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HMW 2 - Family text: Rhinocerotidae (Rhinoceroses)

Class Mammalia

Order Perissodactyla

Suborder Ceratomorpha

Family RHINOCEROTIDAE (RHINOCEROSES)

- Giant mammals; all with distinct horns, long ears tipped with hair, thick skins, three toes, short tails, and often with distinct skin folds on body.
- 240–500 cm.
- Afrotropical and Indo-Malayan regions.
- Tropical montane, lowland, and mangrove forests, short grasslands, tall alluvial grasslands, savannahs, woodlands, semi-desert, scrub.
- 4 genera, 5 species, at least 9 extant taxa.
- 3 species Critically Endangered, 1 Vulnerable; 1 subspecies Extinct in the Wild, 2 subspecies possibly Extinct and 1 subspecies Extinct since 1600.

Systematics

The rhinoceros (rhino) family, until recently, consisted of five extant species: two in Africa, the White Rhinoceros (*Ceratotherium simum*) and the Black Rhinoceros (*Diceros bicornis*), and three in Asia, the Greater One-horned Rhinoceros (*Rhinoceros unicornis*), the Javan Rhinoceros (*Rhinoceros sondaicus*), and the Sumatran Rhinoceros (*Dicerorhinus sumatrensis*). In 2010, a study based largely on genetic evidence suggested separating the geographically distinct Northern White Rhino from the Southern White Rhino as a unique species. Certainly, the two subspecies have been isolated for perhaps as long as 1,000,000 years. Unlike the extant Asian rhinoceroses, White Rhinos are poor swimmers and occasionally drown when trying to cross a major river, so it is likely that the Zambezi River served as a major dispersal barrier, preventing the two races from mingling. The Nile also formed a barrier to movement of the Northern White Rhino. However, the elevation of the

Northern White Rhino has been strongly criticized by several experts who argue for maintaining the subspecific designation based on the limited morphological differences between the two subspecies taxa.

Three features mark the evolutionary history of rhinoceroses: the antiquity of the lineage, the diversity and variety of the feeding niches that they occupied, and numerical abundance. The family to which the five extant species belong, the Rhinocerotidae, flourished in the Oligocene after first appearing in the late Eocene in Eurasia. Paleontologists have inadequately reconstructed the evolutionary lineage of rhinoceros, as mistakes in nomenclature and misconceptions about rhinoceros systematics and phylogenies were common in the scientific literature until 1988. Older phylogenies were based on features now known to be highly variable, such as the molarization of the premolars, resulting in the splitting of primitive rhinocerotids into too many species.

The earliest known rhinoceros-like mammal belonged to the genus *Hyrachyus*, known from late Eocene deposits in Asia, North America, and Europe. These primitive rhinoceroses resembled early horses and tapirs, being diminutive, delicate, and lacking horns. Not until later in their evolutionary history did horns become a defining feature. The first true rhinoceroses that resembled modern forms belong to the family Rhinocerotidae. They also appeared in the late Eocene, but were less dominant than the other two families, the running rhinoceros (*Hydrocodontidae*) and the aquatic rhinoceros (*Amnyodontidae*).

Both families are worth a brief mention. The *Hyracodontidae* are divided into two groups of animals quite different in size: a dog-sized cursorial group, and a lineage of immense forms known as the *Indricotheriinae*. The latter group included some truly spectacular rhinoceroses. For example, the giraffe-rhinoceros (*Paraceratherium grangeri*, formerly known as *Baluchitherium* or *Indricotherium grangeri*) of Mongolia was the largest terrestrial mammal known. It must have been an impressive sight, with a shoulder height of almost six meters and approaching a total length of nine meters. The *indricotheres*, including the giraffe-rhinoceros, disappeared from Asia by the middle Miocene.

Rhinoceroses are considered biologically successful as a lineage because of their evolutionary persistence and their widespread distribution. The aquatic rhinoceroses reached their maximum diversity in the late Eocene and early Oligocene, especially in Asia. The evolutionary persistence of the representatives of this family was remarkable. For example, the hippo-like rhinoceros (*Metamynodon*) ranged for ten million years over much of North America. By the early Oligocene, most aquatic rhinos were in decline, with one genus, *Cadurcotherium*, surviving until the middle Miocene in what is now Pakistan, nearly 15 million years after the demise of the other aquatic rhinoceroses.

The third family, the Rhinocerotidae, flourished in the Oligocene, after first appearing in the late Eocene in Eurasia. Small species came first, followed by middle- and large-sized rhinoceroses during the upper Oligocene. Interestingly, Africa lacked rhinocerotids during the same period. In contrast, North American rhinoceroses increased in size and diversity much earlier than in Eurasia and featured the first rhinoceros with horns, *Diceratherium*. *Diceratherium* also exhibited persistence and dominance. For nearly ten million years, it was the only megaherbivore in North America.

Several evolutionary trends observed in mammals are exhibited by the rhinocerotid lineage. 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 toward gigantism over evolutionary time). Another recent development exhibited by the extant rhinoceroses 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 the 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.

Climatic changes probably triggered the demise of many groups of rhinoceros at the end of the Miocene. In North America, almost the entire rhinoceros fauna was eliminated, and in Eurasia only two lineages survived. One of these, the dicrorhinines, gave rise to a form quite similar to the Sumatran Rhinoceros of today. Perhaps the most famous member of this lineage was the Woolly Rhinoceros (*Coleodonta antiquitatis*), which appeared in the Pleistocene in China and moved westward into Europe. In the Upper Pleistocene, the Woolly Rhinoceros ranged from Korea to Spain, the widest range of all species recorded.

Today, rhinos inhabit only Africa and Asia. Africa's Black Rhinoceros first emerged four million years ago in the Pliocene. Until the last few hundred years, this species ranged widely across sub-Saharan Africa. This establishes the Black Rhino as one of the oldest, most stable, and widely distributed species in the contemporary African megafauna. The other living African species, the White Rhino, appeared more recently, in the middle Pleistocene. Of the living Asian rhinoceroses, the Sumatran Rhino has changed little from its Miocene ancestors, which lived more than 40 million years ago. The Sumatran Rhino is related to the Woolly Rhinoceros and may be more closely related to the African species. The Greater One-horned and the Javan Rhino appeared in the middle Pleistocene.

Occupation of virtually all ungulate feeding niches reflects the diversity of rhinoceroses. Some of the earliest ones were small grazers, and others were small browsers. The giraffe-rhinoceros browsed the treetops, and an assortment of other species grazed or browsed shrubs and saplings in the understory. The semi-aquatic *Teleoceras* is one of a number of species that fed on aquatic plants common to rivers, streams, and oxbows. Other rhinoceroses plucked vegetation with their tapir-like snouts and must have switched seasonally from grass to browse. Perhaps the only feeding behaviors that the prehistoric rhinos failed to exploit were digging and rooting or foraging on bottom plants in lakes. By pushing down saplings and treelets, they even fed in a manner that resembles the primates that eat leaves in the lower stratum of the forest.

Their ability to exploit a variety of habitats explains in part the cosmopolitan distribution of rhinocerotids and helps us to better understand the evolution and ecology of extant species. Rhinoceroses could be found both on flat terrain and in hilly rugged country. Species shared the cold steppes with mammoths, the hot dry savannas of Africa with antelopes, and the humid Asian forests with elephants. From the Oligocene to the Pleistocene, nearly all terrestrial habitats in the Northern Hemisphere contained one or more rhinoceros species as part of their mammal fauna. In the Northern Hemisphere and in Africa, rhinos once occurred in great numbers. In some habitats, they may have outnumbered some of the mid-size ungulates. This aspect is remarkable because rhinoceroses are among the largest herbivores in Tertiary vertebrate communities.

However one chooses to define the evolutionary prominence of a lineage—persistence, geographic range, diversity of feeding niches, variety of habitats used, numerical abundance—the rhinoceroses stand as one of the most successful groups of mammals. The persistence of the rhinoceros over evolutionary time can be explained by a combination of factors, which include large body size, high mobility, invulnerability to non-human predators (both 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 of rhinoceroses 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 rhinoceroses 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 rhinoceroses to switch seasonally between browse and grasses could also have contributed to their wide distribution. For example, Greater One-horned Rhinoceroses are primarily grazers, and have the high-crowned molars characteristic of this feeding niche, but can subsist seasonally on a diet of dicotyledonous plants.

High mobility had numerous benefits, providing a natural escape from changing climates and forage conditions and permitting movement to new areas and habitats. It also helped rhinos cope with local, periodic, and often severe disturbances caused by floods and fires. Four of the five extant species are undaunted by hilly terrain and thus able to cross physical barriers that restrict smaller species. The ability to shift the proportion of graminoid species and browse probably aided rhinoceroses during movements into new habitats. For the three Asian species, their swimming ability also afforded an opportunity to exploit aquatic plants and extended their flexibility in finding food. Greater One-horned Rhinoceroses feed 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 the Sumatran Rhinoceros are tree-fall gaps, where pioneer tree species such as *Macaranga* and *Mallotus* are abundant. Plant succession in the last stronghold of the Javan Rhinoceros—Ujung Kulon National Park, Indonesia—has become widely accepted as a reason why the population stabilized at about 50 individuals and possibly has been declining in recent years. The lack of active biological management of this species (to keep densities lower and at more productive levels) and possible competition from other species are other reasons given for the poor performance of the Javan Rhino. Aside from reduced performance, likely a result of not using translocation to keep densities at lower, more productive levels, having all one's eggs effectively in one basket (and subject to threats of a tsunami, volcanic eruption, disease, or local breakdown in law and order) is not strategically wise. Encouragingly, it has been reported that there are now plans to try to set up a second population using some of the Ujung Kulon animals. The understory in the mature forest is dominated by *Arenga pinnata*, a palm species inedible by rhinos. The eruption of the nearby Krakatau volcano in 1883, and the subsequent tidal wave, created a major disturbance event that triggered succession, and probably allowed for higher densities of Javan Rhinoceroses than at present. Javan and Sumatran Rhinos were both reported in the past as pest species around tea plantations and other large-scale holdings. 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 floodplains of the major river systems of the Indian subcontinent, where annual monsoon floods are the norm.

A morphological feature that the two African and the Greater One-horned seem to share is their rugged nature. Interspecific combat is intense in all five species, and dominant males inflict serious, occasionally fatal, wounds on subordinate males, estrous females, subadult males, and calves. Wounds that would normally lead to mortality in other ungulates have less effect on rhinos, perhaps signalling strong immune response and resistance to infections. One hypothesis is that a strong immune response may have increased their ability to survive disease outbreaks that would have threatened less robust species.

All rhinoceros species have 82 chromosomes, with the exception of the Black Rhino with 84. Remarkably, this total is among the highest for mammals, exceeded only by two rodent species. The reason for such a large number of chromosomes remains unclear. Some Northern White Rhinos also have a Robertsonian translocation.

Morphological Aspects

The unique horns, enormous size, and prehistoric appearance of the rhinoceros family set them apart from all other mammals. Yet a common theme that runs throughout this chapter is how much we know about various aspects of the biology of Black, White, and Greater One-horned rhinos, and how little we know about Sumatran and Javan Rhinos, including basic morphometrics. Many tourists and scientists see the first three species rather easily in favorable locations; hardly anyone has ever seen a Javan or Sumatran Rhinoceros, let alone measured an individual. So while there is a plethora of data on the first three species, data on the two elusive Asian species are quite limited and likely to remain so. As with some other taxa, some care must be taken in interpreting data from animals raised in captivity versus free-ranging individuals. No Javan Rhinos and only a few Sumatran Rhinos exist in captivity today to offer morphological or other useful data.

One of the most striking differences between the two African species and the three Asian species is the first attribute that sets them apart from all other mammals—the smaller horn or horns (for Sumatran) found in the Asian species. A second important attribute is one that most people never see unless they are biologists who obtain a close look at the dentition—the presence of tusks in the lower jaw in the three Asian (but not African) species.

Rhinoceros literally means "nose horn" in Greek. This structure has been the subject of myth, awe, and great scientific interest, and of paramount concern to conservationists. The first stories of the unicorn were fuelled by the discovery of mammals possessing huge facial horns, the rhinos. Recent scientific studies using X-ray computed tomography (CT) scans have offered new insights into the unique nature of rhino "horn." The term horn is used widely in nature to cover the horns of cattle and African antelopes, the upper projection on the beaks of hornbills, and on the faces of reptiles such as chameleons, lizards, and extinct tortoises. In these other species, the horn takes its shape from a bony core, and the outer layer is a thin covering of keratin, as in fingernails and hair. The massive horns of rhinoceros are different in that they lack a bony core and contain only tiny keratin tubes dispersed in a keratinous matrix. CT scans and cross-sections of rhino horns clearly depict a dense central area strengthened by a composite of calcium and melanin. The result is reduced horn loss in the center due to natural wear and exposure to ultraviolet radiation. The softer exterior,

however, is often eroded during use and the wear typically leads to an elongate and sharp-tipped structure, which we call the horn. Attempting to age rhinoceroses from horn wear is challenging, but the same CT scan study offers a new clue. The dark patches of high mineral and melanin concentration within the horn are deposited in a way that reflects annual horn growth in wild rhinos.

Among the five extant wild species, the Black and White Rhinos have the largest horns. Black Rhinoceroses have two horns; the anterior horn can reach 130 cm in some individuals. The posterior horn is much smaller, ranging from 2–55 cm. Average anterior horn length for the White Rhino is 94–102 cm and posterior horn length is up to 55 cm. Among the Asian rhinos, the Sumatran also has two horns, but they are much smaller than in the other four species. The size of the horns varies, but typically they are larger in males. Often only the nasal horn is conspicuous and the second or frontal horn is much reduced in size. Horn lengths from some museum specimens are large (25–80 cm), but may not be indicative of average size. The Greater One-horned and Javan are intermediate in horn size and only possess one horn. Horn length in Greater One-horned Rhinos averages 25 cm in adult males and 24 cm in adult females; in Javan Rhino males it also averages 25 cm. There are reports of female Javan Rhinos without horns. Horn wear can be extensive in older animals; horns can even be broken off. Broken horns regrow over time. Indeed rhino horns grow continually from the base (as much as 7 cm per year in White Rhinos), but horn wear may reduce any actual increase in the size of horns. This means that the chemistry of the base of the horn in an animal translocated in the last few years will differ (reflecting its new home) from the chemistry of the upper part of the horn (reflecting where it was translocated from).

Horns are perhaps the most conspicuous feature of rhinos everyone can recognize. The other important piece of hard anatomy few observers ever see or photograph are the mandibular lower outer incisors often referred to as tusks. One reason why observers fail to see prodigious tusks in the lower jaws of the Black Rhino and the White Rhino is simple—they lack them entirely. In contrast, the Greater One-horned Rhino has impressive, extremely sharp tusks, measuring up to 9.5 cm in the largest bulls. Tusks are smaller in the Javan and Sumatran Rhino, but are still present. The most important point is that the three Asian rhinos use their tusks in combat between breeding males, males use them to subdue breeding females, and females use them to defend their calves from male rhinos or Tigers (*Panthera tigris*). The two African species, because they lack such tusks, use their horns as weapons and for predator defense. This fundamental morphological difference of presence or absence of tusks between the two groups has a tremendous influence on behavior and ecology.

The value of rhino horns and the larger sizes of the African species prompted wildlife conservationists to dehorn rhinos in places where poaching was high and rhinos widely dispersed. Some researchers claimed that dehorning the rhinos led to increased calf loss from lion and hyena predation, as dehorned Black Rhinos were left defenseless, but the data are equivocal.

Besides the horn, the other obvious trait most noticed is body mass. Rhinoceros are truly megafauna. Among the largest terrestrial mammals on the planet, the White Rhino and the Greater One-horned Rhino rank fourth and fifth. Only the three species of elephants are larger. White Rhinos range from 1800–2700 kg. Body mass in the Greater One-horned is reported as high as 2000 kg; it is likely smaller in the Javan Rhino. Body mass in Black Rhinos ranges from 800–1300 kg. The weight of adult Sumatran Rhinoceroses is about 600–

700 kg, making them the smallest, but few data exist on body mass of either Javan or Sumatran wild individuals.

Covering the large bodies is a thick skin that not only makes the rhino a true pachyderm, but also conveys a tank-like appearance. The presence of several skin folds across various parts of the body, especially in Greater One-horned and Javan Rhinos, accentuates an armor-like appearance. Tubercles of skin on these two species lend an appearance of rivets.

The large mass of rhinos belies their ability to run quickly over short distances. Most of the species can reach top speeds of over 55 km/h in brief spurts. These high speeds are generated by powerful legs that seem too short for the body. The three toes of rhinos, placing them in the odd-toed ungulate order Perissodactyla, provide strong traction in muddy to sandy substrate. Black Rhinos that live in the rock deserts of north-western Namibia also run rapidly, aided by fleshy pads on the bottom of the hooves that permit rapid movement across difficult broken terrain.

Another fascinating morphological feature is the prehensile upper lip. When rhinos first evolved, many large mammals across several different orders possessed prehensile lips. This strong extendible lip enables feeding rhinos to pluck leaves and grass stems. The White Rhino differs, having a broad, square lower lip that allows it to crop grasses close to the ground.

Perissodactyls, in general, are noted for near monomorphism, adult males and females being of similar size. This pattern certainly holds for horses and tapirs, the nearest living relatives of rhinos. Among the extant rhinos, the expression of dimorphism is uneven. White rhinos show the greatest degree of differentiation in size. In contrast, Black Rhino adult males and females are similar in size. Evidence from measurements of wild-caught Greater One-horned Rhinos is that males are often stunted and not larger or only slightly larger than the females they breed with. Captive Greater One-horned Rhinos, however, show pronounced size differences, males being demonstrably greater in mass and higher at the shoulder than females. Data on Javan and Sumatran Rhinos are so limited as to restrict comparisons in this aspect.

In Greater One-horned Rhinos, pronounced sexual dimorphism is apparent in the length of the lower outer mandibular incisors (tusks), which are longer and wider in males than in females. Dimorphism is also apparent in their massive neck and upper shoulder muscles, which are more extensively developed in adult males. These muscles provide the force behind the slashing and gouging with the incisors. The extensive primary and secondary neck and shoulder folds found in dominant males may serve 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 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 meters of one another.

Habitat

The extant species of rhinoceros are restricted to the subtropics and tropics in Africa and Asia. Within this belt, they occupy a variety of habitats. Sub-Saharan Africa is for the most

part a dry region. Among the most arid rhino habitats on the continent is in Damaraland in north-west Namibia. Here, Black Rhinos have adapted to living in a red rock desert. They eat the succulent leaves of the sparse plants, and can persist for days without drinking, perhaps extracting water from the vegetation they consume, as do oryx and other desert ungulates. However, rhinos avoid areas with no water. The spread of water points throughout formerly waterless sections of Etosha National Park demonstrates how quickly Black Rhinos will occupy new areas if a reliable source of water becomes available. In this park, just over 1% of Black Rhino sightings were farther than 15 km from a waterhole and 86.5% of sightings occurred in the 16% of the park less than 10 km from water. In much of this habitat, trees are limited to watercourses and rhinos prefer these areas.

As rainfall increases to the north and east, desert grassland and scrub give way to mopane and miombo woodlands and savannas. Black Rhinos formerly occupied tropical scrub across the length of Africa, but shunned true rainforests. At first, it seems odd for a large browser to avoid a forest type filled with broadleaved plants—but in Africa many broadleaved species are chemically defended and rainforests are often nutrient poor. Black Rhinos can cope with a certain quantity of species such as Euphorbia (filled with toxic latex), but there does appear to be a limit as to how much browse containing secondary compounds the rhino can detoxify.

The White Rhinos, both the northern and southern species, favor short grasslands, which they can maintain as grazing lawns. However, when Northern White Rhinos still occurred in Garamba, they lived in areas with tall grass. Nevertheless, they favored short-grass grazing lawns created on nutrient hot-spots. In addition to favoring grazing short creeping grasses such as *Panicum coloratum* and *Urochloa mossambicensis*, the Southern White Rhino also favors taller, leafy *Panicum maximum* and *P. deustum* in shade under trees. Taller *Themeda triandra* can also provide an important dry season food resource. Short grasslands are abundant in the Southern White's range, both at low elevations and in premontane and montane habitats. Short grasses, on average tend to be more nutritious than the more lignified tall grasses, so White Rhinos seek out and through their grazing help maintain this habitat type. Garamba National Park, once home to the now extinct Northern White Rhino, is Sahelian in nature, sitting above the Congo Basin's moist tropical forests. Like the Black Rhino, the Northern White avoided rainforest.

Both species of African rhinos readily ascended into montane forests. Black Rhinos have been recorded in the Aberdares in Kenya at elevations of 2700–2900 m and White Rhinos translocated to Meru National Park in Tanzania also live at elevations that would seem incongruous for such a large-bodied mammal.

Greater One-horned Rhinoceroses flourish in what are arguably the world's tallest grasslands. The floodplains of Royal Chitwan and Kaziranga National Parks support terraces of “elephant grasses” that reach 6–8 m by the end of the monsoon (October). These alluvial grasslands are as threatened as are Greater One-horned Rhinoceros populations, with only a small fraction of the original habitat remaining. The best-conserved examples of floodplain grasslands are in Royal Chitwan National Park, Sukla Phanta Wildlife Reserve, Manas National Park, Dudhwa National Park, and to a lesser extent, Bardia National Park, all part of what is known as the Terai-Duar Grasslands and Savannas ecoregion. This ecoregion, which sits along the base of the outermost foothills of the Himalayas, ranges from Dehra Dun in Uttaranchal, India, across the Nepalese Terai Zone, to the Duar Grasslands of Bhutan.

Rhinoceros populations reached maximum densities in riverine forest (*Saccharum spontaneum* grassland mosaics). The high densities and remarkably small home ranges of adult males and females are explained by: the dominance of *S. spontaneum* along river terraces, its high palatability, and the production of new shoots in response to grazing, burning, inundation, or cutting. Local rhino densities in areas dominated by *Narenga porphyra* and *Themeda arundinacea*, two tall grass species of low palatability for Greater One-horned Rhinoceros, were much lower.

Several important features explain why Greater One-horned Rhinoceroses and other large herbivores and carnivores thrive on the Terai floodplains of the northern Indian subcontinent. The floodplains lie at the base of the Himalaya, the world's youngest, tallest mountain chain. The steepness of the terrain, the fragility of the soils, and the 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 floodplains, burying grasslands in more than a meter of silt. Areas buried in silt return to tall grassland 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 floodplain of the Brahmaputra River in Bangladesh supports high numbers of Greater One-horned Rhinoceros in natural habitats. These predictable, locally severe annual disturbance events are the major structuring forces in this ecosystem. Greater One-horned Rhinoceroses have clearly adapted and prospered in riverine habitats characterized by high levels of habitat disturbance. This disturbance regime, and the productivity of *S. spontaneum* grasslands, rather than habitat diversity, maintain the extraordinary concentrations of the Greater One-horned Rhinoceros along rivers. Furthermore, major floods that occur several times per century shift river courses, create new *Saccharum* floodplains on vast scales, bury areas in silt where non-palatable shrubs have encroached, and periodically reset the successional stages of habitat prevalent on South Asian floodplains.

Along with the importance of riverine grasslands, riverine forests provide browse for rhinos for four months of the year, during the cool season. Many reserves containing Greater One-horned Rhinos are covered mostly by pure or mixed stands of *Shorea robusta* (sal), the dominant forest type over much of northern India and lowland Nepal. Sal is a valuable timber tree, but avoided by rhinoceroses as forage. The high concentrations of tannins in sal likely defend it from herbivory by ungulates. The low palatability of other plant species in sal forests, such as *Terminalia alata*, *T. belerica*, *T. chebula*, *Lagerstroemia parviflora*, *Dillenia pentagyna*, *Syzygium operculata*, *Careya arborea*, and *Buchanania latifolia* reduce the value of the dominant vegetation type for the rhinos. Hill sal forests, a subtype, share the same low level of attraction for rhinos, partly because the soils have poor water retention capacity; 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 rhinos 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 annual monsoon floods. Greater One-horned Rhinos are strong swimmers and are able to 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 until water levels recede.

Range collapse, extirpation of populations, and difficulty in studying free-ranging animals limit our understanding of habitat use by both Javan and Sumatran Rhinos. Much of the literature is anecdotal. Unlike the Black, Southern White, or Greater One-horned, the Javan

and Sumatran Rhinos have never been subjected to study using radio-telemetry to determine habitat use or preference. Some have suggested that where they overlap, Sumatran Rhinos occupy the higher-elevation areas and Javan Rhinos the lowlands forests. Certainly in Kerinci-Seblat and Gunung Leuser in Sumatra, Sumatran Rhinos live in rugged steep terrain, but this may be a function of where they are less likely to encounter poachers than an indication of habitat preference. Both species occupy moist tropical forest, but prefer to forage in openings or secondary forest on pioneer plants. Historically, the Javan Rhino, when it was still found in the Brahamaputra and the Sundarbans, must have occupied mangrove, flooded forests, and alluvial grasslands. One of the last remaining populations of Sumatran Rhinos in Sabah, in the Danum Valley, is an area that has been logged but also contains remnants of some of the most botanically rich dipterocarp forests on earth.

Within a particular area, all five species seek out pools of water, muddy depressions, rivers, or sandy areas as wallowing sites. The five species also vary in their need to remain close to water. Greater One-horned Rhinos are rarely found more than 2 km from water. Biologists assume that the same pattern holds true for Javan and Sumatran Rhinos, but little field data exist to support this claim. In contrast, the White and Black Rhino species of Africa can both go several days without drinking and so are less restricted to living near riparian areas.

Human population densities are much higher in Asian rhino habitats than in Africa, so more is known about interactions between rhinos and humans there. All three Asian species enter crop lands to feed when certain crops such as rice, maize, wheat, and lentils are available. Javan Rhinos were shot when they invaded tea plantations.

General Habits

Some of the most interesting questions about the general habits of rhinos are: to what extent are they diurnal or nocturnal feeders? How do seasonal changes in climate, such as shifts from hot to cool seasons or wet to dry seasons, influence feeding and other activities such as wallowing? To what extent do adult males differ from adult females in activity patterns?

One consequence of very large body size is that species such as rhinos must feed both day and night to ingest enough food to meet their metabolic requirements. This pattern of activity may be modified, as seems to be the case with the dwindling Javan Rhino population in Vietnam, where poaching pressure and human disturbance may have shifted these animals to a more nocturnal existence.

Detailed observations on radio-collared and habituated Greater One-horned Rhinos offer a complete picture of how individual animals of both sexes and various ages spend the 24-hour cycle. This species shifts its activities with the seasons but reveals the following patterns: firstly, in the hot-dry season (mid-February to mid-June), there are two peaks in grazing, in the pre-dawn hours and around dusk. Browsing is very infrequent, as is wallowing, with no real peak activity in these behaviors. Resting peaks at midday and shows smaller peaks at dawn and around midnight. Secondly, in the monsoon (mid-June to mid-October) wallowing increases dramatically and stays high throughout the diurnal period. Browsing is infrequent, and there are two main grazing bouts, just after midnight and from late afternoon through dusk. Resting bouts are scattered through the day. Thirdly, during the cool season wallowing is infrequent, grazing peaks in the late afternoon, and browsing increases dramatically, lasting from just after dark until dawn. The most striking findings are that this species spends half its

time foraging throughout the year, increases browsing ten-fold during the cool season, and can spend up to eight hours per day wallowing during the monsoon.

Wallowing behavior is widespread among large mammalian herbivores and especially among rhinos, so deserves greater examination. The primary function of wallowing is assumed to be heat regulation. Escape from biting insects as well as social communication by scent marking may also encourage this behavior. Greater One-horned Rhinos graze extensively during the day in the hottest, driest month of the year (April) and use wallows infrequently, counter to what might be predicted based on thermoregulatory behavior of other megaherbivores. Conversely, during hot, humid periods (monsoons), the rhinoceroses spend much of the day in wallows, presumably to avoid heat stress. Several factors probably contribute to increased heat stress during the monsoon. The days are longer in the monsoon period, and thus total solar radiation is greater. Wind speed is also reduced in comparison to the other months of the year, so that 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 behavior, which peaks in the monsoon, is correlated with changes in vapor pressure density, a measure of the ability of air to hold water vapor at different temperatures. Thus, problems of heat stress, combined with easy access to preferred forage, probably restrict Greater One-horned Rhinoceroses to riverine habitats during the monsoon. Javan Rhinos make extensive use of wallows, but when wallows dry up, they may use tidal forests and muddy banks to reduce heat stress. They also dip into brackish water in mangroves, perhaps to remove ectoparasites as well. Sumatran Rhinos also make extensive use of wallows. Many camera-trap photos show animals coated in mud, as if they had spent considerable time rubbing and immersed in muddy depressions.

Distinct differences have been detected in the daily activity budgets of megaherbivores. The most striking is that adult females spend more time feeding than do adult males. The Greater One-horned Rhino adheres to this pattern. The simplest explanation for this is that most females observed during the activity studies were pregnant, lactating, or had just completed lactating. The higher nutritional demands placed on females by pregnancy and lactation would result in more time spent foraging. In contrast, the habituated males were typically dominant bulls. Combat among males for control of feeding areas used by breeding females is so intense that males were probably spending their energy keeping track of females and warding off other males, leaving less time for foraging.

Comparing across rhino species, there is some support for the idea that rhinos of larger body size spend more time feeding than those smaller in mass. For example, female White Rhinoceroses spend significantly more time feeding, on average, than do females of the next-largest species, the Greater One-horned Rhinoceros.

So few direct observations of either free-ranging Javan Rhinos or Sumatran Rhinos have been recorded that comparisons are difficult. Camera-trap data help establish presence or absence, but offer a biased view of general habits. Clearly, using radio-telemetry to monitor these two species, as has been done for the other three, would add much valuable information.

White Rhinos have been well studied and their activity patterns are similar to those of Greater One-horned Rhinos. A population in South Africa showed two peaks in activity, early morning and late afternoon, extending into the evening. During the dry season, a considerable amount of time during the evening hours was spent moving to and from waterholes. During cloudy weather, White Rhinos are more active than under sunny conditions. They appear to

reduce their activities at high temperatures under bright sun. Both White and Black Rhinos thermoregulate at midday in summer, either by wallowing or resting under a tree. They sometimes use ridge crests as these usually have a cooling breeze.

White Rhinos and Black Rhinos tend to forage about 50–60% of the time over the 24-hour cycle. Black Rhinos are more nocturnal than White Rhinos, with the Greater One-horned mostly in between. Sumatran Rhinos feed during the morning and spend a lot of time wallowing during the day. It is likely that both Sumatran and Javan Rhinos spend much of the day in wallows of mud or water to cope with the high humidity of their native environments, but little quantitative data exist for comparison.

Asian rhino species routinely use salt licks. Sumatran Rhinos were estimated to visit salt licks about once per week in northern Sumatra. Javan Rhinos in Ujung Kulon routinely visit salt licks. Greater One-horned Rhinos enter *Shorea robusta* forests and visit licks used by other species as well.

Communication

Rhinoceroses rely on vocalizations and urine, feces, and scent to communicate with conspecifics. They possess acute senses of hearing and smell and relatively poor eyesight. These attributes suggest that visual displays are less important than olfactory and auditory cues. The ears of rhinos swivel independently and their elongated shape allows them to detect sounds in a wide arc.

Various field studies have documented the vocalizations of free-ranging rhinos. Greater One-horned Rhinos emit at least ten vocalizations. A common sound is the snort, typically uttered when one individual encounters another, either approaching or being approached. Two snorts are most common, but from one to twenty are possible, depending upon the intensity of the encounter. One of the loudest signals is the honk, which can be heard over several kilometers. The honk is associated with head-to-head encounters, generally occurring during the ensuing flight or chase of one animal by the other. In most cases, the loser in these encounters does the most honking. A bleat is a sound associated with submission during head-to-head encounters or during flight, and often during courtship chases. A roar is restricted to intense encounters, both between males and females and between females. One of the most incongruent sounds uttered by this species is the squeak-pant, normally uttered by males during courtship chases. The moo-grunt is the common contact call between mothers and calves. It is of low intensity and heard over only a short distance, whereas the others are all quite loud and carry far.

Black Rhinos utter some similar and a few different vocalizations. Loud, aggressive sounds occur during confrontations, including growls and trumpet calls. A snort can also serve as a greeting, as in the Greater One-horned Rhino. Black Rhinos snort when angry and make sneeze-like calls as alarms. Fear is expressed as a high-pitched “wonk”, escalating to a scream when terrified. In contrast, a “mmwonk” is a peaceful sound. The squeak in the Black Rhino may be similar to the moo-grunt in the Greater One-horned. Other emotions, such as greetings, anxiety, and reassurance may be expressed through the rapidity of the breathing.

White Rhinos have a similar repertoire. They make a panting sound used as a contact call. They grunt and snort during courtship, often making a “hic-throb” noise when following a

cow in estrus. Agonistic sounds include squeals of distress and deep bellows or growls. If attacked, a male will display a horn-and-head threat posture, with his ears set back, while emitting shrieks.

The Javan Rhino is much less vocal than the other rhinos; in fact, very few Javan Rhino vocalizations have ever been described. In contrast, the Sumatran Rhinoceros is the most vocal species. Zoo observations reveal frequent vocalizing; limited data on free-ranging animals seem to be similar. Three distinct noises have been described. The "eep" is a short, one-second-long yelp, and the most common sound uttered. The "whale," a vocalization that sounds similar to a humpback whale's, is the most song-like and also common. This "song" varies in pitch and lasts from 4 to 7 seconds. The whistle-blow is so named because it consists of a two-second-long whistling noise and a burst of air in immediate succession. This third sound is the loudest of all and can be heard over several kilometers in South-east Asian rainforests.

At least one species, the White Rhino, has been shown to use subsonic or ultrasonic communication similar to elephants. We might assume that Black Rhinos, also a species of open country, might utilize subsonic messaging as well. Use by the three forest dwellers in Asia has yet to be tested.

All extant species possess pedal scent glands and probably use secretions from these to mark territories, home range, or simple presence. Females in estrus are likely detected by males from scent deposited by these glands; several observers have seen males of the African species and the Greater One-horned Rhinoceros follow behind estrous females with their nostrils to the ground prior to catching up to the female and beginning active courtship.

Rhinoceros urine and feces also figure prominently in communication, as is the case with many large mammals. Dominant male Greater One-horned Rhinos perform a dominance display where they are able to evert their penis and shoot sprays of urine up to five meters behind them. Such displays are typically performed in front of other males, breeding age females, or when humans riding elephants approach too closely. Dominant territorial White Rhino bulls also spray urine onto bushes while scraping with their hindlegs. Female Black Rhinos are reported to spray urine more often when receptive for breeding. Rhinoceroses react to the scent of conspecifics by sniffing the ground or vegetation where other males have sprayed urine. Several species are reported to twist or mangle saplings, and make a grimace known as a lip curl, when encountering scent on saplings and other marking spots. This behavior is shown by both males and females; rhinos also use this when smelling urine to assess reproductive status.

The centre for scent deposition, communication, and other social interactions is the latrine. Rhinoceroses, like many ungulates, often return to the same place to defecate. The ecology of latrines has been studied in greatest detail in the Greater One-horned Rhinoceros in Royal Chitwan National Park, Nepal. The majority of defecations occur within 10 m of existing latrines. A mother's defecation often stimulates her calf to defecate.

Latrines occur around feeding stations, tracks leading to wallows, trail intersections, or beneath clumps of shrubby vegetation or trees in grasslands. These sites are very important for individuals to identify each other. Coming upon these spots, rhinos will smell to see who is in the area and add their own marking. In territorial situations in some species, males mark their territory with dung piles and by urine spraying. Scrapes made by the feet in the ground

and by twisting saplings also seem to convey important information. Some rhino species have a peculiar habit of defecating in a latrine, scraping their back feet in the dung, and then leaving the scene in a ritualized display. Sumatran and Javan Rhinoceroses defecate in piles, but do not engage in such scraping, judging from the absence of such tracks. Perhaps in the wet forests of South-east Asia the method is not useful for spreading odors. However, the Greater One-horned Rhinoceros use the same behavior during the monsoon rains. Territorial male White Rhinos also use dung middens, which tend to be concentrated near the boundaries of their territories. Sometimes Black Rhinos defecate on these middens.

Wallowing is an essential behavior to address thermoregulation, but is also often used to exchange information. Male Greater One-horned Rhinos frequently urinate in the large forest pools that serve as wallows and can hold many rhinos. Wallowing sites as a centre for communication may be seasonal in nature, because during cool periods, rhinos may not use wallows. In the ever-humid habitats occupied by Javan and Sumatran Rhinos, wallows may be used regularly throughout the year, so their role as hubs may be of greater importance than they are to the other species.

Because rhinos have poor eyesight in comparison to their other senses, body language is often the least common form of communication. However, at close quarters it can be quite important in influencing outcomes of hostile encounters between males. Male Greater One-horned Rhinos face off, open their mouths to show off the size of their tusks, bellow, and also show the size of their bib and neck skin folds, which likely is a way of advertising the fighting prowess of an individual. Black Rhino bulls will sometimes display an aggressive ritual toward a potential rival. They will smell, spray repeatedly, scrape, trample, and bash bushes with their heads. In attack mode, they combine behavioral posturing with snorts. An uplifted tail in males or females may signify several emotions, including curiosity, alarm, or sexual receptivity. Erect ears perhaps indicate curiosity; as in other species, flattened ears signify anger.

Food and Feeding

Rhinoceros consume a range of plant types, from grasses, sedges, and aquatic plants to evergreen leaves of shrubs and saplings, to fruits and flowers, and also may eat soil. When cultivated plants such as rice, wheat, maize, and lentils are available, the Asian rhinos, especially the Greater One-horned Rhino, can be notorious crop raiders. Rhinoceroses also eat among the most toxic species in the plant kingdom, many avoided by other herbivores, such as a wide range of plants in the spurge family (Euphorbiaceae) and those that are skin irritants (Anacardiaceae and Urticaceae).

A rough classification would place the White Rhino of Africa and the Greater One-horned Rhino of south Asia as grazers and the Black Rhino and two remaining Asian species as browsers. White Rhinos are exclusively grazers and use their wide mouth and a hard pad to clip short grasses. Their repeated feeding in such short grasslands leads to the propagation of "grazing lawns," large open areas where the grass cover is maintained at a golf-course-like height. Grasses in such grazing lawn communities are adapted to intense grazing and trampling by the ponderous animals; they regrow quickly and are high in nitrogen content. Other, much smaller herbivores take advantage of these prime grazing areas, both for their high protein value and as a place to forage where it is safer to feed while remaining watchful for large predators.

Greater One-horned Rhinoceroses eat a wide variety of grasses, but in prime habitat concentrate their feeding along the floodplains of large rivers and streams. Here, the dominant grass is often *Saccharum spontaneum*, a wild sugar cane. *Saccharum spontaneum* produces green shoots throughout the year, stimulated by inundation, fire, cutting by villagers, or previous grazing by rhinos or elephants. Greater One-horned Rhinos wrap their prehensile upper lips around the stems and strip off the tender leaves. One study found that *Saccharum spontaneum* has among the highest protein/fiber ratios of all grasses, and fecal analysis showed that this grass species accounts for 50% of the diet in almost every month of the year, peaking in the pre-monsoon and monsoon (May to September). This species grows among the tallest grasslands in the world, commonly referred to as elephant grasses. Two of the tallest species, *Narenga porphyrocoma* and *Themeda arundinacea*, typically dominate on terraces higher above the floodplain than various *Saccharum* species. These two highly lignified genera, the most common grasses in many of the reserves, are avoided by Greater One-horned Rhinos, except shortly after fires stimulate new shoot growth. The distribution of *Saccharum spontaneum*-dominated floodplains in relation to *Narenga* and *Themeda* predicts the distribution and densities of the Greater One-horned Rhinoceros. These floodplains are maintained by annual, intense disturbance events—monsoon floods—that are tracked by rhinos. Large feeding aggregations form in places buried by silt from such floods.

Unlike the White Rhino, which consumes only grass, the Greater One-horned Rhino greatly increases the amount of browse in its diet during the cool season (mid-October to mid-February). Two species in particular, *Litsea monopetala* and *Mallotus philippinensis*, form the bulk of the diet during this period. Females with calves will walk down saplings of these species to make the most tender leaves available for their young calves. The switch to browse reflects a change in the phenology of the grasses they normally consume, with most going dormant or drying up, so that browse becomes a more palatable option. In winter, scrub vegetation often found along the buffer zones on the edge of parks holds a particular attraction for the rhinoceroses. They feed heavily on several browse species prevalent there, including *Callicarpa macrophylla* and *Cassia tora*.

During the end of the dry season and into the monsoon, Greater One-horned Rhinos increase the amount of aquatic vegetation they consume. Cattails (*Typha*), and aquatic sedges, grasses, and other species figure more prominently in the seasonal diet. The rhinos also help to maintain grazing lawns in grasslands close to rivers. As in Africa, smaller herbivores like Chital (*Axis axis*), Hog Deer (*Axis porcinus*), and Indian Hares (*Lepus nigricollis*) take advantage of the close-cropped lawns for feeding.

The remaining three species, the African Black Rhino and the Sumatran and Javan Rhinos of Asia are all browsers. The main difference between the Black Rhino and the other two species is that the Black Rhino shuns forest while the two Asian species are predominantly forest dwellers and thus forest browsers.

The Black Rhino uses its prehensile upper lip to pluck leaves, grasp stems, and facilitate feeding on broad-leaf shrubs and saplings. The wide range of habitats this species exploits generates a list of over 200 species of browse plants eaten by this large herbivore. Because the distribution of Black Rhinos excludes areas covered by forest, their search for browse includes plant species adapted to life in savannas, grasslands, and woodlands. Of particular interest is the component of the diet from plant genera such as *Euphorbia*, which are highly toxic and avoided by other herbivorous mammals, or whose milky sap causes skin irritation

in humans. Both in East Africa, where the Black Rhino feeds on the candelabra tree (*Euphorbia ingens*) and in the desert grasslands of north-western Namibia, where one of the favorite browse plants is the endemic *E. damariana*, Black Rhinos seem to relish plants with toxic latex. This is an important dietary staple and the rhino is able to detoxify the noxious compounds in its large caecum. The sap from these plants burns the skin of humans. Black Rhinos also ingest fruit, and like the three Asian species, can be important seed dispersers for certain fleshy fruited plants in some parts of their range. *Spirostachys africana* is a Euphorbiaceae and makes up the largest contribution of any species to the woody diet of the Black Rhino in Hluhluwe-Umfolozi Game Reserve, South Africa.

Most of what is known about Javan Rhinos is from indirect signs of browsing. Few direct observations have been recorded and to date, fecal analyses of Javan Rhino diets, from either the Ujung Kulon population, or the Cat Loc remnant, are lacking. Some of the food plants listed for the Javan Rhino in Ujung Kulon may actually have been browsed by the sympatric wild cattle species, the Banteng (*Bos javanicus*). There are more than 100 species in Ujung Kulon listed as browse, but no quantitative data on use are available. The rhinos in Ujung Kulon avoid the understory palm *Arenga pinnata*. Some biologists feel that with the maturing of the Ujung Kulon forest, the spread of *Arenga* has reduced the amount of browse available in the understory for rhinos and limited the growth of this population. Others suggest that the eruption of Krakatoa in 1883, which triggered a tsunami that devastated low-lying areas, likely set back the natural succession of this forest and improved feeding conditions for the Javan Rhino during the first half of the 20th century.

In Vietnam, some of the plants browsed include the climbing acacia (*Acacia pennata*—also eaten by *R. unicornis*), two species of rattan (*Calamus*), two bambusoid grasses (*Bambusia*), *Cyathea* (a tree fern), and *Strychnos nux-vomica*. The last species contains highly toxic seeds and probably toxic compounds in the leaves; it remains unclear if Javan Rhinos eat only the fleshy fruits or browse this species as well.

Historically, the occupation of alluvial floodplains in Bengal and Assam suggests that grasses were a much larger part of the diet in such habitats. When at normal densities, Javan Rhinoceroses, given their size and browsing behavior, might be expected to have a major impact on seedling and sapling recruitment of woody plants, like their congener, the Greater One-horned Rhinoceros.

Information about the diet of the Sumatran Rhinoceros remained largely anecdotal until semi-captive animals in the Tabin Reserve, Sabah, Peninsular Malaysia, and southern Sumatra were provisioned and observed eating browse from adjacent forests. This provisioning became a de facto set of feeding trials. As a strict forest dweller, this species seems to prefer pioneer and second-growth plants. These include young trees, treelets, and saplings from the following genera: *Macaranga*, *Homolanthus*, *Mallotus* (Euphorbiaceae); *Nauclea*, *Neonauclea*, *Hymenodictyon* (Rubiaceae); *Ficus*, (Moraceae); *Poikilospermum* (Urticaceae); *Grewia* (Tiliaceae); *Pterocymbium* (Malvaceae); *Uncaria* (Rubiaceae); and *Merremia* (Convulvulaceae—lianas and vines). Typically, fast-growing trees and treelets of second growth and light gaps are lower in secondary compounds than plants of the primary forest understory, and this factor may also influence diet selection. Like other browsing rhinos, this species will walk over saplings, knocking them down to reach leaves clustered at the tips of branches.

Greater One-horned Rhinoceroses seek out cultivated areas and the same was likely true with Sumatran and Javan Rhinos when they were more abundant. Croplands attract Greater One-horned Rhinos, and require nightly vigilance by farmers to scare the animals away. Rhinoceroses are partial to rice, corn, and wheat at ripening. They seek out and devour hot chilli plants, but feed only sparingly on the mustard crop. Most of the damage to crops by the rhinoceros is restricted to a kilometer from park boundaries. That Sumatran and Javan Rhinos were shot by tea planters as agricultural pests suggest that in the early 19th century, these species played a similar role as crop raiders to the role Greater One-horned Rhinos do today.

Megaherbivores, such as the rhinos, are more than just passive grazers and browsers that occupy wild habitats. Their grazing, browsing, and defecation into latrines change the habitats for other species and the rhinos themselves. Thus, rhinos are true landscape engineers. White Rhinos act like giant mowing machines and their ability to crop short grasses close to the ground creates what ecologists term "grazing lawns." These golf-course-like grasslands are sought out by much smaller grazing ungulates, hares, and other herbivores, who benefit from the nutritious regrowth and probably are better able to detect predators while feeding in open areas. Black Rhinos are generalist browsers, but their feeding behavior also influences the structure and composition of thickets. White Rhino dung middens create nutrient hot-spots and also provide good germination sites for some species. Germination of some woody species such as the sausage tree (*Kigelia africana*) is facilitated by passing through the gut of the Black Rhino.

The best-studied examples of rhinos as landscape architects come from Nepal. In Royal Chitwan National Park, it was found that browsing by Greater One-horned Rhinos suppressed vertical growth for a number of browse species. Essentially, the tree species that reach the canopy of riverine forests are those that as seedlings and saplings are unpalatable to the rhinos and elephants. Greater One-horned Rhinoceroses have other profound effects on their landscape—they exert strong selective pressure on forest structure and canopy composition by inhibiting vertical growth of saplings, by frequent browsing and trampling. Using a series of exclosures, one study demonstrated that the rhinoceros inhibited vertical growth of an abundant tree species, *Litsea monopetala* (Lauraceae). Although stunted saplings of this species dominated the understory 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 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 on the south Asian floodplains, where tree diversity is low and estimates of large browser biomass in riverine forest-grassland mosaics are extremely high.

Exclosures erected in and near river beds following Cyclone Domoina floods indicated that protection from browsing by Black Rhinos (such as that provided by piles of driftwood logs) was important for the successful establishment of new sycamore figs in Umfolozi in KwaZulu-Natal, South Africa. Rhinos also figure into what one biologist termed "the megafauna dispersal syndrome." Certain tree species produce fruits that are large, hard, and dull-colored upon ripening and avoided by bats, birds, and monkeys. Some of these fruits are relished by Greater One-horned Rhinos, and their latrines can contain millions of seeds. Those latrines found in grasslands become beachheads for the colonization of shade-intolerant riverine forest trees. The interaction between rhinos and certain trees producing these megafaunal fruits is such that the feeding behavior of the Greater One-horned Rhino would rapidly convert tall grasslands back to riverine forests if monsoon floods and annual

fires did not cause extensive mortality among tree seedlings. One can only assume that similar interactions occur with Javan and Sumatran Rhinos and rain forest plants.

The Greater One-horned Rhinoceros ingest the fruits of at least 23 species of herbaceous and woody plants. Seeds manured into the rhinos' grassland latrines yield distinct assemblages of dicotyledonous plants. *Trewia nudiflora*, the most common riverine forest tree in Chitwan, and the herb *Cassia tora* accounts 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.

The rhinoceros plays an important role in dispersal and recruitment of woody species in riverine grasslands. In captive rhinos, *Trewia* seeds remained in the gut from three to seven days, but gut treatment itself had no significant effect on germination success. Seeds defecated on grassland latrines developed into robust seedlings, whereas seedlings on forest latrines generally died soon after germination or after the monsoon, 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 fewer than 10% of plant species were dispersed by large mammals, but in floodplain forest and savanna, large-mammal-dispersed species represented the most common trees.

Breeding

Age at first reproduction is usually six to seven years for White, Black, and Greater-one Horned Rhinos, but can vary among individuals and can be shorter or longer depending on conditions. No comparable data are available for the more secretive Javan and Sumatran Rhinos, but their age at first conception is probably similar. Age at first reproduction is a vital life history statistic for endangered species such as rhinos, because shifts in onset to early breeding can help populations recover more quickly and delays in the onset of breeding slow recovery. Based on zoo records from animals of known age, Greater One-horned Rhinos may conceive as early as three years, and White Rhinos at 3-7 years. In the wild, calves of these ages are often still with their mother and do not breed. Age at first reproduction is likely sensitive to forage conditions.

In male Greater One-horned Rhinos, and likely for other species, breeding may be delayed until years after bulls have reached sexual maturity. An individual physiologically capable of breeding may be restricted to areas where breeding-age females rarely congregate. Young adult males venturing into areas where breeding age females cluster are often chased and sometimes killed by the dominant bulls. One study estimated that most bulls likely did not have a chance to breed until at least the age of 13–15 years, at which time they would be strong enough to challenge the dominant male for access to females.

Offsetting a long period until first conception and long inter-calving intervals is the longevity of females. Some individually recognizable Greater One-horned Rhinos were over 40 years old and still breeding. Zoo records show that females can live to nearly 50 years of age. So being able to breed until senescence partially balances the late age at which breeding begins for these megafauna. The lifespan of males seems to be much shorter. Adult male Greater One-horned Rhinos seldom persist past 30 years of age. Once their tusks break off in combat, they are defenseless against bulls with intact tusks and are often killed by other males. These

teeth grow back if broken off, but at a slow rate, leaving adult bulls without their main form of defense for some years.

The extant rhinoceroses are tropical, so we might not expect to see distinct seasonality of births, or if so, to track the oscillation of wet season and dry season. A data set of 113 calf births in Greater One-horned Rhinos showed no discernable peak in births. Gestation for this species is 16 months. In one study in southern Africa, Black Rhinos showed a distinct birth peak in January and February and again between June and August, but in another study in East Africa they exhibited no such seasonal variation. Gestation is 15 months. In the Southern White Rhino a bimodal birth pattern is the norm, with one peak in March and another in July. Gestation is also roughly 16 months. The Garamba population of Northern White Rhinos held too few individuals to discern any pattern of birth interval. Data for free-ranging Javan and Sumatran Rhinos are too few to detect seasonal patterns or to conclude that there is no pattern.

Another vital statistic, interbirth interval, also seems sensitive to environmental conditions. Under excellent forage conditions, where rhinos are not overstocked relative to carrying capacity, both Black and White Rhinos in Africa can have remarkably short interbirth intervals of only 2–2.5 years. Interbirth intervals among 13 known Greater One-horned Rhinos in Nepal was 46 months. Among 87 adult females studied, older females tended to exhibit a longer interbirth interval.

Courtship behavior is rather aggressive across the order Perissodactyla, but seems to peak among the rhinoceros species. Male Black Rhinos engage in intensive struggles to gain access to females, and mortal combat is higher than for any other mammal recorded to date; about 50% of males and 30% of females succumb to injuries associated with males attempting to gain access to females.

In the Greater One-horned Rhinoceros and in the other four species, males actively pursue females during long courtship chases (which can be more than 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. There are also at least two reports of captive females dying from internal injuries sustained during courtship. During one study, a radio-collared dominant male killed a newborn calf that it had not sired. Females begin an estrous cycle again soon after the loss of a calf.

Greater One-horned Rhinoceros males form dominance hierarchies, and an alpha male's tenure is short in comparison with his total longevity. The long interbirth interval (mean, 46 months) and the presence of fewer than 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 behavior when a female cycles into estrus. Non-breeding males seldom use prime grazing areas dominated by the grass *Saccharum spontaneum* and occupied by dominant males. Dominant males attack young-adult males who 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.

During fights to determine dominance, the males slash and gouge one another with the 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. 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 with the incisors. The extensive primary and secondary neck and shoulder folds found in dominant males may serve 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 first, most severe attacks 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 meters of one another.

Young Sumatran Rhino males are often very aggressive toward females and are known to injure or even kill them during courtship. A puzzling aspect about rhinoceros behavior is why courtship is among the most violent among mammals. Such behavior seems maladaptive in light of the few breeding opportunities available to males. Why should a male risk seriously injuring perhaps the only female that could be receptive during his tenure as dominant male in an area? This feature remains a mysterious aspect of the behavior of this species. Violent courtship is typical of the Perissodactyla, and other species of rhinos engage in courtship chases. Females testing the strength of males may intensify the aggressive nature of these chases by running across home ranges of competing males. Alternatively, courtship chases may be required to trigger sex hormones, enabling males to increase the volume of seminal fluid before ejaculation. Mortality of the females may result when courtship chases escalate beyond a safe threshold, or perhaps when a male chasing a female is about to enter the home range of a stronger competitor, so the male must subdue the female at all costs to have a chance to breed.

Movements, Home range and Social organization

Rhinos have the capacity to move rapidly over large areas both daily and seasonally, but as adults they tend to be rather sedentary when in prime habitat. Radio-collared Greater One-horned Rhinos rarely moved more than 5 km during a 24-hour period in any season. Adult breeding males travelled slightly longer distances during the twenty-four hour cycle. These movements were sufficiently large to allow animals to cover most of the core area of the home range in a few days. Most of the daily movements were circular and involved zig-zagging between feeding areas; rarely did the rhinos travel the entire distance in a linear fashion. Viewed from a different perspective, radio-collared rhinos rarely ventured farther than 2 km from riverbanks. Exceptions to this rule occur during periods of inundation during the monsoon. Rhinos and their calves can be swept away by surging waters and typically move to higher ground during floods. Another exception is after translocations, when adult females translocated to new reserves wander over tens of kilometers before settling into a small home range. White Rhinos moved about 5 km during the wet season. During the dry season, however, they routinely moved slightly longer distances to reach water holes.

Among mammals, home range size scales with body size. Thus, the smallest terrestrial mammals show limited movements and narrow home ranges, and at the other extreme, African and Asian elephants may move over large areas, both seasonally and annually, and use enormous home ranges. Despite their size, interpreting movements, home range size, and social organization of megaherbivores is difficult unless data are drawn from individually recognizable and visible individuals or those studied using radio-telemetry. The thick vegetation in most rhino habitats over much of the calendar year precludes following single individuals over a 24-hour period unless the animals are habituated or radio-collared.

Therefore, much of the information in this section is drawn from studies of those rhino populations where individuals have been identified or followed using telemetry.

Home range of Greater One-horned Rhinos in Royal Chitwan National Park are remarkably small for a megaherbivore. Adult female ranges averaged $2.9 \text{ km}^2 (\pm 0.9 \text{ km})$, and showed almost no variation among the three seasons of the year (cool, hot-dry, monsoon). Males also had small annual home ranges (3.3 km^2). Rhinos translocated from Royal Chitwan to Bardia National Park in Nepal occupied much larger home ranges, often 7–10 times larger. The explanation for this marked difference is that Chitwan rhinos live in prime habitat dominated by a highly nutritious forage plant, their staple food, the wild sugar cane (*Saccharum spontaneum*). The Bardia population took a long time to adjust to new surroundings because preferred habitat was much less widespread and the habitat was drier for much of the year. Even so, home ranges in both reserves were distributed close to rivers.

Much of the data on movements and home range of the other Asian species, Javan and Sumatran Rhinos, is anecdotal and remains speculative because both species are extremely difficult to observe in the wild and their presence can be discerned mostly from tracks. Nevertheless, one estimate of home ranges for Sumatran Rhinos was as large as 50 km^2 , based on recognizable footprints of known individuals. Home ranges of Javan Rhinos may be constrained by the small size of the reserves in which they are found.

White Rhinos do not do well in areas subjected to very cold frosty winters or in very arid areas. The highest White Rhino densities occur in savannas where soils are reasonably nutrient-rich and rainfall levels are intermediate (around 700–800 mm), such as in Hluhluwe-Umfolozi Game Reserve (2.3 ind/km^2) in KwaZulu-Natal. In south-western Kruger National Park, the average range of adult males was 9.9 km^2 ; and it was 22.8 km^2 for females. For females, the summer wet season range was larger, 21.4 km^2 as compared with 11.6 km^2 in the winter dry season. One study recorded core areas for territorial males of an average of only 1.7 km^2 in prime Umfolozi habitat, with average female ranges lower than in Kruger, at 16.2 km^2 . However, densities were generally much lower, in the region of $0.1\text{--}0.5 \text{ ind/km}^2$. Home range sizes can be much larger, and in Garamba animals ranged over hundreds of square kilometers.

Black Rhino densities, carrying capacity, and home range sizes have been shown to vary widely over this species' range and even in the same area over time in response to habitat changes. Carrying capacity is particularly dependent on the amount of suitable food, and densities can vary widely, from 0.01 ind/km^2 in poorly vegetated desert plains to up to peak levels of around 1.5 ind/km^2 . The carrying capacity of most areas is in the range of $0.1\text{--}0.4 \text{ ind/km}^2$. Savannas are dynamic, and woody vegetation changes result in the carrying capacity fluctuating in areas over time.

Forage abundance and availability likely influences the annual home-range size of the Black Rhino, a browser like the Sumatran and Javan Rhinos. Female Black Rhinoceroses in the Lerai Forest of the Ngorongoro Crater in Tanzania (*Acacia xanthophloea* woodland with palatable dense understory) used home ranges of less than 2.6 km^2 . They expanded their range to 99 km^2 in the Serengeti grasslands, where browse quality and abundance is much lower. More typical home range sizes across southern and eastern African habitats are $7\text{--}35 \text{ km}^2$. The largest home ranges recorded for all rhinoceros species are those of the desert-dwelling Black Rhinos in Namibia, and for the Northern White Rhino, whose range can exceed 500 km^2 . In southern and eastern Africa, home range sizes vary substantially from

area to area depending on habitat quality and carrying capacity. In general females' home ranges are greater than for territorial adult males. For comparison, the largest Asian megaherbivores, Asian Elephants, occupy home ranges of about 85–115 km².

Defending large feeding areas from conspecifics would seem like a fruitless strategy from the point of view of a grazing or browsing megaherbivore. Greater One-horned Rhinos are not strictly territorial, but form dominance hierarchies. Males vie to maintain control over grazing areas where breeding females tend to concentrate. Home ranges of females overlap extensively, similar to the other grazer, the White Rhino. In one study of radio-collared Black Rhinos, females had overlapping home ranges but adult males occupied exclusive home ranges. Black Rhinos like leguminous herbs, and competition from other browsers can affect them.

Yet in other parts of the Black Rhino range, extensive overlap and even sharing of home range among males has been reported. The most territorial members of the family seem to be White Rhino bulls, who only leave their small territories to visit distant waterholes outside their area. Even in this species, however, the establishment of dominance hierarchies or true territoriality can vary, even within a population. In a study in Royal Chitwan National Park, Nepal, one radio-collared male maintained an exclusive territory for about two years before he was usurped and killed by another bull. Simultaneously, in an adjoining grassland, at least four powerful males rotated through a dominance hierarchy.

Relationship with Humans

Rhinos have been the subject of mythology, awe, and terrible persecution for their horns. The Western world had its first introduction to the rhinoceros through the famous woodcut created by Albrecht Dürer in 1515. The depiction is not entirely accurate, as the artist created his own interpretation from a written account and simple sketch by an unknown artist of a captive Greater One-horned Rhinoceros brought to Lisbon, Portugal from India in 1514. Regardless of the accuracy of his woodcut, or perhaps in part because of it, the image fueled the legend of the unicorn. Here was a living creature with a horn on its face, although a bit more ponderous than the elegant unicorn.

During the colonial era in Africa and Asia, European colonists, especially the nobility, hunting enthusiasts, and naturalists gained much more familiarity with rhinoceroses. All species were abundant then. An oft-repeated story in the literature is that Javan Rhinos, the rarest of all living species, "were once shot by tea planters in Java who regarded the numerous animals as crop pests." In south Asia, Greater-one Horned Rhinos were often found in royal hunting reserves, and commoners entered into these areas at risk of being arrested or shot. Until the end of 20th century in Nepal rhinoceroses were considered holy animals and the property of the reigning monarch; in fact, an inquest for a deceased Greater One-horned Rhino required a more thorough investigation than for that of a human being.

The end of the colonial era brought a shift in circumstances for free-ranging rhinos. Conflicts with agriculturalists greatly reduced habitat. Rhinos became refugees in areas where soils were too poor to farm (Africa) or livestock diseases (sleeping sickness) or deadly malaria (Africa and parts of Asia) kept humans from farming.

The most damaging aspect of the human relationship with rhinos has to be the illegal trade in rhino horn. As stated earlier, the rhinoceros horn is not at all like the horns of cattle, sheep, and goats, which contain a bony core. Rather, rhinoceros horn is composed entirely of densely appressed hairs. According to popular belief, Asian cultures value rhinoceros horn as a powerful aphrodisiac. In fact, traditional Chinese medicine has never used rhinoceros horn as an aphrodisiac; this is a Western misconception that in some parts of Asia is viewed as a kind of anti-Chinese hysteria. Another misconception is that much of traditional Chinese medicine is animal-based. The truth is more than 80% is plant-based.

The reality is that traditional Chinese medicine considers rhinoceros horn an essential curative. Its primary role is to alleviate life-threatening fevers for which no alternative is effective. Thus, rhinoceros horn is more prized than any of the other controversial animal products, such as Tiger bone or penis. Despite the questionable value of rhino horn as a fever reducer, alternatives do exist, and the main consumer nations—China, South Korea, Taiwan, and Hong Kong (when under British governance)—banned the manufacture and trade in powdered rhino horn and its medicinal derivatives by the end of 1993.

The Chinese government allows the use of medicine made from confiscated rhinoceros horns, which were locked up after the ban, as a fever depressant in hospital emergency cases. Traditional medicine specialists in South Korea and Hong Kong calculate that one rhinoceros horn per consumer country per year (covering the ten or so such nations) would provision this need. Rhinoceros horns are typically quite large and the dosage requires a minute shaving from the horn. Thus, the belief that horn is still in high demand is dangerous. Probably in part because of this misconception, poachers and traders are still persecuting rhinos and stockpiling horns.

In recent years Vietnamese citizens have been increasingly implicated in rhino poaching in South Africa, where rhino poaching is currently escalating. It has been rumored that rhino horn is now being used to treat cancer in Vietnam, and this may have fuelled a spike in price and increased poaching. If true, this would represent a new use of horn.

Besides supplying the medical market, the horns have been sought after for dagger handles by men in Middle Eastern countries, especially Yemen and Oman. This problem has been largely solved by the substitution of horns from domestic animal species.

The extensive illegal trade in rhino horn has been well documented. Surveys showed that the horns of the three Asian species are about three times more expensive than those of the two African species, with Asian rhinoceros horn fetching US\$ 30,000/kg. If the large discrepancy between the price of Asian and African horn is accurate, it may in part reflect the historical demography of the five species, in that until quite recently, the African species were much more abundant than the Asian species. More likely, it is attributable to the belief among users of ground rhinoceros horn that the smaller horns of the Asian species yield the most potent medicine.

Status and Conservation

The status and conservation of the rhinoceroses range from extraordinary hopeful to terribly pessimistic, depending on the species in question. Four features deserve closer inspection. First is the truly staggering contrast between the former dominance of rhinoceroses and their

current rarity. Second is the extirpation of populations, reducing the free-ranging animals to a single location or fewer than five locations for several of the species. Third is the negative effect misguided captive breeding programs can have, as opposed to in-situ efforts buttressed by strict protection regimes and incentives to promote community participation in the conservation of endangered species. Fourth is that rhinos will remain what biologists term a "conservation-dependent" species; their survival and recovery depend on strict protection of all populations from poachers who seek their horns and from threats of conversion and degradation of their habitats by agricultural encroachment and infrastructure development.

Rhinoceroses were an abundant, widespread component of large mammal faunas on several continents for eons. The rapid decline of the extant species began at different stages for each of the five species. The Southern White Rhinoceros was abundant prior to the colonization of southern Africa, and dropped to its low point of less than 100 individuals in one game reserve in South Africa around 1900. It has made an astonishing recovery, from that nadir to today's global population, which, exceeding 17,000 animals, is often held up as the most remarkable example of wildlife recovery globally. Through intensive protection and translocation, Southern White Rhinos have been re-established from the founder population in the Hluhluwe-Umfolozi Game Reserve to other parks in southern Africa. That such a large, slow-breeding, long-lived mammal, under acute threat from poachers for its valuable horn, can show such a dramatic recovery buoys hope among conservationists not just for this population and the other rhinos, but for all endangered species.

The decline of the Northern White Rhino paints the opposite picture. In the decades before 1900, there may have been more Northern White Rhinos in Sudan, the Central African Republic, northern Uganda, and the DR Congo than Southern White Rhinos in South Africa. However, by the mid-1980s, civil wars and unrest led to widespread poaching in these countries and the Northern White Rhino population was decimated. The last stronghold became Garamba National Park in the DR Congo. A dedicated group of biologists and park rangers managed to grow this remnant population to at least 32 individuals before a further outbreak of poaching wiped out the rhinos by the mid-2000s. As of 2008, the World Conservation Union considered the remnant free-ranging population of Northern White Rhinos in Garamba National Park (DR Congo), to be extinct; however, there are as yet unsubstantiated rumors that a few animals may survive in a remote part of Sudan. The loss of this last population reinforces the strong link between civil unrest, war, and widespread availability of weapons in the countryside as the death sentence for endangered large mammals. Dedicated rangers can protect and recover endangered large mammals, but if the local populace is engaged in fighting, and if returned soldiers are allowed to keep their weapons upon cessation of armed conflict, extinction is the likely outcome. The demise of this population, considered a subspecies, became all the more tragic when in 2010 a scientific study provided morphological evidence and new genetic data elevating the Northern White Rhinoceros to full species status. This new designation, if it stands, would put the Northern White Rhino in the unenviable situation of going extinct before it was recognized in the scientific literature as a true species. The only hope of reviving this species is through a remnant population relocated from a Czech zoo to a private reserve in Kenya in the hope this will stimulate breeding. However, because these four animals are inter-related (founder genome equivalent of only 1.71), conservation biologists advise that the prognosis for the survival of "pure" Northern White Rhinos is not good and the best hope now is to try to conserve as much adaptive Northern White Rhino genes as possible for their eventual reintroduction into former range or in similar habitat nearby. This will probably require

intercrossing of remaining Northern White Rhino with Southern White Rhino and there can be no guarantees this will succeed.

The Black Rhinoceros was once the most abundant of all five extant species across much of sub-Saharan Africa. Estimates of its numbers around 1900 range from 300,000 to 1,000,000. Black Rhinos experienced what biologists term a range collapse of epic proportions. Core populations were wiped out or greatly reduced in places like the Ngorongoro Conservation Area, Serengeti National Park, and Selous Game Reserve in Tanzania, across much of Zimbabwe, and in south-western Africa. The West African subspecies is likely extinct in the wild. Through intensive efforts by the African range states governments, with assistance from the African Elephant and Rhino Specialists Group of IUCN, NGOs, and foreign donors, the Black Rhino is staging a comeback. In some locales, small breeding populations were established in heavily protected game ranches. These populations recovered rapidly, but the limited spaces quickly reached carrying capacity. Translocations from these small ranches have helped to re-establish rhinos in more free-ranging situations. Perhaps the best success stories for this species both come from Namibia. Strict protection of Etosha National Park in north-central Namibia has allowed the population to grow to over 800 animals, and a massive translocation program has been instigated, supported by the Ministry of the Environment and the World Wildlife Fund. Even more promising is the presence of free-ranging Black Rhinos on communal conservancies in north-western Namibia. Here, local communities own the wildlife on their communal lands and protect it to generate revenues from ecotourism; they also protect game species on their lands for trophy hunting. This ecosystem service has sparked demand and competition from conservancies wanting to be able to show tourists free-ranging Black Rhinos without having to surround the tourists with armed guards as elsewhere in East Africa. The potential for this program bodes well for Black Rhino recovery efforts.

Some southern African countries experimented with a controversial technique to reduce the incentive to poach by dehorning free-ranging rhinos. This response was developed in desperation, poaching being rampant in the early 1990s, and resources inadequate to protect Black Rhinos in large remote reserves. One advantage of dehorning is that animals remain in their native habitats and established territories. Another advantage is that in remote areas, where frequent anti-poaching patrols are too costly, dehorning dissuades poachers from even searching for rhinos. Theoretically, only a portion of the population needs to be dehorned because, given the poachers' high failure rate, they would eventually give up hunting for rhinos with horns. The word would spread among poaching rings that the costs far outweighed the benefits of a successful poaching effort.

Namibia and Zimbabwe continued dehorning for several years, but eventually shut down these programs. The unit cost of dehorning proved too high—some estimates put the cost at US\$ 1500 per individual. Compounding the high unit cost is that rhinoceros horn regenerates quickly. Poachers consider even a few centimeters—the first year's growth—valuable. In many areas, poachers appeared to have killed dehorned rhinos out of spite, or they shot first and looked later to find that the animal was hornless. Although sample sizes were small and the findings were disputed, some researchers suggested that dehorning Black Rhino cows exposed calves to high predation risks by hyenas and Lions. Dehorning, in hindsight, was a valiant but wasteful attempt to save a nucleus population until poaching could be brought under control. Even if initially successful, dehorning is only a stop-gap measure, impossible to maintain once a decimated population has recovered beyond a few dozen individuals.

The current estimate of the total free-ranging population of the three Asian species is less than 2700 individuals. Even more sobering is the statistic that only two populations of Asian rhinoceroses currently contain more than 100 individuals. The rapid decline of Asian rhinoceros populations is a direct result of relentless poaching pressure and loss of habitat.

Poaching has decimated populations among all three Asian species, but each shows a different trajectory and set of secondary threats. The status of the Greater One-horned Rhinoceros more closely resembles the Black Rhinoceros of Africa. Before agriculture spread to the Gangetic and Brahmaputra River floodplains of south Asia in 1400 ad, the Greater One-horned Rhino may have numbered 475,000 or more. The presence of a deadly strain of malaria protected much of their habitat, making it unsuitable for humans until malaria was eradicated in the late 1950s. Only a few indigenous groups resistant to this strain lived near rhino habitat, and they did little poaching. Moreover, many of the current rhino sanctuaries were formerly royal hunting reserves and protected from intruders by the reigning monarchs. Two core populations remained in Royal Chitwan National Park in Nepal and Kaziranga National Park in Assam, India. However, populations declined to as low as 60–80 by the late 1950s and early 1960s in Nepal. Numbers dropped to less than 100 in Kaziranga around 1900. Many smaller reserves in Assam and West Bengal had numbers in the single digits or under 20 individuals in the 1970s.

Since 1986, the turnaround has been dramatic. Following the example of translocation programs designed to rebuild African rhino populations, the government of Nepal began an ambitious effort to translocate animals from Chitwan to other reserves. There are now five reserves in the western Terai zone of Nepal and India that contain rhinos from Chitwan. A similar ambitious translocation program is now underway in Assam with the goal of having a total population of 3000 distributed over seven reserves by 2020.

One major reason why rhinoceroses have persisted in Nepal and recovered from near-extinction, is that very few people have access to sophisticated firearms. Had Nepalese or Assamese villagers possessed the arsenals at the disposal of Somali poachers, the number of Greater One-horned Rhinoceroses would be much below its present level. Two dismal tests of this hypothesis may have already occurred in the Manas sanctuary of Assam, India, and in Bardia National Park, Nepal. An uprising by the Bodo people in Manas wiped out the existing population, estimated at about 80 Greater One-horned Rhinos, prior to the Bodos' temporary take-over of the sanctuary. In Bardia, 85 rhinos translocated to the Babai Valley in the 1980s and early 1990s were killed during a ten-year insurgency by Maoist rebels, which forced the Nepalese army from its guard posts and allowed local poachers access. (A smaller, translocated rhino population remains elsewhere in Bardia.) Even without widespread access to firearms, poaching of Greater One-horned Rhinoceroses in India was reported to have killed as many as 450 rhinos in the ten-year period from 1986 to 1995, and 50 in Nepal over the same interval.

The lessons learned from recovering rhinoceros populations in Nepal offer a comprehensive strategy for long-term conservation. The essential ingredients of the strategy are: strict protection of core areas; powerful economic incentives, and new legislation to promote local guardianship of endangered species and habitats in buffer zones and corridors; 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; and greater conservation

awareness at the local level, regarding the uniqueness, rarity, and value of the species. Successful translocations from Chitwan to Dudhwa, Sukla Phanta, and Bardia demonstrate that recovery of rhinoceros populations within their former range in the Terai is possible if the political will can be mustered. A recent conservation action plan for Asian rhinoceroses incorporates these principles into a suite of actions to enhance conservation of the species, built on the success of efforts in Chitwan and Kaziranga. The most preferred habitats of the Greater One-horned Rhinoceros are floodplains, which are also sites of intensive cultivation. The growth of human populations poses a much greater threat to habitat conservation in Asia than in Africa.

If poaching somehow ceased in Africa, rhinoceros populations would increase rapidly, because extensive habitat still remains. Asia presents a different landscape. There is no habitat block that presently contains rhinos in Asia equivalent to the Selous Game Reserve of southern Tanzania, an area roughly the size of Switzerland, or the Kavango-Zambezi Transfrontier landscape (on the borders of Namibia, Angola, Botswana, Zambia, and Zimbabwe, which is the size of Italy (278,000 km²) and constitutes a potential mega-reserve for the Black Rhinoceros. In Asia, rhinoceros sanctuaries are threatened by rapid deforestation and the spread of oil palm and pulp and paper plantations, and human population growth adjacent to protected areas.

Along the continuum of conservation victories and setbacks, the results of conservation efforts undertaken on behalf of the two remaining Asian species have been underwhelming. Today, Javan Rhinos are widely regarded as the most endangered mammals on earth, numbering no more than 30–50 individuals and now restricted to perhaps a single population in Ujung Kulon National Park, in western Java, Indonesia. Prior to the French-Indochina and the Vietnam Wars, a remnant population of Javan Rhinos on the Vietnam border with Cambodia may have contained a larger population than in Java. Hostilities and the aftermath of poaching reduced that population to a few individuals that survived in a degraded forest area outside Cat Tien National Park, called Cat Loc. Efforts to census what were thought to be four remaining individuals, using scent dogs to locate droppings and DNA extraction to sex and identify the remaining individuals, was completed in early 2010. The most recent discovery was the carcass of what might be the last individual in the population, shot by a poacher. The loss of rhinos in Vietnam has sparked a national controversy, and while too late for this population, may motivate the government to protect other endangered species.

Aside from dehorning, the other great debate in rhino conservation is the value of captive breeding as a conservation tool. The debate reached a climax when the Asian Rhino Specialist Group of the IUCN endorsed a proposal to remove Javan Rhinos from Ujung Kulon to an offshore captive facility. The Indonesian government rejected the proposal, to the relief of field biologists. Finally, in 2010, the government was moving closer to translocating some individuals of the Ujung Kulon population to a safe second site in Java, to ward off the possibility of disease, a poaching epidemic, or a violent eruption of nearby Krakatoa decimating the one remaining population.

Once distributed widely across much of South-east Asia and even reaching Assam, India, Sumatran Rhinos experienced a range collapse similar to the Javan Rhino. The decline was so steep, and remaining Sumatran populations so small, that many conservationists now consider this species the most endangered large mammal on earth. The last strongholds of the species are Taman Negara National Park, peninsular Malaysia; the Danum Valley Conservation Area and Tabin Wildlife Refuge in Sabah, Malaysia; and a few reserves in

Sumatra (Gunung Leuser, Bukit Barisan Selatan, and Way Kambas National Parks). Nowhere are Sumatran Rhinos common.

One of the great debacles in conservation history involved an effort to save the Sumatran Rhino. A group of western zoos and their Asian counterparts formed the Sumatran Rhino Trust, which in the 1980s undertook to rescue otherwise doomed individuals from natural habitats slated for logging or conversion to oil palm or rubber plantations, to provide a chance for the captured animals to survive, breed, and help maintain the genetic vigor of the population. The ultimate goal of the project was the reestablishment in the wild of descendants of captive-bred animals when "suitable areas were secured." The Sumatran Rhino Trust spent at least US\$ 2.5 million to capture 40 doomed individuals, and sent pairs to facilities in Western and Asian zoos. The extent of mortality was shocking, with virtually all the animals dying rather quickly in captivity. One field biologist described this effort in a controversial paper entitled, "Helping a Species To Go Extinct." Eventually, several calves were born at the Cincinnati Zoo. But reproductive rates among wild populations greatly exceeded those in the captive Sumatran Rhino population.

This sad episode forces conservationists to examine the approach they take to saving the most endangered mammals on earth. The first lesson learned is that rhinos, like Tigers, Mountain Gorillas (*Gorilla beringei*), Giant Pandas (*Ailuropoda melanoleuca*), and a few other species, are conservation-dependent—they will only survive and recover by direct intervention and management and permanent protection. They are too commercially valuable to poachers and too susceptible to habitat fragmentation and loss to assume that a few years of protection efforts are enough and we can address other problems. The second lesson is that there is no substitute for political will in the conservation of endangered large mammals like rhinoceros. Declaring populations to be doomed and collecting them for captive breeding is a foolish enterprise. In-situ conservation is often cheaper, but it requires the political will of range state leaders to commit to protecting their endangered species and preventing the complete conversion of their forests and extirpation of large mammals. If the five lessons described above could be effectively applied to all remaining rhinoceros populations, the chances for recovery would increase dramatically.

The situation for the Sumatran Rhino in Sabah, a province in northern Borneo and part of the federation of Malaysia, is an important case study of the challenges conservationists face to recover an endangered large mammal. Less than 40 rhinos are believed to survive in Sabah. If half are females, and some females are too old or too young to reproduce, perhaps only six or seven have the potential to give birth. With a birth interval of three years under optimum conditions, no more than two rhinos are being born annually. At this stage, conservationists begin to worry about the Allee effect, a phenomenon whereby a positive correlation exists between individual fitness (survival probability, fertility, reproductive rate) and population density of the species. As numbers of individuals of a species decline to a very low level, various factors associated with very low numbers—narrow genetic base, locally skewed sex ratio, difficulty in finding a fertile mate, reproductive pathology associated with long non-reproductive periods—conspire to drive the numbers even lower. At some point, the death rate eventually exceeds the birth rate, even with adequate habitat and elimination of poaching. In the absence of specific actions to bring Sumatran Rhinos together and boost production of offspring, therefore, there is a strong possibility that the species may go extinct even if protection of its habitats and the remaining individual rhinos can be maintained and improved.

One rhinoceros biologist summed up the recent conservation history with these words: "That there are any free-ranging rhinoceros alive in 2010 is a miracle. That some populations are actually recovering gives hope for many other species of endangered vertebrates. If strict protection and incentives for communities who live near rhinos are effective, endangered species conservation is far from a lost cause but a noble and hopeful occupation for the 21st century."

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