DEMOGRAPHY AND HABITAT USE BY GREATER ONE-HORNED RHINOCEROS IN NEPAL

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Abstract: We used a register of photographed individuals to census greater one-horned rhinoceros (*Rhinoceros unicornis*, hereafter rhinoceros) in Royal Chitwan National Park (NP), Nepal, between 1984 and 1988. By April 1988, the population was estimated to be 358–376 individuals as determined by regression analysis. The observed rate of increase for the Sauraha population, an intensively monitored subpopulation in the central and eastern part of Royal Chitwan NP, was 4.8% between 1984 and 1988 and 2.5% between 1975 and 1988. The Sauraha population included 87 adult females and 58 breeding-age males, of which only 28 males were judged to have bred during the study period. Annual calf production averaged 7.6 ± 0.8% ($\bar{x}$ ± SE) between 1984 and 1988. No distinct season of parturition was detected. Predation by tigers (*Panthera tigris*) accounted for 4 of 7 calf mortalities, and all 7 calves that died during the study period were <8 months old. Mean annual mortality within the calf, subadult, and adult age categories was estimated to be 2.8, 2.2, and 2.9%, respectively.

Rhinoceros populations reached maximum densities of 13.3/km^2 in riverine forest-*Saccharum spontaneum* grassland mosaics along the Rapti River. Local densities in areas dominated by *Narenga porphyracorma* and *Themeda arundinacea* grasslands were 1.7–3.2/km^2. Annual monsoon floods were responsible for maintaining prime grazing habitat and high population densities.

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Populations of greater one-horned rhinoceros have declined drastically over the last 400 years as a result of land-clearing and poaching (Blanford 1888). By 1988, only 2 populations contained >80 individuals: Royal Chitwan NP, Nepal, and Kaziranga National Park, Assam, India (Dinerstein and McCracken 1990). The Royal Chitwan population is one of the few that has increased over the last decade.

The purpose of our paper is to (1) describe the demography of a subpopulation containing most of the rhinoceros population within Royal Chitwan NP (the Sauraha population); (2) analyze habitat–density relationships within the Sauraha population; and (3) examine population structure of the entire Royal Chitwan population. To this end, we estimated total population size, sex and age composition, seasonality of births, birth rate, interbirth interval, survivorship, mortality, and population growth rate. We also investigated the relationships between proximity to agriculture, the size of flood plain grasslands, and rhinoceros population densities. Finally, we evaluated the importance of annual monsoon floods as a means of maintaining prime grazing habitat and supporting high population densities of this endangered ungulate.

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STUDY AREA

The Royal Chitwan NP is located in the south-central Terai region of Nepal (84°20′E, 27°30′N). Rhinoceros and other large mammals are found in highest densities along the flood plain grasslands and riverine forests bordering the Rapti, Narayani, Reu, Dungre, and Icharni rivers (Fig. 1) (Seidensticker 1976, Mishra 1982, Dinerstein and Wemmer 1988). The most critical habitat is a riverine grassland association dominated by

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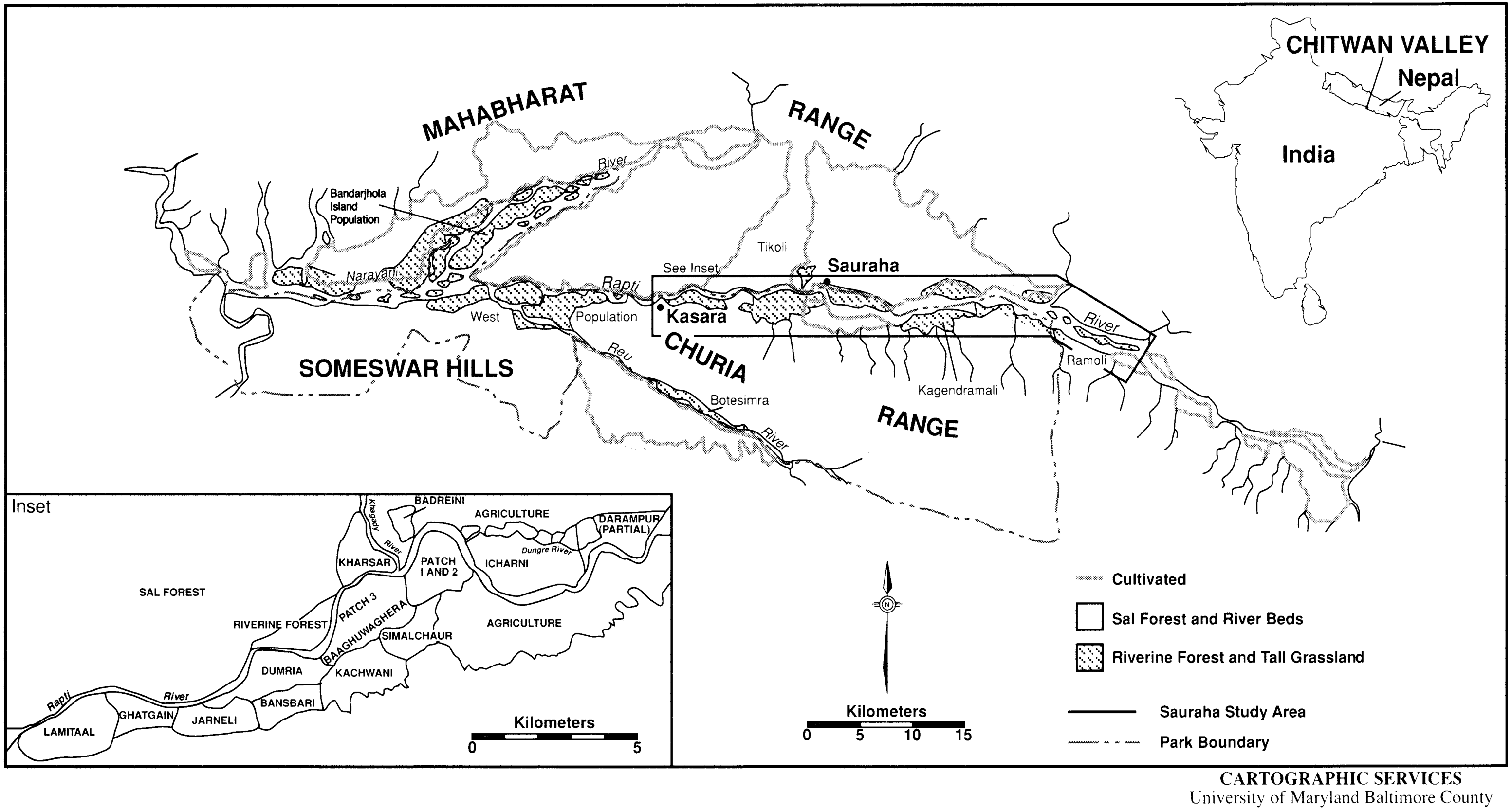

Fig. 1. Royal Chitwan National Park, Nepal, and environs showing major features and location of the 4 subpopulations (Sauraha, West, Bandarjhola-Narayani, and South [Botesimra]) discussed in the text. Inset of the Sauraha area shows blocks searched for greater one-horned rhinoceros (excluding part of Darampur block).

Saccharum spontaneum, 4–6 m in height, which is a major forage plant. Aboveground dry biomass of *S. spontaneum* in this association accounted for 92.0, 99.0, and 99.5% of plant matter sampled during October (end of monsoon), January (cool season), and April (hot season), respectively (E. Dinerstein, unpubl. data). Less frequently used are tall grasslands on higher terraces of the flood plain, dominated by mixed or near monospecific stands of 5–7-m-tall *Narenga porphyracorma*, *Saccharum benghalensis*, or *Themeda arundinacea* (Lehmkuhl 1988, Dinerstein 1989). Interspersed among flood plain grassland associations are patches of riverine forest dominated by *Trewia nudiflora*, *Ehretia elliptica*, and *Bombax ceiba*. During the cool season (Nov–Feb), rhinoceros heavily browse the understory shrubs and saplings common in most riverine forest stands (*Callicarpa macrophylla*, *Litsea monopetala*, *Mallotus philippinensis*, and *Murraya paniculata*) (Gyawali 1986).

Grasslands and riverine forests used by rhinoceros account for only 30% of the Park's 1,038-km^2 area. In contrast, nearly 70% of the Park is covered by sal (*Shorea robusta*) forest (Laurie 1978), an evergreen association on upland, well-drained slopes, that rhinoceros rarely use.

METHODS

Estimation of Abundance

We identified 4 subpopulations that were isolated by physical barriers (rivers and low mountains) or by ecological boundaries (extensive tracts of sal forest or cultivation): the Sauraha, the West, the Bandarjhola-Narayani River, and the South (Fig. 1). The Sauraha was the largest subpopulation (Laurie 1978) and was surveyed most intensively. It spanned the grasslands east of Kagendramali to the edge of the sal forest near Kasara in the west (Fig. 1). Laurie (1978) separated the Kagendramali and Sauraha populations, but we combined them after discovering frequent movement of animals between the 2 areas.

The Sauraha population was separated from the West population by nearly 12 km of unbroken sal forest, which we and Laurie (1978) regarded as a partial migratory barrier limiting extensive movements between areas. Most of the animals in the West population were concentrated within a 3-km radius of the confluence of the Reu, Rapti, and Narayani rivers (Fig. 1). The rhinoceros population on Bandarjhola Island and along the Narayani River flood plain was separated from the West population by several kilometers of agricultural land and the Narayani River. Other populations were separated from the Sauraha population by extensive sal forest and a low mountain range (the South population), or by extensive sal forest, a highway, and cultivation.

We subdivided the Sauraha population into census blocks to examine habitat–density relationships (Fig. 1 inset). We used aerial photos to map the area of each block covered by *Saccharum spontaneum* and riverine forest, the 2 habitats most frequently used by rhinoceros (Laurie 1978). We censused mainly during the hot-dry season (Feb–May) after the tall grass layer had been burned off, when visibility was at a maximum, and when rhinoceros grazed for long periods in the open. After May, grass obscured newborn calves, and recognizing and sexing individuals was difficult.

We used photographs and sketches to identify individuals. Irregularities in skin folds and ear cuts provided the most striking and unambiguous characters for rapid field identification (Dinerstein In Press). All individuals were uniquely identified in our registry.

Between 1984 and 1988 we visited 95% of the Park and adjacent forests where rhinoceros were known to be found. Within each population, we located, identified, and photographed animals from domesticated elephants trained for this task. Searches were confined to morning and late afternoon, when animals were most active. Habituation of many individuals to close approach by elephants increased our ability to obtain detailed photographs. When individuals were less cooperative, they were surrounded by 4 elephants and herded toward the elephant supporting the photographer.

We estimated the minimal time required to find and identify every individual in our study blocks with results from a pilot study on 8 radio-collared animals (2 M and 6 ad F with calves) in the Icharni block. On 5 different days, we determined the number of radio-collared individuals that escaped visual detection during each of 2 searches. We found that about 16 hours of search time with 5 elephants (80 elephant-search hr) were needed to find all 39 animals in the 3.2-km^2 area. We then estimated search time in the other blocks in the Sauraha population by projecting the Icharni results on an area basis ($80/3.2 = 25$ elephant-search hr/km^2). In actuality, we spent far more time between 1985 and 1988 surveying blocks containing high population densities in the Sauraha population than the minimum estimate we computed because we conducted census work and photo-registration while doing other research activities.

We conducted censuses annually, and population sizes were adjusted to account for animals missed from 1 year to the next. Discovery of new animals, other than calves <1 year old, dropped from 10 to <1% from the first census year to the fourth year (also see Laurie 1978).

Sex and Age Criteria and Breeding Status

We determined the sex of animals by observing external genitalia, body size, size of neck folds (which are more pronounced in M), urination, and presence of calves. Also, adult males have wider horns at the base than adult females (Dinerstein In Press). Sex of calves <1.5 years old was difficult to determine and was recorded only if determination had been made by >3 observers or on 3 occasions by 1 observer. Laurie (1978) showed that a significant proportion of calves were incorrectly sexed and that initial sightings were biased towards males. Thus, we cautiously listed a large number of young calves as sex undetermined.

We classified animals in the Royal Chitwan NP population as calves (<4 yr), subadults (4–6 yr), or adults (>6 yr). Age categories were more specific for the intensively studied Sauraha population: calves (0–1, >1–2, >2–3, >3–4 yr); subadults (>4–5, >5–6 yr); young adults (6–12 yr, i.e., breeding F and nonbreeding M); intermediate-aged adults (>12–20 yr); older adults (>20 yr). Calves and subadults could be aged accurately because the birth years of all calves and nearly all subadults were known. Subadults could be distinguished from adults by body size and horn size (Dinerstein In Press). We based our age classification for subadults on the potential for animals to breed. Because captive females and males show signs of reproductive activity by 6 years of age, we considered the subadult category to consist of animals between 4 and 6 years old. Young adults had molars with little wear, small lower incisors, short horns with little wear, few scars or body marks, and were small in size (Dinerstein In Press). Young adult males lacked pronounced secondary neck folds. Individuals in the 12–20-year-old category were distinguished by moderate wear on the molars, horn size and wear, increased amount of facial wrinkles, size, scars, development of secondary neck folds in males, size of outer incisors, and for females, the birth of >1 calf. Individuals in the >20-year-old category had extensive wear on the molars and often displayed a combination of extensive facial wrinkles; major scars on the anal skin folds; torn or notched ears; broken, deeply grooved or eroded horns; and in males, extensive development of secondary neck and shoulder folds (Dinerstein In Press). Differences between age and sex classes were tested using Chi-squared analysis, with significance judged at the 0.05 level.

We identified males as breeders by observing (1) copulations ($n = 7$), (2) tending of estrous females, (3) the outcome of fights among dominant males, and (4) behavioral and morphological features. Breeding males often squirt urine when closely approached, possess extensive secondary neck folds and large procumbent mandibular incisors, and are aggressive toward subordinate males (Laurie 1978, Dinerstein In Press).

Fecundity and Mortality Rates

We estimated interbirth interval in the Sauraha population by monitoring the period between births for 87 registered breeding-age females. Gestation in greater one-horned rhinoceros has been determined in zoos to be about 15.7 months (Laurie et al. 1983). Birth dates were assigned (±1 calendar month) to calves born during the study period in the Sauraha population. We calculated birth rates annually for each age class by dividing the number of live births within a female age class by the total number of females within that age class. For both age-specific fertility and survival, we used data for the entire Sauraha population, calculated these rates each year for all individuals in each class, and averaged them over all years. Our fecundity schedule is based on age-specific births of female offspring.

Mortality data for the Sauraha population was obtained from our searches and from official records of His Majesty's Government. Rhinoceros are considered property of the King, and all mortalities must be accounted for by an official inquest conducted by the Park warden. Animals most frequently died close to river banks, and their carcasses attracted large flocks of vultures, aiding location of dead animals. Drivers frequently grazed their elephants in the same areas. It is unlikely that deaths, other than newborns, escaped detection. We calculated age-specific mortality by dividing the number of individuals dying within an age class by the total number within that class.

Population Growth Rate

We used 2 methods for estimating population growth rate: (1) regression analysis on population estimates to give the observed rate of increase, and (2) instantaneous rate of increase (Caughley's [1977:108] r_s), calculated from survival and fecundity tables. We assumed that the observed vital rates were fixed and that these rates had persisted long enough for the population to stabilize. The validity of these assumptions is examined in more detail in our discussion section.

Habitat–Density Relationships

We recorded habitat selection, feeding, and wallowing behavior by 24-hour activity watches, direct observations recorded during >5,000 locations of 21 radio-collared individuals, and anecdotal observations during censuses. However, only 1988 data were used to compare densities within blocks with habitat variables because 2 of the variables, percent cover of *S. spontaneum* within the block and distance to river bank, were subject to marked annual variation due to siltation and flooding. We determined dominant plant associations within each block and percent cover by *S. spontaneum* by aerial photographs and ground surveys. We measured the distance from the edge of croplands to the center of the highest rhinoceros population density within a block (i.e., the part of the block containing the most frequent sightings of animals) on an aerial photograph. Because blocks ranged in size from 1.05 to 4.76 km^2, we tested to determine if density was positively correlated with block size. We used Spearman rank correlation analysis to test for correlations between rhinoceros densities and habitat variables associated among blocks.

RESULTS

Abundance

Sauraha Population.—The Sauraha population contained 228 registered individuals, 60.0–63.5% of the total estimated population for the Royal Chitwan NP in 1988 (Table 1). We added 3 calves to the 1988 cohort because we missed, on average, 3 births per year,which were subsequently registered in the following census year. This oversight was the result of births occurring after our last month of census work of the year. We also subtracted 15 animals from the subadult cohort registered by 1988. These subadults were registered as 4-year-old calves while still with their mothers, but most likely were re-registered as subadults in subsequent years. Laurie (1978) also adjusted his total estimate to account for this problem.

Royal Chitwan Population.—We estimated that the rhinoceros population in the Park totaled at least 358 individuals in 1988 (Table 1). Because we only censused the West and Bandarjhola-Narayani populations in 1986, we used our estimate for population growth between 1986 and 1988 in the Sauraha as a basis for projecting expected numbers in 1988 in these areas. We also corrected the West and the Bandarjhola-Narayani estimates to account for animals we likely missed; fresh dung and tracks in a few areas indicated the presence of animals we failed to register in both populations. From our data on the Sauraha population, we estimated we missed 7% of subadults and adults during the 1986 census which were subsequently added to the census in the following 2 years of searching (1987–88).

Translocations.—Twenty-four individuals were transferred from Royal Chitwan NP between 1986 and 1988 (Table 1); 17 adults and subadults were translocated to 2 reserves (4 subad F to Dudhwa Natl. Park, India; 5 M and 8 F to Bardia Natl. Park, Nepal). Seven calves were sent to zoos. All of these 24 animals came from the Sauraha population as did another 10 calves sent to zoos between 1978 and 1983. Calculation of vital rates and population growth rates between 1984 and 1988 did not include translocated adults.

Sex and Age Structure and Breeding Status

In the Sauraha population sex ratios for calves, subadults, young adults, and old adults were not significantly different from parity ($P > 0.05$) (Table 2). Intermediate-aged adult females (12–20 yr) were significantly more numerous than males ($\chi^2 = 4.3$, $P < 0.05$). No significant differences in sex ratio were found among adults in the West and Bandarjhola-Narayani populations. Subadults accounted for only 8% of the registered West population but 30% of the Bandarjhola-Narayani population.

Table 1. Total population estimate (*N*) of greater one-horned rhinoceros in the Royal Chitwan National Park, Nepal population, April 1988, excluding 34 animals translocated between 1980 and 1988.

Area	*N*
Sauraha and Kagendramali	252
Relocated animals (1986–88)	24
Subtotal	228
West population (1986)	61
Animals assumed to have been missed (7%) during 1986	4
Estimated population increase between 1986 and 1988	7
Adjusted subtotal West population	72
Bandarjhola Island and Narayani River	34
Animals assumed to have been missed (7%) during 1986	2
Estimated population increase between 1986 and 1988	4
Adjusted subtotal Bandarjhola Island and Narayani River	40
Outlying areas (Ramoli, Tikoli, Botesimra)	18
Total min. estimate for 1988	358

Compared with Laurie's (1978) age distribution in 1975, there appears to be a higher percentage of females with calves in 1975 than in 1978. However, if adult females >6–7 years old are excluded in calculating the 1988 data, then the proportion of females with calves is the same (Table 3). Also, subadults represent a smaller percentage of the Sauraha population in 1988, whereas the opposite is true for adults. These differences in age structure for the populations in 1975 and 1988 largely result from Laurie's (1978) designation of subadults as 3–9 years old, whereas we placed them between 4 and 6 years. If we reclassified our data into the same categories Laurie (1978) used, then age structure was the same in 1975 and 1988.

Male Breeders.—We estimated that 48% of adult males in the Sauraha population (n = 28) mated during the study period. Based on measurements and physical condition of all presumed breeders, we estimated that all but 1 breeding male was >15 years old. Old males (>20 yr) that remained close to high concentrations of breeding females were frequently attacked by younger, stronger males (Laurie 1978). In at least 5 instances during our study such attacks proved fatal. Another 5 breeding males presumed to have bred suffered serious wounds in fights and retreated to blocks with low densities of breeding-age females or to blocks where females and the most aggressive males were uncommon.

Fecundity and Mortality Rates

Seasonality of Births.—Fifty-three calves were born during the study period in the Sauraha population (Fig. 2). We could detect no significant difference in the distribution of births over the calendar year (χ^2 = 2.3, 11 df, P >

Table 2. Sex and age structure of greater one-horned rhinoceros populations in 3 areas in Royal Chitwan National Park, Nepal, April 1988.

	Sauraha						West				Bandarjhola and Narayani River			
Age category (yr)	M	Relocated M	F	Relocated F	Sex unknown	Total	M	F	Sex unknown	Total	M	F	Sex unknown	Total
Calves														
(0–1)	4		2	1	8	15								
(1–2)	3	2	2	3	4	14								
(2–3)	4	1	3	1	9	18								
(3–<4)	5		3	1	2	11								
(0–<4) combined	19		16		23	58	1	1	6	8	2	1	2	5
Subad														
(4–5)	9		3	1	3	16								
(5–<6)	3	1	7		6	17								
(4–<6) combined	13		11		9	33	1	1	2	4	3	4	3	10
Ad														
(6–12)	23	3	37	5	0	60	9	6	7	22	3	1	1	5
(12–20)	16		28	2	0	46	2	9	2	13	2	5		7
(>20)	19	2	22	1	0	44	3			3	7			7
Ad combined	63		95		0	158	14	15	9	38	12	6	1	19

Table 3. Sex and age composition of greater one-horned rhinoceros in the Sauraha subpopulation of Royal Chitwan National Park, Nepal, during 1975 (Laurie 1978) and April 1988.

Parameter	1975	1988
Ad sex ratio (% M)	34.1	39.9
Subad sex ratio (% M)	55.3	54.2
Subad and ad combined sex ratio (% M)	41.0	41.8
Ad as % of *N*	50.9[a]	63.5
Subad as % of *N*	22.8[a]	13.3
Ad F as % of *N*	33.5[a]	38.2
Ad F with calves as % of *N*	26.3[a]	20.9
Ad M as % of *N*	17.3[a]	25.3
% of ad M known or assumed to have bred during study period		48.3
% of ad F with calves	78.6	59.8
% of ad F with calves excluding F 6–7 yr old		77.0
% of ad F (6–12 yr) with calves		54.1
% of ad F (7–12 yr) with calves		90.9
% of ad F (12–20 yr) with calves		64.3
% of ad F (>20 yr) with calves		63.6
% of *N* <12 yr old		62.0

[a] Laurie (1978) classified subadults as 3–9 years old whereas we classified subadults to be 4–6 years old.

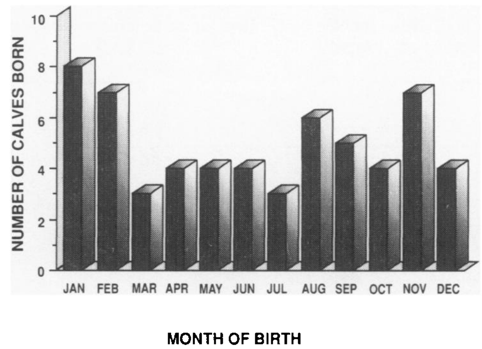

Fig. 2. Greater one-horned rhinoceros calf births by month in the Sauraha population between 1984 and 1988, Royal Chitwan National Park, Nepal.

0.99). We arranged our calf birth data in the same bimonthly format as Laurie (1978) used for the period between 1972 and 1975; the combined data set (n = 113) revealed no seasonality to parturition, either (χ^2 = 8.0, 5 df, $P > 0.10$). However, 43% of all calf births during the 8-year period occurred between 1 November and 28 February.

Age at First Reproduction.—We estimated that the mean age at first birth for 2 known-age females in the Sauraha population was between 7.0 and 7.5 years. An additional 15 (40%) adult females in the 6–12-year-old category (n = 37) had not given birth to their first calf by the end of our study. Of these, 13 were classified as between 6 and 7 years old, 1 between 7 and 8 years old, and 1 >8 years old. Three adult females would have been classified as subadults, based upon horn size, body size, and lack of marks or wrinkles, had they not been observed with young calves. We estimated the age of these 3 females by body size and classified them to be 6 years old when the births occurred, but they may have been younger.

Interbirth Interval.—We discovered either 2 sequential births, or estimated the subsequent calving of a female that was first registered with a calf <6 months old for 16 of 87 adult females. Three females gave birth again at 17, 22, and 31 months. However, each had extenuating circumstances surrounding the subsequent birth: a dominant bull trampled the first calf of 1 female, another calf was captured for shipment to a zoo, and the third calf was thought to have died or been separated from its mother. All 3 incidents apparently shortened the interbirth interval. The interbirth interval based on 13 animals whose calves survived to independence was 45.6 ± 1.8 months (range = 34–51 months). For 6 females with interbirth intervals longer than 48 months, one was 12–20 years old and five were >20 years old.

We estimated much longer interbirth intervals (60.9 ± 3.4 months, range = 48–88 months) for an additional 12 females. They were accompanied by calves of an advanced age and did not give birth during our 48-month study period. Six were categorized as 12–20-year-olds and six as >20 years old. Some of the oldest females may no longer have been reproductively active. Some may have aborted or given birth to a calf that died before it was registered, but this was probably rare. We predict that the mean interbirth interval for rhinoceros in 1988 in the Royal Chitwan NP will likely exceed 48 months, in contrast to Laurie's estimate of 42 months during 1975.

Age-Specific Birth Rate.—Intermediate-aged adult females (12–20 yr old) had higher birth rates than young or old adults (Table 4). Annual variation in birth rate for young adults was 4 times that for intermediate-aged females. Mean annual number of births recorded for the 95 registered adult females (including relocated animals) was 16.3 ± 1.0 calves per year during the study period (Table 4), or an annual birth rate of 7.6 ± 0.8%.

Mortality.—Twenty-eight animals died in the Sauraha population during our study (Table 5). As expected for a long-lived giant herbivore,

Table 4. Age-specific birth rates for adult females, Sauraha subpopulation of greater one-horned rhinoceros, Royal Chitwan National Park, Nepal.

Age category (yr)	Census yr 1984–85	1985–86	1986–87	1987–88	$\bar{x}$	SE
6–12	0.179	0.310	0.138	0.048	0.169	0.048
12–20	0.167	0.233	0.167	0.167	0.183	0.015
>20	0.208	0.130	0.130	0.087	0.139	0.022
No. calves born/yr	13	18	16	18	16.3	1.025

mortality for all age classes was low. The annual mortality rate for calves was 2.8 ± 0.9%, for subadults 2.2 ± 0.7%, and for adults 2.9 ± 0.5%. All calf mortality occurred during the first year of life when calves were prey for tigers. Beyond this age a rhinoceros is largely unaffected by predation. The disproportionate number of mortalities among male adults (15 of 18) suggests that competition for mates may be the most important contributor to deaths of males.

Population Growth Rate

The population growth rate calculated from regression analysis for the Sauraha population between 1984 and 1988 indicated an annual increase of 4.8% (Fig. 3). The population growth rate estimated from schedules of fecundity and survivorship for the same period indicated an annual increase of 2.7% (Table 6). We also combined Laurie's (1978) data from 1975 with our data and used regression analysis to estimate that the growth rate of the Sauraha population from 1975 to 1988 was 2.5% ($r^2 = 0.961$, $P < 0.01$).

Habitat–Density Relationships

The highest rhinoceros densities in the Sauraha area coincided with blocks including large tracts of *Saccharum spontaneum* grassland (Table 7) ($r_s = 0.7750$, $n = 9$, $P < 0.05$). The correlation would have been stronger if translocated and relocated animals had been included. In 1986, prior to the removal of 17 animals for translocation, density in the Icharni block exceeded 10.5/km^2. Blocks covered mainly by *Narenga porphyracorma* grassland, the most common grassland association in the Park (Lehmkuhl 1988), supported lower densities. Dense stands of *Themeda arundinacea* along the edge of sal forest in the Jarneli, Simalchaur-Kachwani, and Bansbari blocks, were avoided.

High densities were not related to proximity to agriculture ($r_s = 0.0297$, $n = 9$, $P > 0.50$). Densities in Dumria, Ghatgain, and Patch 3-Baaghuwaghera exceeded or equaled densities in blocks bordered by croplands. Rhinoceros also reached locally high densities around the Tiger Tops Lodge in the West population, >3 km from the edge of cultivation. However, densities in blocks bordering agricultural areas may fluctuate seasonally in response to ripening of rice, corn, wheat, and lentils. During the rice harvest in October 1987, densities in the Badreini-Kharsar were 8.3/km^2 and declined to 3.0/km^2 by February 1988 after the beginning of grass fires in the Park. New shoots became abundant within 2 weeks after the fires, and most animals vacated the Badreini-Kharsar block to feed on the flush of new growth in *S. spontaneum* grasslands.

Table 5. The numbers and causes of mortalities for greater one-horned rhinoceros by sex and age class in the Sauraha subpopulation, Royal Chitwan National Park, Nepal, 1984–88.

	Ad						Subad			Calves		
	6–<12 yr		12–<20 yr		>20 yr		4–<6 yr					
Cause of death	M	F	M	F	M	F	M	F	Sex unknown	0–<1 yr	1–<4 yr	Total
Poaching			2					1	1			4
Tiger predation										4		4
Intraspecific fighting					5	1	1			1		8
Separation from F										1		1
Flood or quicksand	1				1					1		3
Cause undetermined		1	4	1	2							8
Total	1	1	6	1	8	1	1	1	1	7	0	28

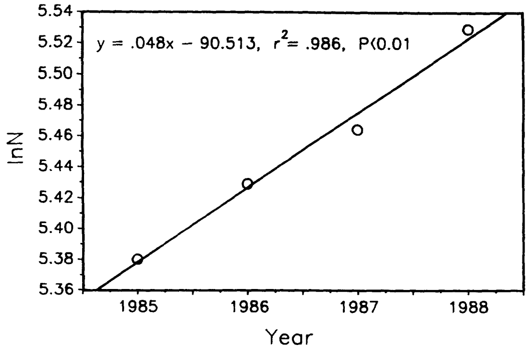

Fig. 3. Population growth of greater one-horned rhinoceros in the Sauraha subpopulation between 1984 and 1988, Royal Chitwan National Park, Nepal.

Table 6. Abridged life table for female greater one-horned rhinoceros in the Sauraha subpopulation, Royal Chitwan National Park, Nepal, based on mean mortality rates (after Caughley 1977).

Age interval (yr)	l_x[a]	p_x[b]	q_x	m_x[c]
0–1	1.000	0.889	0.111	0.0000
1–4	0.889	1.000	0.000	0.0000
4–6	0.889	0.950	0.050	0.0000
6–12	0.802	0.988	0.012	0.0845
12–20	0.746	0.992	0.008	0.0915
20–35	0.700	0.989	0.011	0.0695
35[d]	0.593	0.000	1.000	0.0000

[a] l_x refers only to survivorship to beginning of an interval.
[b] p_x is the average survivorship within an interval.
[c] m_x is the number of female offspring per female per time unit.
[d] Estimated mean maximum age based upon captive animals; females probably do not continue to breed in the wild beyond 35 years.

Blocks with the lowest densities (Simalchaur-Kachwani) lay farthest from the Rapti River and included the most sal forest. In other blocks, rhinoceros concentrated near the Rapti River. Densities were not correlated with the size of blocks (r_s = 0.3333, n = 9, P > 0.20).

DISCUSSION

Population Trend

The increase in number of greater one-horned rhinoceros since the late 1960's demonstrates that populations can rebound vigorously from heavy poaching when provided with sufficient habitat and protection. After declining from an estimated 1,000 animals in 1950 to 60–80 animals by 1962, when land clearing following malaria eradication and heavy poaching decimated the population, the Royal Chitwan NP population has increased by at least 311 individuals during the last 20 years (Caughley 1969; Laurie 1978; H. Mishra, King Mahendra Trust for Nat. Conserv., pers. commun.). Apparently, strict protection is responsible for reversing the decline.

Laurie (1982) estimated that the Sauraha population in 1975 contained 176 animals (adjusted by us to account for more accurate data on poaching and including Laurie's estimate of animals from the Kagendramali area), and he estimated the rate of increase to be between 2 and 6% per year. If we include all animals relocated after Laurie's study and during our study and assume that all individuals would have survived, then the Sauraha population has increased by 86 animals (48.9%) over a 13-year period.

The annual rate of increase estimated by regression analysis between 1975 and 1988 and the one between 1984 and 1988 derived from fecundity and mortality tables are similar. However, use of the life table for calculation of r assumes that observed vital rates are fixed and that these rates have persisted long enough for the population to stabilize. A lack of annual data on vital rates between 1976 and 1984 hinders attempts to determine the validity of the first assumption, and in particular, fixed mortality rates among older age classes. The longevity of rhinoceros and the difficulty of assigning animals to annual or biennial rather than broad age classes inhibit our effort to properly evaluate the assumption of a stable age distribution. However, circumstantial evidence that the second assumption holds is derived from several observations: (1) similarity in age structure of the Sauraha population in 1975 and 1988; (2) mortality rates for subadults and adults are the same; and (3) similarity in birth rates between 1972 and 1975 and between 1984 and 1988. Laurie (1978) estimated birth rates with a different method, but his maximum estimate (8.9%) is close to our estimate of 7.6%. Continued census efforts in Sauraha will determine the validity of assuming a stable age distribution.

In contrast to Sauraha, the West population (Fig. 1) has increased by only 22% since 1975, for a mean annual rate of increase of 1.7%/year. Comparisons were not possible for the Bandarjhola because we estimated population size by photo-registration whereas Laurie (1978) used dung piles and prints.

We predict that the Royal Chitwan NP population will continue to increase by at least another 100 individuals to a population size exceeding 500 by the year 2001. Several large tracts of *Saccharum spontaneum* grasslands,

Table 7. Greater one-horned rhinoceros densities (N/km^2) and some habitat characteristics of blocks censused in Royal Chitwan National Park, Nepal, April 1988. Estimates do not include relocated animals and are from the period when crops were not available in blocks adjacent to farmland.

Area and block	Size (km^2)	Rhinoceros density (N/km^2)	% of block covered by *S. spontaneum* grassland	Distance from croplands to center of highest density (km)	Dominant plant associations in block
Sauraha					
Icharni	4.14	9.4	52.6	0.5	*S. spontaneum*, riverine forest
Darampur	4.16	2.2	0.0	0.5	scrub
Dumria	3.62	9.4	29.6	5.0	*Narenga* grassland, *S. spontaneum*
Badreini–Kharsar	1.05	3.0	0.0	0.5	riverine forest, scrub
Patch 1 and 2	2.41	13.3	43.6	1.0	riverine forest, *S. spontaneum*
Patch 3–Baaghuwaghera	3.15	12.4	29.2	3.0	riverine forest, *S. spontaneum*
Simalchaur–Kachwani	4.76	1.7	0.0	1.0	*Narenga* grassland, sal forest
Bansbari	1.8	1.1	0.0	3.0	*Narenga* grassland, sal forest
Jarneli	1.96	3.6	0.0	3.0	*Narenga* grassland, sal forest
Ghatgain–LamiTaal	3.49	8.3	5.6	3.0	riverine forest, *Narenga* grassland
Subtotal	30.54	6.4			
Kagendramali	6.84	4.7		1.0	
West	60.18	1.2		3.0	
Bandarjhola and Narayani	13.33	3.0		3.0	

suitable to maintain high densities, are currently underpopulated (e.g., LigLige in the East and Chamka in the West). Even patches of *S. spontaneum*-riverine forest mosaic within the Sauraha population (e.g., Ghatgain, LamiTaal) and in the West population are underused. In LigLige and LamiTaal, harassment by cattle herders may have kept rhinoceros from occupying these areas, which as of 1988 were managed strictly for wildlife.

The only comparable data on recovery of other rhinoceros populations comes from South Africa (Owen-Smith 1981). The Umfolozi white rhinoceros (*Ceratotherium simum*) population grew at a constant rate of 9.5%/year over a 13-year interval. High natality rates and short interbirth interval ($\bar{x}$ = 2.2 yr) accounted for this high rate of increase. The interbirth interval for the Umfolozi white rhinoceros population is half that of the Chitwan one-horned rhinoceros population even though the white rhinoceros is slightly larger in body mass.

Habitat Relationships

Densities were positively correlated with the percentage of the block covered by *Saccharum spontaneum* grassland. Along stream banks, *S. spontaneum* can account for >90% of above ground biomass by dry mass (E. Dinerstein, unpubl. data). Not surprisingly, *Saccharum* is a staple in rhinoceros diets; it normally exceeds 50% of the diet each month (Gyawali 1986; E. Dinerstein, unpubl. data). *Saccharum spontaneum* is unique among the common tall perennial grasses of the Park in that new shoots sprout soon after cutting, grazing, or inundation by floods. Other species do not sprout again until the next growing season regardless of these manipulations. New shoots of *S. spontaneum* also provide nutritious forage. Nitrogen content in regrowth is twice that of mature leaves and 10 times that of stems (E. Dinerstein, unpubl. data.).

Laurie (1978) argued that rhinoceros in the Royal Chitwan NP reached highest densities in areas supporting the greatest habitat diversity. He assessed habitat diversity qualitatively by counting the number of different habitat types in a given area. However, we contend that the highest densities are not related to degree of habitat diversity but rather to the abundance of *Saccharum spontaneum* which forms near-monospecific associations within each block. The other common association in the high density blocks is patches of riverine forest (see Dinerstein and Wemmer 1988). This forest association also exhibits low within-habitat diversity where 2 species, *Trewia nudiflora* and *Ehretia elliptica,* dominate 77% of the canopy (Dinerstein and Wemmer 1988).

Long-Term Prospects for Conservation

Severe monsoon floods, disease, and heavy poaching pose major threats to current greater one-horned rhinoceros populations. During the devastating flood of the Brahamaputra River Valley in 1988, about 70% of the Kaziranga National Park remained under 2.7–4 m of water for several weeks. At least 41 animals, including 23 calves, perished (Anonymous 1988). Recent land clearing has limited access to upland forested areas above the flood plain in the Kaziranga sanctuary. If rhinoceros and other vertebrates become isolated from upland forests, floods that normally serve to increase the productivity of critical grasslands and rhinoceros populations could become a major source of calf mortality.

The threat of epidemics and poaching have instigated programs in Nepal and India to move animals to parks that historically harbored rhinoceros populations, are now well-protected from poachers, and contain suitable habitat (Mishra and Dinerstein 1987). Translocated populations have been established in Dudhwa National Park, Uttar Pradesh, India, and in Royal Bardia National Park, western Nepal. Still lacking is a comprehensive plan for conservation of greater one-horned rhinoceros among nations supporting free-living populations (India, Nepal, and Bhutan), international conservation groups, and specialists in captive management.

LITERATURE CITED

ANONYMOUS. 1988. Kaziranga under water. Himal Mag. Nov.–Dec.:33.

BLANFORD, W. T. 1888. The fauna of British India including Ceylon and Burma; Mammalia. Taylor and Francis, London. 617pp.

CAUGHLEY, G. 1969. Wildlife and recreation in the Trisuli watershed and other areas in Nepal. HMG/FAO/UNDP Trisuli Watershed Development Project. Proj. Rep. No. 6., Kathmandu. 54pp.

———. 1977. Analysis of vertebrate populations. Wiley & Sons. New York, N.Y. 234pp.

DINERSTEIN, E. 1989. The foliage-as-fruit hypothesis and the feeding behavior of South Asian ungulates. Biotropica 21:214–18.

———. In Press. Sexual dimorphism in greater one-horned rhinoceros. J. Mammal.

———, AND G. F. MCCRACKEN. 1990. Endangered greater one-horned rhinoceros carry high levels of genetic variability. Conserv. Biol. 4:417–422.

———, AND C. WEMMER. 1988. Fruits *Rhinoceros* eat: dispersal of *Trewia nudiflora* in lowland Nepal. Ecology 69:1768–1774.

GYAWALI, S. R. 1986. Diet analysis of greater one-horned rhinoceros by fecal analysis. M.S. Thesis, Tribhuvan Univ. Kathmandu, Nepal. 34pp.

LAURIE, W. A. 1978. The ecology of the greater one-horned rhinoceros. Ph.D. Thesis, Cambridge Univ. 450pp.

———. 1982. The ecology of greater one-horned rhinoceros. J. Zool. Soc. London. 196:307–341.

———, E. LANG, AND C. P. GROVES. 1983. *Rhinoceros unicornis*. Mamm. Species. 211:1–6.

LEHMKUHL, J. 1988. The ecology of a South Asian tall-grass community. Ph.D. Thesis, Univ. Washington, Seattle. 195pp.

MISHRA, H. R. 1982. The ecology and behavior of chital (*Axis axis*) in the Royal Chitwan National Park, Nepal. Ph.D. Thesis, Univ. Edinburgh, Scotland. 240pp.

———, AND E. DINERSTEIN. 1987. New zip codes for resident rhinos in Nepal. Smithsonian Mag. 18:66–73.

OWEN-SMITH, N. 1981. The white rhino overpopulation problem and a proposed solution. Pages 129–150 *in* P. A. Jewell and S. Holt, eds. Problems in management of locally abundant wild mammals. Academic Press, New York, N.Y.

SEIDENSTICKER, J. 1976. Ungulate populations in Chitwan Valley, Nepal. Biol. Conserv. 10:183–210.

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