates that *Ceratotherium* diverged from the *Diceros* lineage about four million years ago (Hooijer and Patterson, 1972). The differences in dentition between the black rhinoceros and the white rhinoceros are related to their different dietary adaptations as described above, and the morphological adaptations to grazing in *Ceratotherium* evolved independently from those of *Coelodonta*, which they strongly resemble (Owen-Smith, 1973). The radiation of *Ceratotherium* from the *Diceros* stock was probably related to the expansion in the extent of grassland during Pliocene droughts in Africa.

The Rhinocerotinae, which include the two living species *Rhinoceros unicornis* and *R. sondaicus*, can only be traced back as far as the Pliocene *R. palaeindicus* and the Miocene *Gaindatherium browni* from the Siwalik hills of northern India (Osborn, 1900; Colbert, 1935). The origins of the phylum are unknown: no Rhinocerotinae have been found in Europe although they were probably derived from the Oligocene *Caenopus*. They are characterized by a large single horn, a forwardly inclined occiput and well developed lower incisor tusks.

Of the living species, *R. sondaicus* is the more primitive, having altered little since the early Pliocene (Colbert, 1935), and differing from *R. unicornis* in having low crowned cheek teeth, being slightly smaller and feeding mainly on browse rather than grass (Appendix A).

APPENDIX C

Kaziranga National Park and the other reserves for rhinos in India.

1. KAZIRANGA NATIONAL PARK, ASSAM (93°30'E 26°30'N)

The Kaziranga National Park (430 km^2) is situated on the southern bank of the Brahmaputra River at the foot of the Mikir Hills. Numerous rivers and streams flow through the park and there are many permanent 'bheels' or lakes. The soils were all alluvial deposits of the Brahmaputra and its tributaries. The vegetation is mixed grasslands and riverine woodland with grasslands predominating in the west. Tall grasses grow on the higher ground and short grasses grow on the lower ground surrounding the lakes. The climate is monsoonal with a mean annual rainfall of 1,828 mm, 90% of which falls between April and October (see Fig. A.1).

Annual floods inundate almost the whole of the alluvial plain habitats from June to October and even in December much of the lower lying ground is under water. During the dry season the tall grassland is burned by the park staff to encourage the growth of lush young grass. Both fire and floods have helped to maintain the habitat as it is now for thousands of years (Lahan and Sonowal, 1973; Spillet, 1966).

The management of the park is the responsibility of the Forest Department which maintains a staff of 183 men in 34 guard posts and offices. There are 20 elephants attached to the park, which are used for patrol work and for taking tourists on trips to watch animals. Most areas can be visited by four-wheel drive vehicles during the dry season, but boats are necessary for travel within the park during the monsoon. Guards spend long periods during the monsoon cut off from

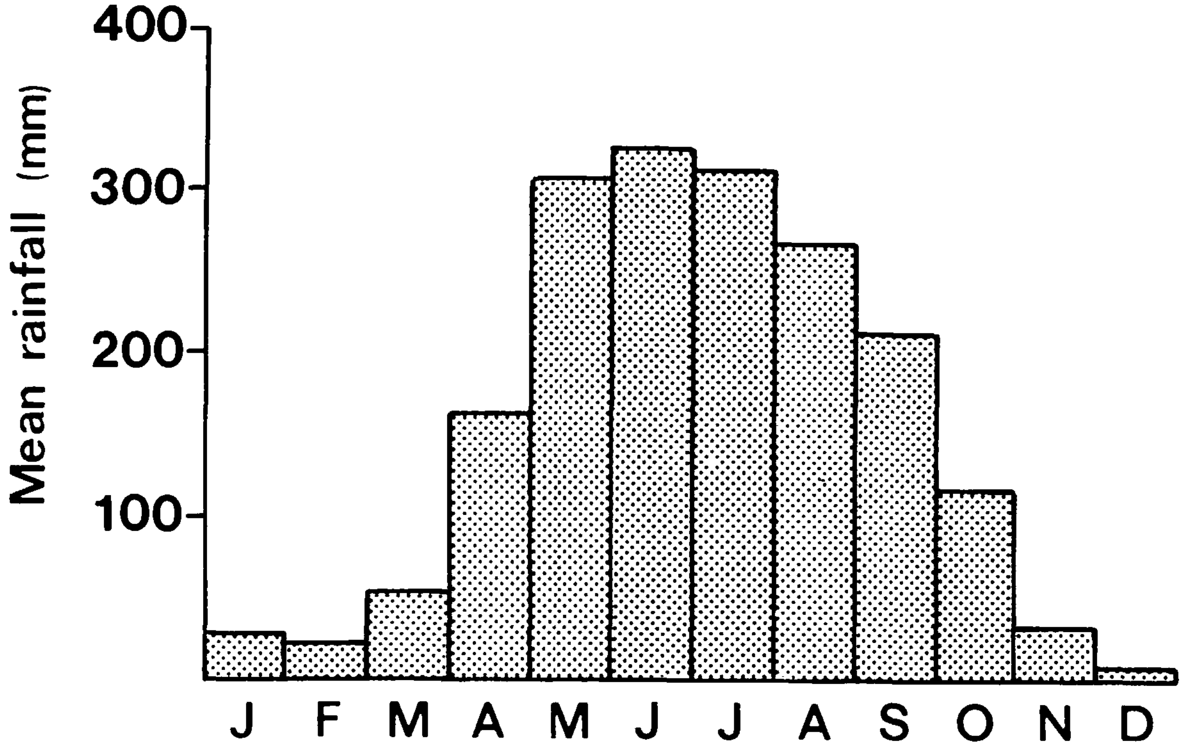

Fig. A.1. Mean monthly rainfall at Hathikuli Tea Garden, 1959-75.

land in guard posts built on stilts. Control of poaching has been very good in recent years. Since the National Park was gazetted in 1975, many professional Nepali graziers have been moved out of the park, but one group remains in the north of the park on the bank of the Brahmaputra. In addition there is some encroachment by cultivators on the southern boundary.

There are probably about 600 rhinos in Kaziranga and their numbers are increasing (Lahan and Sonowal, 1973). Elephant, wild buffalo, swamp deer, hog deer, wild boar and tigers are also common.

2. MANAS WILDLIFE SANCTUARY (90°50'E 26°40'M)

Situated on the Assam-Bhutan border at the point where the Manas River flows out from the hills and splits into three different rivers, the Manas Wildlife Sanctuary covers 580 km^2 of riverine grasslands and forests and subtropical evergreen forests.

The Sanctuary is famous for tiger, buffalo and fishing, and also supports a population of about 40 rhinos. Encroachment, poaching and illegal collection of forest produce have been successfully curbed since the Sanctuary was accorded the status of one of eight Indian Tiger Reserves (Jackson, 1977).

3. ORANG WILDLIFE SANCTUARY (92°5'E 26°20'N)

Situated on the northern bank of the Brahmaputra between Gauhati and Tezpur, the Orang Sanctuary (65 km^2) is also a forest plantation. In an upper dry grassland area the trees are protected from fire by extensive firebreaks dividing the area into fireblocks. Most of this area has been unburned since 1972. As a result, much of it is now covered with thick matted *Saccharum* stalks and leaves - mainly dead and unpalatable to the ungulates. Rhinos and other ungulates graze the fresh shoots during spring in the few burnt areas.

The lower part of the Sanctuary consists of a swampy area annually flooded by the Brahmaputra, which harbours the rhino population during the dry season. As in all the wildlife reserves of Assam, the buffalo grazing rights are sold to Nepali herdsmen who live within the sanctuary: in Orang they have transformed the surroundings of their village into heavily grazed short grassland. Such heavy grazing is a threat to the rhino population which now stands at about 25-30 individuals.

4. LAOKHAWA RESERVE (92°30'E 26°15'N)

Laokhawa Reserve (70 km^2) is situated on the south bank of the Brahmaputra, 80 kms west of Kaziranga. It probably held the third largest population of rhinos in Assam until a few years ago, but it is severely threatened by poaching, cultivation and stock-grazing. People are allowed to live and cultivate in forest villages within the reserve in return for a certain amount of free labour for the Forest Department. Nepali herdsmen and Moslem fishermen pay the Forest Department for the grazing and fishing rights, and the grass-cutting is sold to contractors.

There are large expanses of short grassland, rough *Zizyphus* and *Tamarix* scrub, and *simul* and *koroi* plantations with low sparse undergrowth. The few *bheels*, surrounded by *Typha* and *Arundo* reeds and palatable andropogonous grasses, are frequented by rhinos and buffaloes, but their numbers are very low. Local Forest Department estimates for the rhino population range from 80-150 but I would estimate less than 50. There were 22 cases of poaching discovered during 1974 alone.

5. SONAI RUPAI WILDLIFE RESERVE (92°25'E 26°50'N)

The Sonai Rupai Reserve consists of 195 km^2 of subtropical evergreen forest and patches of grassland beside the Gabru River. Rhinos are restricted almost entirely to a small swampy area beside the Gabru River, which is also used by herdsmen who pay grazing fees and live within the reserve with their large herds of buffalo. There are probably only about 15 rhinos in the area.

6. OCCURRENCE OF RHINOS OUTSIDE RESERVES IN ASSAM

Rhinos are by no means confined to protected areas. Annual flooding causes extensive migration of rhinos from the lower flood plains to higher ground. Apart from these seasonal movements, there are also reports of rhinos in the Singri Hills east of Orang and in the tea estates north of the Brahmaputra, opposite Kaziranga. Until very recently, rhinos existed in forests near North Lakhimpur but such reports are getting less frequent.

7. JALDAPARA WILDLIFE SANCTUARY (89°30'E 26°40'N)

Jaldapara (115 km^2) is located in the flood plains of the Torsa and Malangi Rivers in West Bengal, and is intersected by numerous streams. The vegetation is very similar to that of Chitawan: annual floods and fire maintain a high diversity of early successional stages including grasslands, reedy swamps and riverine forests.

Although collection of forest produce and grazing are prohibited, such practices are difficult to prevent. This is partly due to the unusual shape of the sanctuary - rather like a pair of trousers - which results in a very long boundary. Protection against poaching and encroachment has improved in recent years: armed guards of the National Volunteer force were stationed at the reserve after a period of heavy poaching between 1971 and 1973, during which 29 rhinos were killed. There are now probably 30-40 rhinos in Jaldapara.

8. GORUMARA RESERVE (89°00'E 26°40'N)

This tiny reserve (4 km^2) 80 kms west of Jaldapara, lies at the junction of the Jaldacca and Murti Rivers. It consists of riverine grassland, and is surrounded by commercial sal forest. Rhinos originally travelled between Gorumara and Chapramari Reserve to the north, but a new road now restricts the few (*c.* 5) which remain, to the southern reserve. During the monsoon the whole reserve is flooded, and the animals retreat into the sal forest.

APPENDIX D

A list of plants collected in the study area

* denotes eaten by rhinos.

Family:		
ACANTHACEAE		*Adhatoda vasica* Nees.
		Phlogacanthus thyrsiflorus (Roxb.) Nees.
		Rungia parviflora Nees.
		Goldfussia nutans Nees.
ANACARDIACEAE	*	*Buchanania latifolia* Roxb.
		Lannea coromandelica (Houtt.) Merr.
	*	*Mangifera indica* L.
		Rhus javanica L.
		Semecarpus anacardium L.f.
ANONACEAE		*Miliusa velutina* H.f. & Th.
AMARANTACEAE	*	*Alternanthera sessilis* (L.) DC.
APOCYANACEAE		*Alstonia scholaris* (L.) R. Brown
	*	*Holarrhena antidysentrica* Wallich ex DC.
		Vallaris solanaceae (L.) O. Kuntze
ARACEAE	*	*Pistia stratiotes* L.
	*	*Remusatia* sp.
ASCLEPIADACEAE		*Calotropis gigantea* (L.) Dryand.
BAMBUSACEAE	*	*Dendrocalamus strictus* Nees.
BIGNONIACEAE		*Stereospermum chelonoides* (L.f.) DC.
BIXACEAE	*	*Xylosma longifolium* Clos.
BOMBACACEAE	*	*Bombax ceiba* L.
BORAGINACEAE	*	*Ehretia laevis* Roxb.
	*	*Cordia grandis* Roxb.
	*	*Cynoglossum zeylanicum* Thunberg ex Lehmann
		C. glochidiatum Wallich ex Bentham
		C. bifurcatum L.
BURSERACEAE		*Garuga pinnata* Roxb.
CARYOPHYLLACEAE	*	*Polycarpon indicum* (Forsk) Asher & Schweinf.
	*	*Stellaria* sp.
CAPPARIDACEAE		*Cleome* sp.

CELASTRACEAE		*Cassine glauca* (Rottb.) O. Kuntze
CERATOPHYLLACEAE	*	*Ceratophyllum demersum* L.
CHENOPODIACEAE	*	*Chenopodium album* L.
COMBRETACEAE		*Anogneissus latifolius* (Roxb) Wall.
	*	*Terminalia bellirica* (Gaertn.) Roxb.
		T. chebula Retz.
		T. alata Heyne ex Roth.
COMPOSITAE	*	*Ageratum conyzoides* L.
	*	*Artemisia vulgaris* L.
		A. indica Willd.
		Caesulia axillaris Roxb.
	*	*Cirsium wallichii* DC.
	*	*Eclipta prostrata* L.
	*	*Erigeron bonariensis* L.
	*	*Eupatorium odoratum* L.
	*	*Gnaphalium luteo-album*
	*	*Inula cappa* DC.
	*	*Youngia japonica* (L.) DC.
	*	*Crassocephalum crepidioides*
COMMELINACEAE	*	*Commelina bengalensis* L.
	*	*Commelina* sp.
		Cyanotis sp.
CONIFERAE		*Pinus roxburghii* Sargent
CONVOLVULACEAE	*	*Argyreia speciosa* Sweet
		A. roxburghii Choisy
		Cuscuta reflexa Roxb.
	*	*Ipamoea quamoclit* L.
	*	*I. aquatica* Forsk.
CRUCIFERAE		*Rorippa nasturtium-aquaticum* (L.) Hayek
	*	*Raphanus sativus* L.
CUCURBITACEAE	*	*Zehneria maysorensis* (Wight. & Arn.) Arn.
		Z. indica (Lour.) Keraudren-Aymonin
		Mukia maderaspatana (L.) Roem.
	*	*Trichosanthes dioica* L.
	*	*Cucumis sativus* L.
CUPULIFERAE		*Alnus nepalensis* D. Don
CYPERACEAE	*	*Carex continua* C.B. Clarke
	*	*Scleria laevis* Retz.
	*	*Kyllinga brevifolia* Rottboell
	*	*K. colorata* (L.) Druce
	*	*Mariscus sieberianus* Nees ex Steudl.
	*	*M. paniceus* (Rottb.) Vahl
	*	*Cyperus difformis* L.
	*	*C. digitatus* Roxb.
	*	*C. mersuri* L.

CYPERACEAE (continued)	*	*C. niveus* L.
	*	*C. pilosus* Vahl
	*	*C. rotundus* L.
	*	*Fimbristylis dichotoma* (L.) Vahl
	*	*Schoeno-plectus mucronatus* (L.) Palla
	*	*Pycreus globosus* (All.) Reichenb.
DILLENIACEAE	*	*Dillenia indica* L.
	*	*D. pentagyna* Roxburgh.
DIOSCOREACEAE		*Dioscorea* sp.
DIPTHEROCARPACEAE	*	*Shorea robusta* Gaertn. f.
ELAEOCARPACEAE		*Elaeocarpus tectorius* (Lour.) Poir
EQUISETACEAE		*Equisetum* sp.
	*	*E. debile* Roxb.
EUPHORBIACEAE		*Baccaurea sapida* (Roxb) Muell.-Arg.
	*	*Bridelia retusa* Spreng.
	*	*Croton grandis* Roxb.
		Macaranga denticulata Muell.-Arg.
	*	*Mallotus phillippensis* (Lam.) Muell.-Arg.
	*	*M. nepalensis* Muell.-Arg.
		Macaranga indica Wight.
	*	*Euphorbia hirta* L.
		E. fusiformis Buch.-Ham. ex D. Don
	*	*Phyllanthus emblica* L.
		Drypetes roxburghii (Wall.) Hurusawa
	*	*Trewia nudiflora* L.
		Sapium insigne Benth.
FLACOURTICEAE		*Casearia glomerata* Roxb.
GENTIANACEAE		*Swertia angustifolia* Hamilton ex D. Don
GRAMINAE	*	*Apluda mutica* L.
		Aristida adscensionis L.
	*	*Arundo donax* L.
	*	*Arundinella bengalensis* (Spreng.) Druce
		A. nepalensis Trin.
	*	*Brachiaria ramosa* (L.) Stapf.
	*	*Capillipedium assimile* (Steud.) A. Camus
	*	*Chrysopogon aciculatus* (Retz.) Trin.
	*	*C. gryllus* (L.) Trin.
	*	*Coix lachryma-jobi* L.
	*	*Cymbopogon flexuosus* (Nees ex Steud.) W. Wats
	*	*C. olivieri* (Boiss.) Bor
		C. pendulus (Nees ex Steud.)
	*	*Cynodon dactylon* (L.) Pers.
	*	*Dactyloctenium aegyptium* (L.) P. Beauv.
	*	*Desmostachya bipinnata* (L.) Stapf.
	*	*Digitaria ciliaris* (Retz.) Koeler
	*	*D. setigera* Roth apud Roem et Schult.
	*	*Echinochloa colona* (L.) Link

GRAMINAE (continued)	*	*E. crusgalli* (L.) P. Beauv.
	*	*Eleusine indica* (L.) Gaertn.
	*	*Eragrostis atrovirens* (Desf.) Trin ex Steud.
		E. ciliaris (L.) R. Br.
		E. coarctata Stapf. apud Hook. f.
	*	*E. japonica* (Thunb.) Trin.
	*	*E. tenella* (L.) P. Beauv. ex Roem et Schult.
	*	*E. unioloides* (Retz.) Nees ex Steud.
	*	*Hygrorhyza aristata* (Retz.) Nees ex Wight & Arn.
		Eulalia fastigiata (Nees) Haines
		Eulaliopsis binata (Retz.) C.E. Hubbard
	*	*Hemarthria compressa* (L.f.) R. Br.
		Heteropogon contortus (L.) P. Beauv. ex Roem & Schult.
	*	*Imperata cylindrica* (L.) P. Beauv.
		Leptochloa chinensis (L.) Nees
	*	*Narenga fallax* (Balansa) Bor
	*	*N. porphyrocoma* (Hance) Bov.
	*	*Neyraudia reynaudiana* (Kunth) Kent ex Hitchc.
	*	*Oplismenus* sp.
		Panicum cambogiense Balansa
	*	*Paspalum distichum* L.
	*	*P. scrobiculatum* (L.)
	*	*Paspalidium flavidum* (Retz.) A. Camus
	*	*Phragmites karka* (Retz.) Trin. ex Steud.
		Pogonatherum crinitum (Thunb.) Kunth
		Pseudopogonatherum contortum (Brongn.) A. Camus
		Polypogon monspeliensis (L.) Desf.
	*	*Saccharum arundinaceum* Retz.
	*	*S. munja* Roxb.
	*	*S. procerum* Roxb.
	*	*S. spontaneum* L.
		Erianthus filifolius (Steud.) Hackel
		E. longisetosus Anderson
		E. rufipilus (Steud.) Griseb.
	*	*E. ravennae* (L.) Beauv.
	*	*Setaria glauca* (L.) Beauv.
	*	*S. pallide-fusca* (Schumach.) Stapf. & C.E. Hubbard
		S. plicata (Lam.) T. Cooke
		Sporobolus diander (Retz.) P. Beauv.
	*	*Themeda arundinaceae* (Roxb.) Ridley
		T. caudata (Nees.) A. Camus
	*	*T. villosa* (Poir.) A. Camus
	*	*Thyrsia zea* (Clarke) Stapf.
	*	*Thysanolaena maxima* (Roxb.) O. Kuntze
	*	*Vetiveria zizanoides* (L.) Nash
	*	*Zea mays* L.
	*	*Oryza sativa* L.
	*	*Triticum arvense* L.
GNETACEAE	*	*Gnetum* sp.
HYDROCHARITIACEAE	*	*Hydrilla verticillata* (L.f.) Royle
	*	*Vallisneria natans* (Lour.) Hara
HYPOXIDACEAE		*Cucurligo orchioides*

LABIATAE	*	*Colebrookia oppositifolia* Smith
		Rabdosia coetsa (Buch.-Ham. ex D. Don) Hara
	*	*Leucas mollissima* Wall.
		L. plukenetii Spreng.
		Micromeria integerrimum Benth.
	*	*Pogostemon bengalensis* (Burm.f.) O. Kuntze
LAURACEAE	*	*Litsaea monopetala* (Roxb.) Persoon
		Persea sp.
LECYTHIDACEAE	*	*Careya arborea* Roxb.
LEGUMINOSAE	*	*Acacia catechu* (L.f.) Willdenow
	*	*A. pennata* (L.) Willdenow
	*	*A. concinna* DC.
	*	*A. lenticularis* Buch.-Ham.
		Albizzia gamblei Prain
	*	*A. lebbek* (L.) Benth.
		A. lucida Bentham
		A. odoratissima Benth.
	*	*Bauhinia malabarica* Roxburgh
	*	*B. purpurea* L.
		B. racemosa Lam.
	*	*B. vahlii* Wight & Arnott
		B. variegata L.
	*	*Butea monosperma* (Lam.) Tanb.
		Cassia fistula L.
	*	*Dalbergia sissoo* Roxb.
	*	*D. stipulaceae* Roxburgh
		Erythrina suberosa Roxb.
	*	*Millettia extensa* (Benth.) Baker
	*	*Flemingia strobilifera* (L.) R. Br. ex Ait.
		Desmodium oojeinense (Roxb.) Ohashi
	*	*Spathobolus parviflorus* (Roxb.) O. Kuntze
	*	*Crotalaria albida* Hyne ex Roth
		Indigophera pulchella Roxburgh
		Trigonella sp.
		Caesalpinia bonduc (L.) Roxb.
		C. decapetala (Roth.) Alston
		Cajanus sativa L.
	*	*Cassia tora* L.
		Desmodium sp.
		Lespedeza eriocarpa DC.
	*	*Mimosa rubricaulis* Lam.
		M. pudica L.
LEMNACEAE	*	*Lemna perpusilla* Torrey
	*	*Spirodela polyrhyza* L.
	*	*Wolffia globosa* (Roxb.) Hartog & Plas
LENTIBULARIACEAE	*	*Utricularia aurea* Loureiro
LILIACEAE	*	*Asparagus racemosus* Willd.
		Smilax lanceifolia Roxb.
	*	*S. ovalifolia* (Roxb.) ex D. Don
		Allium cepa L.
		A. sativum L.
		A. wallichii Kunth.

LINACEAE		*Reinwardtia indica* Dumortier
LOGANIACEAE		*Buddleia asiatica* Lour.
LYTHRACEAE	*	*Lagerstroemia parviflora* Roxb.
	*	*Rotala rotundifolia* (Roxb.) Koehne in Engl.
		Woodfordia fructicosa (L.) Kurz.
MALVACEAE		*Kydia calycina* Roxb.
		Hibiscus sp.
		Sida acuta Burman F.
		S. rhombifolia L.
		Thespesia lampas (Cavan.) Dalz et Gibs.
	*	*Urena lobata* L.
MARSILIACEAE	*	*Marsilia tetraphylla* L.
MELASTOMACEAE		*Osbeckia* sp.
		Melastoma malabathricum L.
MELIACEAE	*	*Azadirachta indica* A. Juss
	*	*Toona ciliata* M. Roem.
		Chisocheton paniculatus L.
MENISPERMACEAE		*Stephania japonica* (Thunb.) Miers
		Holoptelea integrifolia Planch
MORACEAE	*	*Ficus semicordata* Hamilton ex J.E. Smith
		F. glaberrima Bl.
		F. racemosa L.
		F. religiosa L.
	*	*F. auriculata* Loureiro
		Cannabis sativa L.
		Streblus asper Loureiro
MUSACEAE	*	*Musa balbisiana* Colla
MYRTACEAE	*	*Syzygium cumini* (L.) Skeels
	*	*S. operculatus* (Roxb.) Merr.
		Eucalyptus sp.
	*	*Psidium guajava* L.
OPHIOGLOSSACEAE	*	*Helminthostachys zeylanicus* (L.) Hooker
		Ophioglossum petiolatum Hooker
ORCHIDACEAE		*Ponerorchis* sp.
OXALIDACEAE		*Oxalis corniculata* L.
PALMAE	*	*Calamus tenuis* Roxb.
	*	*Phoenix acaulis* Buch.
		P. humilis Royle
PIPERACEAE		*Piper nepalense* Miguel
POLYGALACEAE		*Polygala* sp.
	*	*P. abyssinica* R. Br.

POLYGONACEAE	*	*Persicaria barbata* (L.) Hara
	*	*Polygonum plebujum* R. Brown
	*	*Persicaria glabra* (Willd.) Hara
POLYPODIACEAE	*	*Pteris vittata* L.
	*	*Dryopteris* sp.
PONTEDERIACEAE	*	*Monochoria hastata* (L.) Solms.
POTAMOGETONACEAE	*	*Potamogeton crispus* L.
PUNICACEAE		*Punica granatum* L.
RANUNCULACEAE	*	*Ranunculus scleratus* L.
RHAMNACEAE	*	*Zizyphus mauritania* Lam.
		Z. rugosa Lam.
		Rhamnus nipalensis (Wall.) M. Lawson in Hook. f.
ROSACEAE		*Wendlandia tinctoria* (Roxb.) DC.
RUBIACEAE		*Adina cordifolia* (Willd. ex Roxb.) Hooker f.
		Anthocephalus cadamba Miguel
		Eriobotrya japonica Lindl.
		Hymenodictoyon excelsum (Roxb.) Wallich
		Mitragyna parviflora Korth.
		Knoxia corymbosa Willd.
		Mussaenda macrophylla Wall.
		Hedyotis lineata (Roxb.)
		Coffea bengalensis Heyne ex Roem. & Schultes
		Mussaenda frondosa L.
		Xeramphis spinosa (Thunb.) Keay
RUTACEAE	*	*Aegle marmelos* (L.) Correa
		Citrus medica L.
	*	*Murraya koenigii* Spreng.
		Micromelum pubescens Hook. f.
SABIACEAE		*Meliosma simplicifolia* (Roxb.) Walpers
SAPINDACEAE		*Nephelium litchi* Camb.
SAPOTACEAE		*Aesandra butyraceae* (Roxb.)
		Madhuca longifolia (Koenig) MacBride
SAURAUIACEAE		*Saurauia nepaulensis* DC.
SCHIZAECEAE		*Lygodium flexuosum* (L.) SW
		L. japonicum (Thunb.) SW
SCITAMINAE	*	*Zingiber capitatum* Roxb.
		Hedychium spicatum Smith in Rees
		Globba racemosa Smith
		Zingiber officinale Rosc.
SCROPHULARIACEAE		*Scoparia dulcis* L.

SELAGINELLACEAE		*Selaginella fulcrata*
SIMARUBACEAE		*Brucea mollis* Wall.
SOLANCEAE	*	*Solanum indicum* L.
		S. erianthum D. Don
	*	*S. torvum* Swartz.
	*	*S. surabtense* Burm. f.
		Nicotiana tabacum L.
		Datura sp.
		Capsicum annuum L.
SONNERATIACEAE		*Duabanga grandiflora* (Roxb.) Walpers
STAPHYLACEAE		*Bischofia javanica* Blume
STERCULIACEAE		*Sterculia pallens* Wall.
		S. villosa Roxb.
TAMARICACEAE		*Tamarix dioica* Roxb.
		T. indica Willd.
TETRAMELACEAE		*Tetrameles nudiflora* R. Br.
THEACEAE		*Schima wallichii* (DC) Korthals
TILLIACEAE	*	*Grewia subinaequalis* DC.
	*	*G. hainesiana* Hole
		G. pumila Buch.-Ham.
	*	*G. sclerophylla* Roxb.
		Triumfetta sp.
TYPHACEAE		*Typha elephantina* Roxb.
UMBELLIFERAE		*Oenanthe javanica* (Bl.) DC.
		Selinum tenuifolium Wall. ex C.B. Clarke var. *stolonifera* (DC.) Murata
URTICACEAE	*	*Gonostegia pentandra* (Roxb.) Mig.
		Boehmeria macrophylla D. Don
		Urtica dioica L.
		Girardinia diversifolia (Link) Frils *et al* (ined.)
VERBENACEAE		*Gmelina arborea* L.
		Tectona grandis L.
		Caryopteris odorata (D. Don) B.L. Robinson
		Verbena officinalis L.
	*	*Callicarpa macrophylla* Vahl.
		Clerodendron viscosum Ventenat
	*	*Lantana camara* L.
	*	*Premna obtusifolia* R. Br.
	*	*Lippia nodiflora* Rich
VITACEAE		*Leea compactiflora* Kurz.
		L. indica (Burm. f.) Merr.

Sources: Brandis (1906), Kanjilal (1911), Bor (1960), Hara *et al.* (1978).

APPENDIX E

Common and scientific names of animals mentioned in the text

Sources for the Nepalese species are Swan and Leviton (1962), Ellerman and Morrison-Scott (1964), Mitchell (1975), and Fleming *et al.* (1976).

(a) Mammals

	Order Primata	
	Olive baboon	*Papio anubis* Fischer
	Gelada baboon	*Theropithecus gelada* Rüppell
*	Rhesus macaque	*Macaca mulatta* Zimmerman
*	Common langur	*Presbytis entellus* Dufresne
	Order Lagomorpha	
*	Indian hare	*Lepus nigricollis* Cuvier
	Order Carnivora	
*	Smooth Indian otter	*Lutra perspicillata* Geoffroy
*	Sloth bear	*Melursus ursinus* Shaw
*	Asiatic jackal	*Canis aureus* Linnaeus
*	Indian wild dog (dhole)	*Cuon alpinus* Pallas
*	Indian fox	*Vulpes bengalensis* Shaw
*	Striped hyena	*Hyaena hyaena* Linnaeus
*	Jungle cat	*Felis chaus* Güldenstaedt
*	Fishing cat	*Felis viverrina* Bennett
*	Tiger	*Panthera tigris* Linnaeus
*	Leopard	*Panthera pardus* Linnaeus
	Order Pinnipedia	
	Fur seal	*Arctocephalus australis* Schreber
	Order Cetacea	
*	Gangetic dolphin	*Platanista gangetica* Wagler
*	Narwhal	*Monodon monoceros* Linnaeus
	Order Proboscidea	
	African elephant	*Loxodonta africana* Cuvier
*	Asian elephant	*Elephas maximus* Linnaeus

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* denotes animals which occur in Chitawan.

Order Perissodactyla

*	Greater one-horned (Indian) rhinoceros	*Rhinoceros unicornis* Linnaeus
	Lesser one-horned (Javan) rhinoceros	*Rhinoceros sondaicus* Desmarest
	Black rhinoceros	*Diceros bicornis* Linnaeus
	White rhinoceros	*Ceratotherium simum* Burchell
	Sumatran rhinoceros	*Dicerorhinus sumatrensis* Fischer
	Plains zebra	*Equus burchelli* Gray

Order Artiodactyla

	Hippopotamus	*Hippopotamus amphibius* Linnaeus
	Moose	*Alces alces* Linnaeus
	Red deer	*Cervus elephas* Linnaeus
	Reindeer	*Rangifer tarandus* Linnaeus
*	Sambhar	*Cervus unicolor* Kerr
*	Chital	*Axis axis* Erxleben
*	Hog deer	*Axis porcinus* Zimmerman
*	Indian muntjac	*Muntiacus muntjak* Zimmerman
	Swamp deer	*Cervus duvauceli* Cuvier
	Wild goat	*Capra hircus* Linnaeus
	Mountain goat	*Oreamnos americanus* Blainville
	Mountain sheep	*Ovis canadensis* Shaw
	Indian buffalo	*Bubalus bubalis* Linnaeus
	African buffalo	*Syncerus caffer* Sparrman
*	Gaur	*Bos gaurus* H. Smith
	Bison	*Bison bison* Linnaeus
	Waterbuck	*Kobus defassa* Rüppell
	Impala	*Aepyceros melampus* Lichtenstein
	Thomson's gazelle	*Gazella thomsonii* Günther
*	Wild pig	*Sus scrofa* Linnaeus
	Warthog	*Phacochoerus aethiopicus* Pallas
	Bearded pig	*Sus barbatus* Müller
	Collared peccary	*Dicotyles tajacus* Linnaeus

(b) Birds and reptiles

*	Common mynah	*Acridotheres tristis* Linnaeus
*	Gharial	*Gavialis gangeticus* Gmelin
*	Mugger or Marsh crocodile	*Crocodilus palustris* Lesson
*	Indian starred tortoise	*Testudo elongata* Blyth
*	Monitor lizards	*Varanus monitor* Linnaeus *Varanus flavescens* Gray

APPENDIX F

The results of surveys for rhinos in outlying areas

Location	Date (Month, Year)	Distance walked (kms)	Number and types of tracks encountered	Dung-Piles		Population estimate on dung-piles	Number of sightings	Probable number and classes of rhinos	
				No.	No.per km			No.	Classes
West									
SIKRAULI	5.73	2.0	0	0	0	0	0		
	9.73	1.5	0	0	0	0	0		
	11.74	3.0	2 (A♂)	0	0	0	0		
	5.75	3.0	0	0	0	0	0	1	A♂
PIPRAHA	11.74	4.5	3 (S?,A?)	0	0	0	0		
	5.75	3.0	2 (A?)	0	0	0	0	2	A?,S?
KUJAULI	5.73	2.0	0	0	0	0	0		
	9.73	1.5	0	0	0	0	0		
	11.74	1.5	1 (A?)	0	0	0	0		
	5.75	8.0	1 (A?)	1	0.1	1	0	1	A♂
MUKONI	9.73	2.0	1 (A♂)	1	0.5	4	0		
	11.74	13.0	10 (A?,A♀ + c)	0	0.8	7	0		
	5.75	5.0	4 (A♀ + c)	2	0.4	3	0	4	A♂,A♀ + c,A?
BHONSER GHAT	5.73	2.0	5 (A?,A♂,A♀ + c)	5	2.5	22	0		
	9.73	2.0	12 (A?,A♂,A♀ + c)	2	1.0	9	0		
	11.74	12.0	28 (S?,A♂,A♀ + c)	13	1.1	10	1 (S)		
	5.75	10.0	19 (A♂,A♀ + c,S?)	11	1.1	10	1 (A♂)	14	2A♂♂,3A♀♀ + cc, 6S??
LOKHANI	11.74	7.5	8 (A?,S?,A♂,A♀ + c)	2	0.3	3	0		
	5.75	2.0	6 (A?,A♀ + c)	1	0.5	4	0	5	A♂,2A♀♀ + cc
JUNGLE	5.73	9.0	3 (A?.A♀ + c)	1	0.1	1	3 (3A♂♂)		
	9.73	5.0	12 (S?,A♀ + c)	3	0.6	5	0		
	11.74	18.0	62 (S?,A♀ + c)	9	0.5	4	3 (A A♀ + IIIc)		
	5.75	16.0	26 (A♀ + c,A♂,A?)	18	0.1	1	2 (A?)	6	A♂,2A♀♀ + cc,S?
MAGARKHOT	11.74	9.0	5 (A?,A♀ + c)	1	0.1	1	0	3	A♂,A♀ + c
SHERGUNJ	11.74	2.5	1 (A?)	0	0	0	0	1	A♂
AMALTARI	11.74	2.0	5 (A♂,A?)	0	0	0	0	2	A♂,A?

Continued/.....

APPENDIX F (continued).

Location	Date (Month, Year)	Distance walked (kms)	Number and types of tracks encountered	Dung-piles		Population estimate on dung-piles	Number of sightings	Probable number and classes of rhinos	
				No.	No.per km			No.	Classes
West(cont.)									
SERHI	11.74	3.5	14 (A♂,A♀ + IIIc, A♀ + Ic)	2	0.6	5	2 (A♀ + IIIc)	6	2Ao♂,2A♀♀ + cc
JHANGARA	11.74	3.5	10 (A♂,A♀ + IIIc, A♀ + Ic)	2	0.6	5	0	6	2A♂♂,2A♀♀ + cc
KOLKUTTA	11.74	4.5	6 (A?,A♂)	1	0.2	2	0	2	2A♂♂
TAMASPUR	11.74	3.5	2 (A♂)	0	0	0	0		
	5.73	5.0	2 (A♀ + c)	0	0	0	0	4	2A♂♂,A♀ + c
BINAI KHOLA	11.74	21.0	0	0	0	0	0	0	
East									
IMRATANI	11.73	12.0	3 (A♂,A♀ + c)	1	0.1	1	0		
	5.74	6.0	4 (A?,A♂)	0	0	0	0	3	A♂,A♀ + c
JAGHDARI	11.73	14.0	7 (A?,S?,Ao)	4	0.3	3	0	3	A♂,A?,S?
KAHENDRAMOLI	11.73	12.5	9 (A♂,A♀ + c)	2	0.2	2	0	3	A♂,A♀ + c
KUCHKUCHIA	11.73	16.0	21 (A?,S?,A♀ + c)	14	0.9	8	7 (3S??,A♂, A♀ + c)		
	5.74	8.0	11 (A?,S?,A♀ + c)	5	0.6	5	0		
	9.74	19.0	25 (S?,A♀ + Ic, A♀ + c,A)	14	0.7	6	0	9	2A♂♂,2A♀♀ + cc, 3S??
LOTHAR	11.73	9.0	1 (A♂)	0	0	0	0	1	A♂
LIGLIGDOMAR	11.73	36.0	7 (A?,A♂,A♀ + c)	2	0.1	1	0	3	A♂,A♀ + c
JITPUR	11.73	10.0	9 (A?,S?,A♀ + c)	1	0.1	1	0	4	A♂,A♀ + c,S?

Continued/.....

APPENDIX F (continued).

Location	Date (Month, Year)	Distance walked (kms)	Number and types of tracks encountered	Dung-piles		Population estimate on dung-piles	Number of sightings	Probable number and classes of rhinos	
				No.	No.per km			No.	Classes
South									
AMWA	1.73	9.0	0	0	0	0	0		
	8.73	11.0	0	0	0	0	0		
	10.74	11.0	0	0	0	0	0		
BAGAI	8.73	14.0	2 (2A♂♂)	2	0.1	1	0		
	10.74	10.0	1 (A?)	0	0	0	0	2	2A♂♂
BOTESIMRA	8.73	9.0	0	0	0	0	0		
	10.74	9.0	4 (A♀ + c)	1	0.1	1	0	2	A♀ + c
BANKATTA	8.73	5.0	3 (A♂,A?)	0	0	0	0		
	10.74	12.0	2 (A♂,A?)	2	0.2	2	0	2	2A♂♂
North									
GORUA	1.74	9.0	6 (A♂♂,A?)	2	0.2	2	0	2	2A♂♂
TIKOLI	1.74	10.0	4 (A♀ + c)	1	0.2	2	0		
	6.74	22.0	14 (A♀ + Ic,A♀ + c,A♂)	5	0.4	4	4 (2A♀♀ + cc)	5	A♂,2A♀♀ + cc

APPENDIX G

The results of time-sampling observations on feeding, lumped for each habitat and season

SAL FOREST	FMAM 1 period 44 minutes	
Food types	Number of minutes Available	Eaten
Saccharum spontaneum (M)	22	0
S. munja (M)	23	0
Phragmites karka	5	0
Themeda villosa	42	38
Vetiveria zizanoides	10	2
Imperata cylindrica	23	3
Clerodendron viscosum	13	0
Callicarpa macrophylla	11	0
Acacia concinna	28	0
Phyllanthus emblica	10	0
Litsaea monopetala	2	0
Bauhinia malabaricum	1	0
Mallotus phillippensis	15	0
Syzygium cumini	5	0
Spatholobus parviflorus	10	0
Syzygium operculatus	12	0
Bauhinia vahlii	32	0
Shorea robusta	27	2
Sterculia villosa	16	0
Ficus semicordata	6	0
Bridelia retusa	12	0
Mimosa rubricaulis	10	0
Careya arborea	6	0
Wendlandia tinctoria	2	0
Dillenia indica	27	0
Terminalia chebula	4	0
Terminalia bellirica	13	0
Miliusa velutina	5	0
Buchanania latifolia	15	0
Unidentified trees	16	2

Continued/.....

APPENDIX G (continued).

TALL GRASSLAND Food types	FMAM 34 periods 563 minutes		JJAS 9 periods 159 minutes		ONDJ 10 periods 205 minutes	
	Number of minutes Available	Eaten	Number of minutes Available	Eaten	Number of minutes Available	Eaten
Saccharum spontaneum (M)	38	17	22	10	199	132
" " (B)	125	13				
" " (R)	264	182				
S. munja (M)	39	21	13	6	111	59
" (B)	237	84				
" (R)	299	165				
Narenga porphyrocoma (M)	10	8	12	8	32	29
" " (B)	45	0				
" " (R)	147	92	7	4		
Erianthus ravennae	4	1			23	3
Saccharum procerum	43	10			22	2
Arundo donax	8	2	3	0	20	12
Phragmites karka	13	2			3	1
Thyrsia zea	2	1				
Themeda villosa	8	6			12	1
Vetiveria zizanoides			3	3		
Apluda mutica	5	0	9	0		
Typha elephantina					10	0
Imperata cylindrica			11	6	5	5
Cynodon dactylon	165	10	24	14	100	15
Setaria pallide-fusca	19	2	20	8		
Hemarthria compressa	2	0				
Fimbristylis dichotoma	14	0				
Ageratum conyzoides					18	0
Zehneria maysorensis					19	2
Clerodendron viscosum	31	0	1	0		
Artemisia vulgaris	123	12	7	0	83	12
Callicarpa macrophylla	110	31	11	0	101	22
Calotropis gigantea	1	0	1	0	127	0
Colebrookia oppositifolia	196	16	18	0	86	5
Pogostemon bengalensis	27	10	5	0	96	35
Eupatorium odoratum	1	0			44	1
Zizyphus jujuba	4	0	8	0	2	0
Cassia tora					1	0
Ranunculus scleratus	7	0				
Cordia grandis	1	0				
Litsaea monopetala			1	0		
Bombax ceiba	67	0			42	3
Bauhinia malabaricum	47	0	7	0	21	1
Trewia nudiflora	77	0			33	0
Mallotus phillippensis	10	1				
Butea monosperma	3	3				
Unidentified creeper			4	0		
Trewia nudiflora (fruits)			2	0		
Hydrilla verticillata and other aquatic plants	7	7	5	5		

Continued/.....

APPENDIX G (continued).

SHORT GRASSLAND	FMAM 17 periods 319 minutes		JJAS 9 periods 159 minutes		ONDJ 10 periods 205 minutes	
Food types	Number of minutes Available	Eaten	Number of minutes Available	Eaten	Number of minutes Available	Eaten
Saccharum spontaneum (M)			11	3	59	33
" " (B)	3	0				
" " (R)	25	3	48	38		
S. munja (M)					33	23
" (B)	16	0				
" (R)	39	32				
Narenga porphyrocoma (B)	6	2				
" " (R)	6	6				
Vetiveria zizanoides	3	1	12	5		
Imperata cylindrica	10	0	21	10	13	0
Cynodon dactylon	231	197	76	60	130	91
Chrysopogon aciculatus					60	44
Fimbristylis dichotoma			10	3	2	2
Kyllingia colorata			2	2		
Carex continua			2	2		
Cyperus spp. (small)			44	32	23	22
Polygonum plebujum			3	1		
Equisetum sp.	5	3				
Erigeron bonariensis	2	1				
Ipomaea quamoclit	3	0				
Dryopteris sp.	2	0			3	3
Cirsium wallichii	4	0				
Artemisia vulgaris	53	19	17	0	25	6
Callicarpa macrophylla	38	4	8	0	44	20
Calotropis gigantea					5	0
Colebrookia oppositifolia	63	0	13	0	28	0
Pogostemon bengalensis	6	0			16	8
Eupatorium odoratum	2	0			4	2
Zizyphus jujuba	15	0			9	3
Cassia tora			2	1		
Solanum indicum	2	0				
Phyllanthus emblica					5	3
Ranunculus scleratus			3	1	5	1
Litsaea monopetala			1	0	4	0
Trewia nudiflora	7	0	4	0	11	0
Bombax ceiba (flowers)	10	9				
Hydrilla verticillata and other aquatic plants	24	17	47	28	44	25
Hygrorhyza aristata			39	28		

Continued/.....

APPENDIX G (continued).

TALS Food types	FMAM 14 periods 183 minutes		JJAS 8 periods 92 minutes		ONDJ 1 period 26 minutes	
	Number of minutes Available	Eaten	Number of minutes Available	Eaten	Number of minutes Available	Eaten
Saccharum spontaneum (M)	47	20	18	3		
Arundo donax	37	19	39	21		
Phragmites karka	5	0				
Themeda villosa	2	1				
Vetiveria zizanoides			8	5		
Typha elephantina	10	2				
Imperata cylindrica	16	0				
Cynodon dactylon	22	2	6	1	14	10
Paspalidium flavidum	6	2			13	8
Paspalum scrobiculatum	6	1				
Oplismenus sp.			14	10		
Aquatic grasses			34	19	13	9
Cyperus spp. (large)	13	8	11	8		
Cyperus spp. (small)	11	0			8	3
Polygonum plebujum	6	6				
Piper nepalense	4	0				
Pteris vittata	15	2				
Gonostegia pentandra	1	0	10	0		
Dalbergia sissoo	16	14				
Bombax ceiba	2	1				
Hydrilla verticillata and other aquatic plants	152	127	79	54	17	10

Continued/.....

APPENDIX G (continued).

RIVERINE FOREST	FMAM 7 periods 123 minutes		JJAS 9 periods 145 minutes		ONDJ 4 periods 67 minutes	
Food types	Number of minutes Available	Eaten	Number of minutes Available	Eaten	Number of minutes Available	Eaten
Saccharum spontaneum (M)	56	46	22	15	25	13
S. munja (M)	28	12	22	0	19	3
Narenga porphyrocoma			24	13		
Saccharum procerum	3	1				
Narenga fallax	8	2				
Themeda villosa	3	0	13	8		
Imperata cylindrica	18	4			22	0
Cynodon dactylon	97	39	126	24	39	0
Setaria pallide-fusca	8	3	12	7	5	0
Brachiaria ramosa	10	8	25	0	5	0
Hemarthria compressa	8	3				
Chrysopogon aciculatus	14	3	5	1	21	0
Cyperus spp. (small)			14	1		
Ageratum conyzoides	5	0				
Erigeron bonariensis	2	2				
Zehneria maysorensis			8	0		
Gonostegia pentandra	9	1				
Oxalis corniculata	3	2				
Unidentified herbs			9	3		
Adhatoda vasica	2	0				
Clerodendron viscosum	24	0	2	0		
Artemisia vulgaris	43	3	22	0	7	0
Callicarpa macrophylla	63	25	6	1	29	15
Calotropis gigantea	10	0	1	0		
Colebrookia oppositifolia	34	0	82	0	41	0
Pogostemon bengalensis	11	0				
Eupatorium odoratum	8	0	14	0		
Zizyphus jujuba	23	1	4	0	8	4
Cassia tora	9	0			3	0
Cirardinia diversifolia			6	0		
Acacia concinna			2	0		
Dead leaves			3	1		
Solanum indicum	4	0				
Phyllanthus emblica	3	0	32	14	14	2
Cordia grandis	3	3			4	3
Dalbergia sissoo	7	5				
Litsaea monopetala	3	0	1	0	14	10
Ehretia laevis	5	3			5	4
Bombax ceiba	4	0	4	0	7	0
Bauhinia malabaricum			1	0		
Trewia nudiflora	42	0	71	0	27	0
Mallotus phillippensis	5	0	12	0	24	19
Trewia nudiflora (fruits)			83	83		
Murraya koenigii	2	0	6	0	7	2
Unidentified shrub					5	3
Hydrilla verticillata and other aquatic plants	6	6				

Continued/.....

APPENDIX G (continued).

SCRUB	FMAM 3 periods 30 minutes		JJAS 3 periods 60 minutes		ONDJ 6 periods 82 minutes	
Food types	Number of minutes Available	Eaten	Number of minutes Available	Eaten	Number of minutes Available	Eaten
Saccharum spontaneum (M)	2	0	5	3	27	18
S. munja (M)	3	1			10	1
Vetiveria zizanoides			8	2		
Imperata cylindrica	3	0	2	0	19	0
Cynodon dactylon	27	23	57	43	65	14
Setaria pallide-fusca			16	4		
Brachiaria ramosa			22	10		
Chrysopogon aciculatus			32	29	43	3
Aquatic grasses			4	4		
Cyperus spp. (small)	3	3	4	1		
Pteris vittata			2	0		
Gonostegia pentandra			7	0		
Oxalis corniculata	3	0				
Artemisia vulgaris	10	0	11	5	18	8
Callicarpa macrophylla	6	4	18	6	45	32
Calotropis gigantea	3	0			23	0
Colebrookia oppositifolia	7	0	30	3	40	0
Pogostemon bengalensis	4	2			18	2
Eupatorium odoratum	4	2			5	1
Zizyphus jujuba	6	0	11	0	24	8
Solanum torvum	1	0	1	1		
Calamus tenuis					4	0
Cordia grandis			7	4		
Litsaea monopetala	4	0	1	0		
Ehretia laevis	2	0	2	0		
Bombax ceiba	3	0	14	2	3	0
Trewia nudiflora	6	0	6	0	7	0
Mallotus phillippensis	2	0	3	0	16	0
Murraya koenigii			3	2		

APPENDIX H

The numbers of visits, hours of searching time and rhinos sighted in each block of the Sauraha study area in each month of the study period.

MONTH	Blocks A + B			Block C			Block D			Block E			Block F			Block G		
	No.of visits	No.of hours	No.of sightings	No.of visits	No.of hours	No.of sightings	No.of visits	No.of hours	No.of sightings	No.of visits	No.of hours	No.of sightings	No.of visits	No.of hours	No.of sightings	No.of visits	No.of hours	No.of sightings
1972 DEC	1	4	1	0	0	0	5	16	16	5	14	5	4	3	0	0	0	0
1973 JAN	1	3	1	0	0	0	6	25	7	11	55	37	5	13	8	0	0	0
MAR	1	2	2	0	0	0	15	72	108	15	101	59	8	11	11	0	0	0
APR	1	4	5	0	0	0	15	126	175	14	44	47	7	6	3	0	0	0
MAY	2	5	3	0	0	0	20	92	141	20	44	44	9	16	14	0	0	0
JUN	4	10	0	1	2	1	8	29	5	8	22	39	1	1	0	0	0	0
JUL	1	2	1	1	3	1	24	66	111	25	137	213	1	3	1	0	0	0
AUG	5	5	5	0	1	0	12	40	20	18	125	112	1	2	0	1	2	0
SEP	5	4	0	1	0	0	9	19	14	19	43	36	10	78	60	1	1	0
OCT	3	9	1	0	1	0	11	25	17	13	40	17	24	170	70	0	0	0
NOV	0	0	0	2	15	8	6	10	5	7	29	29	77	81	33	6	33	45
DEC	3	5	1	3	10	14	14	36	11	14	31	16	20	90	39	2	5	8
1974 JAN	10	10	1	10	50	27	21	43	28	23	64	32	24	120	82	6	20	20
FEB	10	14	10	6	33	13	21	59	89	24	76	38	22	80	58	3	4	3
MAR	4	8	7	1	6	3	17	67	116	17	49	27	14	70	74	3	11	14
APR	9	6	19	0	0	0	22	85	240	23	53	117	17	55	62	5	7	11
MAY	2	6	1	6	64	14	14	54	58	14	24	9	15	53	34	3	6	1
JUN	1	1	0	0	0	0	7	10	20	10	28	50	19	139	205	0	0	0
JUL	2	3	2	3	15	5	4	27	20	14	56	65	19	102	158	1	3	7
AUG	0	0	0	1	4	5	4	7	10	7	36	12	13	75	141	1	4	10
SEP	2	3	0	2	8	3	7	17	17	8	37	27	23	99	139	5	17	27
OCT	2	3	1	2	17	3	5	6	4	8	43	19	12	59	45	2	5	4
NOV	1	1	0	3	21	2	7	10	19	8	35	19	15	52	35	2	4	7
1975 JAN	2	3	0	1	2	0	2	5	4	3	6	3	5	21	20	1	3	4
MAR	7	16	34	2	4	2	18	67	14	28	128	103	22	10	76	1	5	9
APR	14	40	63	1	3	0	29	76	159	35	123	164	28	77	88	2	8	10
MAY	8	13	23	0	2	0	29	85	227	32	92	106	25	137	93	1	0	0
JUN	6	9	5	0	0	0	10	17	57	15	27	49	14	48	46	3	3	3
JUL	0	0	0	1	7	2	5	12	17	18	70	97	18	84	119	6	15	41
AUG	2	3	0	0	0	0	2	3	13	2	3	7	2	7	9	0	0	0
NOV	3	13	0	2	7	1	4	10	1	6	19	11	6	30	22	1	4	4
1976 JUN	2	3	3	1	2	7	3	9	5	9	56	134	10	63	124	2	5	12

APPENDIX J

The distribution of the sightings of 37 individuals over the 15 sub-blocks of the study area

	Number of sightings														
Sub-blocks	A1	A2	B1	B2	C1	C2	D1	E1	E2	F1	F2	F3	G1	G2	G3
Individual															
M001	0	0	0	5	8	2	95	10	8	1	2	0	0	0	0
M002	0	0	0	4	1	2	27	1	0	2	1	0	0	0	0
M004	0	0	0	2	0	0	56	0	1	0	0	0	0	0	0
M005	0	0	0	3	1	0	87	27	35	23	2	7	0	1	0
M013	0	6	6	2	2	2	4	0	0	0	0	0	0	0	0
m032	0	0	0	0	0	0	0	0	6	3	0	0	3	3	7
M045	0	0	0	0	0	0	14	19	13	56	20	36	0	2	1
m054	0	0	0	0	0	0	4	5	0	21	18	16	0	0	0
m055	0	0	0	0	0	0	1	4	1	43	26	26	0	0	0
M056	0	0	0	0	0	0	0	0	0	0	0	0	6	7	7
m057	0	0	0	0	0	0	0	2	0	10	6	9	0	0	0
m060	0	0	0	0	0	0	0	3	0	8	4	6	0	0	0
F073	0	0	0	3	0	0	105	62	35	3	0	3	0	0	0
F075	0	0	0	2	0	1	94	17	12	0	0	12	0	2	0
m076	0	0	0	0	0	0	1	5	3	6	13	24	0	0	0
F078	0	0	0	0	0	0	34	14	21	1	0	0	0	0	0
F081	0	0	0	0	0	0	40	37	41	3	1	0	0	0	0
F084	0	0	0	0	0	0	29	10	19	0	0	0	0	0	0
F086	0	0	0	0	0	0	37	18	11	7	20	27	1	0	0
m087	0	0	0	0	0	0	18	13	11	4	10	20	2	0	0
F090	0	2	1	1	1	3	72	12	14	4	4	1	0	0	0
f098	0	0	0	1	0	0	46	8	13	0	0	0	0	0	0
F099	0	0	0	1	0	0	33	17	33	0	1	0	0	0	0
f100	0	0	0	1	0	0	28	20	35	0	0	0	0	0	0
F110	0	0	0	0	0	0	8	16	5	4	10	14	0	0	0
F113	0	0	0	0	0	0	5	2	0	6	6	6	0	0	0
F122	0	0	0	0	0	0	5	2	33	0	0	0	0	0	0
F130	0	0	0	0	0	0	10	8	5	8	1	18	0	1	0
F139	0	0	0	1	0	0	2	1	0	0	0	0	4	5	8
F141	0	0	0	0	0	0	0	0	0	0	0	0	0	8	15
f160	0	0	0	0	0	0	1	3	5	11	15	35	3	1	0
F161	0	0	1	0	0	8	7	2	0	6	12	0	0	0	0
F163	0	0	0	0	2	0	8	28	3	18	14	7	0	0	0
f165	0	0	0	0	0	0	0	4	5	9	1	2	2	1	3
F170	0	0	0	0	0	0	7	4	9	6	12	7	0	1	0
f179	0	0	0	0	0	0	0	2	0	8	16	25	0	0	0
F192	0	0	0	0	0	0	7	9	25	1	0	2	0	0	0

APPENDIX K

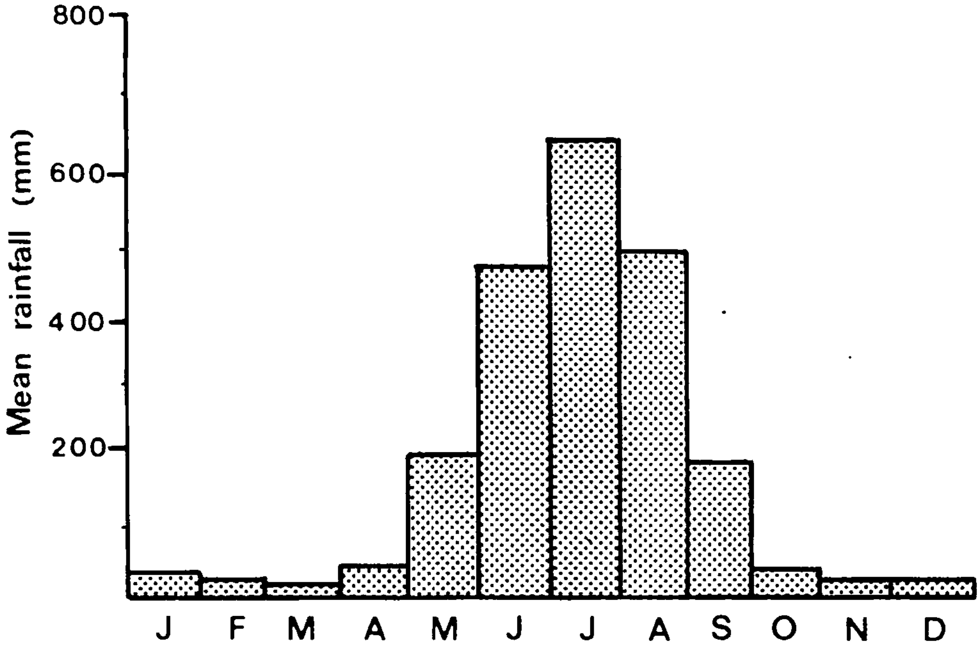
The distributions of the sightings of 37 individuals between two parts of the study area in each season

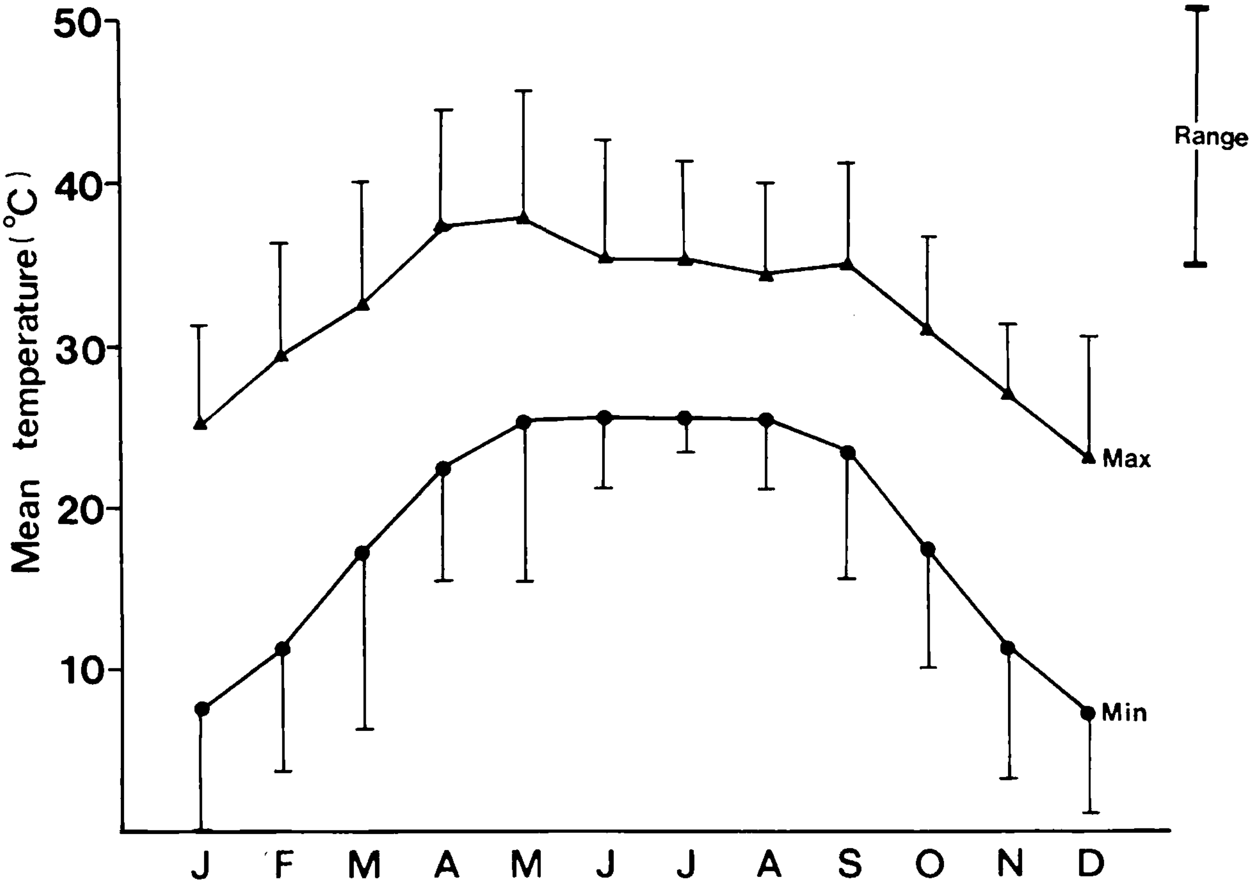
	Blocks A to D				Blocks E to G			
Season	FMAM	JJAS	ONDJ	Total	FMAM	JJAS	ONDJ	Total
Numbers of visits	190	95	81	366	222	153	98	473
Individual								
M013	18	4	0	22	0	0	0	0
M004	45	11	2	58	1	0	0	1
M001	95	7	8	110	3	10	8	21
M002	28	4	2	34	1	1	2	4
F075	80	14	3	97	10	30	3	43
F090	52	23	5	80	8	23	4	35
f098	36	10	0	46	2	19	0	21
F084	25	3	1	29	0	25	4	29
F073	82	15	11	108	34	47	22	103
F078	22	6	6	34	8	22	6	36
M005	69	18	4	91	30	37	28	95
F099	23	11	0	34	14	35	2	51
f100	14	4	0	18	16	8	4	28
F081	32	7	1	40	26	47	9	82
F122	2	1	2	5	1	33	1	35
F192	4	1	2	7	2	33	2	37

	Blocks A to E				Blocks F to G			
Season	FMAM	JJAS	ONDJ	Total	FMAM	JJAS	ONDJ	Total
Numbers of visits	222	153	98	473	167	130	132	429
Individual								
F161	11	4	3	18	17	1	0	18
F163	40	0	1	41	13	20	6	39
f165	9	9	0	18	4	5	1	10
F086	45	17	4	66	6	39	10	55
F110	22	7	0	29	5	18	5	28
m087	8	9	2	19	5	20	0	25
M045	32	13	1	46	37	20	14	71
F170	13	7	0	20	4	12	10	26
F113	7	0	0	7	0	15	3	18
F130	18	4	1	23	6	26	4	36
m060	0	3	0	3	4	13	1	18
m054	9	0	0	9	6	44	5	55
m055	6	0	0	6	16	71	8	95
m076	10	3	0	13	5	34	4	43
f179	2	0	0	2	9	35	5	49
m057	2	0	0	2	4	16	5	25
f160	4	5	0	9	10	40	15	65
m032	6	0	0	6	5	6	5	16
M056	0	0	0	0	9	8	3	20
F139	4	0	0	4	2	8	7	17
F141	3	0	0	3	3	9	8	20

APPENDIX L

Meteorological data recorded at Rampur, 1958 to 1966





APPENDIX M

Some measurements of rhinos in Chitawan and Kaziranga

(a) Photographic measurements of height

Adult males (n = 3): 170.0 - 183.0 cms; mean, 177.0 cms
Adult females (n = 5): 160.0 - 173.0 cms; mean, 165.0 cms

Sub-adults:
  Class 6 (n = 6): 144.0 - 155.0 cms; mean, 149.3 cms
  Class 5 (n = 3): 135.0 - 142.0 cms; mean, 137.3 cms.

(b) Some of the measurements made on carcases (all in cms)

	Aoo (n = 2)	A♀♀ (n = 4)	So Class 6 (n = 1)	o Calf *c*.4 mo. (wt 158 kgs) (n = 1)	o Calf < 1 mo. (n = 1)
Shoulder height	171.0 - 176.0	148.0 - 164.5	155.0	71.0	63.0
Body length (tail base to nose)	368.0 - 380.0	310.0 - 341.0	298.0	140.0	117.0
Tail length	68.0 - 88.5	65.0 - 69.0	51.0	31.0	28.0
Neck girth	153.0 - 169.0	138.0 - 145.0	104.0	66.0	48.0
Forefoot width	24.0 - 27.5	21.0 - 23.5	20.0	12.8	10.0
Hindfoot width	22.5 - 27.0	20.0 - 22.0	18.0	12.8	10.0
Circumference of foreleg just above foot	50.0 - 53.0	45.0 - 51.0	45.0	27.0	21.0

(c) Some skull measurements (all in cms)

	Aoo (n = 3)	A♀♀ (n = 6)	o Calf *c.* 2 yrs. (n = 1)	o Calf *c.* 4 mo. (n = 1)	o Calf < 1 mo. (n = 1)
Height	49.0 - 52.5	49.5 - 50.5	38.0	23.5	11.0
Length	61.0 - 64.0	60.0 - 63.5	44.5	35.0	25.5
Max. width	31.0 - 33.0	24.0 - 31.0	20.5	15.5	12.0
Zygomatic arch length	27.0 - 28.5	25.0 - 28.0	20.0	14.5	11.0
Mandible length	55.0 - 56.0	50.0 - 54.5	41.0	28.0	21.5
Mandible height	31.5 - 32.5	27.5 - 30.5	23.0	14.0	10.0
Upper tooth row length	26.5 - 28.5	23.0 - 27.5	18.0	14.5	12.0
Lower tooth row length	24.5 - 26.5	22.0 - 25.0	17.0	13.5	12.5

Measurements of teeth and tooth wear data will be published elsewhere.

(d) Horn weights

In a sample of 86 rhino horns collected and weighed in the Kaziranga National Park (Assam Forest Dept. Records, 1965-1975), adult males had significantly heavier horns than adult females:

Aoo (n = 42), 1,167.6 ± 501.4 gms: A♀♀ (n = 44), 536.8 ± 259.3 gms.

APPENDIX N

The relative importance of each habitat type for feeding, according to the season

Habitat	Area (km^2) % of total (=A)		FMAM	JJAS	ONDJ
Tall grassland	4.5 42.3%	F*	39.6	15.8	11.8
		F x A$^{x10^{-2}}$	16.75	6.68	4.99
		RI[†]	69.3	34.4	35.9
Short grassland	11.5 33.5%	F	12.1	27.6	11.8
		F x A$^{x10^{-2}}$	4.05	9.25	3.95
		RI	16.8	47.7	28.4
Tals	0.1 0.3%	F	16.4	21.9	28.1
		F x A$^{x10^{-2}}$	0.05	0.07	0.08
		RI	0.2	0.4	0.6
Riverine forest	5.1 14.9%	F	7.4	4.8	9.0
		F x A$^{x10^{-2}}$	1.10	0.72	1.34
		RI	4.6	3.7	9.6
Scrub	3.1 9.0%	F	24.5	29.8	39.3
		F x A$^{x10^{-2}}$	2.21	2.68	3.54
		RI	9.1	13.8	25.5

* F = the mean rate of sightings of feeding rhinos (from Fig. 4.4) expressed as a percentage of the total of the rates in each habitat type.

[†] RI = the relative importance of each habitat type for feeding in each season (= F x A x 10^{-} expressed as a percentage of the total for each season).

APPENDIX P

Parasites collected from rhinos in Chitawan

Leeches : (unidentified) frequently observed on rhinos' softer parts. Specimens at British Museum (Natural History).

Ticks : include *Dermacentor auratus* (identified by H. Hoogstraal). Rarely found on carcases.

Tape worms : (unidentified) frequently found in the dung.

Nematodes : Some individuals had heavy infestations. Mrs. M. Chitwood examined one female strongylid nematode from a young male rhino and concluded that it belonged to a new genus and species. Other specimens were identified as *Decrusia* sp. by Ms. E. Harrison.

Biting flies : *Tabanus* spp. Three species.

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Plates 3 to 42

Plate 3. A painting depicting a rhino hunt in Chitawan. Kaiser Library, Kathmandu.

Plate 4. An aerial view of a tributary of the Rapti in the Sauraha study area.

Plate 5. A female Indian rhino with her calf in tall grassland near Khoria, west Chitawan.

Plate 6. My elephant, Devi Kali, and her driver, Naryan, in tall grassland near Sauraha. The Himalayas are visible in the background.

Plate 7. A cow and her calf standing alert after being disturbed by the observer.

Plate 8. A calf fleeing behind his mother.

Plate 9. *A cow charging the observer, followed by her calf.*

Plate 10. *Bumps and irregularities in the fold patterns such as those shown, and the loss of parts of the tail and ears all helped in the identification of individuals.*

Plate 11. *A photograph taken through the Rank image-intensifier (I.W.S. SS.20 Mk.1.) at a range of eight metres on a moonlit night.*

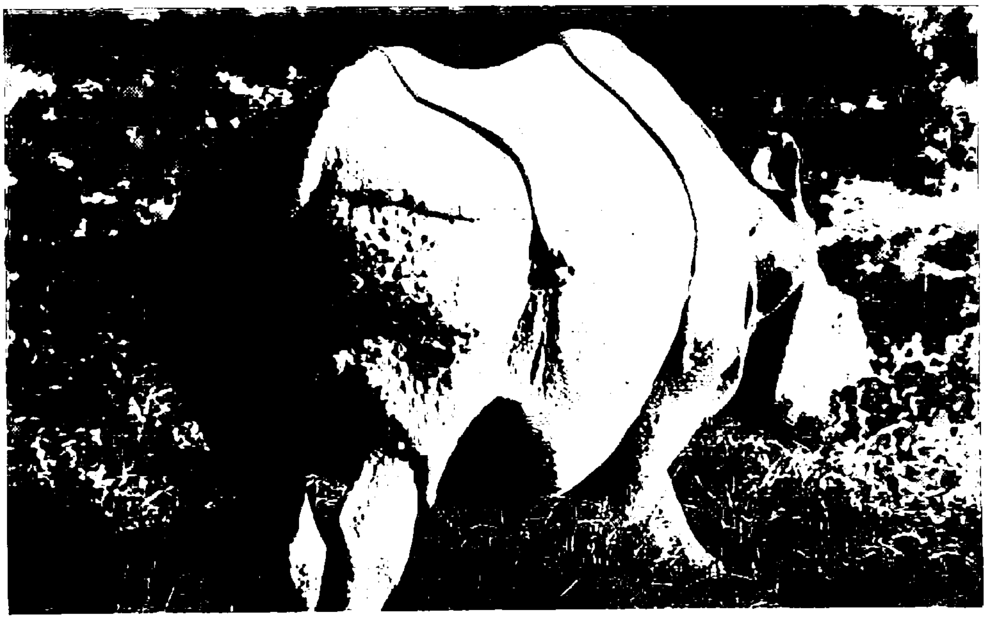

Plate 12. *An adult female Indian rhino in side view. Note the shallow neck folds and small bib in comparison with those of the adult male below. See also Plates 41 and 42.*

Plate 13. *An adult male Indian rhino in side view. The deep neck-folds and bib are probably important in close-up displays. See also Plates 41 and 42.*

Plate 14. *A photograph taken through the image-intensifier, of a young female urinating. The image intensifier enabled me to reliably determine the sex of rhinos from a considerable distance even at night.*

Plate 15. A cow with her three-month old calf.

Plate 16. A cow with her 18-month old calf.

Plates 17 and 18. A sub-adult rhino measured photographically by later photographing a graduated pole placed in its footprint.

Plate 19. A sub-adult male, class 5.

Plate 20. Two sub-adult males, class 6. Note the greater development of the neck-folds than in the class 5 sub-adult pictured above.

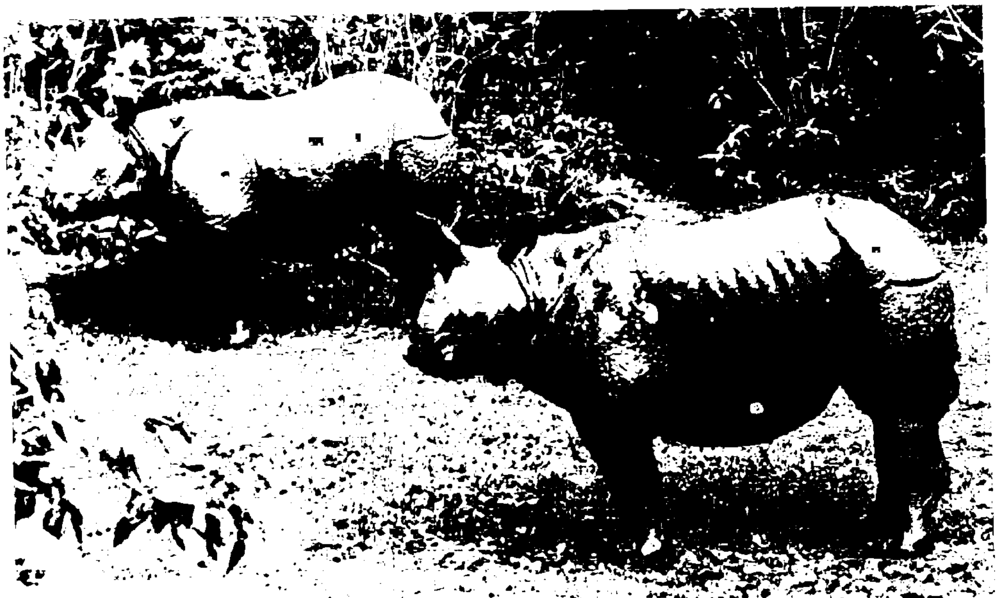

Plate 21. *The lower jaw of an Indian rhino, showing the very sharp incumbent lower incisors.*

Plate 22. *An adult female feeding on tall grass (*Saccharum spontaneum*). Note the mobile, prehensile lip.*

Plate 23. Dalbergia sissoo *trees bent over by rhinos and browsed upon repeatedly, on Bandarjola Island.*

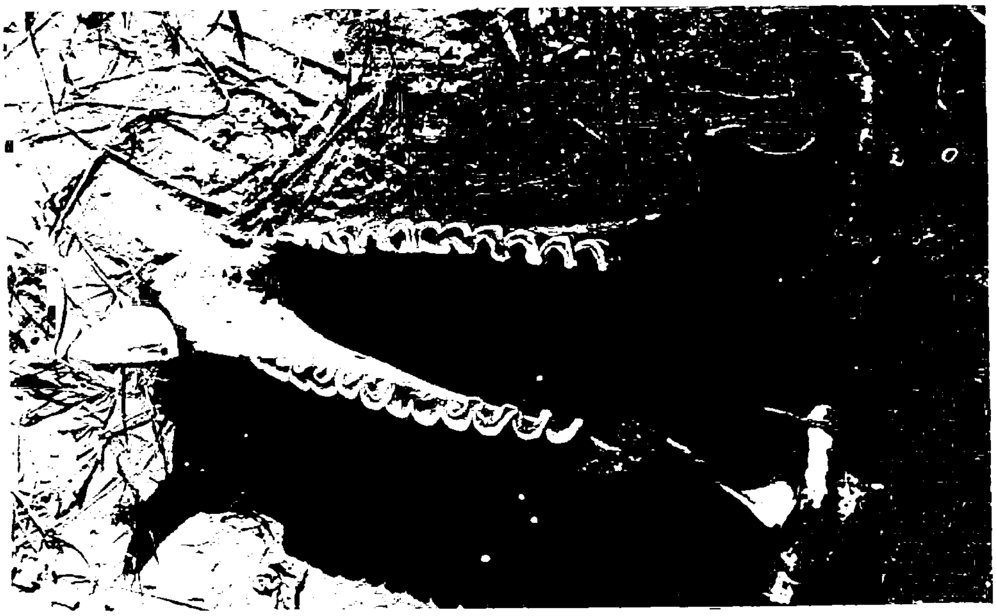

Plate 24. A sub-adult grazing on short grass using its opposed lips to pluck the grass.

Plate 25. A cow and her calf wallowing in a muddy pool, at the start of the monsoon.

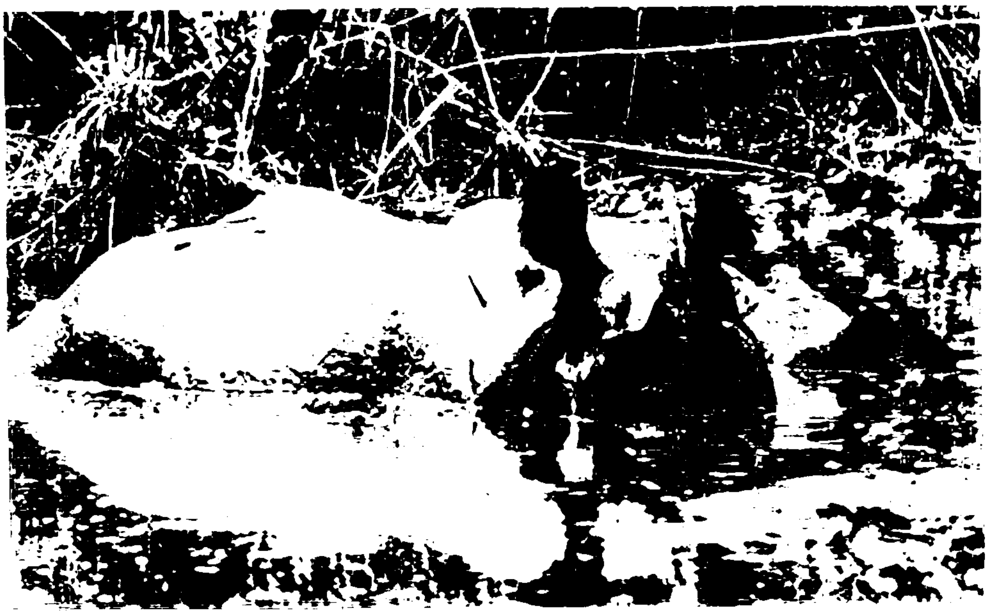

Plate 26. A group of sub-adults wallowing together.

Plate 27. An aggregation of three cow-calf pairs and one adult male grazing in short grassland at the edge of riverine forest.

Plate 28. An adult male (M045) squirt-urinating.

Plate 29. *Drag-marks created by an adult male dragging his hind-feet through a dung-pile.*

Plate 30. *A sub-adult female performing* flehmen *in reaction to the urine of another rhino.*

Plate 31. *A calf nuzzling her mother's head.*

Plate 32. A sub-adult female licking another sub-adult's back.

Plate 33. An infant mounting his mother's head.

Plate 34. Two sub-adult males sparring.

Plate 35. An agonistic interaction between two adult females at a wallow. The animal on the left is displaying her tusks.

Plate 36. The suppurating wounds sustained by an adult male (M062) in fights with other adult males. He later died from the wounds.

Plate 37. This third year calf, attacked repeatedly by an adult male, died from internal injuries and tusk wounds.

Plate 38. A calf touches his mother for 'reassurance' in the presence of the observer.

Plate 39. A copulating pair of Indian rhinos.

Plate 40. Two calves approaching each other while their mothers graze.

Plates 41 and 42. A comparison of the front views of the neckfolds and bib of an adult male (above) and an adult female (below).