GREATER ONE-HORNED RHINOCEROS POPULATIONS IN NEPAL

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ABSTRACT

We report on the status of two greater one-horned rhinoceros (*Rhinoceros unicornis*), hereafter rhinoceros) populations in Nepal: 1) the world's second largest free-ranging population in Royal Chitwan National Park; and 2) a translocated population, from Chitwan founders, established in the Royal Bardia National Park. The Royal Chitwan NP population is one of the few rhinoceros populations in the world to have increased dramatically during the past two decades. 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. Increase in the population is the result of adequate protection of critical grassland habitats and control of poaching.

In 1986 and 1991, 13 and 25 individuals, respectively, were successfully translocated from Royal Chitwan NP into two discrete areas of Bardia National Park in southwestern Nepal. Population growth rate of the population translocated in 1986 has averaged 6.5% year between 1986-1991. The successful re-establishment of rhinoceros in Nepal suggests that translocation should form an important component of recovery of Asian rhinoceros populations in other countries.

INTRODUCTION

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 Price, 1991; Dinerstein and McCracken, 1990). In this paper we describe the demography of a subpopulation containing most of the rhinoceros population within Royal Chitwan NP (the Sauraha population) and examine population structure of the entire Royal Chitwan population and for a newly translocated population in Royal Bardia National Park (NP), Nepal. We report on total population size, sex and age composition, seasonality of births, birth rate, interbirth interval, survivorship, mortality, and population growth rate. These data are of particular interest because the Royal Chitwan NP population is one of the few populations of rhinoceroses of any species that has increased over the last two decades. The Royal Bardia NP population is the result of the first successful translocation of an Asian rhinoceros species.

STUDY AREAS

The Royal Chitwan NP is located in the southcentral Terai region of Nepal (84°20'E, 27°30'N). Rhinoceros and other large mammals are common 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).

Grasslands and riverine forests used by rhinoceros account for only 30% of the Park's 1,038 km² 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. A more detailed description of the study area, habitat use by rhinoceros, and feeding ecology can be found in Dinerstein and Price, 1991; Dinerstein, 1989a; 1989b).

The Royal Bardia National Park (968 km²) is located 250 km west of Royal Chitwan NP in the southwestern Terai zone. Royal Bardia NP contained rhinoceros until about 200 years ago; today it is well-protected and still includes excellent habitat for rhinoceros. A detailed description of the vegetation and ecology of Royal Bardia NP can be found in Dinerstein (1979a; 1980a; 1980b; 1977).

METHODS

Estimation of Abundance

<u>Royal Chitwan NP</u>

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 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).

The Sauraha population was separated from the West population by nearly 12 km of unbroken sal forest, which Laurie (1978) and we 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.

The Sauraha population was subdivided into census blocks (Fig. 1 inset). 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.

Photographs and sketches were used to identify individuals. Irregularities in skin folds and ear cuts provided the most striking and unambiguous characters for rapid field identification (Dinerstein, 1991). All individuals were uniquely identified in our registry.

Between 1984 and 1988 we visited 95% of the Park and adjacent forests where rhinoceros are known to be found. Within each population we located, identified and photographed animals from domesticated elephants trained for this task. Specific techniques for censusing rhinoceros are reported elsewhere (Dinerstein and Price, 1991).

<u>Translocated population (Royal Bardia NP)</u>

The 13 animals translocated in 1986 were released without radio-collars. Subsequently, most of the animals were recaptured and fitted with radio-collars to monitor movements and reproductive activity.

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 males), urination, and presence of calves. Also, adult males have wider horns at the base than adult females (Dinerstein, 1991). 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. We classified animals in the Royal Chitwan NP population and in the translocated Royal Bardia NP population as calves (<4 yrs), subadults (4 to 6 yrs), or adults (>6 yrs). Age categories were more specific for the intensively studied Sauraha population of Royal Chitwan NP: calves (0-1, >1-2, >3-4 yrs); subadults (>4-5, >5-6); young adults (6-12 yrs, i.e., breeding female and nonbreeding male); intermediate-aged adults (>12-20 yrs); older adults (>20 yrs). 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, 1991). We based 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, 1991). 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, 1991). Differences between age and sex classes were tested using Chi-squared analysis, with significance judged at the 0.05 level.

For the Royal Chitwan NP population 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, 1991).

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 this species 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 annually birth rates 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. 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 are fixed and that these rates have persisted long enough for the population to stabilize. The validity of these assumptions is examined in more detail in our discussion section.

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 because 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).

Royal Bardia NP population and other 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 subadult F to Dudhwa National Park, India; 5 M and 8 F to Bardia NP, 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. An additional 25 rhinoceros were translocated to the Babai Valley area in January and February of 1991, after demographic analyses of the Royal Chitwan NP population was completed.

Sex and Age Structure and Breeding Status

Royal Chitwan NP. In the Sauraha population sex rations 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 yrs) were significantly more numerous than males ($X^2 = 4.3$ $P < 0.05$). 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.

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 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 ($\underline{n}$ = 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 yrs) 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.

Royal Bardia NP populations. The 1986 translocated population released in the Karnali floodplain (N=13) consisted of 2 adult males, 3 subadult males, 5 adult females, and 3 subadult females. The 1991 translocated population released in the Babai floodplain (N=25) consisted of 6 adult males, 2 subadult males, 11 adult females, and 6 subadult females.

Fecundity and Mortality Rates

Seasonality of Births. Fifty-three calves were born during the study period in the Sauraha population. We could detect no significant difference in the distribution of births over the calendar year (X^2 = 2.3, 11 df, $\underline{P}$ > 0.99). Arranging our calf birth data in the same bimonthly format as Laurie (1978) used for the period between 1972 and 1975, the combined data set ($\underline{n}$ = 113) revealed no seasonality to parturition, either (X^2 = 8.0, 5 df, $\underline{P}$ > 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 ($\underline{n}$ = 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 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 one female, another calf was captured for shipment to a zoo, and the 3rd 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, 1 was 12-20 years old and 5 were >20 years old.

We estimated much longer interbirth intervals (60.9 ± 3.4 months, range - 44-88 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 6 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 yrs 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, mortality for all age classes was low. Annual mortality rates 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.

Of the 13 animals translocated to Bardia in 1986, one of the adult males died within 12 days after release, and a subadult male was poached outside of the park, approximately 39 months after release.

Population Growth Rate

Sauraha population. 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). 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).

Royal Bardia population. After the loss of two males, the number of animals from the 1986 translocation has increased to 16 by January 1991 from the recruitment of five calves. Two calves were born in 1987, and one each in 1988, 1989, and 1990, a mean annual rate of recruitment of 1 calf per year (Wegge, et al., 1990). Population growth rate over this period as determined by regression analysis was 6.4% (r^2 = 0.86).

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 Nature Conservation, 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 hinder 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 2001. Several large tracts of *Saccharum spontaneum* grasslands, 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 are managed strictly for wildlife.

The rapid recruitment begun in the Bardia NP population translocated in 1986 bodes well for establishment of this founder group. All of the females which gave birth in Bardia were bred after release rather than some females having conceived prior to capture. Growth rate of the Babai population released in 1991 will be monitored closely over the next three years. It remains unclear if the two populations, separated by over 25 km of sal forest and a major river gorge, will commingle.

With the successful recovery of the Chitwan population, conservation of rhinoceros in Nepal and India has entered a new phase in which translocation efforts will form the basis of conservation strategies. Two such efforts have already proved successful in Nepal. A regional strategy for rhinoceros conservation will require cooperation between the Indian and Nepalese governments to guarantee the long-term viability of rhinoceros sanctuaries and rhinoceros populations in the wild.

ACKNOWLEDGMENTS

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Table 1. Total population estimate (N̲) of Greater one-horned rhinoceros in the Royal Chitwan National Park, Nepal population, April 1988, excluding 23 animals translocated between 1980 and 1988.

Area	N̲
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
Bandarjola 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 Bandarjola Island and Narayani River	40
Outlying areas (Ramoli, Tikoli, Botesimra)	18
Total minimum estimate for 1988	358

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

Age category (yr)	Sauraha						West				Bandarjola and Narayani River			
	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	51	1	1	6	8	2	1	2	5
Subadult														
(4-5)			3	1	3	16								
(5<6)		1	7		6	17								
(4<6) combined			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	60	9	6	7	22	3	1	1	5
(>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
Subadult sex ratio (% M)	55.3	54.2
Subadult and ad combined sex ratio (% M)	41.0	41.8
Ad as % of N	50.9 [a]	63.5
Subadults 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 yrs 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 placed them between 4 and 6 years.

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

Age category (yrs)	Census yr				$\bar{X}$	SE
	1984-85	1985-86	1986-87	1987-88		
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

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

Cause of death	Ad 6 <12 yrs M	F	12 <20 yrs M	F	>20 yrs M	F	Subadults 4 <6 yrs M	F	Sex unknown	Calves 0 <1 yrs	1 <4 yrs	Total
Poaching			2					1	1			4
Tiger predation										4		4
Intraspecific fighting					5	1	1			1		8
Separation from female										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

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

Age interval	l_x	p_x	q_x	m_x
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*	0.593	0.000	1.000	0.0000

* Estimated mean maximum age based upon captive animals.
It is unlikely that females continue to breed in the wild beyond 35 years.

l_x refers only to survivorship to beginning of interval

p_x is the average survivorship within interval

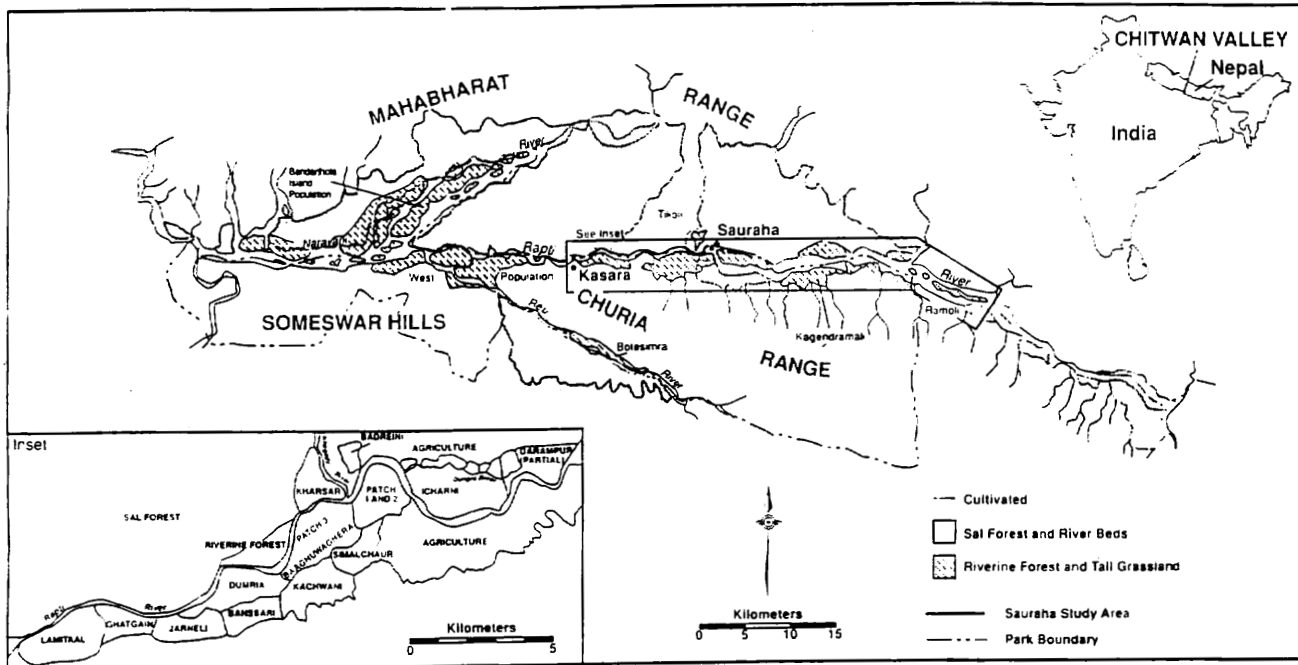m_x is the number of female offspring per female per time unit

r = 0.027

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).
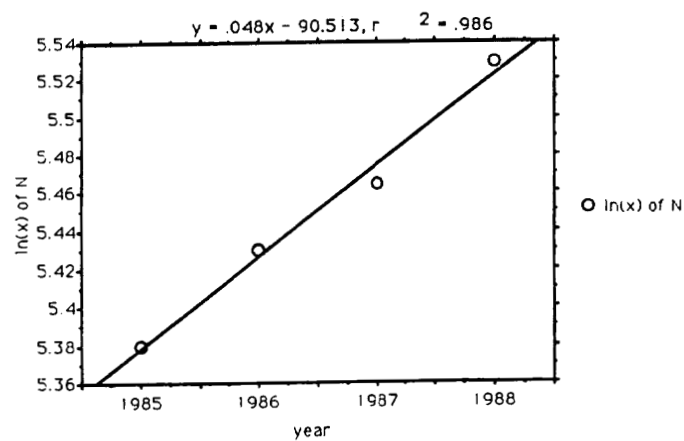

Fig 2. Population growth of Greater one-horned rhinoceros in the Sauraha population between 1984 and 1988, Royal Chitwan National Park, Nepal.