

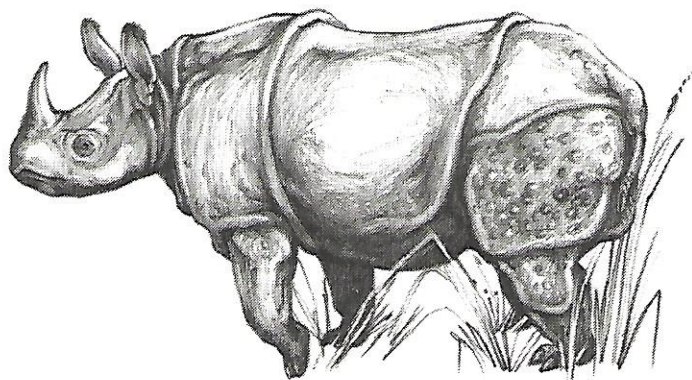
Mammals of South Asia

Volume Two

Edited by
AJT JOHNSINGH and NIMA MANJREKAR

Foreword by GEORGE B SCHALLER

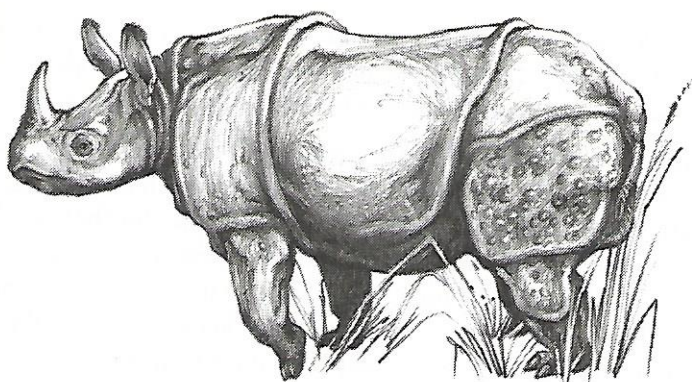
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GREATER ONE-HORNED RHINOCEROS

Rhinoceros unicornis

Eric Dinerstein

Order	Perissodactyla
Family	Rhinocerotidae
Genus	Rhinoceros
Species	unicornis

The enormous size, unique horn and prehistoric appearance of the greater one-horned rhinoceros sets it apart as one of the most conspicuous mammals of South Asia. Because of its highly valued horn, it is also one of the most endangered.

The common name of this species is derived from its Latin epithet (*Rhinoceros unicornis*). Also called the Indian rhinoceros, the species was first described by Linnaeus in 1758. It is the largest of the three extant species of rhinoceroses found in Asia, the other two being the Javan rhinoceros (*Rhinoceros sondaicus*) and the Sumatran rhinoceros (*Dicerorhinus sumatrensis*), both of which have been extirpated from northeast India.

Evolution and Taxonomy

The family to which the greater one-horned rhinoceros belongs, the Rhinocerotidae, flourished in the Oligocene after first appearing in the Eocene in Eurasia. Several evolutionary trends observed in mammals are exhibited by this lineage and by the greater one-horned rhinoceros

in particular. Perhaps the most dramatic is the increase in body size over ancestral, diminutive Rhinocerotids, an example of Cope's Rule (i.e., species within a lineage tend towards gigantism over evolutionary time).

Another development exhibited by the greater one-horned rhinoceros was the appearance on the skull of a unique, boneless horn, which its ancestors lacked. The evolution of broad feet with three toes became another modification important in adapting to marshy habitats. Less conspicuous, but of considerable ecological importance, were changes in dentition: the premolars became more like molars, the crowns of the cheek teeth lengthened, and the enamel patterns became more complex—modifications which increased efficiency in handling a diet of coarse grasses (Prothero and Schoch 1989).

Description

The greater one-horned rhinoceros is the second largest among living rhinoceroses, and the fourth largest terrestrial mammal. The author captured and collected dimensional data on 50 free-ranging rhinoceroses (Dinerstein *et al.* 1990, Dinerstein 1991a). This effort was part of a larger study on the biology of the species in Royal Chitwan National Park, Nepal. This total represented about 4 per cent of the wild population in 1988. A large adult male captured for translocation to Royal Bardia National Park in 1986 exceeded 2000 kg. Based on measurements of other males, this is probably close to the upper limit in body mass. In captivity, adult male greater one-horned rhinoceros may reach 2100 kg (Lang 1961), but data on captive-born individuals must be treated with caution.

Laurie (1978) and Dinerstein (1991a) considered animals to be calves until they separated from their mother, at about four years of age (Plate 38.1). This classification is based on longitudinal studies of known-age, free-ranging individuals. Subadults were 4–6 years of age. Subadult females at the upper end of this age class were occasionally difficult to separate from young-adult females that were small in total body length.

Three age categories for adults, based largely on dental condition and horn length (and these features related to other non-mensural characters), were considered. These categories are essential for accurate assessment of the demographic features of the population. Young adults possessed sharp occlusal ridges on the lower molars, and the lower outer incisors were <5 cm long and <3 cm wide at the base (males only). The horn was intact, with no erosion around the base, and short (<15 cm for females; <18 cm for males). Young adults developed small secondary shoulder and neck folds, and were relatively small in size.

Intermediate-aged adults showed moderate wear on the occlusal surface of the lower molars, with mandibular outer incisors 4–5 cm long and >3 cm at

the base (females) and more elongated in males (range: 4.5–8.7 cm). Horns showed moderate erosion at the base, were 20–28 cm long in females and 20–30 cm in males, and mostly entire. The circumference at the base of the horn was 48–54 cm for males. Intermediate-aged adults were greater in length and girth than most young adults. Males showed extensive development of the neck, shoulder and secondary shoulder skin folds and thick upper-neck muscles. Both sexes had moderate wrinkles around the mouth, under the zygoma and around the eyes and forehead. Deep scars on the anal folds, face and back of the legs were uncommon. A female that had successfully weaned its first calf, and was nursing its second calf, was considered an intermediate-aged animal.

Old adults showed heavy wear on the molars, with well-formed depressions on the occlusal surface. Lower outer incisors were 4–5 cm long and >3 cm at the base (females) and elongated in males (range, if entire: 5.1–8.9 cm) though often broken. The horn was either long (20–33 cm) or broken and heavily worn and eroded, often with deep anterior and occasionally posterior grooves. In males, the horn base was large in circumference (55–95 cm), commonly with signs of breakage and subsequent regrowth. Old males often had major scars on the second cross-skin fold and minor scars on the face and other areas. Shoulder girdles, hip girdles and ribs were prominent in old females. Old adults often had cuts or pieces missing in one ear, and occasionally both.

Dimensional data on young-adult males and females showed considerable overlap (Dinerstein 1991a). Like other perissodactyls, adult males and females showed near monomorphism except in a few key characters. Adult males developed significantly longer mandibular incisors (tusks) and significantly greater neck musculature than females. In contrast, the female greater one-horned rhinos often have longer horns (though slightly narrower) than the males that breed with them. Long incisors provide formidable offensive and defensive weapons. Long incisors (rather than horns), powerful neck and shoulder musculature, and extensive neck and shoulder skin folds figured prominently in fights and displays between breeding-age males.

Males born in zoos are often >25 cm taller at the shoulder and considerably larger in mass than females. Larger samples will most likely show that old adult males are taller at the shoulder and slightly heavier than most old females. However, slight differences in body mass may not be a critical dimorphic feature in a species whose adults exceed 1500 kg. Among free-ranging rhinos, adult males are essentially a slightly larger version of females. The most conspicuous differences in morphometrics are directly related to the dental weapons and the enlarged neck and shoulder musculature of males, relied upon during the frequent inter-male fights that determine dominance and access to estrous females. Reduced size dimorphism in free-ranging animals may be explained by greater stress on males, and poor nutrition during the

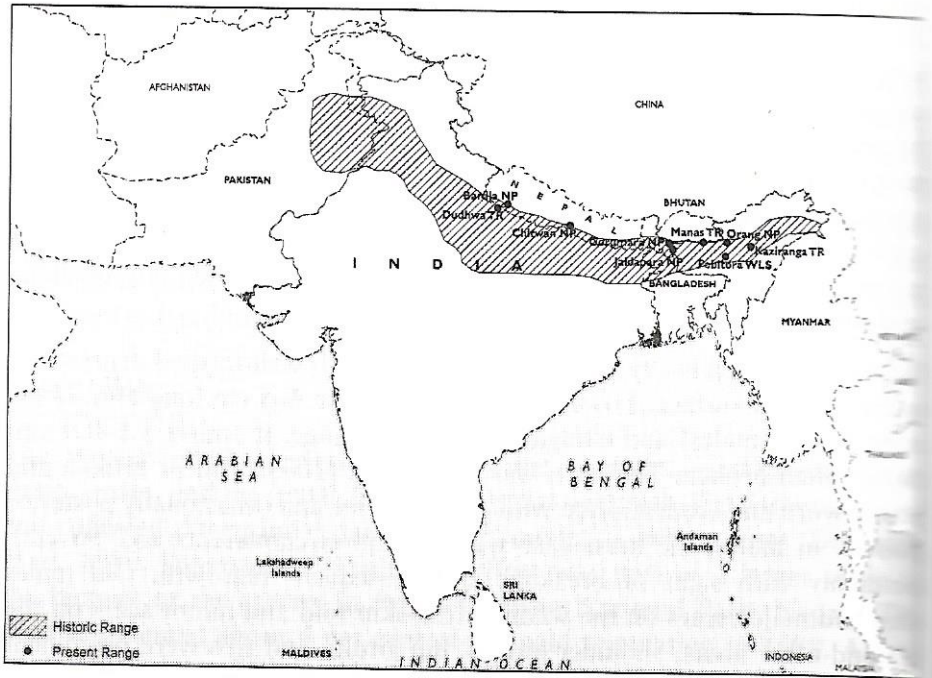


Figure 38.1. Distribution of greater one-horned rhinoceros in South Asia

long non-breeding interval when young adults are harassed by dominant males and excluded from prime grazing areas.

Distribution, Historical Demography and Genetics

Unlike the other two Asian species, the greater one-horned rhinoceros was historically limited to the flood plains and forest tracts of the Brahmaputra, Gangetic and Indus river valleys (Figure 38.1). Artifacts from the Mohenjodaro era accurately depict the greater one-horned rhinoceros, suggesting that the species occupied what is now Sind province in Pakistan in 2000 BC (Laurie 1982, Rookmaaker 2000). Dinerstein and McCracken (1990) estimated that prior to 1400 AD, the beginning of intensive agricultural settlement, prime habitats supported a minimal total population of 476,140 individuals. The greater one-horned rhinoceros maintained its extensive distribution until relatively recently. Today, however, no more than 2800 individuals remain in the wild, with only three populations containing more than 100 individuals: Kaziranga National Park in Assam, India (with an estimated 2050 individuals), Jaldapara WLS in West Bengal and Chitwan (with about 534 individuals in 2012) (Table 38.1). Smaller populations occur in 11 other reserves in Nepal and India (Dinerstein 2011).

Table 38.1.

Important greater one-horned rhinoceros populations for long-term conservation. The population data is from Yonzon (1994), Foose and van Strien (1997), Dinerstein (2003), B. Talukdar, Asian Rhino Specialist Group (2009, pers. comm.). Protected area data only includes core reserves without buffer zones.

Protected area (ha)	PA area	Estimated population 1993	Estimated population 1995	Confirmed population	2005-06	2009
India						
Kaziranga	43,000	1164±134	1300	1200	1855	2048
Orang	7260	90+	100	90	68	64
Pobitora	3883	56	76	68	81	84
Jaldapara	21,651	33+	35	35	108	108
Gorumara	852				27	31
Manas	50,000	60+	20	4	0	3
Dudhwa	49,029	11	13	13	29	
Katamiaghat	40,069				0	1-2
Nepal						
Chitwan	93,200	375-400	466	460	372	408
Bardia	96,800	40+	45	40	32	21
Sulia Phanta	30,500					5

The Chitwan population was reduced to 60-80 individuals in 1962, with an estimated effective population size (N_e) of 21-28 animals. The Kaziranga population was reduced to less than 100 animals around 1900, but both populations have rebounded. These demographic patterns presume a population bottleneck effect in Chitwan. However, protein electrophoresis showed that heterozygosity remains very high in this population ($H_o = 9.9$ per cent) despite its near extinction. Dinerstein and McCracken (1990) attributed the high heterozygosity to large N_e s prior to the population bottleneck, the recent occurrence of the bottleneck, and long generation time. Studies of the greater one-horned rhinoceros illustrate the importance of considering historical demography and life history parameters when evaluating the possible genetic effects of bottlenecks in wild populations.

Ecology

Habitat

The greater one-horned rhinoceros flourishes in what are arguably the world's tallest grasslands. The flood plains of Chitwan and Kaziranga support terraces of 'elephant grasses' that reach 6-8 m by the end of the monsoon (October). These alluvial grasslands are as threatened as the populations of the greater one-horned rhinoceros, with only a small fraction of the original habitat

remaining (Olson and Dinerstein 1998). The best-conserved examples of flood plain grasslands are in Chitwan, Sukla Phanta Wildlife Reserve, Manas Wildlife Sanctuary, Dudhwa National Park, and to a lesser extent, in Royal Bardia National Park. A global analysis of biodiversity identified the 'Terai-Duar Savannas and Grasslands' as part of the Global 200, a representative example of one of the most biologically outstanding grassland ecoregions on earth (Olson and Dinerstein 1998). This ecoregion, which lies along the base of the outermost foothills of the Himalaya, ranges from Dehradun in Uttarakhand, India, across the Nepalese Terai Zone, to the Duar Grasslands of Bhutan.

Rhinoceros populations reached a maximum density of 13.3/sq km in riverine forest-*Saccharum spontaneum* grassland mosaics (Dinerstein and Price 1991). The high densities and remarkably small home ranges of adult males and females are explained by: 1) the dominance of *S. spontaneum* along river terraces, 2) its high palatability and 3) the production of new shoots in response to grazing, burning, inundation or cutting (Dinerstein 2003). Local density in areas dominated by *Narenga porphyracoma* and *Themeda arundinacea*, two tall grass species of low palatability for the greater one-horned rhinoceros, was 1.7-3.2/sq km.

Several important features explain why the greater one-horned rhinoceros and other large herbivores and carnivores thrive on the Terai flood plains of the northern Indian subcontinent. The flood plains lie at the base of the Himalaya, the world's youngest, tallest mountain chain. The steepness of the terrain, fragility of the soil and high rainfall occurring in a condensed period from July to early September result in tremendous rates of soil erosion and frequent, severe monsoon floods. Every year, the major rivers meander across the flood plains, burying grasslands in more than a metre of silt. Areas buried in silt return to tall grasslands by the end of the following monsoon, and low-lying areas merely inundated for a few days are recharged with an annual load of nutrients. Thus, the same phenomenon that maintains high rice yields and astounding human population densities along the flood plains of the Brahmaputra in Bangladesh, supports high numbers of greater one-horned rhinoceros in their natural habitat. These predictable, locally severe, annual disturbances are the major structuring forces in this ecosystem. The greater one-horned rhinoceros has clearly adapted and prospered in riverine habitats characterised by high levels of habitat disturbance (Dinerstein and Price 1991). It is this disturbance regime and the productivity of *S. spontaneum* grasslands, rather than habitat diversity, that maintain extraordinary concentrations of the greater one-horned rhinoceros along rivers (cf. Laurie 1978). Rhinoceros densities are much lower in areas of high habitat diversity that lack *S. spontaneum* grasslands than in landscapes dominated by these grasslands.

Despite the importance of riverine grasslands, many reserves containing the

greater one-horned rhinoceros are mostly covered by pure or mixed strands of *Shorea robusta* (sal), the dominant forest type over much of northern India and lowland Nepal. Sal is a valuable timber tree, but is avoided by rhinoceros as forage. The high concentration of tannins in sal likely defends it from herbivory by ungulates. The low palatability of other species in sal forests such as *Terminalia alata* (saj or asna), *T. belerica* (barro), *T. chebula* (harro), *Lagerstroemia parviflora* (bhotdhairo), *Dillenia pentagyna* (tantari), *Sicygium operculata* (jamun), *Careya arborea* (kumbi) and *Buchanania latifolia* (kalikat) reduce the value of the dominant vegetation type for the rhinoceros.

Hill sal forests, a subtype, share the same low level of attraction for the rhinoceros, partly because the soil has poor water retention capacity; thus, seasonal streams in the hilly tracts of their range hold water only during the monsoon and for a short time thereafter. Perhaps the most important use of upland sal forests by the rhinoceros is as a refuge during floods. The absence of safe high ground areas in Kaziranga National Park in Assam, India poses a serious threat during and after monsoon floods. Rhinos are strong swimmers and cross flooding rivers (note: not all rhinos are great swimmers; white rhinos sometimes drown and would not cross flooding rivers!). However, during periods of high water, they, like other large mammals, require higher ground. Where inundation has been severe, these sites must support browsing by rhinos until the water levels recede.

Food habits and impact on the landscape

The greater one-horned rhinoceros is primarily a grazer, with *S. spontaneum* comprising a major part of the diet in all months of the year. In winter, the rhinoceros browses much more frequently, as determined by fecal analysis and direct observation (Gyawali 1986). In winter, scrub vegetation, often found along the buffer zones on the edge of parks, holds a particular attraction for the rhinoceros. They feed heavily on several browse species prevalent there, including *Callicarpa macrophylla* (daikamala) and *Cassia tora* (saano taphre). Even the stick-tight fruits and stems of the weedy *Xanthium stromarium*, (shadi kuro, cocklebur), an introduced weed normally dispersed on animal dung, is sought out by the rhinoceros.

Croplands attract rhinoceros and all of the other ungulates, and require nightly vigilance by farmers to scare animals away. Rhinoceros are partial to rice, corn and wheat at ripening (Gyawali 1986). They seek out and devour hot chilli plants, but feed only sparingly on mustard crop. Most of the damage to crops by the rhinoceros is restricted to a kilometre from park boundaries (Laurie 1978, Gyawali 1986). However, when Dinerstein and Price (1991) compared the densities of the greater one-horned rhinoceros in extensive *S. spontaneum* grasslands far from agriculture, and too far to include crops in the diet (Gyawali 1986), with densities in grasslands in close proximity to

agriculture, they found no statistically significant difference.

The greater one-horned rhinoceros ingested the fruits of at least 23 species of herbaceous and woody plants (Dinerstein 1991b). Seeds manured into grassland latrines used by the rhinoceros yielded distinct assemblages of dicotyledonous plants. *Trewia nudiflora*, the most common riverine forest tree in Chitwan, and *Cassia tora*, a herbaceous plant, accounted for most of the herbaceous cover. Although unattractive to arboreal and volant frugivores (monkeys, bats and birds), *Trewia* fruit is an important food source for the rhinoceros during the monsoon (Dinerstein and Wemmer 1988).

The rhinoceros plays an important role in the dispersal and recruitment of woody species in riverine grasslands. *Trewia* seeds remained inside the gut of captive rhinoceros for 3–7 days, but gut treatment itself had no significant effect on germination success. Seeds defecated on grassland latrines created by rhinoceros developed into robust seedlings, whereas seedlings on forest latrines generally died soon after germination or after the monsoon. This is because *Trewia* is shade-intolerant. Despite abundant fruit fall and reasonable seed germination, seedling recruitment was poor under the forest canopy. A survey of the woody flora of Chitwan revealed that <10 per cent of plant species were dispersed by large mammals, but in flood plain forest and savanna, large mammal-dispersed species represented the most common trees.

The greater one-horned rhinoceros has other profound effects on its landscape: it exerts strong selective pressure on forest structure and canopy composition by inhibiting the vertical growth of saplings, by frequent browsing and trampling (Dinerstein 1992). Using a series of exclosures, Dinerstein (1992) demonstrated that the rhinoceros inhibited the vertical growth of an abundant tree species, *Litsea monopetala* (Lauraceae). Although stunted saplings of this species dominated the understorey of riverine forests, it was rare as a canopy species in forests occupied by the rhinoceros.

This study and others on the feeding ecology of Asian megaherbivores (Mueller-Dombois 1972) suggest a significant evolutionary impact of selective browsing by large mammals, with potential cumulative effects on forest structure and canopy composition. The impact may be particularly conspicuous in the South Asian flood plains, where tree diversity is low, and estimates of large browser biomass in riverine forest-grassland mosaics are extremely high (Seidensticker 1976).

Behaviour

General behaviour patterns of rhinoceros are described in Laurie (1982). The three conspicuous aspects of behaviour are courtship, male–male interactions and thermoregulation.

Courtship behaviour in the greater one-horned rhinoceros is rather aggressive.

and perhaps the most violent among the Perissodactyla. Males actively pursue females during long courtship chases (>2 km), and attack females with their incisors or ram into them in an attempt to subdue them. On one, and possibly two, occasions, females died from wounds suffered in attacks by males. Reports of females dying from internal injuries sustained during courtship were also recorded on at least two occasions in captivity (M Dee pers. comm.). During the author's study, a radio-collared dominant male killed a newborn calf that it had not sired. Females begin an estrous cycle soon after the loss of a calf.

Males of the greater one-horned rhinoceros form dominance hierarchies, and an alpha male's tenure is short in comparison with its longevity (Dinerstein 2003). The long mean interbirth interval (46 months) and the presence of <150 breeding-age females in the Chitwan population indicate that breeding opportunities are probably few for individual males. Limited chances for copulation probably heighten aggressive behaviour when a female cycles into estrus. Non-breeding males seldom use prime grazing areas dominated by the grass *S. spontaneum* and occupied by dominant males. Dominant males attack young-adult males if they remain in areas where breeding females concentrate. In contrast, females may occupy such areas even as subadults, and continue to occupy the maternal home range as adults (Dinerstein 2003, Laurie 1978).

During fights to determine dominance, the males slash and gouge one another with their razor-sharp lower outer incisors, rather than relying on the horn. Three dominant males in Royal Chitwan National Park maintained their status with broken horns but intact incisors (Dinerstein 2003). Pronounced sexual dimorphism is observed in the massive neck and upper shoulder muscles, which are more extensively developed in adult males. These muscles provide the force behind the slashing and gouging. The extensive primary and secondary neck and shoulder folds found in dominant males may be used for display in head-on confrontations between rival males, and to deflect the penetration of an opponent's incisors from the neck, chest and shoulder area. This is the region where the most severe attacks first occur before one male inevitably turns and runs from the other. The greater one-horned rhinoceros is believed to have poor eyesight. The head-on display, which often precedes combat, occurs when males are within a few metres of one another. All three species of rhinoceros in Asia possess elongated lower outer incisors, but they are smaller in the Javan and Sumatran rhinoceros.

One of the most prominent behaviours of the greater one-horned rhinoceros is wallowing. Wallowing (Figure 38.2) is widespread among large mammalian herbivores (Owen-Smith 1988). Dinerstein (2003) observed that they grazed extensively during the day in the hottest, driest month of the year (April) and used wallows infrequently, counter to what might be predicted based on the thermoregulatory behaviour of other megaherbivores. Conversely,

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Figure 38.2. Wallowing is important for rhinos in the summer months. A mother and a calf in Jaldapara Wildlife Sanctuary.

during hot, humid periods (monsoons), the rhinoceros spent much of the day in wallows, presumably to avoid heat stress. Several factors probably contribute to increased heat stress during the monsoon. Days are longer and thus total solar radiation is greater. Wind speed is also reduced in comparison to the other months of the year, so heat loss through evaporative cooling is less. Most importantly, the high atmospheric humidity reduces the ability of large-bodied herbivores to use evaporative cooling to deal with heat stress. Wallowing behaviour, which peaks in the monsoon, is correlated with changes in vapour pressure density, a measure of the ability of air to hold water vapour at different temperatures. Thus, problems of heat stress, combined with easy access to preferred forage, probably restrict the greater one-horned rhinoceros to riverine habitats during the monsoon.

Unlike young and intermediate-aged males, old males seldom ran from human observers riding on domesticated elephants (*Elephas maximus*), and most old males squirted urine back between their legs in a dominance display.

Population Dynamics and Reproduction

The greater one-horned rhinoceros population in Royal Chitwan National Park has been the subject of two detailed studies of population dynamics (Laurie 1978, Dinerstein and Price 1991), using a register of photographed individuals. One study, conducted between 1984 and 1988, estimated the Chitwan population to be 358–376 individuals, as determined by regression analysis (Dinerstein and Price 1991). The observed rate of increase for the Sauraha population, an intensively monitored subpopulation in the central

and eastern part of Chitwan, was 4.8 per cent between 1984 and 1988, against 2.5 per cent between 1975 and 1988 (1975 marking the end of Laurie's study). This population included 87 adult females and 58 breeding-age males, of which only 28 were judged to have bred during the study period (Table 38.2).

Annual calf production (per cent of females in the population producing calves) averaged 7.6 ± 0.8 per cent ($\bar{x} \pm \text{SE}$) between 1984 and 1988. No distinct season of parturition was detected based on the birth of 53 calves during the 1984–88 study period. Age at first reproduction for two known-age females was between 7.0 and 7.5 years. Interbirth intervals based on 13 females whose calves survived to independence was 45.6 ± 1.8 months, range: 34–51 months (Dinerstein and Price 1991). Even longer interbirth intervals were estimated for an additional 12 females (60.9 ± 3.4 months, range: 48–88 months). Age-specific birth rates for the Chitwan population are published elsewhere (Dinerstein and Price 1991). As might be expected for a long-lived megaherbivore, mortality for all age classes was low. Mean annual mortality within the calf, subadult and adult age categories was estimated to be 2.8 per cent, 2.2 per cent and 2.9 per cent, respectively. Predation by tigers accounted for four of seven calf mortalities, and all seven calves that died during the study period were less than eight months old.

Table 38.2.

Sex and age structure of the greater one-horned rhinoceros (Sauraha population only) in Royal Chitwan National Park, 1988.

Age Category (yr)	Relocated		Relocated		Sex unknown	Total
	M	M	F	F		
Calves						
(0–1)	4	2	2	1	8	15
(1–2)	3	1	2	3	4	14
(2–3)	4		3	1	9	18
(3–<4)	5		3	1	2	11
combined	19		16		23	58
Subadult						
(4–5)	9		3	1	3	16
(5–6)	3	1	7		6	17
combined	13		11		9	33
Adult						
(6–12)	23	3	37	5	0	68
(12–20)	16		28	2	0	46
(>20)	19	2	22	1	0	44
combined	63		95		0	158

Conservation

The contrast between the former abundance of rhinos and their current rarity is truly staggering. The current estimate of the total free-ranging population of the three Asian species is less than 2800 individuals (Dinerstein 2011). Even more worrying is the statistic that only two populations of Asian rhinoceros currently contain more than 100 individuals. The decline and fragmentation of rhinoceros populations worldwide is alarming because most of the species were abundant until recently and, with the exception of the greater one-horned rhinoceros, were distributed continent-wide.

The rapid decline in rhinoceros populations is a direct result of relentless poaching pressure and loss of habitat. The extensive illegal trade in rhino horn has been well-documented by Esmond Martin and colleagues. These surveys uncovered three important findings. First, they showed that the horns of the three Asian species are about three times more expensive than those of African species, with Asian rhinoceros horn fetching \$30,000/kg (in 2012, the price increased to an estimated \$100,000/kg for all five species). Presumably, Asian traders and users believe that the Asian horn is more potent than the African horn. No published data is available on the sample size used to determine prices, or if prices fluctuate. If the large discrepancy between the prices of the Asian and African horn is valid, it may in part reflect the historical demography of the five species, in that, until quite recently, the African species was much more abundant than the Asian species. More likely, it is attributable to the belief among users of ground rhinoceros horn that the Asian species yield the most potent medicine.

Second, the demand for powdered rhinoceros horn is not fuelled by its mythical powers as an aphrodisiac, but as a fever depressant. In Vietnam, the myth has extended to curing cancer and treating hangovers. Third, in north Yemen, another major smuggling depot, the main use of rhinoceros horn is as dagger handles. This trade has been largely solved by the substitution of horns from other domestic animal species, and efforts by conservation groups provide some hope that Chinese traditional medicine can utilise other ingredients to combat fever than precious rhinoceros horn. Efforts to promote substitutions for rhinoceros horn, as has been done for tiger bones, are underway.

If poaching somehow ceased in Africa, the rhinoceros population would increase rapidly because extensive habitat still remains to re-establish the species throughout their range. Asia presents a different landscape. There is no habitat block that currently contains rhinos in Asia equivalent to the Selous Game Reserve of southern Tanzania, an area roughly the size of Switzerland, constituting a potential mega-reserve for the black rhinoceros. In Asia, rhinoceros sanctuaries are threatened by rapid deforestation and human population growth adjacent to protected areas. The most preferred habitats of the greater one-horned rhinoceros are flood plains, which are

also sites of intensive cultivation and weed invasion. The growth of human populations poses a much greater threat to habitat conservation in Asia than in Africa.

Finally, insurgencies and the proliferation of automatic weapons in rural areas have taken their toll on the rhinoceros. Rhinoceros populations could withstand the pressures of poaching by traditional methods. In South Asia, pit traps and spears and occasionally firearms are the techniques most commonly used to kill the greater one-horned rhinoceros, whereas in Southeast Asia, snares and pit traps are commonly used to capture the Sumatran rhinoceros.

One major seldomly stated reason why rhinoceroses have persisted in Nepal and recovered from near-extinction is that, aside from strict protection by the Nepalese Army in core reserves, very few private individuals have access to sophisticated firearms. Had the Nepalese or Assamese villagers possessed the arsenals at the disposal of Somali poachers, it is unlikely that the numbers of the greater one-horned rhinoceros would be even at their present levels. A dismal test of this hypothesis may have already occurred in the Manas Sanctuary of Assam, India. There, an uprising by the Bodo people has nearly wiped out the existing population, estimated at about 80 greater one-horned rhinoceros prior to their temporary takeover of the sanctuary (Foose and van Strien 1997). Even without widespread access to firearms, poaching of the greater one-horned rhinoceros in India was reported to be as high as 450 individuals in the 10-year interval of 1986–95 (Menon 1996), and only 50 in Nepal over the same interval (Martin and Vigne 1995).

Poaching had been well controlled since 1993 in Chitwan, through the joint activities of the Nepalese Army stationed inside the park and an active anti-poaching information network operating outside the park. Dinerstein (2003) summarises the lessons learned from experiences in recovering rhinoceros populations in Nepal, and offers a comprehensive strategy for long-term conservation.

The essential ingredients of the strategy are:

- Strict protection of core areas (Plate 38.2)
- Powerful economic incentives and new legislation to promote local guardianship of endangered species and habitats in buffer zones and corridors (Dinerstein *et al.* 1999)
- Effective anti-poaching information networks and anti-poaching units
- Bold leadership to carry out essential conservation measures such as translocations, fair resettlement of villages located inside reserves, and equitable distribution of ecotourism revenues (Figure 38.3)
- Greater conservation awareness at the local level, regarding the uniqueness, rarity and value of the species

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Figure 38.3. Tourists on the back of an elephant watching rhinos in Kaziranga Tiger Reserve

Successful translocations from Chitwan to the Dudhwa and Royal Bardia National Parks demonstrate that recovery of rhinoceros populations within their former range in the Terai is possible if the political will can be mustered (Dinerstein and Gyawali 1993). A conservation action plan for Asian rhinos incorporated these principles into a suite of actions to enhance conservation of the species, built on the success of efforts in Chitwan and Kaziranga (Wikramanayake and Dinerstein 1998).

Beginning in the late 1990s, an insurgency movement in Nepal threatened to undermine all of the progress made in rhinoceros conservation in the previous three decades. The Nepalese Army vacated many of their guard posts to join other troops in fighting the Maoists far from the Terai. The rhinoceros population was left essentially unguarded for several years. The population in Chitwan crashed from a high of 550 in 2000 to 372 in 2005. To put the decline in perspective, the poaching epidemic reduced the number of rhinos alive in Chitwan in 2005 to the level observed in 1990.

Bardia fared much worse. More than 80 rhinos were translocated to the Babai Valley, an inner Dun valley of the Terai Zone during the late 1980s and early 1990s. By 2008, all had been poached. Rhinos still persist in Bardia; a subpopulation released in 1986–87 near the Karnali river has grown very slowly and now numbers about 21 individuals, several of which cross the Indian border into the neighbouring Katarniaghat Wildlife Reserve.

From a total population perspective, the decline in rhinos in Bardia is a

tragedy. Had the founder populations been well protected, Bardia would easily be supporting a population of over 250 rhinos today. Yet, that there are any rhinos alive today in Nepal is something of a small miracle and a tribute to the dedication of the national park staff that remained at their posts during a very challenging period for conservation. From a species recovery strategy perspective, there is a more optimistic interpretation: rhinos are now present in five reserves in the Terai Zone (Chitwan, Bardia, Sukla Phanta, Dudhwa and Katarniaghat), up from only one location until the early 1980s.

In India, the rapid increase of rhinos in some of the smaller protected areas has created opportunities for translocations, and ambitious plans are underway to repopulate Manas from neighbouring reserves. The population in Kaziranga continues to rise. Here the challenge remains the need to secure a corridor linking Kaziranga with upland habitats to create a refuge for rhinos and other wildlife during the monsoon floods.

Despite setbacks in Nepal during the Maoist insurgency period, rhino conservation is on the upswing in both Nepal and India. One area where a small population of ca. 15 rhinos can be introduced and managed is the Dhikala and Paterpani grasslands in Corbett Tiger Reserve (Johnsingh *et al.* 2007). Rhino conservation will require constant vigilance, however, or the recent gains could be wiped out in short order.

Conclusion

The persistence of the rhinoceros over evolutionary time can be explained by a combination of factors—large body size, high mobility, invulnerability to non-human predators (as juveniles and adults) and an ability to process a low-quality, high-roughage diet. Large body size and high mobility emerge as prominent factors in the success of the lineage. The large size conveyed two important advantages: an effective defence (at least as adults) from decimation by predators, and an ability to subsist on relatively coarse vegetation. The digestive strategies of the rhinoceros allowed them to subsist on plant matter that would normally yield too little energy to meet the metabolic demands of smaller herbivores. The development of molars adept at handling coarse grasses, which are often protected by guard cells of enamel-grinding silica, also allowed these large mammals to process the most abundant forage plants.

The ability of some rhinoceros to switch seasonally between browse and grasses could also have contributed to their wide distribution. For example, the greater one-horned rhinoceros is primarily a grazer, and has the high-crowned molars characteristic of this feeding niche, but can subsist seasonally on a diet of dicotyledonous plants. The ability to shift the proportion of graminoid species and browse probably aided rhinoceroses during movements into new habitats. Their swimming ability also afforded an opportunity to exploit

aquatic plants and extended their flexibility in finding food. The rhinoceros in Chitwan feeds extensively on aquatic vegetation during the hot-dry season.

Another reason for their persistence and abundance might be their ability to thrive in areas of high habitat disturbance. All three surviving Asian species reach highest densities in early successional habitats maintained by local disturbance regimes. Preferred foraging areas for Sumatran rhinoceros are tree-fall gaps, where pioneer tree species such as *Macaranga* are abundant. Plant succession in the last stronghold of the Javan rhinoceros—Ujung Kulon National Park, Indonesia—has become widely accepted as the reason why the population has stabilised at under 50 individuals (N Foehad pers. comm.). The eruption of the nearby Krakatau volcano, and the subsequent tidal wave, created a major disturbance that triggered succession, and probably allowed for higher densities of Javan rhinoceros than at present. The greater one-horned rhinoceros reaches extraordinary local densities because it is well adapted to feeding in one of the most dynamic landscapes on earth—the flood plains of the major river systems of the Indian subcontinent, where annual monsoon floods are the norm. High mobility provides a natural escape against changing climates and forage conditions, and permits movement to new areas and habitats. It also helps the rhinoceros cope with local, periodic and often severe disturbances caused by floods and fires.

The decline of the rhinoceros is attributable to heavy poaching pressure for their highly valued horns and to habitat loss. A new era of greater one-horned rhinoceros conservation is underway, marked by extensive translocation programmes. The goal is to re-establish at least 10 populations supporting at least 100 individuals each, across northern India and Nepal, from several source populations.

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