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Rhinoceros behaviour: implications for captive management and conservation

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All species of rhinoceros are, to varying degrees, threatened with extinction because of poaching, habitat loss, human–rhinoceros conflict, hunting and civil unrest. Clearly the threats facing the five remaining species (Black rhinoceros *Diceros bicornis,* White rhinoceros *Ceratotherium simum,* Greater one-horned rhinoceros *Rhinoceros unicornis,* Javan rhinoceros *Rhinoceros sondaicus* and Sumatran rhinoceros *Dicerorhinus sumatrensis*) are anthropogenic. Although many disciplines are important for conservation, understanding the behaviour characteristics of a species should be considered a key component when developing wildlife-management and conservation strategies. A general overview of the behaviour of rhinoceros is presented, addressing ecology and social organization, activity and habitat use, feeding strategies, courtship and reproduction, and anti-predator behaviour. The implications of behavioural studies for successful management and husbandry of rhinoceros in captivity are discussed in sections on group size and composition, enclosure design and enrichment programmes, activity patterns, introductions, reproduction, hand-rearing, and health and stress. Finally, there is some discussion about the implications of this knowledge for *in situ* conservation in relation to designing protected areas, further aspects of animal health and stress, and reintroduction and translocation. A detailed understanding of rhinoceros behaviour is important for survival both in range-country protected areas and captivity, and such knowledge should be used to provide the most appropriate animal care and environments for these species.

Key-words: animal care, behaviour, black rhinoceros, greater one-horned rhinoceros, human–rhinoceros conflict, husbandry, *in situ* conservation, Javan rhinoceros, reproduction, Sumatran rhinoceros, white rhinoceros

> ‘The big beast stood like an uncouth statue, his hide black in the sunlight; he seemed what he was, a monster surviving over from the world’s past, from the days when the beasts of the prime ran riot in their strength, before man grew so cunning of brain and hand as to master them. So little did he dream of our presence that when we were a hundred yards off he actually lay down.’ *Theodore Roosevelt, 1910.*

Humans have apparently admired rhinoceros for some time; these massive creatures are not only featured on prehistoric cave paintings and petroglyphs but also in modern advertisements for rugged all-terrain vehicles and computer software. While many rhinoceros and rhinoceros-like species have come and gone since the Eocene epoch (*c.* 58 million years ago), only five species remain. The Black rhinoceros *Diceros bicornis* and White rhinoceros *Ceratotherium simum,* including the Southern white rhinoceros *Ceratotherium simum simum* and the Northern white rhinoceros *Ceratotherium simum cottoni,* are native to Africa, while the Greater one-horned rhinoceros *Rhinoceros unicornis,* Javan rhinoceros *Rhinoceros sondaicus* and Sumatran rhinoceros *Dicerorhinus sumatrensis* are found in Asia.

Unfortunately, all of these species are, to varying degrees, threatened with extinction. The Black rhinoceros population declined from 65 000 animals in 1970 to 2300 in 1992 because of rampant poaching: a 96% decrease (IRF, 2005). The International Rhino Foundation (IRF) estimated that there were about 3610 wild Black rhinoceros as at February 2005 (IRF, 2005). The Southern white rhinoceros population was reduced to between 50 and 200 animals by the end of the 19th century but conservation efforts have increased that number to about 11 330 (IRF, 2005). The Greater one-horned rhinoceros has recovered from less than 200 animals in the early 20th century to around 2400 as a result of protection throughout India and Nepal (IRF, 2005). While these species still have not recovered to their earlier peaks, their outlook for survival is far less bleak than other species or subspecies. In contrast, only about 60 Javan rhinoceros, 300 Sumatran rhinoceros and ten Northern white rhinoceros are estimated to survive in the wild (IRF, 2005).

Threats to survival vary by species. They include poaching for products that are made from rhinoceros horn (i.e. traditional medicines, ceremonial dagger handles and/or decorative carvings), habitat loss from clear cutting for logging or agriculture and human settlement, human–rhinoceros conflicts, unsustainable hunting for sport and food, and civil unrest (Foose & Van Strien, 1997; Emslie & Brooks, 1999). The common thread among all these threats is that they are all anthropogenic. Thus, the survival of the world's rhinoceros species depends on human decisions. Such decisions, whether for management or conservation of rhinoceros in the wild or in captivity, must consider the behaviour of these species.

An understanding of animal behaviour is a key component of wildlife management and conservation, whether the goal is to: (1) develop successful methods of breeding and maintaining animals in captivity (Eisenberg & Kleiman, 1977; Kleiman, 1980; Boyd, 1991), (2) promote animal welfare (Broom & Johnson, 1993; Mench & Mason, 1997; Poole, 1998), (3) reintroduce captive-bred wildlife back into nature (Kleiman, 1989; Hutchins *et al.,* 1995; Miller *et al.,* 1998) or (4) conserve extant wildlife populations *in situ* (Hutchins & Geist, 1987; Clemmons & Buchholz, 1997; Festa-Bianchet & Apollonio, 2003).

The goal of this paper is to briefly review our current knowledge of rhinoceros behavioural biology and, furthermore, to summarize its implications for *ex situ* and *in situ* management and conservation. This review is not intended to be comprehensive; however, it does include many topics of interest to animal managers and conservationists. Animal training and its use in captive-animal management and husbandry is not addressed here as that topic is the focus of another article in this volume (Holden *et al.,* this volume). Finally, we recognize that many other disciplines affect the conservation of rhinoceros, including veterinary medicine, nutrition, reproductive biology and ecology. However, as we hope to demonstrate, rhinoceros behaviour should be considered when making conservation or management decisions.

RHINOCEROS BEHAVIOUR: AN OVERVIEW

Ecology and social organization The social organization of rhinoceros species varies widely depending on the ecological circumstances in which the species or population occurs (Laurie, 1982). Rhinoceros inhabit a wide range of habitats across sub-Saharan Africa and South and South-east Asia. Sumatran rhinoceros and Javan rhinoceros inhabit dense tropical evergreen rainforests; the Greater one-horned or Indian rhinoceros lives in swamps and adjacent meadows; White rhinoceros inhabit savannah grasslands and Black rhinoceros range through dry bushland or semi-desert (Owen-Smith, 2004).

There is still much to learn about the details of rhinoceros social organization and behaviour; however, a basic picture has emerged as the result of field studies conducted over the past three decades. There are many similarities and some subtle differences between species, populations and individuals. The most stable social bond among rhinoceros is that between a ♀ and her most recent offspring. Adult ♂♂ tend to be solitary and aggressive (Owen-Smith, 2004). Males separate themselves spatially and temporally through olfactory communication; dung piles (lavatories) and urine spraying, are commonly used olfactory signals, while scrapes and broken vegetation may offer visual evidence of the presence of other individuals (Black rhinoceros, Schenkel & Schenkel-Hullinger, 1969a; Javan rhinoceros, Schenkel & Schenkel-Hullinger, 1969b; White rhinoceros, Owen-Smith, 1975; Greater one-horned rhinoceros, Laurie, 1982; Sumatran rhinoceros, Van Strien, 1986). Urination in rhinoceros is highly ritualized; the animals can either urinate in a continuous stream on the ground or squirt urine 3–4 m behind them (Laurie, 1982). Adult ♀ Greater one-horned rhinoceros only squirt-urinate when they are in oestrus, whereas some ♂♂, particularly socially dominant ♂♂, always urinate this way. White rhinoceros bulls squirt-urinate most frequently while patrolling their territorial borders (Owen-Smith, 1975).

Rhinoceros tend to defecate near other rhinoceros dung. Laurie (1982) found only 13% of freshly deposited faeces were more than 10 m from existing dung and, during normal activities, rhinoceros defecated directly on existing dung piles 88% of the time. African rhinoceros scrape their back feet through dung piles to spread odours that advertise their presence. Sumatran and Javan rhinoceros do not scrape and this divergence in behaviour is likely the result of ecological differences (Schenkel & Schenkel-Hullinger, 1969b). Greater one-horned rhinoceros do scrape but dung piles tend to occur at the borders of forest and grassland, on riverbanks, near wallows and paths, roads or ditches (Laurie, 1982). Scraping may not be as an effective method for spreading odours in wet, densely forested habitats as it is in open, dryer habitats. Forest-dwelling Javan rhinoceros frequently urinate and defecate in water or wallowing sites and this may help to impregnate their bodies with distinctive odours. Odours are subsequently disseminated throughout the habitat as the animals move through vegetation and are presumably recognized by others (Schenkel & Schenkel-Hullinger, 1969b).

The home ranges of adult ♂ rhinoceros may overlap those of several adult ♀♀ but this is not always the case. Core areas of some ♂ home ranges may be exclusive and thus represent territories in some species or populations (e.g. Black rhinoceros, Klingel & Klingel, 1966; Frame, 1980; White rhinoceros, Owen-Smith, 1971; van Gyseghem, 1984; Sumatran rhinoceros, Van Strien, 1986). However, in others, adult ♂ home ranges may overlap but ♂♂ defend oestrous ♀♀ from the close approach of other ♂♂ (e.g. Greater one-horned rhinoceros, Laurie, 1982). In some species, adult ♀♀ and sub-adults are semi-social. Although close physical contact among rhinoceros is restricted primarily to the mother–offspring relationship and to brief mating encounters between adults, adult ♀♀ and/or sub-adults of some species will congregate in either temporary or semi-stable groups (e.g. Black rhinoceros, Schenkel & Schenkel-Hulliger, 1969a; White rhinoceros, Owen-Smith, 1975; van Gyseghem, 1984; Greater one-horned rhinoceros, Laurie, 1982).

The Asian species are the least social of the Rhinocerotidae. Adults are normally solitary and rarely come together except to mate, although sub-adults will sometimes associate with one another temporarily (Schenkel & Schenkel-Hullinger, 1969a,b; Laurie, 1982; Van Strien, 1986; Owen-Smith, 2004). The African species appear to be the most gregarious (Estes, 1991). While adult ♂♂ of these species tend to be solitary and territorial (at least in some populations), adult ♀♀ and sub-adults occasionally gather in groups (Owen-Smith, 1971, 1975; Estes, 1991). Although Black rhinoceros ♀♀ are most frequently solitary, groups of three to five individuals form on occasion (Schenkel & Schenkel-Hullinger, 1969a; Owen-Smith, 2004). In White rhinoceros, stable herds of up to six form occasionally and larger aggregations of up to ten can occur (Owen-Smith, 1975, 2004; Estes, 1991). Adult ♀♀ and sub-adults frequently graze together in groups (van Gyseghem, 1984). Furthermore, bonds among ♀♀ may be quite strong and they will co-operate to defend themselves against predators. Even among the most solitary species, adults occasionally congregate around limited resources, such as wallows, water sources, feeding areas and salt licks (e.g. Javan rhinoceros, Schenkel & Schenkel-Hullinger, 1969b).

Activity patterns, habitat use and movements Free-ranging rhinoceros may be active both day and night (Goddard, 1967; Schenkel & Schenkel-Hullinger, 1969a,b; Owen-Smith, 2004). As in most large mammals, activity patterns are influenced by a variety of factors, including ambient temperature and the relative abundance and distribution of food and other essential resources, such as water and mates. Activity levels tend to be lowest during the hottest time of the day and increase as conditions become cooler, which may assist thermoregulation (e.g. Black rhinoceros, Goddard, 1967; Javan rhinoceros, Schenkel & Schenkel-Hullinger, 1969b). During the dry season, Northern white rhinoceros may graze in the shade of trees for up to 30 minutes before and after resting in the shade (van Gyseghem, 1984). In this subspecies, most grazing activity takes place beginning around 1600 hours and continues throughout the evening. During seasonally colder nights in some habitats, however, rhinoceros become less active (e.g. Black rhinoceros, Mehradadfar, 1999). Rhinoceros may spend the middle of the day lying in mud wallows. Wallowing appears to be important in thermoregulation, repelling biting insects and external parasites, and protecting the skin from dehydration and sun (e.g. Black rhinoceros, Goddard, 1967; Javan rhinoceros, Schenkel & Schenkel-Hullinger, 1969b; Greater one-horned rhinoceros, Dutta, 1991). However, rhinoceros may use wallows at any time, both day and night. Where deeper water is present, they may spend their time standing or lying in pools or streams. The Asian species particularly have a strong affinity for water (Schenkel & Schenkel-Hullinger, 1969b; Laurie, 1982; Van Strien, 1986). Other maintenance or comfort behaviours are also performed, such as scratching or rubbing the body against trees or other vegetation, which removes dead skin (Roosevelt, 1910).

Rhinoceros movements and home-range sizes vary tremendously depending on habitat type and quality. Large mammals tend to be energetically conservative. The availability of critical resources, including food, water and mates, governs the extent to which animals range throughout their habitats. Black rhinoceros home-range size, for example, varies from 2·5 km^2 in Nogorogoro Crater in Tanzania to 500 km^2 in the Namib Desert of Namibia (Owen-Smith, 2004), presumably as the result of resource availability and dispersion. In arid habitats, rhinoceros must move to water every 2–5 days, but may roam great distances away from water, presumably to find food (Black rhinoceros, Mehradadfar, 1999). In contrast, Sumatran rhinoceros do not range as widely, preferring an extensive system of trails running through dense topical evergreen forests (Van Strien, 1986). Because food and water are generally abundant, the home-range size of Sumatran rhinoceros is limited by the occurrence of salt licks that provide essential minerals to their diet. While Javan rhinoceros also use trail systems, their primary source of salt appears to be sea water rather than salt licks, but that may be the result of ecological factors in their last remaining habitat, Ujung Kulon National Park, Java, Indonesia, an isolated peninsula surrounded by ocean on three sides (Schenkel & Schenkel-Hullinger, 1969b). Table 1 shows the home-range sizes recorded for rhinoceros species by gender.

Foraging and feeding behaviour

Rhinoceros species differ significantly in their feeding ecology and foraging behaviour (Owen-Smith, 2004). White rhinoceros are primarily grazers that feed on grasses. Black rhinoceros are primarily browsers that feed on herbs and shrubs. Greater one-horned rhinoceros forage on both grasses and aquatic plants in their marshy habitats; Sumatran and Javan rhinoceros feed on a wide variety of tropical vegetation, including some fruits. Wild rhinoceros eat a wide variety of plants. For example, Mukinya (1977) found that Black rhinoceros ate 70 different plant species, representing 30 different botanical families in the Masai Mara Game Reserve, Kenya. Patterns of food selection by rhinoceros are often related to the relative abundance and distribution of various plants in a given habitat and season (van Gyseghem, 1984). As in other ungulates, young rhinoceros probably learn what to eat by foraging in close proximity to their mothers.

Because of their great size, the bulky, low-quality nature of their food and the inefficiency of the digestion process, rhinoceros must spend a good deal of their active time foraging (Field, 1968). Northern white rhinoceros at Murchison Falls National Park, Uganda were

SPECIES	SEX	SIZE	REFERENCE
Black rhinoceros			
Diceros bicornis	♀	2·59–90·6 km^{2}	Goddard (1967)
	♀	12·5–47·3 km^{2}	Kiwia (1989)
	♂	2·59–51·8 km^{2}	Goddard (1967)
	♂	69 km^{2}	Kiwia (1989)
Greater one-horned rhinoceros			
Rhinoceros unicornis	♀	20 km^{2} (2–4 km^{2} core)	Laurie (1982)
	♂	3–4 km^{2}	
Javan rhinoceros			
Rhinoceros sondaicus	♀ (no calf)	10 km^{2}	Schenkel & Schenkel-Hullinger (1969b)
	♀ (with calf)	2–3 km^{2}	
	♂	20 km^{2}	
Sumatran rhinoceros			
Dicerorhinus sumatrensis	♀	10–15 km^{2}	Van Strien (1986)
	♂	50 km^{2}	
White rhinoceros			
Ceratotherium simum	♀	9–20 km^{2}	Owen-Smith (1975)
		97 km^{2}	van Gyseghem (1984)
	♂	0·75–2·6 km^{2}*	Owen-Smith (1975)
	♂	30 km^{2}	van Gyseghem (1984)

* Breeding territories.

Table 1. Home-range sizes reported in the literature for the five remaining rhinoceros species.

observed grazing in groups, spaced apart from each other by one body length (van Gyseghem, 1984). They grazed sporadically throughout the day in between bouts of wallowing, resting and wandering, with a peak grazing period between 1600 and 1900 hours. Interestingly, Black rhinoceros in the Masai Mara Game Reserve, Kenya, also had a peak feeding period between 1400 and 1900 hours (71% of their activity during that period) (Mukinya, 1977). Both species displayed a morning and afternoon feeding peak, but foraging and feeding occurred throughout the day and, the authors believed, throughout the night as well (Mukinya, 1977; van Gyseghem, 1984).

Courtship and mating behaviour All rhinoceros species are polygamous and polyandrous, with both ♂♂ and ♀♀ seeking multiple mates (Owen-Smith, 2004). Courtship and mating behaviour are similar across species and can occur at nearly any time of day (Goddard, 1967). However, there are some subtle interspecific differences and individuals may differ in their behaviour as well. Rhinoceros courtship can be protracted and aggressive. Male rhinoceros engage in mate-guarding behaviour, following the ♀ until she comes into full oestrus and will tolerate close approach and physical contact with a ♂ (Estes, 1991; Owen-Smith, 2004). Oestrous ♀♀ urinate frequently. Bulls test a ♀'s reproductive status by tasting her urine, which is then followed by a pronounced curling of the upper lip, known as the Flehmen response (Goddard, 1967; Laurie, 1982). Until she is receptive, a ♀ rhinoceros may repeatedly drive the ♂ away with mock charges and other defensive behaviours.

Loud whistling by ♀ Greater one-horned rhinoceros announces reproductive condition and location. This typically occurs 6–10 hours prior to courtship or breeding activity. The whistling attracts bulls that respond with precopulatory behaviour, such as prolonged chases of 1–2 km. Laurie (1982) suggested that such behaviour ensured that the ♀ ultimately mated with the 'strongest' (i.e. most dominant) ♂ in the vicinity.

During its final stages, bull courtship consists of a complex combination of approaches, followed by dominance and threat displays (e.g. rushing at and jabbing or pushing with the head and/or horn) (Black rhinoceros, Ritchie, 1963; Estes, 1991); however, this is not always the case (Goddard, 1967). Females may become aggressive too, especially during courtship chases in captivity, which may result in scrapes, cuts or deeper wounds (Dutta, 1991).

As a prelude to copulation, the ♂ stands behind the ♀, rests his chin on her back and slides his head up her spine (Goddard, 1967; Owen-Smith, 1975). He then uses his neck as a lever to raise his forefeet off the ground and into a copulatory position, with his tail raised and forefeet placed behind the shoulders of the ♀. A ♂ may stand in this position for long periods prior to intromission. In some cases, the ♀ will move off and dislodge him. In the Black rhinoceros, multiple mountings may extend over several hours before actual copulation takes place. Coitus itself can be a prolonged affair, lasting up to an hour or more. In some cases vocalizations occur but in others the activities are completed in relative silence (Goddard, 1967). When mounting is successful, four to five thrusts made in rapid succession indicate ejaculation (Dutta, 1991). In some cases, ejaculations have occurred at the rate of one per minute (Lang, 1975).

Adult ♂♂ attending oestrous ♀♀ may become very aggressive towards other ♂♂ during chance encounters and Kretzschmar *et al.* (2004) found that free-ranging territorial ♂ White rhinoceros had higher levels of androgen metabolites in their faeces when accompanying a receptive ♀ than when alone. Thus, high levels of testicular activity were correlated with the peak of intra-sexual competition and mating; this also occurred during the rainy season (September–February), suggesting an environmental influence on reproduction. Goddard (1967) described an incident in which three Black rhinoceros bulls fought over access to an oestrous ♀. In this species, a ♀ may mate with several bulls during her 3 day window of peak receptivity (Estes, 1991). In the White rhinoceros, not all confrontations between territorial ♂♂ result in fighting. When it does occur, ♂–♂ aggression is highly ritualized, consisting of reciprocal horn against horn staring, vigorous wiping of the horn on the ground and brief clashes of horns in only about a quarter of cases (Owen-Smith, 1975). Among Greater one-horned rhinoceros, adult ♂♂ are attracted to the vocalizations associated with mating and will approach mating pairs. Subsequent aggressive interactions can become very violent, sometimes resulting in serious wounds or even fatalities (Laurie, 1982; Dutta, 1991). While Greater one-horned rhinoceros ♂♂ are not territorial, 'strong' ♂♂ limit access to oestrous ♀♀ by other adult ♂♂. Submissive ♂♂ may share the home ranges of strong ♂♂ but do not scent mark (squirt-urinate) and usually retreat at the approach of a strong ♂. Among White rhinoceros, dominant ♂♂ occupy clearly demarcated breeding territories and defend them from other dominant ♂♂. However, these territories are not exclusive; ♂♂ share their space with cows, subadults and even with subordinate (or 'subsidiary') ♂♂ (Owen-Smith, 1971, 1975). Occasionally, fighting between ♂♂ may lead to a shift in dominance status. When this occurs, the previous owner may stay in his former territory, as long as he remains submissive and refrains from scent marking (Owen-Smith, 1971, 1975, 2004). Black rhinoceros show considerable variation in mating system, depending on their ecological circumstances: while their behaviour is similar to that of White rhinoceros in wetter habitats, they are apparently not territorial in arid habitats (Klingel & Klingel, 1966; Schenkel & Schenkel-Hullinger, 1969a; Mukinya, 1977; Frame, 1980; Laurie, 1982; Kiwia, 1989).

Females are sometimes intolerant of mounting even while in heat, suggesting that they may be exercising mate choice. Male physical and behavioural characteristics are thought to influence ♀ mate selection (Dutta, 1991; Estep & Dewsbury, 1996). Female Greater one-horned rhinoceros will go to great lengths to avoid the advances of undesirable ♂♂, either running away or even fighting when cornered. In turn, this may cause the ♂♂ to become even more aggressive, and the ensuing chases and fights may result in serious injury to ♀♀ while they are fleeing, or even death if they succumb to wounds inflicted by the ♂ (Laurie, 1982; Dutta, 1991). Dominant ♂ White rhinoceros sequester cows within their territories and consort with them for as long as 2–3 weeks, thus preventing interference by other ♂♂ (Owen-Smith, 1971). If an oestrous ♀ attempts to roam outside his territorial boundary, a ♂ will block her path. Little is known about the details of courtship and mating in free-ranging Sumatran and Javan rhinoceros because of the difficulty of observation in dense rainforest. However, observations of Sumatran rhinoceros in captivity suggest that courtship and mating are generally similar across the species.

Pregnancy, parturition, maternal care and infant development Female rhinoceros exhibit several behavioural and physical signs of pregnancy and parturition (Fouraker & Wagener, 1996). For example, the udder and vulva may become noticeably swollen 30 days prior to birth and the abdomen may appear distended (Gowda, 1969; Buechner & Mackler, 1976). Milk production begins at this time and is accompanied by waxy plugs on the teats. The size of the udder may increase dramatically within 48 hours of delivery. The ♀'s appetite may also decrease, the vulva may dilate, and a mucous plug forms. In addition, as the time of birth approaches, the ♀ may become more restless, alternately standing and lying. Free-ranging pre-parturient ♀♀ generally seek seclusion in dense vegetation or in areas where few other rhinoceros travel prior to giving birth (Owen-Smith, 2004). At this time, and for a period of time post partum, ♀♀ may become more irritable and aggressive towards other rhinoceros; this occurs both in nature and in captivity (Dittrich, 1967; Gowda, 1969; Buechner & Mackler, 1976; Laurie, 1982; Estes, 1991). Pre-partum social isolation is common among social ungulates and may have many functions, including reducing the risk of predation, allowing the ♀ and her infant to bond without interference, preventing chance 'kidnappings' and protecting the infant from injuries that might occur as the result of interactions with older, potentially aggressive conspecifics (Hutchins, 1984). Greater one-horned rhinoceros ♂♂ have been known to attack calves in captivity (Dutta, 1991). In addition to these behavioural clues, pregnancy can also be detected by measuring ♀ hormonal changes (e.g. Southern white rhinoceros: Patton *et al.,* 1999). Dates of impending parturition can be predicted based on observed matings and known gestation lengths for the species in question (Hutchins *et al.,* 1996).

A single calf is typical among all rhinoceros species (Owen-Smith, 2004). Observations of births are rare, except in captivity. Frame (1971) reported on the birth of a free-ranging Black rhinoceros. The mother stood during birth and the calf emerged within 10 minutes of first becoming visible. The mother removed the amniotic sac by licking and the calf first stood within 10 minutes post partum. During a Greater one-horned rhinoceros birth at the Smithsonian National Zoological Park, Washington, DC, the pregnant ♀ paced back and forth within her enclosure (Buechner & Mackler, 1976). Her udder and vulva were enlarged and red. At 0840 hours, an amber coloured fluid emerged from the birth canal, probably signalling the rupture of the amniotic sac. Four-hours later, the ♀ was lying on her side, breathing heavily and appeared to be straining. Forty-minutes later, the calf's forefeet and foetal membranes were seen protruding from the birth canal. The ♀ alternately lay down, then rose to her feet and walked slowly during labour. At 1355 hours, complete parturition occurred with the ♀ standing. As soon as the calf was on the ground, the ♀ pivoted around and touched the calf with her nose, licked it and exhibited the Flehmen response. She expelled the afterbirth about 2 hours post partum and subsequently consumed it, a common behaviour among ungulates (Hutchins *et al.,* 1996). Similar descriptions, albeit with some individual variation, are recorded in the literature (Dittrich, 1967; Bhatia & Desai, 1975; Dutta, 1991).

Among free-ranging Greater one-horned rhinoceros, calves under 2 months of age may be left lying alone while the mother moves up to 800 m away to forage on vegetation. However, after this time, they rarely wander more than a few meters away from their mothers (Laurie, 1982). Black rhinoceros newborns may remain hidden for the first week after birth but once their legs have strengthened, typically remain in close vicinity of their mothers (Goodard, 1967; Schenkel & Schenkel-Hullinger, 1969a; Mukinya, 1977; Frame, 1980; Kiwai, 1989). When separated temporarily, mother–infant pairs maintain contact through vocalizations, the mothers calling with pants and the infants responding with high-pitched squeals. However, this behaviour may be variable, depending on ecological circumstances. Berger (1993) documented the temporary separation of Black rhinoceros mothers and calves under 6 months old in two populations in Namibia. In these cases, mothers moved as far as 19 km from their young when travelling to water. The author speculated that the probability of a calf–predator encounter might be higher at watering places; thus, the chances of predation may be lower when the calf stays in one place where it would be less vulnerable. Small calves and sub-adults up to 3 years of age are at risk from predation by Lions *Panthera leo* and Spotted hyenas *Crocuta crocuta* (Goddard, 1967; Kruuk, 1972). Female rhinoceros are protective of their young and behave aggressively towards predators and conspecifics that approach too closely (Dutta, 1991).

Infant rhinoceros typically stand for the first time from 30 minutes to an hour post partum (Bhatia & Desai, 1975). Calves search for their mother's nipples as soon as they can walk; first nursing typically begins within 1–2 hours after the calf is on its feet (Fouraker & Wagener, 1996). Few data exist on the frequency and duration of nursing by rhinoceros calves and particularly on changes in nursing frequency and duration over time. For example, Laurie (1982) reported that free-ranging Greater one-horned rhinoceros calves suckled 'frequently' until 1 year of age but started to feed on grass, herbs and creepers at 2–3 months. Second-year calves suckled less frequently and calves older than 18 months rarely suckled. Dutta (1991) reported that Greater one-horned rhinoceros calves suckled 'every half hour or so' and that this typically continues until the calf is 2 years old or the mother conceives again. What little detailed data do exist on nursing frequency and duration are primarily from studies in captivity. Gowda (1969) recorded suckling durations over 3 days (days 3–5 post partum) in a Greater one-horned rhinoceros calf born at Mysore Zoo, India. He observed 19 suckling bouts lasting 2–10 minutes (mean 5·32 minutes per bout).

Greater one-horned rhinoceros calves remained with their mothers until about a week before the next calf was born (Laurie, 1982). Cows became aggressive towards their older calves only during the week prior to parturition; before that, they simply snorted at the calf when it tried to approach or threatened it with a tusk display. Some sub-adults attempted to remain in contact with their mothers and younger siblings post partum and, in those cases, termination of the relationship was gradual. In others, however, separation was immediate (Dutta, 1991). Generally, however, ♂ and ♀ Greater one-horned rhinoceros calves left their mothers at a mean age of 39·4 and 34·1 months, respectively (Laurie, 1982). One 4 year old ♂ rejoined his mother after the loss of the new calf. Observations of single adult ♀♀ and sub-adult ♂♂ travelling together may have also been examples of mothers with their 4 or 5 year-old calves (Laurie, 1982). Retention of older offspring after reproductive failure or loss of young-of-the-year has been reported in numerous other ungulate species (Hutchins, 1984). Suckling may even occur but may be non-nutritive, as it has been confirmed that some suckling ♀♀ are not producing milk. In such cases, the advantages accrued to offspring may include sharing in their mother's dominance status and knowledge of the location of critical resources.

Anti-predator and alarm behaviour Free-ranging adult rhinoceros show a variety of behaviours in response to the approach of their only significant natural enemies: humans. While Lions may also pose a threat to adult African rhinoceros, proven cases are rare (Goddard, 1967). Reactions of rhinoceros to humans vary, depending on the sensory system involved. According to Schenkel & Schenkel-Hullinger (1969a), Black rhinoceros had the most intense alarm response when exposed only to the scent of humans. In such cases, rhinoceros often fled at great speed up to several hundred meters before stopping. Flight responses can also be elicited by the warning cries of Oxpeckers *Buphagus* sp, birds that are frequently associated with Black rhinoceros. The degree of alarm appears to be lessened when the animals are able to locate the source of the stimulus either visually or acoustically. If the distance between rhinoceros and humans is not less than 30–40 m, then acoustic stimuli alone do not elicit a fear response. Rhinoceros vision is comparatively poor but the animals can detect a moving person as far as 60 m away. The animals' ability to detect humans by sight alone is limited when humans remain motionless. Reactions of Black rhinoceros to humans in vehicles are varied and can range from a complete lack of response to flight and/or attack. In addition, there is great individual variation in such behaviour. It has been suggested that young rhinoceros learn how to react to humans while observing the reactions of their mothers (Schenkel & Schenkel-Hullinger, 1969a).

Forest dwelling and mostly solitary Sumatran rhinoceros are reportedly very sensitive to any kind of human disturbance (Van Strien, 1986). Upon detecting the presence of humans, Sumatran rhinoceros will run for long distances through the densest and thorniest undergrowth and often abandon areas with a high degree of disturbance. Rhinoceros habitat is lost through clear cutting from forest logging operations or to conversion of land for agriculture. In addition, hunters and settlers may subsequently occupy these areas. Javan rhinoceros exhibit a variety of responses towards humans, ranging from silent alertness to immediate escape (Schenkel & Schenkel-Hullinger, 1969b). They, like Greater one-horned rhinoceros, have also been known to attack humans that have approached too closely, inflicting wounds by biting with the incisors on the lower jaw; bites are delivered with an upward thrust of the head (Schenkel & Schenkel-Hullinger, 1969b; Dutta, 1991).

IMPLICATIONS FOR ANIMAL MANAGEMENT AND HUSBANDRY IN CAPTIVITY

Group size and composition Rhinoceros behaviour has many implications for zoo exhibit design. The social organization of the species in question, as well as the number, age and sex of animals in the collection, dictate the size of the enclosure required. The less social a species is, the fewer the number of adult animals that can be kept together. In addition, housing these animals together is not recommended given the competitive nature of bulls. Fouraker & Wagener (1996) listed possibilities for rhinoceros social groupings in captivity based on social biology. Keeping adult ♂ Greater one-horned, Black and White rhinoceros together was not recommended. However, the authors also indicated that ♂ White rhinoceros could be kept together in rare cases but only in extremely large exhibits, such as game parks or ranches. Furthermore, given their relatively gregarious nature, keeping adult ♀ White rhinoceros in groups was not only possible but also desirable (Fouraker & Wagener, 1996). In contrast, keeping Greater one-horned and Black rhinoceros ♀♀ together was recommended only in very large enclosures. Fouraker & Wagener (1996, p. 12) also noted that 'numerous variables affect the probability of success with any captive social group, including the animals' dispositions and available holding space.'.

In most cases sub-adult rhinoceros can be kept with their mothers until they reach puberty. Short periods of separation should begin when a calf is quite young to stimulate the mother to breed again. As in nature, aggressive behaviour by the mother towards an older calf may escalate at the birth of a new calf. Zoos can simulate normal dispersal by separating mothers and older calves at this time (Fouraker & Wagener, 1996). If the calf is ♀ efforts should be made to extend the mother–offspring relationship or re-establish a relationship after a birth and bonding period.

Enclosure design and environmental enrichment There are several factors that result in the variability in size of rhinoceros home ranges in nature (Table 1). The primary factors are the abundance and availability of food, water and minerals. Few zoos, if any, can recreate even the smallest home range but that does not free zoos from providing facilities that meet the spatial and behavioural needs of rhinoceros species in captivity. Climate is a factor that is a great challenge for zoos that experience long, cold winters, because rhinoceros will be held indoors for extended periods of time. In cold climates, it is strongly recommended that rhinoceros be allowed outdoors as often as safely possible even if it is for short periods of time.

Fouraker & Wagener (1996) provided specific recommendations for the size of indoor and outdoor housing, including holding areas, breeding and communal areas, and exhibit-only enclosures for rhinoceros. Minimum outdoor exhibit areas per rhinoceros ranged from 771 m^2 for Black rhinoceros to 929 m^2 for White and Greater one-horned rhinoceros. The figures for communal and breeding areas ranged from 2322 m^2 to 2787 m^2. Recommended indoor holding areas ranged from 18 m^2 for Black rhinoceros to 30 m^2 for White and Greater one-horned rhinoceros. Outdoor individual holding yard recommendations are 204 m^2 for Black and 215 m^2 for White and Greater one-horned rhinoceros. The authors also recommended the minimum enclosure sizes for Black rhinoceros for Sumatran and Javan rhinoceros enclosures. These guidelines were the product of workshops organized by the American Zoo and Aquarium Association (AZA) Rhino Taxon Advisory Group (TAG) and took into consideration the experience of managers of rhinoceros in captivity and available scientific literature. However, the compilers acknowledge deficiencies in our knowledge about the needs of rhinoceros in captivity. Obviously, these sizes are much smaller than the smallest recorded home ranges for free-ranging rhinoceros. Further studies are needed to ascertain the amount and quality of space required to maintain physical and psychological health of rhinoceros in captivity. In addition, it is important that zoos develop specific measures to gauge their success. For example, Carlstead & Brown (2005) found that stress levels (as measured by faecal corticoids) were highest in rhinoceros maintained in enclosures that allowed visitor viewing around a greater portion of their perimeters. This suggests that the presence of humans is potentially stressful for rhinoceros in captivity, especially when there is no opportunity to hide or escape.

For the well-being of rhinoceros species, it is extremely important that enclosure design replicates as many features of the natural habitat as possible. This also allows zoo visitors to observe typical rhinoceros behaviour similar to what they might see in a range country, thus fostering appreciation and a conservation concern for the species. The efforts of zoo biologists to provide stimulating and appropriate environments for animals in captivity have evolved into the relatively new science of environmental enrichment. Shepherdson (1998, p. 1) defines environmental enrichment as '... an animal husbandry principle that seeks to enhance the quality of captive animal care by identifying and providing the environmental stimuli necessary for optimal psychological and physical well-being. In practice, this covers a multitude of innovative, imaginative and ingenious techniques, devices and practices aimed at keeping captive animals occupied, increasing the range and diversity of behavioral opportunities, and providing more stimulating and responsive environments.'.

Environmental enrichment is an animal-husbandry principle that enhances the quality of animal care by identifying and providing the environmental stimuli necessary for optimal psychological and physiological well-being (Shepherdson, 1999). It includes physical elements of an enclosure that improve the quality of the space allowed for the animal. Using rhinoceros behaviour in the wild as a guide, it seems logical to provide rhinoceros in captivity with wallows, pools, sand pits, rubbing posts and other items that provide opportunities to perform activities the animals seem to 'enjoy' in the wild (as opposed to evading or defending against predators). Forthman (1998) offered some basic principles for providing rhinoceros in captivity with an appropriate and enriching environment. Her recommendations included providing the animals with species-appropriate climate and vegetation density; large exhibits with varied substrates and terrain and long views to minimize startle responses that might occur at the sudden appearance of people; non-contact training to facilitate restraint, transport, veterinary care and other management-related behaviours. She further suggested enhancing olfactory stimulation by leaving some dung piles intact and by applying novel scents within the enclosure and enhancing tactile stimulation by providing rubbing/scratching surfaces at various heights and wet and dry wallows. To reduce negative stress (distress), she recommended minimizing auditory stimulation, both indoors and outdoors. In addition, she suggested that bulk food, such as fresh browse, fruits, aquatic plants and grasses, be dispersed widely and unpredictably throughout the enclosure to stimulate the animals to exercise and explore. Lastly, she recommended that rhinoceros in captivity have an opportunity to choose between social or solitary settings. When individual animals exert some measure of control over their environments, it can greatly reduce their stress levels (Shepherdson, 1998). Visual barriers within an enclosure, such as rockwork or vegetation, can provide animals with a sense of social isolation, thus also contributing to their perception of 'control'.

Environmental-enrichment programmes need to do more than simply provide objects to manipulate. There needs to be a scientific component, which involves monitoring the use of enrichment items and activities; what is used by one rhinoceros may not be used by others. Animals may lose interest in certain items over time or show a preference for them at certain times of the day. Alternatives, such as rotation of items and living space, may re-stimulate activity. Thus, it is important to record data such as the time and date enrichment items are presented, degree of use, and when and how an item is used.

Activity patterns Ideally, the activity patterns of animals in captivity should resemble those of their wild counterparts, as this could provide evidence that the behavioural needs of the animals are being met. O'Connor (1986) examined the activity cycles of a herd of 14 Southern white rhinoceros at Whipsnade Wild Animal Park, UK, with the duel goal of comparing them to free-ranging rhinoceros and encouraging more natural behaviour. The author found that the animals exhibited three peaks of activity: early morning (0200–0500 hours), mid-morning (0800–1100 hours) and evening (1600–2100 hours). Over a 24 hour period, rhinoceros spent 49% of their time feeding, 43·5% resting and 7·5% engaged in other behaviours. As in nature, rhinoceros in captivity became inactive during the hottest part of the day. In general, the activity patterns of White rhinoceros in captivity were remarkably similar to those observed in free-ranging animals by Owen-Smith (1973). It was suggested that there are numerous important factors required to stimulate natural activity cycles in captive environments. The size of the enclosure was considered to be the most significant factor, especially if it influenced the amount of food available to grazing animals, such as White rhinoceros. Climate and the provision of adequate numbers of wallows, rubbing posts and shaded resting places, were also considered important.

Introductions Owing to the aggressive nature of adult rhinoceros, great care must be taken when introducing animals into new social situations. Based on the collective experience of rhinoceros managers, Fouraker & Wagener (1996) offered guidelines for introductions of Black, White and Great Indian rhinoceros. Zoos have maintained few Javan and Sumatran rhinoceros so these species are not addressed by the guidelines. The guidelines consider the sociality of the species and the type of introduction, such as ♂ to ♀ or vice versa for breeding purposes, ♀ with new calf to a ♂–♀ group and/or new ♂ to a ♀ group. Species-typical social behaviour may affect whether or not aggression will occur during an introduction. Rhinoceros managers have observed five levels of aggression during introductions. These range from rhinoceros charging each other but making no physical contact to aggression and pursuit resulting in one or both rhinoceros sustaining subcutaneous wounds or arterial blood flow. Therefore, monitoring behaviour pre-introduction, during introduction and post-introduction is critical for determining if intervention is necessary.

The guidelines identify five general steps to rhinoceros introduction. First, animals should have olfactory and auditory contact with each other prior to introduction. The next step is providing the animals with visual contact. They should be moved close to each other but separated by physical barriers. Actual physical introduction should occur in the largest enclosure available and should be carried out with full consideration of species-specific guidelines, including social behaviour and aggression levels. Finally, it may be necessary to separate rhinoceros for brief periods until aggression levels decrease.

Aggression should not be the only behaviour monitored during and after an introduction. Persistent abnormal behaviours and other indicators of elevated stress (such as high faecal cortisol levels) may be detrimental to the well-being of the animals and lead to diminished health or reproduction (Carlstead & Brown, 2005). This can occur not only in the newly introduced animal but also in the rhinoceros to which it is being introduced or to other members of the established group. There may be cases where certain individuals are simply not compatible. If this occurs in a breeding situation, artificial insemination provides an alternative solution. The guidelines recommend that rhinoceros exhibiting stress-related behaviours for more than 2–3 hours should return to the previous step in the introduction process.

Reproduction Because rhinoceros are potentially aggressive during courtship and mating, mate compatibility is a major issue affecting captive-breeding success (Smith & Read, 1992). In nature, ♀♀ can avoid overly aggressive ♂♂; however, in spatially restricted captive environments, this may not always be possible. Forced proximity of large, potentially aggressive animals can exacerbate fighting and increase the probability of serious injury or even death. Adult rhinoceros should be monitored carefully during courtship and mating. Carlstead, Mellen & Kleiman (1999), using rapid behavioural-assessment techniques, found a correlation between breeding success and the temperament of ♂♂. Males that scored high on dominant behaviours were less likely to reproduce successfully, whereas ♀♀ that scored high on dominant behaviours relative to their mates tended to be more successful breeders. These findings suggest that reproductive success may be dependent on pairing assertive ♀♀ with ♂♂ that are 'submissive, adaptable and interactive'. Furthermore, this illustrates the importance of understanding individual differences in personality for achieving reproductive success.

When aggression becomes too intense, it may be necessary to separate pairs before they can cause serious damage. On the other hand, overly cautious managers who do not recognize that aggression is a normal part of rhinoceros courtship may be more likely to separate a pair prematurely, thus interfering with successful reproduction. Crandall (1964) and Smith & Read (1992) speculated that this has been a major cause of poor reproductive performance by rhinoceros in captivity.

New technologies that allow the monitoring of ♀ reproductive cycles have also been useful for determining precisely when ♂♂ and ♀♀ should be put together. For example, Roth *et al.* (2001) described the use of ultrasonography and hormonal analysis to monitor ovarian activity in ♀ Sumatran rhinoceros. Aggression between ♂♂ and non-oestrous ♀♀ has been a barrier to successful captive reproduction in this species (Khan *et al.,* 1999). Because ♀♀ do not exhibit overt behavioural changes during oestrus, it has proven difficult to determine the optimal time for introduction. In addition, unlike other Rhinocerotidae, the Sumatran rhinoceros appears to be an induced ovulator; the stimulus for ovulation is associated with mating activity (mounting and attempted copulation) (Roth *et al.,* 2001). By closely monitoring the ♀'s reproductive cycle and placing a pair together during her peak oestrus, a captive-bred calf was born in 2001 at Cincinnati Zoo, Ohio, USA. This was the first calf bred in captivity since 1889 (Kahn & Van Strien, 2001). Carlstead & Brown (2005) found that captive Black rhinoceros pairs that were kept separated until the ♀ was in peak oestrus exhibited less variation in faecal corticoid levels. This is significant because higher variability in corticoid excretion was correlated with higher rates of fighting and mortality.

Another potentially important factor influencing successful reproduction is the presence or absence of adult conspecifics. For example, mate novelty, the 'Coolidge Effect', is known to heighten ♂ libido in some mammalian species (see Dewsbury, 1981), so that presenting ♂ rhinoceros with several potential mates, rather than just one, may prove to be advantageous. The presence or absence of other adult ♂♂ can also affect ♂ sexual response (Estep & Dewsbury, 1996). While adult ♂ rhinoceros typically cannot be held together in the same enclosure, some believe that the visual or olfactory presence of other ♂♂ and competitive interactions among them may heighten libido and, thus, help increase the chances of successful mating (Fraser, 1968). In the absence of such competition ♂♂ may become lethargic and their interest in sexual activity may wane. This would argue for having adult ♂♂ in adjacent enclosures, where they can see, smell and hear their rivals but where they are prevented from potentially dangerous fighting. Conversely, the mere presence of dominant ♂♂ and ♀♀ also may suppress sexual behaviour in subordinates, as has been shown for other mammals (e.g. Stumptail macaques *Macaca arctoides,* Estep *et al.,* 1988; elephants, Freeman *et al.,* 2004). Changes in environment are also known to reinstate declining sexual behaviour in some species (e.g. domestic cattle, Hale & Almquist, 1960), while in others it can induce fear and stress responses that may interfere with normal sexual behaviour, at least temporarily (Hediger, 1965; Fraser, 1968). Further research is needed to assess the degree to which rhinoceros sexual behaviour may be affected by social and environmental factors. By manipulating the social and physical environment, managers may someday be able to influence the probability of successful reproduction (Estep & Dewsbury, 1996).

Hand-rearing and separation of mothers and offspring Normative data on early mother–infant behaviour and behavioural development in rhinoceros calves can be useful in determining if veterinary or other intervention is necessary to ensure calf survival (Hutchins *et al.,* 1996). For example, Greed (1967) reported that an infant Black rhinoceros had not suckled for the first time 26 hours post partum. Based on previous experience, this was considered too long; keepers subsequently milked the mother in an attempt to provide supplemental nutrition to the calf.

Hand-rearing may be necessary in those instances in which mammalian mothers are not exhibiting appropriate maternal care towards their offspring (Read & Meier, 1996). A detailed knowledge of what constitutes appropriate care can assist zoo managers in deciding when to intervene. Hagenbeck (1969) described the artificial rearing of a Greater one-horned rhinoceros calf that was rejected by its mother. Such intervention may also be necessary in free-ranging animals when management activities interfere with the mother–infant bond. For example, Wallach (1969) described a White rhinoceros and her calf that were chemically immobilized for tagging and translocation. The calf subsequently failed to rejoin its mother for 24 hours post-translocation and release, apparently as a result of maternal rejection. The infant had to be hand-reared. The lesson here is that every effort should be made to avoid separating ♀♀ from very young calves unless absolutely necessary. Minimizing disturbances to the mother post partum also reduces the likelihood that she may reject or become aggressive towards her calf when agitated.

Animal health and behavioural stress

Behavioural research has important implications for maintaining the health of animals in captivity. For large mammals, such as rhinoceros, where the opportunity for direct physical examination is rare, keepers and veterinarians look for changes in behaviour that may indicate emerging health problems. These include lethargy, excessive aggression, signs of discomfort, pain or irritation, or other behavioural cues (Broom & Johnson, 1993). In rhinoceros, changes in dietary and excretory behaviour may be the first indicators of a health problem.

Adequate nutrition and, consequently, feeding behaviour is important for the health of rhinoceros in captivity. Their inefficient digestive system and large size mean that they require large quantities of forage throughout the day (Field, 1968). Southern white rhinoceros in captivity have been shown to spend *c.* 49% of their time feeding over a 24 hour period, alternating between sleeping and feeding throughout the day and night (O'Connor, 1986). Dittrich (1976) suggested supplementary forage should be constantly available or at least offered two or three times per day. Dierenfeld (1996) also states that hay and fresh water should be available *ad libitum* but that the concentrate or pelleted portion of the diet should be offered in at least two daily feedings to maximize utilization. Poor-quality hay (i.e. dusty, wet or mouldy) can cause colic and impactions (Dierenfeld, 1996; Von Houwald, 2002). Dierenfeld (1996) warned that high-quality legume or small-grained hay may be so readily digested that when fed with concentrates, loose faeces or colic may result. These legume hays should be mixed with grass hays (see also Clauss & Hatt, this volume).

It is important to monitor the feeding behaviour of each rhinoceros to ensure that all individuals have access to the appropriate quantity of food (Dittrich, 1976; Dierenfeld, 1996; Von Houwald, 2002). Rhinoceros that are given diets that vary by life stages or condition, such as growing, sub-adult or lactating ♀, should be fed separately (Von Houwald, 2002). To minimize competition for food, rhinoceros can be fed at multiple feeding stations or large communal feeding areas. Providing food on a dirt substrate has been discouraged because of the possibility of impaction from ingesting soil or sand; concrete floors or troughs are recommended (Dierenfeld, 1996; Von Houwald, 2002).

There is an increasing appreciation of the role of behavioural stress in animal and human health (Broom & Johnson, 1993). There is a direct correlation between stress, as measured by cortisol levels and other physiological and behavioural indicators, and the incidence of disease and mortality in animals in captivity. Stress certainly occurs in free-ranging animals as well as animals in captivity (Sapolsky, 1990) but chronic, low levels of stress in captivity may be particularly deleterious to animal health.

Humans are a potential source of stress for rhinoceros in captivity (Carlstead & Brown, 2005). How rhinoceros perceive humans may depend on whether that person is a familiar caretaker or an unfamiliar visitor. Despite their apparent fear of humans in their natural habitats rhinoceros will rapidly become 'tame' in captivity. This is likely a simple form of habituation, whereby humans, once perceived as a threat, eventually become perceived as either a neutral or even a positive stimulus. Some rhinoceros seem to derive 'pleasure' from being scratched behind the ears or will lie down to have their bellies rubbed by keepers. This positive stress or 'eustress' also occurs in mammals in nature in such forms as comfort behaviours (e.g. grooming) and copulation. The more familiar negative stress or 'distress' can result in impaired health and mortality over the long term (Moberg, 1993). In the wild, finding adequate food and water, avoiding predators, fighting over mating opportunities and resisting disease are likely to be distressing events. In captivity, however, there are indications that distress may also be related to the presence of humans. Carlstead, Fraser *et al.* (1999) found a positive correlation between mortality, percentage of public access to the exhibit and behaviours suggestive of fear in ♂ Black rhinoceros. While correlation does not imply causation, these findings are at least suggestive that a high degree of exposure to the noises, smells and sight of the visiting public can be stressful for ♂ Black rhinoceros. Many rhinoceros managers in zoos believe that stress can be reduced by ensuring that visitors cannot completely surround a rhinoceros on exhibit and that they are unable to interact with the animals in an abusive way (Carlstead & Brown, 2005; J. Doherty, pers. comm.). Further studies are needed to understand the effects of stress on rhinoceros morbidity and mortality in captive environments (Kock & Garnier, 1993).

Acute stress or brief periods of stress may or may not have long-term consequences (Moberg, 1993; Mench & Mason, 1997). For example, one rhinoceros charges another but does not make physical contact and the recipient of the charge retreats. Physiologically, there may be an increase in adrenal stress hormones (such as epinephrine) but the episode was brief and the stress-hormone levels return to their normal values. The retreating rhinoceros has altered its behaviour to cope with the perceived stressor. If the stressor is infrequent, depending on the magnitude of the event, the recipient of the charge may not suffer any long-term physical or psychological consequences. Persistent or chronic stress can result in negative consequences, such as weakened immunity and impaired reproduction. Chronic stress can be minimized through appropriate management. For example, separation anxiety, indicated by increased vocalizations and locomotion, was observed in a mother and daughter White rhinoceros, which were separated after 9 years to improve their chances of reproducing (Hodgden, 1991). This stress was managed by slowly reducing the time the mother and offspring spent with each other, while increasing the time each spent with a bull.

Chronic stress, boredom or frustration can also result in behavioural abnormalities (Carlstead, 1996). A common behavioural abnormality observed in rhinoceros in captivity is excessive horn rubbing against abrasive objects, such as concrete surfaces and steel cable, which can cause extensive horn wear (Fouraker & Waggener, 1996). Covering surfaces where horn rubbing occurs with non-abrasive materials, such as smooth plastic or wood, can prevent such horn wear, although this does not eliminate the cause of the behaviour.

Another abnormal behaviour observed in domestic livestock as well as rhinoceros is bar-biting or licking metal barriers (Dittrich, 1976). This stereotypic behaviour (repetitive and apparently functionless, like pacing) may be indicative of frustrated foraging behaviour, such as when prepared diets are rapidly consumed (Dittrich, 1976). The provision of browse or hay throughout the enclosure allows rhinoceros to approximate more closely the time spent foraging and feeding in the wild.

The causes of behavioural abnormalities are difficult to identify unless they first occur immediately after some abrupt change in husbandry and management procedures. Often the long association animal caretakers have with a particular rhinoceros enable them to identify abnormal behaviours. Indeed, it is difficult to identify what is 'abnormal' for rhinoceros in captivity if there is little scientific study on what constitutes normal rhinoceros behaviour in the wild.

IMPLICATIONS FOR *IN SITU* CONSERVATION

An understanding of rhinoceros behaviour has important implications for *in situ* conservation. Of particular interest are implications for (1) the design and management of national parks and reserves, (2) behavioural stress and animal health and (3) reintroduction and translocation as conservation tools.

Reserve design and management

Monitoring rhinoceros behaviour is critical to reserve design and management. By observing diurnal and seasonal movements, social behaviour and foraging behaviour, appropriate decisions can be made regarding habitat needs of a species or population, home-range size and management in protected areas (e.g. Boyce, 1991; Penzhorn & Novellie, 1991).

Wild animals do not recognize the artificial boundaries that humans impose on natural landscapes when national parks or reserves are established. Consequently, animals may be at greater risk from poachers or for coming into conflict with humans and livestock when they roam outside protected areas (Sinha & Sawarker, 1993). In addition, a park or reserve must also contain suitable tracts of all habitat types used by the species at various times of the year. An increase in the distances travelled by Black rhinoceros during a dry season, for example, has indicated a need for the provision of supplemental food and water to maintain the animals within the boundaries of protected areas (Bhima & Dudley, 1996).

Wildlife managers must carefully consider both the size and location of parks or reserves based on a detailed knowledge of the habitat needs and movement patterns of the animals, and on vegetation types and other characteristics of the site (Owen-Smith, 2003). Almost all of the known Javan rhinoceros population (*c.* 60 individuals) is located in Ujung Kulon National Park in Indonesia (30 000 ha) (Foose & Van Strien, Unpubl.). Within the confines of the Park, Javan rhinoceros compete with Banteng *Bos javanicus* for food. In addition, rhinoceros habitat is degraded by the invasive plant species Langkap *Arenga obtusifolia.* However, the effects of this competition and habitat loss on the rhinoceros population are unknown, as is the reproductive behaviour of this reclusive species. Managers have expressed the need for behavioural studies as a conservation priority to determine appropriate management techniques (Foose & Van Strien, Unpubl.).

Behavioural studies also have implications for protected-area design and management. When managing for the conservation of territorial species, such as White rhinoceros, careful thought must also be given to the number of individuals that can be sustained in a given location. In the case of smaller national parks and reserves, overpopulation might lead to increased stress, aggression and mortality, and reduced reproductive success. Since 2000, in southern Zimbabwe, the growth of subsistence farming and emergence of rhinoceros custodianship areas (private ranches) has resulted in about 230 Black rhinoceros becoming displaced from their home ranges. The increased concentration of animals in new areas has caused fighting, injuries and death (Du Toit, 2002). When protected areas are left unfenced, subordinate individuals may move onto lands where they may come into direct conflict with humans. Similarly, as a given population reaches the carrying capacity for its habitat, natural dispersal of sub-adults can also result in emigration and thus put many animals at risk.

Given the limited space of some fenced areas, ♂-biased Black rhinoceros populations in Namibia have resulted in injuries and mortalities to reproductive-age ♀♀ and calves as well as to other ♂♂ that are genetically valuable. In fenced areas with restricted resources, any food consumed by less-valuable (and often post-reproductive) ♂♂ is no longer available for reproductive-age ♀♀ and this may have an adverse affect on reproduction. Because ♀ reproductive success might be higher in populations with a greater proportion of ♀♀ to ♂♂, managers must plan for how to manage surplus bulls (Emslie, 2004). The translocation of White rhinoceros into a fenced area at Matobo National Park, Zimbabwe, from Umfolozi Game Reserve, South Africa, resulted in the removal of 20 individuals because of increased levels of aggression-related injuries from resident rhinoceros (Rachlow & Berger, 1998). Three young ♂♂, aged 15–27 months, died of injuries, stress and harassment resulting from interactions with resident ♂♂.

The higher concentration of animals in fenced areas may degrade the habitat and could also, over time, change the genetic structure of the population as a result of inbreeding. Thus, population sizes and habitat quality must be carefully monitored and actively managed. This might involve the capture and translocation of rhinoceros to other areas or, in some cases, even culling for population-management purposes.

Stress, animal health and mortality

Recent research has shown a clear connection between stress and the incidence of disease and mortality (Broom & Johnson, 1993). This has implications for conservation, because efforts to conserve a species or population often involve reducing the incidence of early death (Festa-Bianchet & Apollonio, 2003). Individuals must survive to reproductive age if they are to contribute their genes to the population and, if too few individuals are reproducing, populations are not sustainable. Free-ranging rhinoceros, with the possible exception of those in heavily visited national parks, are particularly sensitive to the encroachment of humans into their habitats. In addition, management-related actions, such as capture, reintroduction or translocation, can also be stressful and result in stress-induced abortions (Sinha & Sawarkar, 1993). Protection of rhinoceros for conservation may, therefore, involve limiting human–rhinoceros interactions to the extent possible.

Acute and chronic stress can be the result of aggression or the threat of aggression. In rhinoceros, intraspecific aggression can cause debilitating injuries and even death so, during translocations and reintroductions, the animals should be monitored closely (Emslie, 2004). Concerns about aggression and stress have deterred range-country breeding programmes from introducing Sumatran rhinoceros to potential mates as some have been wounded or killed during introduction attempts in zoos and breeding facilities. However, once biologists established effective methods for how and when to introduce potential mates at the Sungai Dusun Sumatran Rhino Conservation Center in Malaysia, it resulted in over 70 matings since 2001, when previously there had been no successful matings since the programme's inception in 1992 (Khan, 2004).

Reintroduction and translocation Rhinoceros population models have generally indicated that growth rates of 5% per year are desirable for sustainability and to recover from periodic losses. The recommendations are that at least five populations of 100 or more individuals are necessary to meet the long-term conservation goals for each species or subspecies (Foose & Van Strien, Unpubl.). There is a concern that Black rhinoceros populations are not growing quickly enough to withstand the effects of poaching. There are also some areas that cannot support additional rhinoceros population growth because the population has exceeded ecological carrying capacity. This has resulted in strategies for rhinoceros translocation to control populations in some areas, while employing other management options to encourage population growth in areas where populations are small (Emslie, 2001; see also Amin, Thomas *et al.* this volume; Amin, Okita-Ouma *et al.* this volume).

Behavioural considerations are important for reintroductions or translocations. Both are becoming important tools for re-establishing extirpated or augmenting existing but rapidly declining wildlife populations (Kleiman, 1996). Behavioural considerations are included in reintroduction guidelines (IUCN, 1998). It is especially important that behaviourists study the activities of reintroduced or translocated animals post-release, so that the success and cost-effectiveness of such procedures can be improved (Kleiman, 1989). For example, reintroduced animals often have little or no knowledge of the location of important resources, such as prime feeding areas, shelter or other important aspects of their new habitats. Thus, they often move great distances, presumably in search of appropriate habitat (e.g. Black-footed ferrets *Mustela nigripes:* Miller *et al.,* 1998). Similar patterns have been observed in reintroduced rhinoceros. Jnawali & Wegge (1993) studied the movement and habitat-use patterns of nine radio-collared Greater one-horned rhinoceros after their reintroduction to the Royal Bardia National Park, Nepal. Several animals dispersed widely after release, some wandering as far as 15–40 km from the release site. In addition, the average annual home-range size of reintroduced animals was about ten-times larger than that observed in the host population in Chitwan National Park. Some of this may have been the result of increased exploration; however, ecological differences between the two sites probably also played a role.

For Black rhinoceros, experience has demonstrated that optimal translocations require large numbers of rhinoceros (20 or more) that are moved into an understocked or vacant area in a short time (Brett, 1998). The large numbers of animals introduced in a short time frame give resident rhinoceros, particularly dominant bulls, less opportunity to injure or kill newcomers. Introduction of small groups tends to result in higher mortality rates. In one successful translocation, 15 Black rhinoceros were translocated onto Mun-ya-Wana Game Reserve in northern KwaZulu-Natal, South Africa, to reduce pressure on existing reserves (Sherriffs, 2004). All were released over 3 days. Dung from each animal was spread around the release sites, and the largest and most dangerous bulls were placed at extreme ends of the reserve to minimize aggressive contact. Each animal was also fitted with a radio transmitter to allow close monitoring.

Local knowledge of rhinoceros behaviour is used to locate individuals for translocation (WWF Nepal Program, Unpubl.). Capture of the Greater one-horned rhinoceros for translocation often involves using a semicircle of domesticated Asian elephants *Elephas maximus* to drive the rhinoceros into a brushy area, away from water, where it can be safely darted.

Captive-bred animals have also been used in reintroductions. Osofsky *et al.* (2001) enumerated conditions that would favour when captive-bred Black rhinoceros should be used for reintroduction. The authors stated that reintroductions should occur only if the captive population can contribute biologically significant numbers to a population that is below its ecological carrying capacity but within the species' historic range, when the wild population is in need of new genetic material or when reintroduction methods have been tested (Osofsky *et al.,* 2001). From a behavioural perspective, reintroductions of captive-bred Black rhinoceros must involve consideration of group size if the animals are to be introduced into an area already occupied by the species.

Monitoring of habitat use and movement patterns is critical for reintroduced animals. In particular, it is important that attempts to re-establish animals in areas of their former range do not result in human–animal conflicts. Sinha & Sawarkar (1993) closely monitored the movement and habitat-use patterns of a reintroduced population of Greater one-horned rhinoceros in Dudhwa National Park, India. There was particular concern expressed about the possible future movement of rhinoceros into sugar-cane crops and rice paddies along the southern edge of the Park. The authors noted that such conflicts could be exacerbated by an already existing problem: man-eating Tigers *Panthera tigris* in the region that may or may not be originating from within the park. Human–wildlife conflicts, if left unresolved, have the potential to erode public support for wildlife conservation and for national parks and equivalent reserves. The proposed solution was the installation of an electric fence designed to prevent reintroduced rhinoceros from crossing the Suheli River and straying into adjacent agricultural areas.

Other behavioural characteristics are also important for improving the success of reintroductions and translocations. For example, The Zoological Society of San Diego, California, USA, and the University of Port Elizabeth, South Africa, are researching dung and urine olfactory communication in Black rhinoceros. The results of this study may facilitate the development of techniques that can be used to disperse newly introduced and resident rhinoceros (USFWS, 2004).

CONCLUSIONS

A detailed understanding of rhinoceros behaviour can assist wildlife managers in both zoos and range-country protected areas. The behaviour of wild rhinoceros provides guidelines for managing the species in appropriate group size, sex and age ratios in captivity. Environmental-enrichment programmes can be designed to encourage activities and time budgets similar to those observed in the wild. Facilitating species-specific reproductive behaviour in captivity will result in the birth of offspring, increasing the number and, with careful management, genetic diversity of rhinoceros both in captivity and in the wild. In addition, visitors will benefit from viewing healthy rhinoceros behaving much as they would in nature and this increases the animals' value as conservation ambassadors for their species. Understanding rhinoceros behaviour in the wild is important to wildlife management. As we have shown, behavioural studies have tremendous application to population management in terms of designing new protected areas, making decisions about carrying capacity of existing protected areas, translocations and reintroductions. Theodore Roosevelt's statement that the fate of the rhinoceros rests in our hands was undoubtedly correct. By using rhinoceros behaviour as a tool for rhinoceros management, perhaps we will ultimately make decisions that favour the perpetuation of these ancient species in a human-dominated world. The loss of these magnificent animals would represent a significant defeat for the conservation movement.

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